INTRODUCTION

Understanding how the phenotypic composition of animal groups acts as a selective force on individual group members, although simultaneously being an emergent property of individual decision-making, has been the focus of much work within behavioral ecology (Krause and Ruxton 2002; Farine et al. 2015). Central to this objective is determining the role played by group phenotypic composition in shaping individual fitness and group-level outcomes. Selective targeting of phenotypically different individuals by predators can promote behavioral conformity between group members (Day et al. 2001), as well as the formation of morphologically homogeneous groups that are assorted by factors such as body size, species, or sex (Krause and Ruxton 2002). Conversely, phenotypic diversity can be selected for by mechanisms such as social heterosis (Nonacs and Kapheim 2007) or negative frequency dependence (Maynard Smith 1982); for example, in the producer–scrounger game, in which producers locate resources and scroungers paritize their efforts, scrounger success is positively associated with the frequency of producers within the group (Barnard and Sibly 1981).

Consistent between-individual differences in behavior represent a key component of phenotypic variation within groups. Such stable differences have been observed for numerous traits, including the propensity to use social information (Kurvers et al. 2010), leadership tendencies (Leblond and Reebs 2006), or averseness toward risk (Laskowski and Pruitt 2014; Modlmeier et al. 2014). The mixture of behavioral types within a group can shape both the social decision-making of individuals (Cote et al. 2012) and the group-level outcomes (Dyer et al. 2009; Modlmeier et al. 2012; Pruitt and Goodnight 2014). In the social spider Anelosimus studiosus, for example, colony survival and reproductive success depends on matching the within-colony ratio of aggressive to docile individuals to the environmental conditions experienced by the colony (Pruitt and Goodnight 2014). In some contexts, association between unlike individuals can generate benefits for one or both parties, such as in socially foraging shoals of Trinidadian guppies (Poecilia reticulata), in which mixed shoals of bold and shy fish experienced higher
foraging success than pure shoals of either behavioral type (Dyer et al. 2009). Consistent differences in social behavior can also derive from variation in the extent to which individuals are familiar with their group mates, defined here as condition-independent recognition of unrelated individuals (Griffiths and Ward 2011). Across a wide variety of taxa, familiarity has been shown to influence social preferences, including in fish (Griffiths and Magurran 1997; Atton et al. 2014), birds (Kohn et al. 2013), and mammals (Keller et al. 2011). Familiarity can arise through learned recognition of specific individuals (Griffiths and Magurran 1997; Ward et al. 2009), as well as via mechanisms that facilitate a more general recognition of particular classes of individual. For instance, fish can distinguish between individuals on the basis of olfactory cues derived from recent habitat use or diet (Webster et al. 2007; Ward et al. 2009).

The presence of familiar individuals within a group can have potentially large impacts on group dynamics and individual fitness. Familiarity can facilitate behavioral coordination between group members by allowing them to tailor their interactions with specific individuals based on past experience (Wolf et al. 2011). Such an effect may be responsible for the more cohesive shoaling behavior, reduced aggression, and more effective antipredator responses exhibited by familiar shoals of fish compared with unfamiliar ones (Chivers et al. 1995; Griffiths et al. 2004; Granroth-Wilding and Magurran 2013). By promoting social cohesion, familiarity can also enhance the transmission of social information through a group. Guppies learned the route to a foraging site from a trained demonstrator more rapidly when the demonstrator was also familiar to them as a result of stronger tendencies to follow familiar group mates (Swaney et al. 2001). Familiarity may also generate consistent behavioral differences between group members through the process of social niche specialization, which proposes that repeated interactions between group members promote behavioral diversification due to individuals adopting different social roles in order to reduce competitive costs (Bergmüller and Taborsky 2010; Montiglio et al. 2013). An individual’s adoption of a social role is then stabilized by positive feedback mechanisms or costs associated with role switching. Support for this hypothesis has been found in social spiders (Laskowski and Pruitt 2014; Modlmeier et al. 2014), in which spiders exhibited more pronounced individual differences in boldness when they belonged to colonies in which group members were more familiar with one another; such between-individual variation has been linked to positive colony-level outcomes in both spiders and ants (Pruitt and Richeart 2011; Modlmeier et al. 2012).

