Individual- and population-level drivers of consistent foraging success across environments

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Abstract

Individual foraging is under strong natural selection. Yet, whether individuals differ consistently in their foraging success across environments, and which individual- and population-level traits might drive such differences, is largely unknown. We addressed this question in a field experiment, conducting over 1,100 foraging trials with subpopulations of guppies, *Poecilia reticulata*, translocated across environments in the wild. We show that individuals consistently differed in reaching and acquiring food resources, but not control 'resources', across environments. Social individuals reached and acquired more food resources than less social ones and males reached more food resources than females. Yet, overall, individuals were more likely to join females at resources than males, which might explain why individuals in subpopulations with relatively more females reached and acquired, on average, more food resources. Our results provide rare evidence for individual differences in foraging success across environments, driven by individual and population level (sex ratio) traits.

Keywords

Behavioural consistency, environment, foraging, field study, guppy, individual, social dynamics, social networks, social preferences, uncertainty.

Animals strongly depend on successful foraging (i.e. the localization and acquisition of food resources), for their survival and reproduction. Animals regularly forage in dynamic environments in which they have incomplete information on the local resource distribution[1,2] and in which they cannot rely on long term memory of static landscape features such as landmarks[3,4] to forage successfully. In these situations, they have to rely on other types of behaviours, such as strategic movement patterns[1,5] or social behaviours[2,6]. Yet, it remains unclear if such behavioural mechanisms indeed allow animals in the wild to maintain a certain level of foraging success. Evidence that differences in individual foraging behaviour in the wild can be consistent over time is accumulating[7,8], but evidence for such repeatability of individual foraging behaviour across environments remains rare and evidence for repeatability of individual foraging success across environments is, to our knowledge, absent. Translocating individuals across environments in the wild is crucial to break individual by environment correlations[9] and reveal which individual traits and behaviours causally underly individual foraging success.

In addition to individual traits, group and population-level traits could also play a key role in affecting individual foraging success. When animals forage in dynamic environments, living in groups can be especially beneficial since it allows individuals to take advantage of the foraging information of others[2,10–13]. Previous studies in a wide range of species, have indeed identified the social environment as a crucial factor for successful foraging under environmental uncertainty[2,6,14,15]. Through social foraging, animals can obtain information[12,16] and increase foraging success without the need to individually sample the whole environment[17–19]. Further, the mere presence of others may result in increased foraging success (i.e. social facilitation)[20,21]. Individual great and blue tits (*Parus major*, *Cyanistes caeruleus*), that joined larger flocks, for example, profited from a higher intake of a novel and difficult to acquire food source[22]. Likewise, individual barnacle geese (*Branta leucopsis*) which followed information provided by group members benefited from an increased feeding time[23].

To address whether foraging success can indeed vary consistently between individuals across environments in the wild and whether (and which) individual and population-level traits may underly such variation, we combined over 1,100 ecologically realistic foraging trials with dynamic social (Markov Chain) modelling[24] in nine subpopulations of guppies, *Poecilia reticulata*. Multiple factors make guppies an ideal study system to address these fundamental questions in (social) foraging ecology. First, they inhabit rainforest streams that change dynamically throughout the year and frequently forage on resources that are patchily and sporadically distributed in time and space. During the dry season, the period in which this study took place, guppies often form ephemeral subpopulations in temporarily isolated pools and stay together for weeks, or even months. The term ‘subpopulation’ refers here to a number of individuals that, for a significant period of time, is more socially and spatially associated to each other than to other conspecifics in the overall population. Second, guppies in the wild show consistent individual difference in their social tendencies across environments[25,26], allowing us to investigate how such between individual differences in social tendencies impact foraging success across environments. Finally, both male and female guppies show strong evidence for socially mediated foraging, albeit stronger in females[27–31]. Though male guppies prioritize shoal size over (female-biased) sex ratios[32], use social information to get to resources[33] and spend an equal amount of time socializing as females do, they are also known to show less distinct preferences for certain social partners or shoals[26,34] and to disrupt female social behaviour[35,36]. The mixed-sexed groups in which guppies often occur, thus allowed us to also examine the role of sex in, socially mediated, individual foraging success.

Prior to the foraging trials, we quantified the social dynamics of each subpopulation via focal observations of individually-marked fish. The individual marks allowed us to obtain information on the social tendency of each unique individual. During the foraging trials, we presented food resources at various locations in a novel environment (pool) and determined the identity, order and feeding behaviour of each fish that arrived within one minute of the first arriving fish. We used the proportion of novel food resources reached as the primary measure of foraging success. We examined repeatability of individual foraging success across environments by translocating the subpopulations between different natural pools. Furthermore, we accounted for success driven merely by individual differences in movement behaviour by additionally testing individual responses towards unpredictably distributed control ‘resources’ (i.e. items without food).

An important aim of this study was to find out whether individuals consistently differ in their ability to find resources across environments and to identify which traits underlie this ability, which should increase our understanding of how natural selection might act upon such traits. Trinidadian guppies have been naturally selected to cope with a dynamic environment and recent studies have revealed that their social dynamics can be consistent across environments[25,26]. Given the evidence for socially mediated foraging, we therefore expected guppies to indeed show consistent individual differences in foraging success across environments. Moreover, we expected females and more social individuals to be the consistently superior foragers.

Results

In total, 92% of all the presented resources (89% control, 94% food) were 'detected', i.e. reached by at least one fish of the subpopulation. A subpopulation was overall significantly, though only slightly, more likely to detect a food resource than a control resource ($\chi^2 = 10.99$, $P < 0.001$, *Relative Risk* = 1.05 (1.03-1.06), $N = 1{,}135$). The likelihood of food over control resource detection did not change over time ($\chi^2 = 0.10$, $P = 0.75$, $N = 1{,}135$). Control resources thus mimicked food resources very closely, but not perfectly (see also Supplementary Fig. 1). For the remainder of the Results section we consider only detected resources (i.e. the 92% of the resources with the potential to provide social information).

Individual foraging success is consistent across environments

Individuals consistently differed in the proportion of food resources they reached across different pools (Repeatability (R) = 0.34, $SE = 0.13$, $CI = 0.09 – 0.59$, $P = 0.02$, $N = 114$; Fig. 1). That is, individuals that reached more food resources in their initial pool also reached more resources after being translocated to another pool. Individuals, however, did not differ in the proportion of control resources they reached, even though these resources were presented at the same locations ($R = 0.00$, $SE = 0.10$, $CI = 0.00 – 0.34$, $P = 0.50$, $N = 114$; Fig. 1). This suggests that the individual repeatability we observed in food resource visitation was not merely a reflection of individual differences in movement behaviour. Individuals that reached a higher proportion of food resources also took more foraging bites ($\chi^2 = 100.10$, $P < 0.001$, $N = 114$; Supplementary Fig. 2). Correspondingly, individuals also consistently differed in the total number of foraging bites across pools ($R = 0.36$, $SE = 0.13$, $CI = 0.12 – 0.62$, $P = 0.01$, $N = 114$; Supplementary Fig. 3).

