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Pair foraging degrades socially transmitted food preferences in rats

Chelsey C. Damphousse[1] · Diano F. Marrone[1] · Noam Miller[1]

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Abstract
Following presentation of a novel food odor on the breath of a conspecific, naïve rats will exhibit a preference for that food, a form of learning called social transmission of food preference (STFP). When tested in isolation, STFPs are robust, persisting for up to a month and overcoming prior aversions. This testing protocol, however, does not account for rats' ecology. Rats and other rodents forage in small groups, rather than alone. We allowed rats to forage in pairs and found that, following social foraging, they no longer displayed a food preference, i.e., that STFPs degrade during social foraging. Non-foraging rats exposed to the same foods for the same amount of time in isolation maintained their preferences. We also examined whether individual differences between rats affect STFP. Neither boldness nor sociability predicted initial STFP strength, but bolder rats' preferences degraded more following social foraging. Shyer rats were more likely to eat at the same time as their partner. By tracking rats' interactions during social foraging, we show that they use complex rules to combine their own preferences with socially acquired information about foods in their environment. These results situate STFP within the behavioral ecology of foraging and suggest that individual traits and the interactions between them modulate how social learning is maintained, modified, or lost.

Keywords Social transmission of food preference (STFP) · Foraging · Behavioral syndromes · Information sharing · Exploration · Rat

Background

The transmission of foraging-related information between members of rat colonies has been extensively studied (Steiniger 1950; Inglis et al. 1996). From fetal development (Smotherman 1982) through adulthood (Galef and Clark 1971; Galef 1981), conspecifics' interactions bias food choices (Galef et al. 1984). If, after consuming a particular food, an individual interacts with a conspecific, that conspecific will later show a preference for the breath-borne food odor it detected, even if the food is novel; a phenomenon referred to as the social transmission of food preference (STFP; Galef et al. 1984).

The sharing of food-related information occurs within, and is a major benefit to, living in groups. For individuals that explore and forage in groups, as rats do (Inglis et al. 1996), not only does STFP mediate safer consumption of novel food types (Galef and Clark 1971), but also shared information can increase the efficiency of foraging (Krause and Ruxton 2002; Beauchamp 2013). In addition to increasing foraging time, due to a decreased need for individual vigilance, information may be shared amongst group members regarding food location (Galef and Giraldeau 2001), type (Real 1992), predation risks (Ward et al. 2008), and the quality of a foraging patch (Marler et al. 1986). When exploring novel environments, rats organize their behavior around a "home base" (Eilam and Golani 1989) to which they frequently return and which may serve as an information center (Galef and Giraldeau 2001) where informative interactions with conspecifics are concentrated.

Despite several decades of research (Galef 2012), no study has examined how foraging in a group may alter the expression of preferences or how long such socially acquired preferences are retained. We, therefore, explored how food preferences established via STFP impact social foraging in

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✉ Chelsey C. Damphousse
damp7000@mylaurier.ca

[1] Department of Psychology, Wilfrid Laurier University, 75 University Ave. West, Waterloo, ON N2L 3C5, Canada

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a novel environment, and whether foraging with a partner alters food preferences.

In addition to qualities of the food itself, social transmission of information is likely to be affected by consistent individual differences in behavioral characteristics, often referred to as "animal personality" or "behavioral syndromes", common across a wide range of species (Gosling 2001; Sih et al. 2004), which have been shown to predict social behaviors in pairs of rodents (Dochtermann and Jenkins 2007). Since the proportion of preferred food consumption, a proxy for the strength of an acquired preference, varies between subjects during STFP testing, we also examined how individual differences might influence the transmission and utilization of STFP-related information.

After assessing rats for individual differences, using both social and exploratory assays (often assumed to capture "boldness"; Réale et al. 2007), we gave each rat a preference for either cinnamon- or cocoa-flavored food, using well-established methods (Posadas-Andrews and Roper 1983; Galef and Whiskin 2003; Galef 2002). Rats in the experimental group were then allowed to repeatedly forage for both food types in an open arena (containing a home base) with a partner of the same or differing preference. Compared to a control group of rats that did not forage socially but were given both food types in their cages for exactly the same duration, we found that pair foraging caused previously acquired preferences to be extinguished, leaving subjects indifferent between the two foods. This is in stark contrast to the extremely robust preferences that are observed when animals are tested in isolation (e.g., Galef and Whiskin 2003). To further explore the mechanisms by which this degradation of preference occurs, we examined the interactions that took place during social foraging. Individual behavioral differences were re-assessed at the end of the experiment.

Methods

Subjects

Subjects were 80 male Sprague–Dawley rats (Charles River Breeding Farms, St. Constant, QC, Canada), approximately 60 days old at the start of the experiment. 44 rats formed the experimental group. One rat died before the end of the experiment and its data were discarded. 20 rats constituted the control group. Two rats from this group were excluded for failing to acquire a food preference. In both the experimental and control groups, equal numbers of rats were given each preference. A further 16 rats served as demonstrators (8 for cocoa, 8 for cinnamon; see below). Demonstrator rats did not undergo any of the testing for individual differences or social foraging.

Subjects were pair-housed upon arrival in the lab and, a week later, were transferred to individual cages. Rats were handled for 10 days prior to the start of the experiment. The colony room was maintained at 21–22 °C on a 12-h reversed light–dark cycle (lights off at 0700 h). During most of the experiment, as noted below, animals were fed a restricted diet of standard rat chow (20 g per day per rat) and given water ad libitum. The procedures used followed the Canadian Council on Animal Care guidelines and were approved by the Wilfrid Laurier University Animal Care Committee (AUP R16001).