Familiarity is generally associated with stronger social preferences between individuals. Fine-scale patterns of social structure—conceptualized as a social network—are an emergent outcome of such preferences (Wilson et al. 2014). Even within fission–fusion social systems, in which group size and membership changes frequently, social connections between familiar individuals can persist. Female brown-headed cowbirds (Molothrus ater) maintained stable social bonds with familiar females over time and across shifting group compositions (Kohn et al. 2015). Similarly, persistent social preferences were detected between females in a wild Trinidadian guppy population, and these strong network connections were correlated with greater cooperation during predator inspections (Croft et al. 2006). The structure of a social network can also shape group-level outcomes, such as the speed and pathways by which information flows through a group (Claidière et al. 2013; Aplin et al. 2015). Within three-spined stickleback (Gasterosteus aculeatus) shoals, information regarding the location of a novel foraging task was more likely to spread between familiar shoal mates than between unfamiliar ones, facilitating information transfer within—and restricting it between—clusters of familiar individuals (Atton et al. 2014).

The influence of between-group variation in terms of familiarity on individual success and group-level outcomes has been well-studied, particularly in fish (reviewed in Griffiths and Ward 2011). However, despite the importance of social recognition in many studies of animal networks, less is known about how this variation shapes the emergent social structure of a group and how social structure might mediate these group-level outcomes (though see Morrell et al. 2008). We therefore asked whether the proportion of familiar individuals composing a group affected the fission–fusion decisions of its members, its network structure, as well as diffusion processes occurring within it.

For our study, we used the Trinidadian guppy. The guppy has long served as a model system in which to investigate questions related to social information use (Dugatkin 1992; Lachlan et al. 1998; Swaney et al. 2001; Morrell et al. 2008) and the influence of familiarity on social decision-making (Griffiths and Magurran 1997; Lachlan et al. 1998; Swaney et al. 2001; Ward et al. 2009; Granroth-Wilding and Magurran 2013). Guppies have also served as a popular study system in which to use social network analysis to probe the causes and consequences of variation in fine-scale social structure (Croft et al. 2006; Morrell et al. 2008; Croft et al. 2009; Wilson et al. 2015).

We formed groups of female guppies in which individuals were either: 1) all familiar with one another, 2) all unfamiliar with one another, or 3) a mixed group of familiar and unfamiliar fish. Each group was placed within an arena and the shoaling decisions of group members were recorded. Fission–fusion models of shoaling behavior were used to characterize the social dynamics occurring within each treatment and to infer the social network structure of each group (Wilson et al. 2014, 2015). Next, groups were presented with a hidden food patch and the order in which individuals discovered the patch was recorded (as in Webster et al. 2013). Network-based diffusion analysis was then used to examine whether network structure predicted information flow and to estimate the strength of social effects on patch discovery (Franz and Nunn 2009; Hoppitt and Laland 2013).

We tested the following predictions: 1) that individuals in groups of familiar fish would express more cohesive shoaling behavior, such that they would be less likely to remain swimming alone; 2) that individuals in unfamiliar groups would be more likely to switch between social partners, as familiarity-based social preferences would not yet have formed; 3) that networks based on shoaling associations would predict the diffusion of information through social groups; and 4) that the highest diffusion rates would be observed in familiar groups.

METHODS

Study subjects and rearing conditions

Study subjects were lab-reared descendants of wild-caught fish collected in 2003 from the Quaré River in Trinidad. The study was conducted in two replicate blocks from February to June 2014. Juvenile guppies (ca., ≤7 mm in length) were collected from four 208-L stock tanks, each of which contained several hundred fish. To reduce the likelihood of social preferences expressed during the experiment being systematically influenced by kinship or by familiarity developed within the stock tanks early in life, juveniles were randomly assigned to one of the fifteen 37.9-L rearing tanks and
were reared together in groups of 24 fish. Rearing tanks were visually and chemically isolated from one another, filtered, and maintained at 26-27 °C on a 12-h:12-h light–dark cycle. Fish were fed TetraMin® Tropical Flakes daily.

Once fish had matured, six size-matched, non-gravid females were selected from each rearing tank for the experiment; at this point, population sizes varied between rearing tanks due to mortality (mean ± standard deviation [SD]: 21 ± 2.2 individuals). All individuals besides the selected females were then returned to the stock tanks. We used female guppies because they are more likely to express persistent social preferences (Griffiths and Magurran 1998; Croft et al. 2006) as well as tend to be more food motivated than males (Reader and Laland 2000). At the time of testing, rearing groups had been together for 51 to 55 days. Learned familiarity can develop in guppies under captive conditions in as little as 12 days (Griffiths and Magurran 1997), so we considered fish reared in the same tank to be familiar with one another and fish reared in separate tanks to be unfamiliar. Olfactory cues originating from the unique chemical mélange within each rearing tank may also have contributed to social recognition (Ward et al. 2009). To permit individual identification, each female was anesthetized with MS-222 and injected with a combination of two colored elastomer tags. This method has been extensively used in guppies (e.g., Croft et al. 2006; Morrell et al. 2008; Croft et al. 2009; Wilson et al. 2015) and does not appear to influence shoaling decisions (Croft et al. 2004). Females recovered quickly after marking and no mortalities occurred as a result of this procedure.