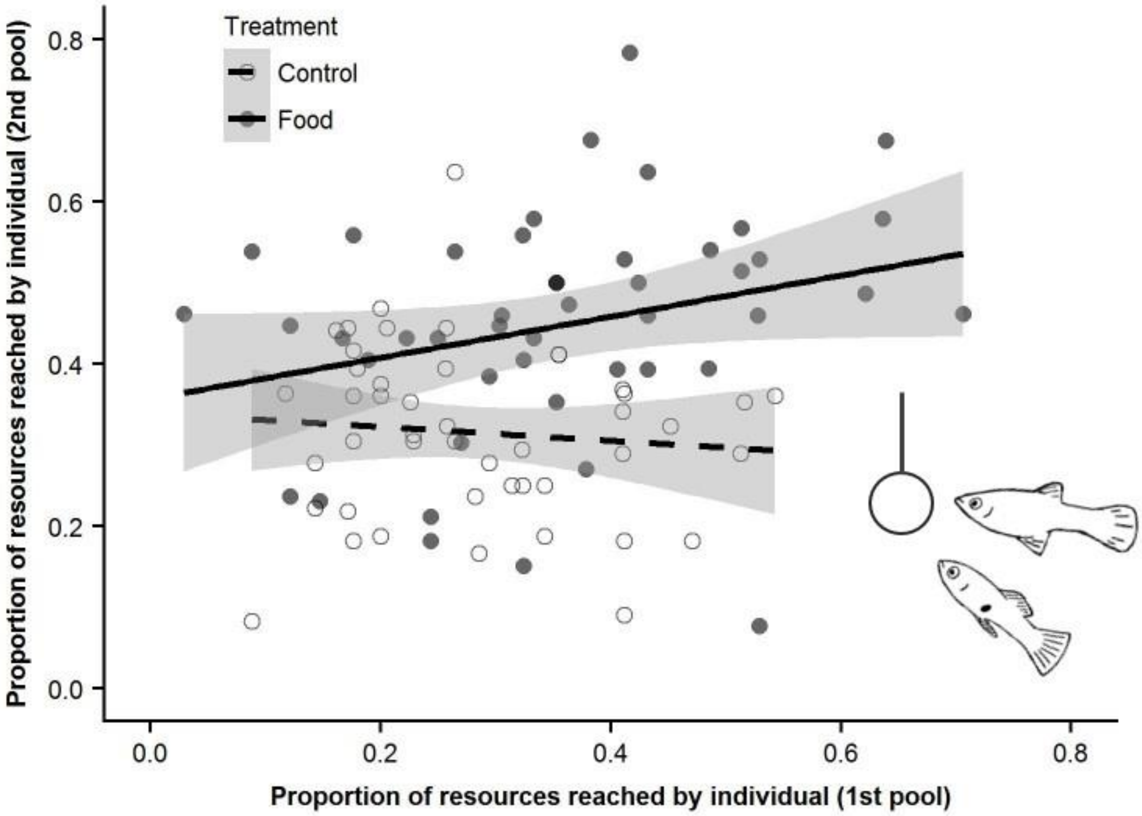

Figure 1 | The relationship between the proportion of food and control resources reached by an individual fish in its initial pool (1st pool) and after translocation (2nd pool). Fish showed consistent individual differences in the proportion of food resources reached between pools (solid marker, solid line), but not in control resources reached (open marker, dashed line; R food = 0.34, P = 0.02; R control = 0.00, P = 0.50, N individuals = 68, including 6 juveniles). Note that the figure shows only translocated individuals (N individuals = 46). Proportions are calculated relative to the total number of food or control resources detected by the subpopulation. Regression lines and 95% *CI* (shaded area) are based on fitted values for proportion of resources reached in the 2nd pool against the 1st pool.

Social fish and males reach a higher proportion of resources

More social individuals, i.e. fish which spend more of their time near conspecifics (Fig. 2), reached more resources than less social ones and this effect was stronger for food than control resources (*10,000 randomization steps*, Food: *coefficient* = 0.20; P = 0.001, N = 107; Control: *coefficient* = 0.05; P = 0.07, N = 107; Fig. 3). Furthermore, males reached more food resources, but not control resources, than females (χ^2 = 9.02, P = 0.003, N = 214; pairwise contrast of females to males during Food treatment: *Z ratio* = -5.31, *P* < 0.001; Control treatment: *Z ratio* = -2.08, *P* = 0.16; Fig. 4). When sex and social tendency were accounted for (i.e. could explain individual variation), individuals were no longer significantly repeatable in the proportion of food resources they reached across environments (Supplementary Table 1), emphasizing the importance of both traits in explaining individual variation in locating food resources. Accounting for body length and bite rate (as a proxy for foraging motivation) did not significantly reduce repeatability in the proportion of food resources reached (Supplementary Table 1).

Males visited fewer control than food resources (pairwise contrast of control to food treatment in males: *Z ratio* = -7.28, *P* < 0.001; Fig. 4), which suggests that the higher number of food resources reached compared to females was not merely driven by sex-differences in movement activity. Additionally, sex-differences in exploratory tendency are unlikely to have been a driver, since males were not more likely to be the first to arrive at a resource (Supplementary Information; Supplementary Fig. 4) and we found no evidence for consistent individual differences in 'producer- scrounger' ratios, i.e. being the first versus being a follower at a reached food resource (*R* = 0.06, *SE* = 0.11, *CI* = 0.00 – 0.36, *P* = 0.35, *N* = 114; Supplementary Fig. 5). Instead, or additionally, sex-differences in social behaviour might have played an important role. In line with earlier findings[26], males and females did not differ in their overall time spent in a social state (within-subpopulation permutation: *10,000 randomization steps*, *difference of means* = 0.02, *P* = 0.46, *N* = 62). Yet, males spread their contact moments more evenly over social partners, while females showed stronger individual preferences for specific social partners (within-subpopulation permutation: *10,000 randomization steps*, *difference of means* = 0.02, *P* = 0.02, *N* = 62). Individuals that spread their social contacts more evenly indeed reached more food and, to a weaker extent, control resources (*10,000 randomization steps,* Food: *coefficient* = -0.12, *P* = 0.03, *N* = 107*;* Control: *coefficient* = -0.04, *P* = 0.048, *N* = 107).