Procedure

Figure 1 shows a schematic of the experimental timeline. Subjects in both experimental and control groups were first given 5 days of testing to assess individual differences (days 1–5), followed by a demonstration of one food odor (counterbalanced across subjects) and a preference test (T1; day

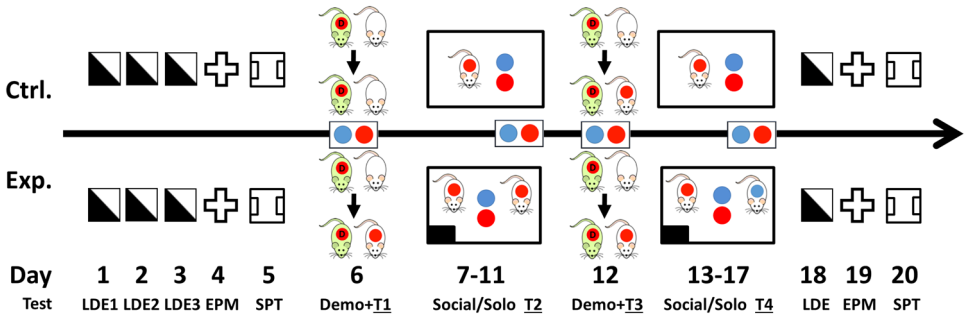

Fig. 1 Schematic of the experiment timeline. Control group rats are shown above the arrow, experimental group below. Days of the experiment are listed below, along with the test conducted on that day. *LD* light/dark emergence test, *EPM* elevated plus maze, *SPT* social preference test, *Demo* odor demonstration, *T1–T4* preference tests, *Social/Solo* social (experimental group) or solo (control) foraging. Demonstrator rats are shown shaded in green and labeled with a "*D*". For simplicity, all rats are shown being given the same preference (red) and doing social foraging with a partner of the same preference first, though both these things were counterbalanced in the experiment (color figure online)

6). Experimental group rats then had 5 days of social foraging (SF), in an arena containing both foods, with a partner that had either the same or the opposite food preference (counterbalanced across rats); control group rats had the same amount of time to forage on both foods, but remained alone in their home cages (days 7–11). On the last day of foraging, rats in both groups received a second preference test (T2; day 11). The following day (day 12), all rats received a second demonstration (of the same odor as before), and a third preference test (T3). Days 13–17 were identical to days 7–11, but experimental group rats that had a partner with the same preference as themselves on days 7–11 now had a partner with the opposite preference, and vice versa. On the last day of this second round of social/solo foraging (day 17), rats received a fourth preference test (T4). On the last 3 days (days 18–20), rats in both groups went through the same three individual difference assays as at the start of the experiment.

Individual differences

For both groups, the first 3 days of individual difference testing (days 1–3) consisted of a light/dark emergence task (LDE1-3; Fig. 1; Bourin and Hascoët 2003; Crawley 1985), followed by 1 day (day 4) of elevated plus maze (EPM; Montgomery 1955), and ending with 1 day (day 5) of social preference testing (SPT; Moy et al. 2004). All sessions were recorded under white room lighting with a webcam attached to a laptop mounted on the ceiling of the testing room. Subjects were not food-deprived during this phase of the experiment. Between trials, the arena and apparatus were sanitized using spray disinfectant and then wiped dry.

The LDE task took place in a 122 cm × 122 cm × 44 cm high arena with 122 cm × 122 cm black haircell acrylonitrile butadiene styrene (ABS) plastic flooring (Piedmont Plastics, Kitchener, ON, Canada). A 41 cm × 24 cm × 18 cm high, lidded start box with a 10 cm × 15 cm opening in the center of the front face was placed by the middle of one wall of the arena. Rats were placed inside the start box, the lid was closed (so that the box was dark inside), and the subject left undisturbed to explore the arena for 30 min. The proportion of the session time that the rats spent out of the start box was recorded. Each rat had one trial per day on three consecutive days; scores from all 3 days were averaged to give one LDE score per subject.

The EPM consisted of two open sided and two walled black PVC arms, each measuring 57 cm × 10 cm × 42 cm high, with black ABS flooring. Arms were arranged in a cross-elevated position, 53 cm from the ground. Rats were placed into the center of the maze oriented toward an open arm, and left undisturbed for 10 min. The proportion of the session spent on the open arms of the maze was recorded.

For the SPT, two clear acrylic cages measuring 45 cm × 25 cm × 20 cm high with a wire mesh lid were placed halfway down the opposite walls of the arena previously used for the LDE task. Cages were placed on sides not previously used for the LDE start box and were equidistant from its previous location. Cages contained wood chips and a piece of PVC piping for environmental enrichment. In one of the cages, a decoy stuffed rat was placed. The other cage contained an unfamiliar male Sprague–Dawley rat, not otherwise involved in the experiment. The subject was placed into the center of one side of the arena, equidistant from both cages, and left to explore undisturbed for 10 min. The proportion of time that the subject spent within 30 cm of the cage containing the conspecific was calculated as a proportion of the total amount of time spent within 30 cm of either cage. Time spent in the area between the two cages was ignored. The positions of the decoy and live rat were counterbalanced across subjects.

Following testing, the three raw measures produced across the three behavioral assay tasks (EPM, SPT, and LDE) were reduced using principal components analysis. We found two significant factors, giving a pair of scores for each rat. In the experimental group, foraging pairs were created by selecting rats with the greatest possible differences in these scores, and then establishing their food preferences accordingly.

Individual differences were re-assessed following the SF stage of the experiment (days 18–20). Each rat was given one session each of LDE, EPM, and SPT. Scores on these sessions were compared to the pre-SF scores.

Social transmission of food preferences

Immediately following the individual difference assays, rats were food restricted for the remainder of the experiment. The first STFP demonstrator/observer interaction was given 24 h later (day 6). Although familiarity does not appear to influence preference acquisition (Galef et al. 1984), we used demonstrators that were unfamiliar to the subject rats. STFP procedures used closely followed those suggested by Galef (Galef 2002; see also Galef and Wigmore 1983).