Testing procedure

Prior to testing, rearing groups were habituated to the test arena; at the start of habituation, rearing groups had been together for 40 days. The test arena was a black rectangular tank measuring 62 × 44 cm with black gravel substrate and water 5 cm deep (Figure 1). Black cloth was hung around the arena setup to minimize disturbance from any visual cues in the room. Each rearing group was released within the arena for 30 min on 5 separate occasions. Each time, flake food was sprinkled over the water’s surface in sufficient amounts to minimize competition, as judged by the presence of uneaten flake food at the end of each session. The arena and gravel were rinsed and scrubbed between subsequent uses. Habituation sessions for a rearing group occurred every other day for a 10-day span. Testing began on the day after the final habituation sessions.

Three treatment groups were tested each day. Our study had 3 treatments: 1) familiar (n = 9 groups), in which all 6 fish originated from the same rearing group, 2) unfamiliar (n = 10 groups), in which all 6 fish originated from separate rearing groups, or 3) mixed (n = 10 groups), in which 3 fish were familiar with one another, whereas the remaining 3 originated from 3 separate rearing tanks. Unfamiliar and mixed groups were formed immediately prior to being transferred to the arena. One familiar group was lost due to mortality unrelated to the study. The mean (±SD) standard length of fish in this study was 16.9 ± 1.4 mm; within each group, all individuals were within 3 mm standard length of one another. This was done to minimize the impact of size-based preferences (Krause and Ruxton 2002; Wilson et al. 2014) in order to better isolate any influence of familiarity on shoaling decisions.

The testing procedure was adapted from Webster et al. (2013). The arena was as described above, with the addition of eighteen 10 cm² partitions setup perpendicular to one another to break up sight lines between fish in the arena (Figure 1). The foraging and control patches were located at the arena center. The foraging patch was a transparent cylindrical container (3.5 cm diameter) containing flake food that was recessed into the gravel and sealed to prevent release of olfactory cues; fish had to pass over the foraging patch in order to locate it. An area of substrate identical in size to the foraging patch, but containing no food and possessing no topological features distinguishing it from the surrounding gravel, was designated as the control patch. Two black cylinders (10.5 cm diameter) concealed both patches from groups for the first 120 min in the arena. Overhead illumination was provided by four 23 W compact fluorescent lights. Groups were filmed by a Canon Vixia HG21 camcorder suspended 1.2 m above the arena.

Groups were given 30 min of acclimation before being recorded for 90 min to collect shoaling association data. Focal individuals were randomly selected and observed continuously for 4 min. Every 10 s, we recorded whether the focal fish was asocial—that is, no group mates were within four body lengths—or social. If the latter, we recorded the identity of its nearest neighbor as measured from the center of their heads. We also recorded activity based on whether the focal had moved ≥10 cm since its prior observation. After 4 min, a new focal fish was randomly selected until all group members had been observed. This process was repeated twice more, allowing 6 min to elapse between consecutive sessions, to provide 72 observations per individual. After this 90-min period, we gently removed the cylinders to reveal the foraging and control patches. Groups were filmed for an additional 30 min, during which we recorded the time of first arrival for each individual at both the real and control patch for use in the network-based diffusion analysis. The arena, gravel, and all items within the arena were scrubbed and rinsed on trial completion.

All experimental procedures, as well as animal care and maintenance protocols, were approved prior to the study’s commencement by the University of Louisville’s Institutional Animal Care and Use Committee (IACUC #13020).

Fission–fusion dynamics and social network structure

To characterize the social dynamics acting within our treatments, we used the fission–fusion model of shoaling behavior originally...
developed by Wilson et al. (2014). The shoaling behavior of a focal individual is described by a sequence of behavioral states, where swimming alone is denoted by $s_p$ and shoaling is denoted by $s_h$, where $g$ is one of $k$ potential nearest neighbors (Figure 2). If $a$ and $s_i$ ... then the probability of transitioning between states is determined solely by an individual’s current state. Transition probabilities were estimated as simple proportions from the observed sequences of shoaling behavior. Three individuals, 2 from mixed groups and 1 from an unfamiliar group, were not visible throughout their trial. Focal follows were conducted on 54 fish in familiar groups, 58 fish in mixed groups, and 59 fish in unfamiliar groups.