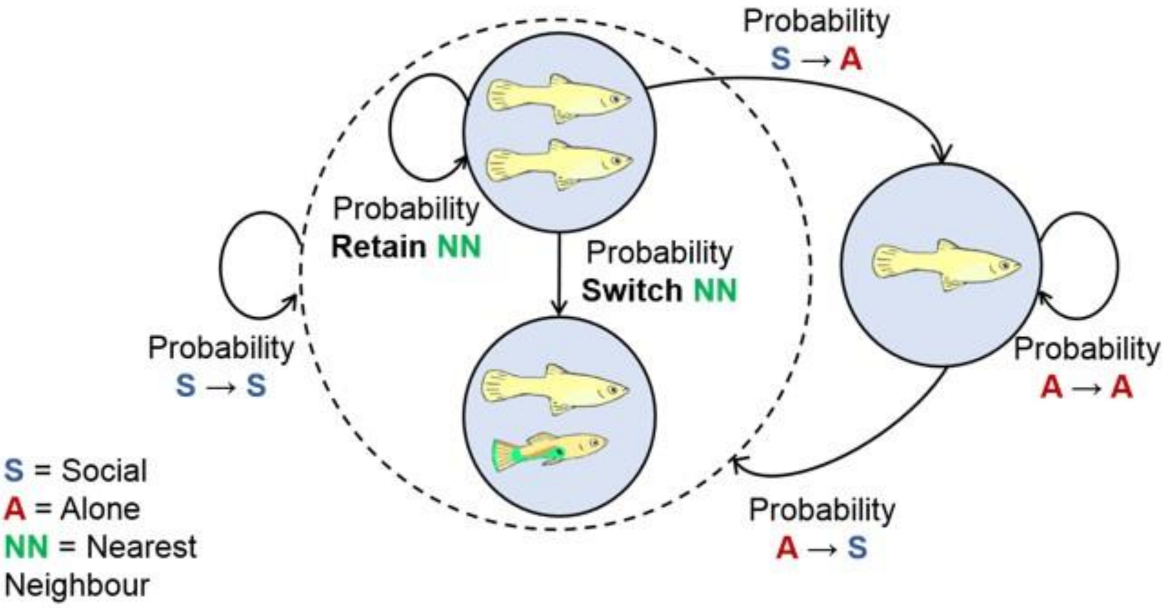

Figure 2 | Markov chain model of the guppy fission-fusion social system. When an individual is alone it can, in the next time step, stay in the state ‘Alone’ or go to the state ‘Social’. When in state ‘Social’, an individual can go to the state ‘Alone’ or stay in state ‘Social’. Within a social state an individual can stay with its current nearest neighbour or switch to another. The individual transition probabilities between these states, quantified before the foraging trials, were used to calculate the proportion of time an individual spends near any other individual (i.e. in the social state).

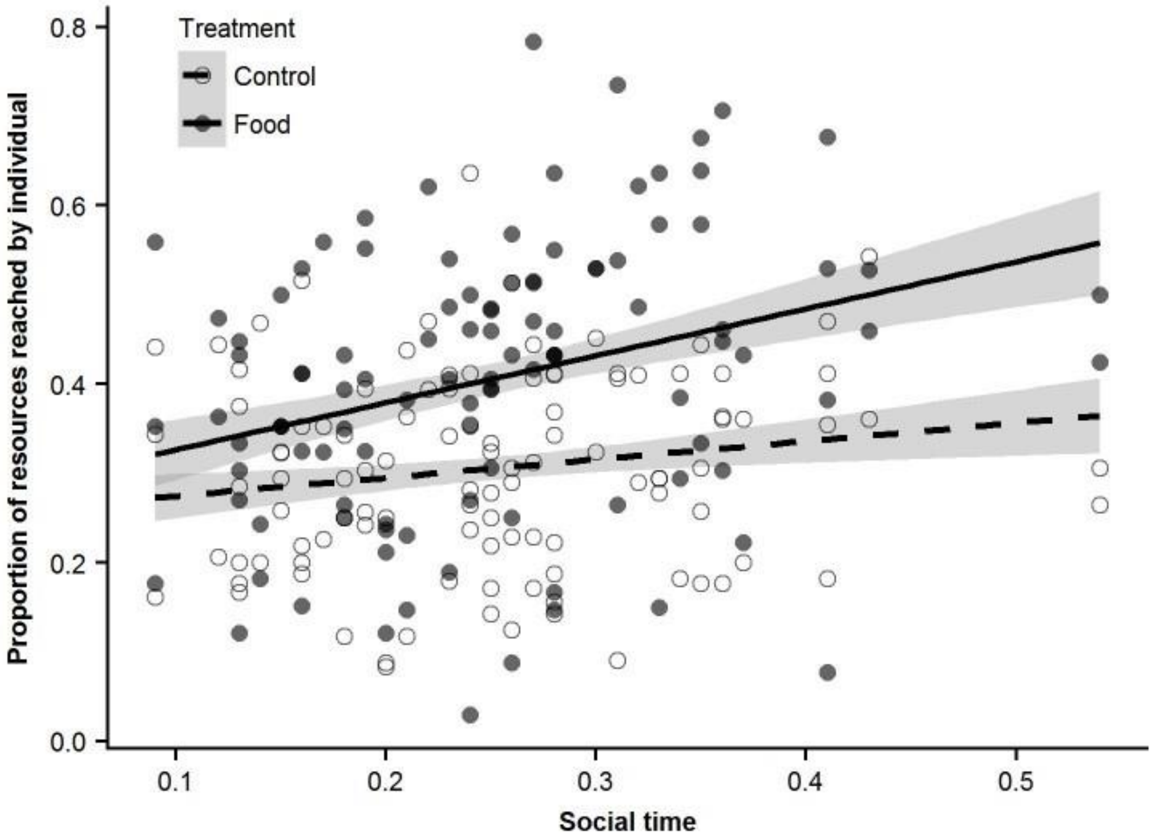

Figure 3 | The proportion of food and control resources reached per pool in relation to individual Social time. A higher Social time value indicates a stronger propensity to spend time in proximity of conspecifics (before the foraging trials). In food treatments (solid marker, solid line), but less in control treatments (open marker, dashed line), more social fish reached more resources (*10,000 randomization steps*, Food: *coefficient* = 0.20; *P* = 0.001, *N* = 107, *N* individuals = 62; Control: *coefficien*t = 0.05; *P* = 0.07*,* *N* = 107, *N* individuals = 62). Proportions are calculated relative to the total number of food or control resources detected by the subpopulation. Regression lines and 95% *CI* (shaded area) are based on fitted final model values.

Males and females take similar numbers of foraging bites

Next to reaching more resources, social individuals also took more foraging bites than less social individuals (*10,000 randomization steps*, *coefficient* = 1.87, *P* = 0.004, *N* = 107). Fish that spread their contacts more evenly did not take more bites (*10,000 randomization steps, coefficient* = 0.62, *P* = 0.83, *N* = 107). Males and females also did not differ significantly in how many foraging bites they took (χ^2 = 2.53, *P* = 0.11, *N* = 107). Females may have compensated their lower proportion of resources reached with a stronger foraging motivation, driven by a higher dependency on resources[37,38]. Indeed, females exhibited a significantly higher bite rate than males when they were present at a resource ($\chi^2 = 10.13$, $P = 0.001$, $N = 107$) and bite rate (similar to the proportion of resource visits) positively correlated with the total number of foraging bites taken by an individual ($\chi^2 = 103.85$, $P < 0.001$, $N = 114$). In fact, bite rate, as a proxy for foraging motivation, explained a substantial proportion of the variation in the total number of forging bites an individual took, more than the other individual traits considered (Supplementary Table 1). Moreover, after initially arriving at a food resource, females stayed substantially longer than males (*Median (Inter Quartile Range*) for percentage of time stayed after arrival: females: 100% (9), males: 78% (45) for males), further suggesting a stronger foraging motivation in females.