Demonstrators were trained by giving them approximately 30 g of the designated flavored foods for 1 h in their home cages. The bowls used for training were constructed of a plastic container (Rubbermaid® 7J55 Easy Find Lid square food storage containers; 1/2 cup in size) that was glued inside the bottom of a 7 cm × 7 cm × 6 cm (length, width, height) metal water dish, so that any spilled food could be salvaged and accounted for. The metal dish was secured to a 9 cm × 9 cm Plexiglas base to prevent the rats from tipping it over. Consuming at least 3 g of the food during the 1-h presentation was required, as this was considered as a sufficient amount to successfully transmit the

information to a conspecific. Immediately following this training, a demonstrator was placed with a naïve observer rat in a novel cage to interact undisturbed for 30 min. Immediately following interactions, observers were given a 4-h preference test. 60 g each of cocoa and cinnamon-flavored foods were presented simultaneously in the rat's home cage in a pair of bowls identical to those used during demonstrator training. If > 50% of the total food consumed was of the demonstrated flavor, the transmission of food preference was considered successful (Countryman and Gold 2007). If this did not occur, the observer was given another demonstration on the following day and re-tested. Two rats failed to acquire a preference even after two demonstrations and were dropped from the experiment.

Social/solo foraging

For the experimental group, social foraging (SF) sessions took place in a 183 cm × 183 cm open-field arena with black ABS flooring, in a different room to that used for testing individual differences (Fig. S1). Using three walls of the room to surround the arena, a fourth wall was constructed out of 23.5 cm high white PVC. Across the open end of the arena, a plastic shower curtain was suspended from the ceiling to isolate the testing area. In one corner of the arena, a 35.5 cm × 20 cm overhang of white gatorboard was attached to the wall approximately 20 cm above the floor, providing a home base for the rats (Eilam and Golani 1989). Within the foraging arena were two pairs of bowls. One bowl in each pair contained cinnamon-flavored food and the other contained cocoa-flavored food (Fig. S1). Rats' movements were recorded using a video camera (Panasonic HC-V770) attached to the ceiling such that the entire arena was visible, with the exception of the area underneath the home base. Analysis of feeding times (start and end of each feeding event), type of food consumed (cocoa or cinnamon), and bowl pair (A or B) for every feeding event of each rat was manually coded from the videos, as well as all interactions between the two partners when outside the home base (start and end times). Interactions between the rats were coded whenever the rats were touching or sniffing each other. Partners were additionally assumed to be interacting whenever they were both in the home base (which was barely large enough for both rats to fit underneath), and these times were also coded. The amount of food consumed was estimated from the time spent eating (i.e., we assume that rats eat at a fixed rate which does not vary between rats).

Each rat in the experimental group underwent two phases of SF (days 7–11 and 13–17), each consisting of five sessions on consecutive days with the same partner, 30 min per session. Half of the rats were first paired with a partner that had the same food preference and then a partner of the opposite food preference; the other half had a partner of the opposite food preference first.

Following the first phase of SF, rats' preferences were re-tested (day 11) and then re-established (day 12) prior to start of the second phase. Rats were all given a demonstration of the same odor that they had previously observed (i.e., the preferences were not changed). Demonstrators were fed the same food that they had previously demonstrated, but were paired with a different observer rat than in the first demonstration. Preferences were tested one more time at the end of the second phase of SF (day 17).

Rats in the control group did not undergo SF sessions. Control group rats remained in their home cages and were given a bowl pair containing both the cinnamon-flavored food and the cocoa-flavored food for 30 min on 5 consecutive days (days 7–11), exactly mirroring the exposure schedule of the experimental group rats. They were then also given a second test of their preference (day 11) and a second demonstration (day 12), identical to the procedure followed with the experimental group rats, followed by a second round of 5 days of choice (days 13–17) and a final preference test (day 17). In other words, control group rats went through the same schedule as the experimental group, except that they did not forage in pairs.

Analysis

Individual behavioral assay videos were tracked using custom in-house software that extracted the position of the rat in every frame of the video. These trajectories were then analyzed in *Mathematica* (v. 10, Wolfram Research) to extract the following measures: proportion of time spent on the open arms (elevated plus maze), proportion of time spent near the live conspecific (social preference test), and proportion of time spent outside the start box (three light/dark emergence tests). Individual scores on all these measures were entered into a principal components analysis, and the eigenvalues and loadings of each measure were explored to determine how many significant components there were and what they represented.

SF videos were coded manually by recording rat identity, time (start and end), type of food (cocoa or cinnamon), and bowl pair (A or B) for every feeding event for each rat. All data were entered into Microsoft Excel spreadsheets. Repeatability analyses for individual difference scores were conducted in *R* (R Core Team) using the ICC function in the *Psych* package. All *t* tests were two-tailed. We used a *t* test for testing the significance of correlation coefficients, and the two-way Kolmogorov–Smirnov test [K–S test] to compare data distributions. A significance cut-off of $\alpha = 0.01$ was used for all statistical tests. Raw data are archived at https://osf.io/rcj34/.

Results

Individual differences

A principal components analysis of the measures from the LDE, EPM, and SPT tests returned two significant factors (eigenvalues of the correlation matrix: 1.70, 0.93, 0.37). Two of the three measures loaded heavily and positively onto factor 1 (EPM 0.87, LDE 0.89, SPT 0.40), which we, therefore, label "boldness". The social preference task score loaded most heavily onto Factor 2 (SPT 0.92, EPM −0.26, LDE −0.16), which we, therefore, label "sociability".