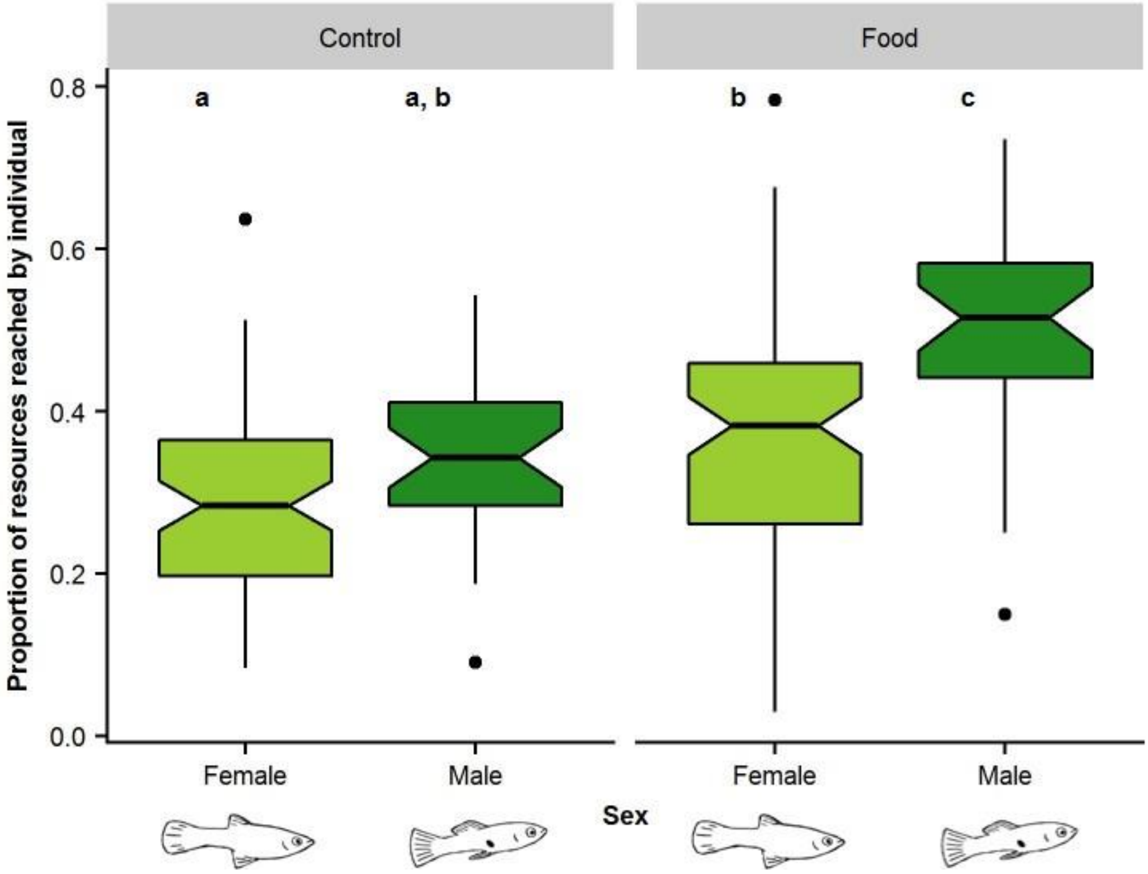

Figure 4 | The proportion of food and control resources reached per pool for individual males and females. Males (dark fill) reached more food resources than females (light fill), but not significantly more control resources ($\chi^2 = 9.02$, $P = 0.003$, $N = 214$, N individuals = 62; pairwise contrast of females to males during Food treatment: Z *ratio* = -5.31, $P < 0.001$;

Control treatment: *Z ratio* = -2.08, P = 0.16). 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. Letters ‘a’ to ‘c’ indicate significant differences revealed by post-hoc tests.

Individuals in subpopulations with relatively more females reach more resources and take more bites

Individuals were more likely to join others at food resources than at control resources (χ^2 = 76.03, $P < 0.001$, N = 907). Over time (i.e. trial number), individuals became more likely to join at a resource at which a female arrived first compared to a male arriving first (χ^2 = 10.99, $P < 0.001$, N = 907; Supplementary Fig. 6). Congruently, over time, a bigger proportion of the subpopulation reached a resource when a female was first (χ^2 = 5.59, P = 0.02, N = 907; Fig. 5). When subpopulation members profit more from a female than a male reaching a food resource, we would expect individuals to experience an increase in foraging success with a relative increase of females in the subpopulation. Indeed, individuals (both males and females) were more likely to reach food resources, but not control resources, the greater the proportion of females in a subpopulation (χ^2 = 12.18, $P < 0.001$, N = 214; Fig. 6). Accordingly, individuals in subpopulations with a greater proportion of females also took more foraging bites (χ^2 = 5.82, P = 0.02, N = 107).

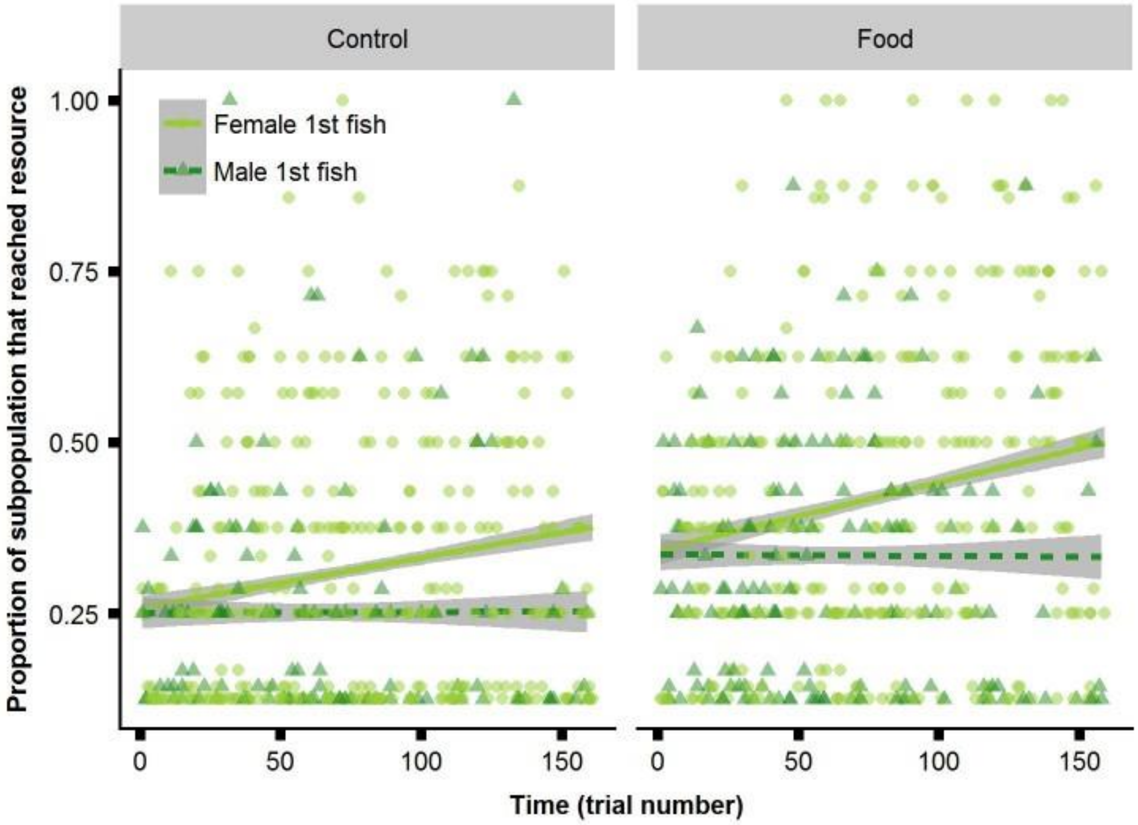

Figure 5 | Joining of first arriving fish by subpopulation members in relation to its sex. Proportion of the adult subpopulation that joins a first male (dark triangle) or female (light circle) at a food or control resource, over time (trial number). Over time, fish were more likely to reach a food or control resource when a female was the first to arrive than when a male was the first ($\chi 2 = 5.59$, $P = 0.02$, $N = 907$). Regression lines and 95% *CI* (shaded area) are based on fitted final model values.

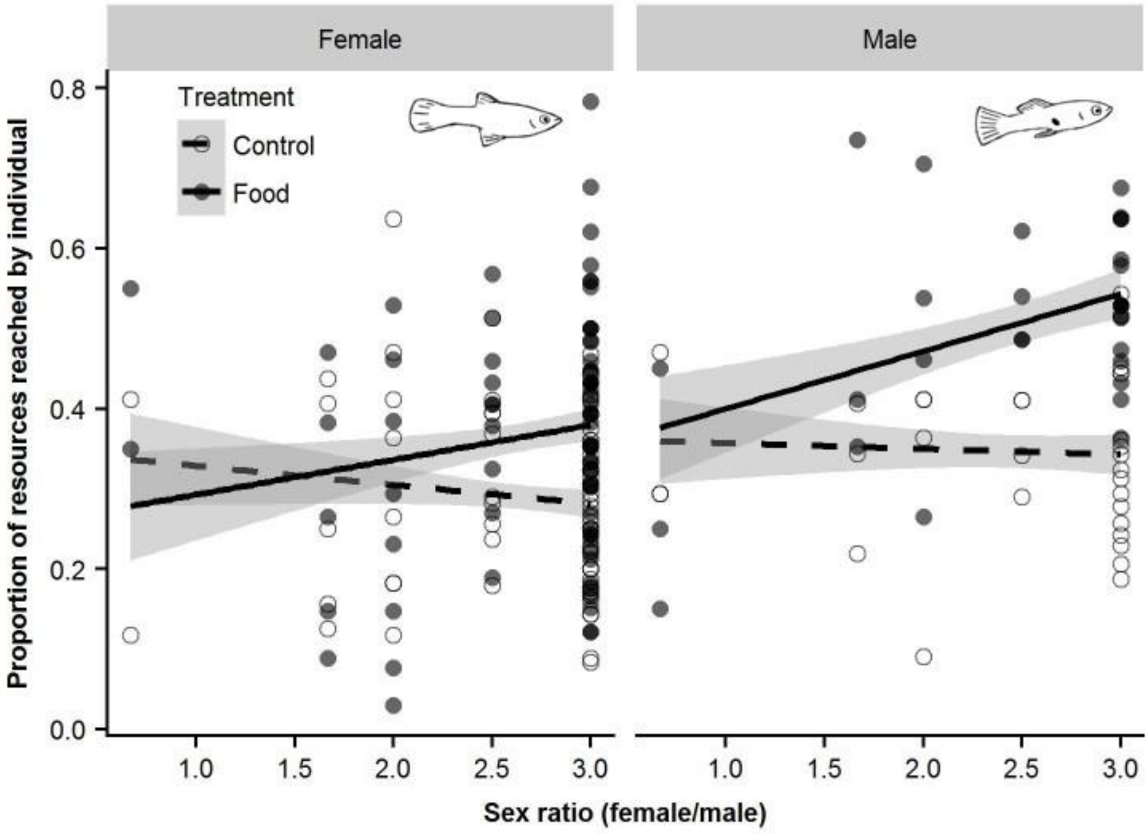

Figure 6 | The proportion of detected resources reached by an individual per pool in relation to the sex ratio of its subpopulation. Individuals (males and females) were more likely to arrive at food resources (solid marker, solid line), but not control resources (open marker, dashed line) in subpopulations with stronger female-biased sex ratios ($\chi^2 = 12.18$, $P < 0.001$, $N = 214$, N individuals = 62). Proportions are calculated relative to the total number of food or control resources detected by the subpopulation. Regression lines and 95% *CI* (shaded area) are based on fitted final model values.

Discussion

We showed that animals living in dynamic environments in the wild can exhibit individually consistent differences in foraging success. We expected females and more social individuals to be consistently better foragers across environments. Indeed, more social fish reached more food resources than less social fish, yet males were, unexpectedly, more successful in reaching food resources than females. Importantly, males and females did not differ in their likelihood to reach a control resource nor did they differ in their likelihood to be the first at any resource, suggesting that our findings were not merely driven by potential sex differences in activity or exploratory tendency. It is intriguing that males reached more food resources than females, since female guppies are generally considered more food motivated[31,37–41]. Resources at which a female arrived first were subsequently also more likely to be visited by subpopulation members, which might explain why individuals in subpopulations with relatively more females reached and acquired, on average, more food resources.

These findings may have important implications. Social animals are known to typically attend to some group members more than others[11,42]. As in many animal species[43,44], both male and female guppies prefer to associate with females over males[32,45] and as a consequence they could miss foraging opportunities provided by males. Males might 'attract' fewer conspecifics because they provide weaker foraging cues (e.g. lower bite rate[46]) or because subpopulation members try to avoid male-initiated costs (e.g. sexual harassment, male-male aggression)[35,41,47]. The costs of foregoing or missing foraging opportunities provided by males is probably negligible when natural populations are strongly female-biased[48]. However, based on our findings, when populations become less female-biased, individuals are likely to experience reduced foraging success. Interestingly, natural guppy sex ratios are known to fluctuate heavily through time (i.e., season) and space[49]. One appealing next step is therefore to test whether individuals reared in male-biased captive populations or living in natural populations with male-biased sex ratios, respond more strongly to foraging males compared to populations with female-biased sex ratios. They might learn (lab) or be naturally selected (field) to be more socially responsive to males. Alternatively, such a study might reveal that avoiding the costs of being alone with a male (e.g. sexual harassment or aggression) generally outweighs the costs of missed foraging opportunities[38], irrespective of sex ratio. Our study showed that male guppies were better than females in terms of reaching resources, but not necessarily in initially detecting them. More research is needed to understand how they exactly managed to reach more food resources than females and why the other (female) guppies in the subpopulation did not appear to take advantage from their ability.

We further showed that more social individuals were able to reach more food resources than less social ones. This result strongly indicates that the social environment was indeed an important component in facilitating foraging success. Our study builds further on former social foraging studies[6,13,22,23] by showing that social effects play a significant role in determining foraging success even across natural environments in the wild. Yet, the exact social mechanism(s) remain undetermined. Individuals with a higher propensity to be social might, for example, reach more food resources because they are more attentive to social (foraging) cues[50] or because they have an increased close-range exposure to social cues emitted by companions. Alternatively, being social could also increase the chance of a long-range foraging cue being noticed, i.e. the many-eyes theory[10]. Fish that spread their social contacts more evenly were also more likely to reach more food resources. It is possible that individuals who spread their social contacts more evenly also spread their social attention more evenly, and so more quickly pick up relevant foraging information. This might partly explain why males, who distributed their contact more evenly, reached more food resources than females.