All rats completed a second set of behavioral assays following both social foraging phases (SF1 and SF2). This included a single test of each type (LDE, EPM, and SPT). Scores on the LDE and EPM tests were strongly correlated between pre- and post-SF assays (experimental group: LDE, $r=0.72$, $t\ (41)=6.66$, $p<0.00001$; EPM, $r=0.67$, $t\ (41)=5.71$, $p<0.00001$. Control group: LDE, $r=0.70$, $t\ (16)=3.90$, $p=0.0006$; EPM, $r=0.71$, $t\ (16)=4.03$, $p=0.0005$). However, pre- and post-SF scores for the SPT were not correlated (experimental group: $r=0.13$, $t\ (41)=0.83$, $p=0.21$; control group: $r=0.07$, $t\ (16)=0.26$, $p=0.40$). A repeatability analysis confirmed that LDE [ICC (3,1) = 0.60, $F\ (42,126)=7.0$, $p<0.00001$] and EPM [ICC (3,1) = 0.51, $F\ (42,42)=3.1$, $p=0.0002$] scores were significantly repeatable but SPT scores were not [ICC (3,1) = −0.019, $F\ (42,42)=0.96$, $p=0.55$], suggesting that boldness did not change appreciably during the course of the experiment, but rats' motivation to be social did. There was no significant difference between the experimental and control groups on the LDE or EPM tests (K–S test, LDE1: $D=0.29$, $p=0.18$; LDE2: $D=0.21$, $p=0.57$; LDE3: $D=0.16$, $p=0.84$; post-SF LDE: $D=0.41$, $p=0.02$; EPM: $D=0.34$, $p=0.09$; post-SF EPM: $D=0.23$, $p=0.42$). In the SPT, rats in the control group spent less time near a live conspecific than those in the experimental group before the social foraging phase of the experiment ($D=0.56$, $p=0.0003$), but not after ($D=0.22$, $p=0.5$).

Social transmission of food preference

During the first demonstration (day 6), 7 of 63 rats required a second demonstration to acquire a preference (i.e., to consume > 50% of the demonstrated food). During the second demonstration (day 12), 14 of 61 rats required a second demonstration (2 of the control rats never acquired a preference in this phase and were dropped from the experiment). In both cases, rats that required a second demonstration did not end up with a stronger or weaker preference than those that only required a single demonstration [two-sample t test. day 6: $t\ (61)=0.35$, $p=0.50$; day 12: $t\ (59)=0.27$, $p=0.86$], nor were there significant differences in their boldness [day 6: $t\ (61)=0.40$, $p=0.08$; day 12: $t\ (59)=0.39$, $p=0.18$] or sociability [day 6: $t\ (61)=0.35$, $p=0.48$; day 12: $t\ (59)=0.30$, $p=0.76$], suggesting that the individual differences we measured do not affect how easily rats acquire a STFP.

To assess the transmission and maintenance of socially acquired preferences, rats in both the experimental and control groups were tested four times: before SF1 (T1), after SF1 (T2), before SF2 (T3), and after SF2 (T4). Tests for both groups were identical, consisting of a single 4-h exposure to both food flavors, conducted in isolation, in their home cages. Preferences were re-established after SF1 (between T2 and T3; see "Methods"). Cocoa- and cinnamon-flavored foods were previously tested in a separate population that was not used for the rest of the experiment and proved to be equally palatable (Mann–Whitney test on all preference tests for both groups: $U=421.5$, $p=0.54$; Galef 1989).

Strength of food preference (as measured by proportion of demonstrated food consumed) at T1, before any social foraging, did not correlate with boldness [$r=-0.20$, $t\ (59)=-1.56$, $p=0.062$] or sociability [$r=-0.24$, $t\ (59)=-1.88$, $p=0.032$], suggesting that individual behavioral differences do not directly affect the strength of socially acquired food preferences. We also found no difference between the experimental and control groups in the total amount of food they consumed during any of the four preference tests [repeated-measures ANOVA, main effect of group: $F\ (1,41)=3.06$, $p=0.09$].

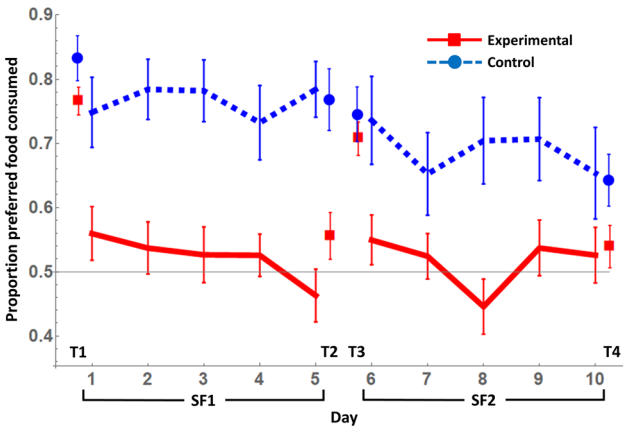

Fig. 2 Proportion of food consumed by test rats that was of their demonstrated flavor in each of the preference tests (T1–T4) and on each day of social foraging (SF1 and SF2). Experimental group: solid red line, square markers; control group: dashed blue line, round markers. The gray horizontal line indicates chance levels. Error bars show ± SEM (color figure online)

Figure 2 shows the proportion of consumed food of the demonstrated flavor for the four preference tests (separate markers) and during the two SF phases (lines). Rats in the experimental group (solid red lines) displayed a strong preference for their demonstrated food following both demonstrations (T1 and T3) but this preference was eliminated following social foraging trials (K–S test. T1 vs. T2: $D=0.47$, $p=0.0001$; T3 vs. T4: $D=0.44$, $p=0.0004$). Preferences were successfully re-established by interaction with a demonstrator following SF1 (T2 vs. T3: $D=0.37$, $p=0.005$). The degradation of preference did not depend on whether the subject's foraging partner had the same or opposite food preference (K–S test. $D=0.159$, $p=0.639$), suggesting that it was not simply demonstration of the alternate odor that caused preferences to disappear. Rats in the control group (Fig. 2, dashed blue lines) displayed no degradation of preference as a result of their exposures to both foods (T1 vs. T2: $D=0.22$, $p=0.77$; T3 vs. T4: $D=0.39$, $p=0.13$), suggesting that social foraging itself results in a loss of preference. Similarly, preferences in the experimental group were not significantly different from those in the control group immediately after demonstrations (T1: $D=0.32$, $p=0.11$; T3: $D=0.31$, $p=0.13$) but were significantly lower after the first round of social foraging (T2: $D=0.46$, $p=0.006$; T4: $D=0.30$, $p=0.15$).

For subjects in the experimental group, degradation of preference during social foraging was correlated across the two SF phases [correlating individual T1–T2 scores with T3–T4: $r=0.348$, $t\,(42)=2.409$, $p=0.01$]. We assigned each subject an averaged degradation score, which was the mean of their change in preference across the two SF phases. Degradation scores were significantly correlated with boldness ($r=0.34$, $t\,(41)=2.75$, $p=0.004$) but not with sociability [$r=0.08$, $t\,(41)=0.62$, $p=0.27$], suggesting that bolder rats experience a larger preference degradation following social foraging.

Social foraging

To explore the mechanisms by which social foraging degrades food preferences, we examined the behaviors of rat pairs in the experimental group during SF. Pairs of rats spent more time eating overall (summing over both rats) when both partners had the same food preference than when their preferences were different (K–S test. $D=0.22$, $p=0.01$), and time spent eating was correlated between partners [same preference: $r=0.79$, $t\,(41)=18.85$, $p<0.00001$; different preference: $r=0.73$, $t\,(41)=15.71$, $p<0.00001$], which suggests that partners influence each other's decision to engage in eating and this partly depends on their relative food preferences. Time spent eating correlated negatively with individual boldness [$r=-0.55$, $t\,(41)=-4.30$, $p<0.0001$], but did not correlate with sociability [$r=-0.23$, $t\,(41)=-1.51$, $p=0.07$], suggesting that bolder rats spend less time eating, possibly because they are exploring the arena more.

The preferences, boldness, and sociability of the foraging partners had no discernible effect on which foods they consumed. The proportion of food consumed during SF sessions that was of an individual's preferred flavor did not depend on whether the partners had the same or opposite preferences (K–S test. $D=0.12$, $p=0.11$), nor did it correlate with the differences between them in boldness [same preference, $r=-0.02$, $t\,(41)=-0.15$, $p=0.44$; different preference: $r=0.25$, $t\,(41)=1.65$, $p=0.05$] or sociability [same preference, $r=-0.31$, $t\,(41)=-2.14$, $p=0.02$; different preference: $r=0.13$, $t\,(41)=0.84$, $p=0.20$].

We next studied the timing of feeding events to examine the potential for coordination during social foraging (Rook and Penning 1991; Conradt and Roper 2000). We defined a measure, 'overlap', as the proportion of the time of one rat's feeding during which the other rat was also feeding (an overlap score of 1 indicates that the subject only ate at the same time as its partner; a score of 0 indicates it never ate at the same time as its partner). The overlap score for each individual was calculated for every SF session and then averaged, giving each individual a single score.

Figure 3a shows the distribution of mean overlap scores. Visual examination of this distribution suggested that it was bimodal. We confirmed this using a maximum likelihood estimation procedure with 1, 2, and 3 component Gaussian mixture models fitted to the data distribution (Everitt 1981). The Akaike information criterion (AIC) values for the three models were: −37.096, −37.901, and −32.455, respectively, suggesting that the distribution was most likely bimodal.

We divided the data by which component of the overlap distribution each rat inhabited using the intersection of the two distributions, overlap = 0.387, to assign each individual to a component (Fig. 3a, inset). Ten of the 43 experimental group subjects fell into the high-overlap component. Rats in the high-overlap component had lower boldness scores than rats with low overlap (Fig. 3b; K–S test. $D=0.88$, $p<0.00001$). In other words, bolder rats were less likely to eat at the same time as their partner than less bold rats. There was no significant difference in sociability between overlap components (Fig. 3c; $D=0.22$, $p=0.75$). Overlap scores did not correlate with preference degradation scores (see above; $r=0.289$, $t\,(42)=1.96$, $p=0.03$), suggesting that whatever causes rats to lose their preferences during social foraging does not depend on the relative timing of their eating.

Overlap scores were then calculated for each 5-day SF phase separately, so that each rat received two scores: one for their sessions with a partner of the same preference and one for sessions with a partner that had the opposite preference. Overlap distributions did not differ between SF phases (K–S test. $D=0.27$, $p=0.08$). Overlap scores for the