Guppies live in a fission-fusion social system, in which they alternate between being alone and associating with one or a few ephemeral companions. Fission-fusion systems are widespread throughout the animal kingdom[51,52], including species of primates (e.g. chimpanzee, *Pan troglodytes verus*), cetaceans (e.g. bottlenose dolphin, *Tursiops* spp.), bats (e.g. Bechstein's bat, *Myotis bechsteinii*), songbirds (e.g. great tit), teleost fish (e.g. threespine stickleback, *Gasterosteus aculeatus*) and social insects (e.g. Argentine ant, *Linepithema humile*). Such social systems would allow for several of the above-mentioned social foraging mechanisms to operate in synergy. Our findings may thus have consequences for other fission-fusion species living in dynamic environments with heterogenous resource distributions.

Both control and food resources in which a female arrived first were, over time, reached by more conspecifics than resources at which a male arrived first. When food resources start to appear more frequently (e.g. ripe fruits falling from trees), guppies might quickly 'learn' to become more socially attracted and attentive to female conspecifics (no harassment) and forage more effectively on an individual level, especially in food-limited habitats. Individuals managed to reach more resources in the second pool compared to the first pool ($\chi 2$ = 28.09, P = 0.004, N = 214), which suggests that some form of (social) learning took place. They might have arrived at more resources passively by more frequently moving together with a (female) companion, i.e. via 'un-transmitted social effects'[13,53], or by more hastily responding to food cues[54]. Individuals frequently arrived quickly after one another, which was also true at control resources, but quickly left control resources after arrival (*Median* (*Inter Quartile Range*) for percentage of time spent at a resource after arrival: Food: 96% (26), Control: 12% (21)). In fact, 56% of the second fish arrived within three seconds of the first fish. These short latencies and frequent control resource visits suggest that fish were making very fast but potentially inaccurate following decisions (i.e. speed-accuracy trade-offs)[55]. Acceleration when swimming to a food resource (or mistaken control resource) might have been used as a food cue. Such a cue may produce many false positives, since it signals what an individual "thinks" it might have found, but not what it actually found[56]. In animal populations in which the costs of falsely responding (e.g. increased predation risk, energy loss) are relatively low, or when food resources are especially scarce, conspecific cues might often be wrong[57], yet right often enough to offset these costs. Indeed, there is evidence that guppies from low-predation sites, like in this study, make more 'hasty' and potentially incorrect decisions than guppies from high-predation sites[58]. Alternatively, social individuals might put up with incorrect information just to stay near a companion[54].

After having established that individuals consistently differ in foraging success in the wild, apparently using foraging abilities that are transferable across locations, the next step would be to test under which specific abiotic and biotic (including social) environmental conditions this finding might no longer hold. The novel environments (i.e. pools) in our study varied in their physical characteristics in an, for our study area, ecologically relevant way (Supplementary Fig. 7). However, the generality of our findings could be further tested in several ways. First, physical characteristics, such as pool size, shape, substrate and depth, but also turbidity[59], could be further manipulated to their extremes to investigate their importance in mediating individual foraging success. Second, the fish in our study subpopulations generally experienced little predation, were overall food limited, showed little aggression and spent most of their time alone or in pairs (75% alone, 22% pair and only 3% triplets or more). Yet, Trinidadian guppy populations vary widely in the food availability and predation risk levels they experience and (consequently) their social compositions (sex ratios) and dynamics[48,60–63]. It would thus be very interesting to repeat our study across populations that vary in food availability and predation regime. Such a comparative approach would give us more insights into the underlying (social) mechanisms, i.e. it might reveal which population-level social attributes (e.g. familiarity, female biased sex ratio, low density, small shoal sizes or low aggression levels) are essential for facilitating consistency in individual foraging success. Finally, the method of resource presentation (e.g. quality, quantity, frequency, number of locations) could be varied to change the opportunities for individual learning[3,4,64,65] and to encompass various levels of resource exploitation potential and difficulty[66], something which is expected to change the social behaviour of the foragers. Subpopulations could, for example, change from showing individualism (no competition) to showing collective searching or scrambling competition[66].

Animals can possess several physical and behavioural traits that are consistent over time and/or space[67]. Interestingly, such stable individual traits commonly interact with the social environment[68–70]. Consistent individual traits that interact with potentially important components of foraging, such as the social environment, but also learning strategies[71], movement patterns and search strategies[1,72], could generate consistent individual differences in foraging success and so promote selection on these traits. However, to infer selection, it is important to link such traits to consistent foraging success, independent of the individual's current environment. In many ecological systems, it is extremely challenging and often unfeasible to completely take individuals out of their local environment and place them repeatedly into new ones while remaining under the selective forces of the wild. Here, we took advantage of a key study system in evolutionary ecology, the Trinidadian guppy[73], and were able to show that individual level traits such as sex and social tendency as well as subpopulation sex ratio can be important drivers of consistent foraging success across different novel environments in the wild.

Methods

Study area

The study took place in Trinidad in the Upper Turure rainforest region (10°41'8"N, 61°10'22"W) from 11 to 30 March 2016. Our study site was located upstream in an area with little exposure to the sun, which is likely to have lower primary productivity than further downstream[74], making our fish relatively food-limited. Moreover, our study location is a 'low predation' site, meaning relatively low predation levels as compared to other guppy populations and (consequently) less sex-segregation[60]. It is also important to note that our Upper Turure guppy subjects were 'original' Turure fish and not the translocated fish often mentioned in other studies.

For our study, we used four natural pools that varied in shape, surface area, depth profile, substrate and canopy cover (see Supplementary Fig. 7 for details). The in- and outflow of the pools was slightly altered to reduce potential fish migration but a continuous water-flow was maintained. All guppies that originally occurred in these pools were removed. From nearby source pools we caught guppies and individually marked them using an established method of fluorescent elastomer (VIE) colouring[75,76]. We collected two subpopulations of seven fish and seven subpopulations of eight fish within the natural range of sex and age compositions[48,49], including 38-75% females, 13-38% males and 0-50% juveniles; comprising a total of 45 females, 19 males and 6 juveniles. Because a few fish escaped after the observations of social behaviour, we finished with one subpopulation of six, two subpopulations of seven and six subpopulations of eight fish in the foraging trials. These numbers created densities that were typical for our local population and within the natural range of Trinidadian guppy densities[61]. After marking, fish were released in the study pool and kept overnight to recover. We caught all fish within one subpopulation from the same source pool to ensure familiarity (but used different pools across subpopulations). Source pools never contained more than 30 guppies. 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.

Social phenotypes

To quantify the social phenotypes, we performed focal follow observations between 09:00 and 15:00. Each fish was followed for 2 min, recording its nearest neighbours every 10 sec (see also[24]). A fish was considered a neighbour if it was within four body lengths of the focal fish[24–26]. After following all fish in a subpopulation, each fish for two min, we waited for 10 min to ensure independence of focal sessions[24], upon which we repeated the procedure for the same subpopulation. This procedure was repeated for a total of 12 times for each subpopulation over two or three days (depending on weather conditions), resulting in a total of 24 min of focal follows for each individual fish. To quantify an individual's propensity to be social, we used Markov Chain analysis (see below) to calculate the proportion of time an individual spends near other individuals (i.e. Social time[24,25]). To quantify the degree to which individuals have social preferences, we calculated the Υ-measure as the sum of squares of the normalized association strengths (relative number of contact moments) between one individual and all others[26]. In previous studies with Trinidadian guppies, these social measures have been shown to be consistent throughout habitat alterations and translocations[25,26].