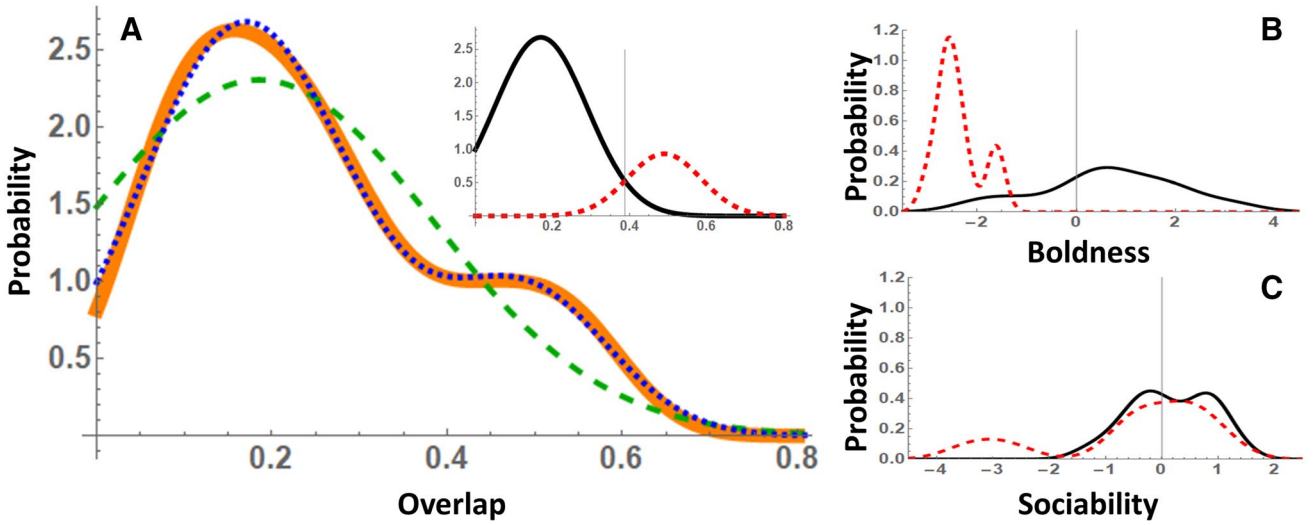

Fig. 3 **a** Density distribution of mean overlap per rat (solid orange line). The distribution is bimodal: the best-fit single Gaussian model (dashed green line) fits less well than a 2-Gaussian model (dotted blue line; see text for details). The inset shows the two components of the best-fit bimodal model (low overlap in solid black; high overlap in dashed red) and the criterion used for assigning rats to a component (vertical line; overlap = 0.387). Boldness (**b**) but not sociability (**c**) predicts overlap mode. Rats in the low-overlap component (solid black lines) tend to have higher boldness scores than rats in the high-overlap component (dashed red lines) (color figure online)

same rat across both SF phases were correlated [$r = 0.40$, $t\,(41) = 2.82$, $p = 0.004$], suggesting—in combination with the results reported above—that the degree to which a subject coordinates its foraging behavior with a partner, by eating at the same time as its partner (regardless of food type or location), is mostly determined by that subject's boldness.

Interactions

Finally, we explored the interactions between partners during social foraging, defined as any time the rats were touching or sniffing each other, or together inside the small home base. The total amount of time that partners spent interacting did not correlate with their mean boldness [$r = 0.11$, $t\,(41) = 1.45$, $p = 0.07$], sociability [$r = 0.05$, $t\,(41) = 0.61$, $p = 0.27$], or the differences in those scores between the partners [Δboldness: $r = -0.10$, $t\,(41) = -1.40$, $p = 0.08$; Δsociability: $r = -0.32$, $t\,(41) = -0.38$, $p = 0.35$], suggesting—somewhat surprisingly—that individual differences do not drive interactions in a novel, potentially anxiogenic, environment. Total amount of interaction also did not differ between pairs of rats that had the same preference or those that had different preferences (K–S test. $D = 0.20$, $p = 0.04$), which suggests that rats do not preferentially associate with conspecifics that share their food preferences. However, same preference rats spent more time interacting outside of the home base than inside it (Fig. S2; $D = 0.31$, $p = 0.0002$); while, rats of opposing preferences showed the opposite effect, spending more time interacting inside the shelter than out ($D = 0.31$, $p = 0.0003$). Same preference rats interacted more than rats with opposite preferences outside the home base (Fig. S2; $D = 0.26$, $p = 0.004$), but interacted less inside the home base ($D = 0.31$, $p = 0.0003$). These results suggest that rats modulate their interactions differently when sheltering inside the home base than when they are outside, foraging in or exploring their environment. We discuss this idea further below.

To examine the effects of interactions on foraging choices in greater detail, we measured the amount of interaction that took place between each two consecutive bouts of eating, classified by the flavor of food eaten during each bout (i.e., preferred or non-preferred) and by the preferences of the partners (Fig. 4). When not switching foods, rats interacted significantly more between two eating events if their partner had the same preference than if they had opposing preferences, whether both events consisted of eating their preferred food (Fig. 4a; K–S test. same vs. diff: pref. → pref., $D = 0.185$, $p < 0.00001$) or their non-preferred food (same vs. diff: non → non, $D = 0.217$, $p < 0.00001$). This effect was driven by differences in interaction durations outside the home base (outside same vs. diff: pref. → pref., $D = 0.19$, $p < 0.00001$; outside same vs. diff: non → non, $D = 0.22$, $p < 0.00001$) but not inside it (inside same vs. diff: pref. → pref., $D = 0.05$, $p = 0.10$; inside same vs. diff: non → non, $D = 0.01$, $p = 0.99$). Conversely, rats interacted more if their preferences were different than if they had the same preference when switching foods, either from their preferred to their non-preferred food (Fig. 4b; same: pref. → non vs. diff: pref. → non, $D = 0.08$, $p = 0.004$) or from their non-preferred to their preferred food (same: non → pref. vs. diff:

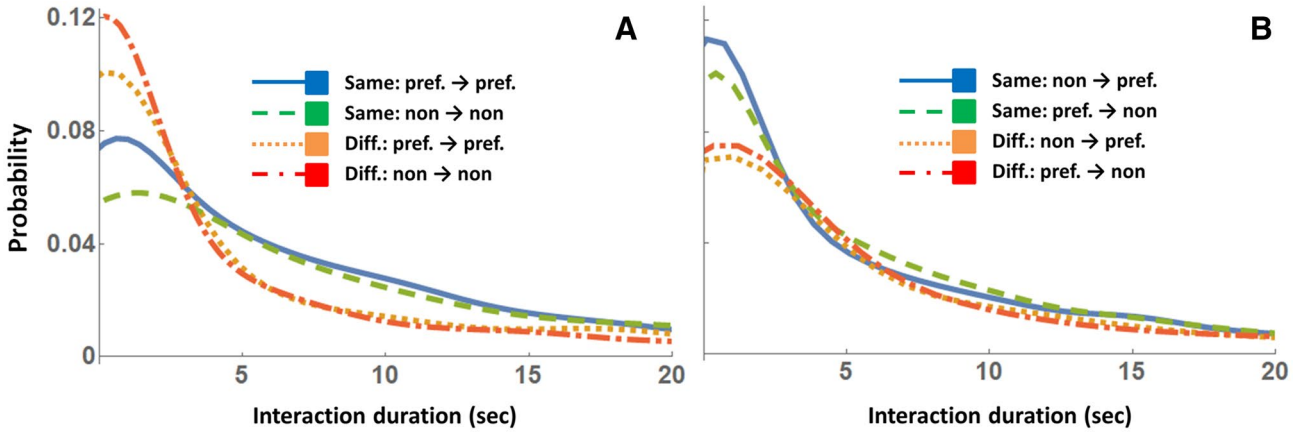

Fig. 4 Distributions of interaction durations between two eating events. Each event in each pair of eating events was classified as being of the subject's preferred (pref.) or non-preferred (non) flavor, and separate distributions are shown for sessions in which partners had the same or different preferences. **a** Durations of interactions between eating events of the same food type (pref. → pref. or non → non). **b** Durations of interactions between eating events of differing food types (color figure online)

non → pref., $D = 0.11$, $p < 0.0001$). This effect was driven by differences in interaction duration within the home base (inside same vs. diff: pref. → non, $D = 0.08$, $p = 0.006$; inside same vs. diff: non → pref., $D = 0.13$, $p < 0.00001$) but not outside it (outside same vs. diff: pref. → non, $D = 0.06$, $p = 0.04$; outside same vs. diff: non → pref., $D = 0.05$, $p = 0.23$). These results do not show that interacting with a partner that has the same preference makes an individual more likely to copy that preference (or vice versa), as might be expected. Rather, the data suggest that interacting with a partner that has the same preference (outside a home base) makes a rat more likely to continue to eat what it has been eating (Fig. 4a), whether or not that is its—or its partner's—preferred food. Conversely, interacting with a partner that has a different preference (in the home base) appears to make rats more likely to switch foods (Fig. 4b), even if that means switching away from their preferred food. Note that we cannot distinguish whether the durations of interactions drive food choices, as in this proposed explanation, or whether upcoming food choices determine the amount of interaction rats engage in. As above, it is also not immediately apparent why interactions inside the home base have a different effect on (or are differentially affected by) food choices than interactions outside the home base. We discuss this finding further below.

Though the data presented above indicate that the dynamics of social foraging in partners with the same preferences differ from those of partners with opposing preferences, it is unclear what indicates a partner's original preference. When placed into the SF arena, neither rat has eaten that day, allowing us to assume that their breath carries no specific food information. We, therefore, re-analyzed the interactions between partners, taking into account the last thing each rat had eaten, which is presumably what its breath smelled most strongly of. We note, however, that rats' breath may contain multiple cues and rats that have consumed several foods can transmit more than one preference at a time (Galef et al. 1990a). Eating events that were preceded only by interactions with a partner who had not yet eaten that day were excluded. For simplicity, we ignored the locations of the interactions. Before eating their preferred food, subjects interacted for longer with a partner whose breath smelled of their preferred food than one whose breath smelled of the other food (K–S test. $D = 0.06$, $p < 0.00001$). Similarly, subjects interacted for longer with a partner whose breath smelled of their preferred food before consuming that food than before consuming their non-preferred food ($D = 0.04$, $p = 0.007$), suggesting that what a partner's breath smells of most strongly at least partially mediates the amount of interaction rats engage in.

Discussion

Rats in nature are known to forage in groups (Barnett 1963) and frequently return to a shared burrow where they likely interact and share food-related information with conspecifics (Galef 2012). Despite the complexity of rats' foraging ecology, STFP has most often been studied in isolation from possible external factors, such as individual differences between group members, and under artificially simplified conditions, where a completely naïve rat is exposed to a single trained demonstrator and then tested alone for its acquired preference (Galef 2012). In the current experiment we attempted to place STFP in context by testing socially acquired preferences against individual differences and examining how preferences change as a result of foraging in a small group (of two individuals). Clearly, our paradigm is

still far from the natural complexity of social interactions in rodent groups, but it nonetheless reveals that STFPs can be dramatically altered by social foraging.

We find that STFPs, traditionally described as long-lasting and robust, completely degrade as a result of social foraging. Preferences in our Experimental Group were reduced to chance levels after just one or two 30-min sessions of foraging with a partner (Fig. 2), irrespective of whether that partner had the same or a different food preference, and independent of the absolute or relative boldness or sociability of the two partners. Moreover, this result is not a function of failing to create robust preferences. When tested under conditions that mimic the typical behavioral protocol for STFP induction, control group rats—who were exposed to both flavors of food in their home cages under exactly the same schedule as rats in the experimental group—showed almost no degradation of their preferences (see also Galef and Whiskin 2001, experiment 2). There were two differences between the rats in our experimental and control groups that might account for the difference in the robustness of their preferences: rats in the experimental group foraged for their food in a large open arena, and they did so with a partner. Control group rats received both foods in their home cages, alone. Though our current results do not allow us to disambiguate how much each of these differences contributed to the observed effect, it is likely that they were both important. Both regularly interacting with one or more partners and having to search for food outside a shelter are important elements of natural foraging in rats which are not present in most studies of STFP.

Since no significant sex differences have been found in the STFP paradigm (Choleris and Kavaliers 1999), we used only male subjects. However, foraging strategies do vary slightly between sexes (Inglis et al. 1996), and female exploration of novel environments may be modulated by estrous cycle (Palanza et al. 2001), suggesting that using mixed-sex groups, which are what we might expect to find in the wild, might alter our results somewhat.