Foraging experiment

To study how individual and population-level social traits influence foraging success we conducted food provisioning experiments. As a novel food resource we used a small lead ball (8 mm diameter) covered in a mix of gelatine and fish food (TetraMin©), including carotenoids (a valuable resource for guppies[77]). This food resource was gently lowered in the pool using a monofilament fishing line attached to a rod. Once in the water, the food resource was kept approximately 5 cm above the bottom. Upon detection by a guppy, the resource was gently lowered to the bottom, with the exception of the first trials in the first subpopulations. As control treatment, we used an identical procedure except that the lead balls were not covered with gelatine or food. These food and control presentations mimic natural events of either food (e.g., insects, fruits) or non-edible items (e.g., leaves, twigs) falling on the water surface and slowly sinking to the bottom, being available for only a limited time[71]. We presented the food and control resources in pre-determined feeding locations (zones). We created ten feedings locations in pools 1 to 3 and six feeding locations in pool 4 (because this pool was smaller), assuring roughly equal distances between feeding locations. We presented control and food resources at each location in a randomized order, with the constraint that a location was not used twice in a row. After presenting a resource, we waited for a fish to detect it (defined as approaching the resource within two body lengths). Upon detection, the resource was left in the water for 1 min after which we removed it and the trial ended. A food resource was never completely depleted at the end of a trial. If the resource was not detected within 3 min, the trial also ended. After finishing a trial, we waited for 3 min before starting a new trial. After presenting a food and control treatment at each location, we waited for 30 min upon which we started a new sequence. We performed four such sequences for fish in pools 1 to 3 (over a period of two or three days depending on weather conditions), resulting in 40 food and 40 control trials per subpopulation per pool. In pool 4, which had only six feeding locations, we performed this sequence seven times, resulting in 42 food and 42 control trials per subpopulation per pool. Six of the nine subpopulations of fish were, after their respective foraging trials, caught and relocated to another study pool. The next day, we repeated the foraging experiment in the new pool to study if the observed foraging success was consistent across environments. Twice an entire subpopulation emigrated out of their study pool, most likely because of heavy overnight rain, reducing the number of foraging trials in comparison to the other subpopulations (see Supplementary Tables 2-3 for more details on the study time line and subpopulation compositions). In total, we conducted 1,141 trials (incl. one replicate trial).

Video observations

We recorded all trials with Panasonic and Sony HD Handycams mounted on tripods. From these recordings, we scored the identity, order and feeding behaviour of each newly arrived individual for the 1 min following initial discovery. When a resource remained undetected, we recorded for a maximum of 3 min. Six trials were excluded because the observation time was too short (< 3 min) to reliably quantify a resource as undetected, leaving 1,135 trials with binary data (yes/no) on resource detection (of which 94 resources/trials were not detected). Due to poor video quality (e.g., water surface glare), some videos were not or only partly useable (e.g. arrival first fish). We could determine the identity of all visiting fish for 963 videos and the feeding behaviour of those fish (e.g. time spent within two body lengths of the (food) resource, number of bites taken from the resource) for 944 videos. We analysed the videos using the open-source event-logging software BORIS[78] (v 4.0). For each detected resource, we recorded for 1 min the following variables for each individual fish arriving at the resource: arrival time, duration present (i.e., within two body lengths of the resource), number of bites at the resource, aggressive behaviour and sexual behaviour (display or harassment). Only one aggressive event took place per 434 bites and one sexual event per 133 bites. Fish identification during the video analysis was cross-validated with the identities reported in the field notes. Two observers analysed all of the videos and showed high inter-observer agreement in individual identification and behaviour (Supplementary Information).

Statistical analysis

To analyse our foraging experiments, we ran general and generalized mixed models (LMM & GLMM) with R[79] version 3.4.1 in R Studio version 1.0.153 (© 2009-2017 RStudio, Inc.), using the *lmer* and *glmer* functions in the '*lme4'* package[80]. Variables of specific interest (e.g. Sex, Social time) and control variables inherent to the research design were kept in the model at all times, including when they remained non-significant in the final model. These control variables included: Treatment (Control/Food), Relocation (1st/2nd pool), Pool identity (Pool 1 to 4), Zone identity (36 resource locations nested in Pool identity), Subpopulation identity (9 subpopulations) and Fish identity (62 adults and six juveniles nested in Subpopulation identity). Since the sex of juvenile guppies could not be reliably determined, models including Sex excluded data for juveniles (3% of the data).

We always started with full models, containing all variables (see Supplementary Table 4 for an overview). To test the significance of fixed effects (two-tailed), we compared models with and without the fixed effect of interest, using Log Likelihood Ratio (LLR) tests.

Fixed effects with $P > 0.1$, that were not variables of interest or the above-mentioned control variables, were removed from the model starting with the highest-level interactions. Significance of pairwise contrasts was evaluated using the Tukey method. All continuous variables were centred and scaled. We evaluated model fit of linear models via visual inspection of the fitted versus residual plot and the residual frequency distribution. Binomial models (proportions) were tested for over-dispersion. For further information on model validation, see the Supplementary Information and see Supplementary Tables 5 to 13 for the final model statistics. We based conclusions for social phenotypes on permutation models (see 'analysis of social effects').

Treatment detection

To test if there was an effect of treatment (control or food) on detection probability, we ran a GLMM (binomial) with resources as unit of analysis ($N = 1{,}135$). Whether a resource was visited by at least one fish (yes/no) was used as the binary dependent variable. The interaction between Treatment and Time (i.e. trial number, continuous), resource Drop after first arrival (yes/no) and Relocation were included in the full model as fixed effects. Subpopulation identity and Zone identity (nested in Pool identity) were included as random effects (Supplementary Table 5). See Supplementary Table 4: 'model 1' for model details. Relative risk of control versus treatment was calculated based on the odds-ratio of Treatment in the final model.

Consistent individual differences in resources reached across environments

We quantified foraging success as the number of resources reached by an individual relative to the total number of resources detected by its subpopulation. We calculated foraging success for each Treatment*Pool combination that an individual had experienced, thus resulting in four values for individuals in the six translocated subpopulations and two values for individuals in the other three subpopulations. To test whether foraging success was consistent across environments, we calculated the individual repeatability (R) of the proportion of resources reached per pool. We additionally calculated repeatability of the proportion of visited resources an individual reached first. We derived repeatability values and their 95% confidence intervals using the 'rptR' package[81]. Repeatability was calculated separately for food and control treatments. To assess how much variation in foraging success could be attributed to the individual, repeatability values were calculated based on a model that only included Pool identity and Relocation as fixed effects and Individual identity as random effect. Excluding Pool identity did not lead to a qualitatively different outcome. To study the individual drivers of repeatability, we additionally assessed models including individual traits. See Supplementary Table 1 and 4: ‘model 2a, 2b and 7a’ for model details.