In addition to testing STFPs, we gave each subject a series of tests to establish their individual behavioral norms, sometimes referred to as 'animal personality'. Rats were tested on emergence into and exploration of a brightly lit novel environment (LDE), an elevated plus maze (EPM), and preference for an unfamiliar conspecific over a stuffed decoy (SPT). Scores on these tests were put into a principal components analysis, which returned two axes which we labeled boldness (LDE: exploring more; EPM: more time on open arms) and sociability (SPT: more time close to conspecific). Neither boldness nor sociability affected the strength of STFP, though bolder individuals held on to their preferences marginally less strongly after social foraging than shyer rats. Bolder rats spent less time eating overall during social foraging, possibly because they spent more time exploring the environment (Kurvers et al. 2010a, b). When bold rats did eat, they were more likely than shyer rats to eat when their partner was not also eating, which we call having low 'overlap'. Shy rats mostly ate at the same time as the bolder rats, suggesting that the bolder rats initiated most feeding events and the shyer rats then joined in. These results reinforce findings showing that shyer individuals are more likely to copy the foraging choices of their bolder group mates (Kurvers et al. 2010a, b; Harcourt et al. 2009; Nakayama et al. 2012; Kurvers et al. 2009), scrounging from their finds (Kurvers et al. 2010b). However, in our data, only the decision to begin (or cease) eating appears to have been socially affected, not the decision of which food to sample. This effect aligns with earlier results on STFP that show the process has limited ability to drive avoidance of specific foods (Galef et al. 1990b) or to affect general preferences for odors (e.g., of bedding; Galef and Iliffe 1994). Additionally, feeding appears to have been modulated by whether or not the partners shared a preference, with rats eating more when their preferences aligned than when they did not, and amount eaten correlating between members of a pair.

When exploring a novel environment, as in the current experiment, rats' behavior is organized around a home base to which they frequently return and where some behaviors (e.g., grooming) are concentrated (Eilam and Golani 1989). We note that rats were not habituated to the SF arena before the experiment began; doing so might alter their exploration of the environment (Fonio et al. 2012) and possibly affect our results. The home base may correspond to the communal burrow, which serves as an 'information center' (Galef and Giraldeau 2001) where rats interact with conspecifics, in the process transmitting information about the foods they have consumed. We provided our foraging pairs with a home base in the form of a shelter in one corner of the social foraging arena and recorded their interactions both inside and outside it. Rats with the same food preference interacted more while outside of the home base than while inside it (Fig. S2). Rats with opposing preferences showed the opposite pattern. This suggests that rats manage their interactions differently depending on what task they are engaged in. When foraging, rats prefer to engage with partners of similar preference, who are more likely to locate a food source that they will want to scrounge from. Foraging with partners of differing preferences may more often lead to differences of opinion on whether or not to exploit some food source, which may reduce the efficiency of foraging. Conversely, when sheltering in a home base, rats interact more with partners of opposing preference, possibly because acquiring information about novel foods is more important than confirming what they know about an already preferred food.

Interacting with a partner whose breath smelled of a rat's preferred food increased its probability of then consuming that food, but interacting with a partner whose breath

smelled of the non-preferred food had no effect on subsequent choice. This suggests that rats are biased in their use of information sources, altering their behavior more in response to some social interactions than others. Similarly, interacting with a partner of the same preference while foraging increased the probability of continuing to consume the same food as previously, whether it was the preferred or non-preferred food, and interacting with a partner of differing preference while in the home base increased the probability of switching foods (Fig. 4), suggesting—as we propose above—that rats' use of food-related information is dependent on its source and on whether they are currently foraging or sheltering.

We propose the following, speculative, explanation for our results. Rats that have previously acquired food preferences, either socially or through their own past experiences with various food items in their environment, engage in social interactions that are modulated by these preferences. When in a shelter, which has been proposed to serve as an 'information center' (Galef and Giraldeau 2001), rats interact more with conspecifics that provide information about novel potential food sources, information that may help them expand their foraging repertoire. These interactions increase rats' subsequent probability of switching foods (i.e., consuming a food different from the one they chose in their immediately previous eating event), whether this is a switch to or away from their preferred food. We can summarize this by saying that gaining new information increases the variability of rats' foraging choices. Conversely, when rats are outside the shelter, presumably foraging (or exploring the environment), they engage more with conspecifics that provide confirmatory information about the food they are searching for. Interacting with those rats increases their chances of continuing to eat the same food they have been eating.

Conclusion

As the differences between our experimental and control groups show, when tested under marginally more naturalistic conditions than is usual, socially acquired food preferences degrade rapidly and may not have as dominant an effect on rats' food intake as previously suggested. Our results suggest that foraging in groups might preclude strong socially transmitted preferences from forming in the first place, though this is not something we tested. Our rats were given pre-existing socially acquired food preferences and only then allowed to forage in pairs. It is possible, given the degradation of preference that we then observed, that rats which began to forage naturally without a food preference might never acquire one, due to the variability of the information they were exposed to, from both environmental and social sources. Rats with pre-existing food preferences, foraging in pairs in an open environment, do not simply consume their preferred food, nor do they consume their partner's preferred food, or the food their partner's breath currently smells of most strongly. Instead, rats' choices of food depend on a number of interacting factors, including their boldness, their partner's food preferences, and the amount of time they spend interacting with that partner. Rats interact with their partners differently when foraging than when they are sheltering in a home base, suggesting that they prioritize new information (about novel foods) when in a shelter, and information about the food they are currently searching for when outside the shelter. Selecting which foods to consume is a complex task for rats, which are dietary generalists and often confronted with novel, potentially poisonous, foods (Galef 2012). Rats rely heavily on social learning to solve this problem and, as our data show, combine the information they extract from conspecifics with their own information and preferences in complex ways.

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Author contributions All authors designed the experiment. CD ran the experiment, CD and NM analyzed the data, and all authors wrote the manuscript.

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Compliance and ethical standards

Conflict of interest Chelsey C. Damphousse declares that she has no conflict of interest. Diano F. Marrone declares that he has no conflict of interest. Noam Miller declares that he has no conflict of interest.

Statement on welfare of animals All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The procedures used followed the Canadian Council on Animal Care guidelines and were approved by the Wilfrid Laurier University Animal Care Committee.

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