Individual social tendency, sex and sex ratio in relation to resources reached

To test for the effects of social tendency and sex on foraging success, we ran a GLMM with the proportion of resources reached as dependent variable (N = 214). Sex, Social time, Sex ratio and their interaction with Treatment were added as fixed effects. As a proxy for foraging motivation, Bite rate (centred on Sex since Sex influenced Bite rate) was added as additional control variable. Pool identity and Relocation were again added as fixed effects and Individual identity (nested within Subpopulation identity) as random effect (Supplementary Table 6). Sex ratio was not correlated to the number of foraging adults in a subpopulation (*Spearman Rho* = 0.38, P = 0.31, N = 9) and replacing Sex ratio with the absolute number of males or females in a subpopulation did not lead to a better model fit (ΔAIC = + 4.1 & ΔAIC = + 7.4, respectively). To test for a potential effect of body size (i.e. Body length (mm)), we ran the final model again, replacing Social time with Body length, since Social time was correlated to Body length (Within-subpopulation permutation, overall correlation coefficient = 0.40, P < 0.01, N = 68). Body length did not significantly affect the proportion of food or control resources reached (Body length*Treatment: χ^2 = 3.78, P = 0.052, N = 214, but χ^2 = 4.06, P = 0.044 after removal of a potential outlier; Supplementary Table 7). See Supplementary Table 4: ‘models 3a and b’ and for model details.

Total number of bites and bite rate

To test for the effects of (1) individual foraging behaviours and (2) individual and subpopulation traits on the total number of bites, we ran two models (due to collinearity issues). For each individual, we calculated its total number of bites as the sum of all its bites per pool, divided by the total number of resources detected by its subpopulation per pool (only food treatment). This measure thus expresses the average number of bites taken by an individual over all resources detected by its subpopulation. For each individual, we also calculated its bite rate as the sum of all its bites per pool, divided by the sum of time (seconds) present at a resource per pool (only food treatment). The first model (LMM) included the Proportion of resources reached and Bite rate (not centred on sex) as independent variables (N = 114; Supplementary Table 8) and the second model (LMM) included Sex, Social time and Sex ratio (*N* = 107; Supplementary Table 9). Both models included Pool identity and Relocation as fixed effects (not as random effects due to a low number of factor levels) and Individual identity (nested in Subpopulation identity) as random effect. To test for sex differences in Bite rate, we ran an additional third model (LMM) with Sex, Pool identity and Relocation as fixed effects and Individual identity (nested in Subpopulation identity) as random effect (*N* = 107; Supplementary Table 10). See Supplementary Table 4: ‘models 4a and b’ and ‘model 5’ for model details. Repeatability of total number of bites taken (only food treatment) was calculated similar to the method described above. See Supplementary Table 4: ‘model 6a for model details.

Overall, we lay more emphasis on the proportion of resources reached as a measure of foraging success than the number of total bites taken for several reasons. First, it is challenging to distinguish which parts of the variation in the foraging success measures will be driven by ability, motivation, necessity and/or ‘random’ processes. The proportion of resources reached we can compare to a control treatment, but this is unfortunately not possible for the total number of bites taken (fish barely bite the control ball). Second, our subpopulations showed only little sexual harassment and even less aggression (see *‘Video observations’*), thus competitive ability is likely to play only a minor part in achieving a high number of bites. Indeed, the food resources never got depleted and fish were thus, after reaching a food resource, relatively free to take as many bites as the wanted. The number of bites is therefore likely to (more) strongly reflect individual variation in foraging necessity than ability (e.g. a higher number of bites taken by females versus males is likely to reflect a higher foraging motivation[41], driven by a stronger dependence on resources[37,38]). Finally, it is not possible to exactly determine how much food/energy an individual takes in with each bite and bite size is likely to differ among guppies depending on physical (e.g. body size) differences.

Likelihood of conspecifics joining at a resource

To test if males and females differed in how likely they were to be joined at a resource, we quantified for each resource whether a first arriving individual was joined the following 60 seconds (yes/no) and calculated what proportion of the subpopulation reached the resource. We ran two GLMM’s (binomial) for both dependent variables, including Sex and Social time and their interactions with Time and Treatment as fixed effects. Relocation and resource Drop after first arrival were added as additional fixed effects and Zone identity (nested in Pool identity) and Individual identity (nested in Subpopulation identity) as random effects (*N*

= 907 both models; Supplementary Tables 11 and 12). See Supplementary Table 4: ‘model 8 and 9’ for model details.

Analysis of social effects

Markov Chain analysis

We used the Markov chain based fission-fusion model by Wilson et al. (2014)[24] to describe the underlying social dynamics of the observed focal fish and determine the social phenotype of each individual. The social behaviour of each 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. We used the collected observational data to estimate the transition probabilities between each state for each individual fish [see the Supplementary material of Wilson et al. (2014)[24] for more details]. The individual proportion of Social time equals $P_{a \rightarrow s}$ / ($P_{s \rightarrow a}$ + $P_{a \rightarrow s}$), where $P_{a \rightarrow s}$ is the probability of ending being alone and $P_{s \rightarrow a}$ is the probability of ending a social contact (Fig. 2).

Preferred relationships

We analysed the presence of preferred relationships between the individuals using a randomisation test where we permuted the identities of the focal individuals’ contact partners within each subpopulation. We computed the variation coefficient of the association strengths (numbers of contact moments) for each subpopulation and used the sum of these values as our test statistic. The social structures indeed showed evidence of significant individual social preferences within the subpopulations (within-subpopulation permutation: *10,000 randomization steps, sum of variation coefficients* = 5.7, $P < 0.001$, $N = 70$), making the so-called Υ-measure[82], a measure of the spread of social contact moments across conspecifics, a relevant social measure. The Υ-measure, was not correlated with Social time (within-subpopulation permutation: *10,000 randomization steps, coefficient* = -0.06, $P = 0.39$, $N = 68$).

Randomization tests

Effects of social traits (Social time and Υ-measure) on the proportion of reached resources and the number of bites were tested by randomizing the social metrics between individuals within a subpopulation and calculating the coefficient for the effect of the social trait 10,000 times. The original coefficient in the final model was then compared to the distribution of the coefficients of the permutated final models[83]. We conducted this procedure separately for food and control trials. Because the Υ-measure is sensitive for differences in subpopulation size, we ran the analyses with Υ-measure values corrected for subpopulation size (see Supplementary Information). Details of the final models can be found in the Supplementary Tables 6 and 9. To test if the effect of Sex on foraging success could be explained by males spreading their contacts more evenly (smaller Υ-measure value, see Results), we replaced Sex in the models with Υ-measure.

To analyse the influence of Sex on Social time, we permuted the individual Social times within each subpopulation and used as a test statistic the absolute value of the difference of the mean Social times between males and females. We analysed the influence of Sex on the Υ-measure in the same way. To analyse the relationship between Social time and Υ-measure, we permuted the individual Social times within each subpopulation and used as a test statistic Pearson's correlation coefficient between Social time and Υ-values. Similarly, we analysed the connection between Social time and Body length. Social time and Υ-measure were computed based on the complete subpopulations ($N = 70$ individuals). For our tests, however, we only used those (adult) individuals that were present in the foraging trials ($N = 62$). Also, as in the above described tests regarding the effect of social traits, we ran these analyses with Υ-measure values corrected for subpopulation size (see Supplementary Information).

Code availability

The R codes used for analyses of social effects during the current study are available from the corresponding author on request.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on request.

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Author contributions

All authors contributed significantly to the design of the study and the collection of the primary data. L.S. and S.K. analysed the data and L.S. wrote the main manuscript. All authors commented on the manuscript and accepted its last version.

Additional information

Supplementary material is available for this paper.

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Competing financial interests

The authors declare no competing financial interests.