The model can be characterized by the probabilities of an individual switching from being alone to shoaling [$p(a,s)$], of ending social contact [$p(s,a)$], and of switching between nearest neighbors though remaining social [$p(switch)$] (Figure 2). The probability of a focal individual maintaining its current state is determined by the respective transition probability—for example, $p(a,a) = 1 - p(a,s)$. As some behavioral states—for example, swimming alone—were not observed with sufficient frequency to permit accurate estimation of individual-specific transition probabilities, data were pooled across all focal follows within each group. Weighted mean transition probabilities were then calculated for each treatment, where weighting was based on the relative frequency of opportunities for state transitions within a group. Nonparametric bootstrapping was used to generate 95% confidence intervals (CIs) using the boot package (Davison and Hinkley 1997; Canty and Ripley 2015) in R version 3.2 (R Core Team 2015).

To test whether fish expressed social preferences for particular individuals, we first quantified the association strength between each pair of group mates in terms of: 1) the average duration of a contact phase between them and 2) the total number of distinct contact phases with each other. A contact phase between two individuals was one or more consecutive observations in which a focal individual was recorded as being nearest neighbors to one another. We then employed randomization tests where, for each focal individual, we kept constant their observed number of contact phases and their lengths but randomized the identities of their nearest neighbors prior to recalculating association strengths using both methods described above. This randomization procedure was carried out $10^4$ times. The test statistic was the sum of squares of the association strength across all pairs within a group. If the observed test statistic was in the top 5% of the distribution generated by the randomization procedure, this was used as evidence that focal fish were expressing individual-specific nearest neighbor preferences. We then calculated combined $P$ values using Fisher’s omnibus procedure to examine treatment-level patterns (Haccou and Meelis 1994).

Using networks based on the total number of contact phases between pairs (see Results), we tested whether a pair’s association strength was correlated with their similarity in terms of body length, activity level, or shoaling tendency using Mantel tests. Activity level and shoaling tendency were calculated as the proportion of observations in which a focal individual was recorded as being active or shoaling respectively. Similarity was calculated by subtracting the difference between two individuals in terms of the variable of interest from the maximum value possible—for example, for body length, this was the maximum length measured within a group. Similarity matrices for each group were then constructed from these values. Two-tailed Mantel tests were conducted in SORC-PROG version 2.5 with $10^4$ permutations per test (Whitehead 2009). The $P$ values within a treatment were subsequently combined using Fisher’s omnibus procedure (Haccou and Meelis 1994).

**Network-based diffusion analysis**

We used the order-of-acquisition diffusion analysis (OADA) variant of network-based diffusion analysis (NBDA) to examine the rate and pattern of information diffusion in our groups (Hoppitt and Laland 2013). OADA examines whether the order in which individuals acquire information is predicted by their social network. The time of first arrival at a patch was used to indicate when an individual became knowledgeable about its location. A general form of the NBDA model, extended to consider diffusions in separate groups, is given by:

$$\lambda_k(t) = \lambda_a(t)(1 - z_a(t))\left(\sum_{j=1}^{N_s} p_{ij} z_i(t) + 1\right)$$

![Figure 2](https://example.com/figure2.png)

**Figure 2**

Markov chain model of shoaling behavior. A focal individual can either be swimming alone—$a$—or shoaling with some nearest neighbor—$s_i$—where $g$ is one of $k$ potential nearest neighbors. A focal individual that is alone remains so during the next observation with probability $p(a,a)$ or will begin shoaling with another individual with probability $p(a,s)$. An individual shoaling with a nearest neighbor will either continue shoaling with that individual at the next observation with probability $p(same)$, begin shoaling with a different nearest neighbor with probability $p(switch)$ or cease shoaling entirely with probability $p(a,s)$. This model does not include individual-specific nearest neighbor preferences; when an individual switches nearest neighbors, it selects its new partner with probability equal to $p(switch)/(k-1)$. The probability of maintaining shoaling behavior rather than beginning to swim alone is given by $p(s)$. 

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in which \( \lambda_k(t) \) is the rate at which individual \( i \) in group \( k \) discovers the patch at time \( t \), \( \lambda_i \) is the baseline rate of acquisition, \( z_i(t) \) is the informational status of individual \( i \) in group \( k \) at time \( t \) where \( z = 1 \) is informed and \( z = 0 \) is naive, \( a_{ij} \) is the association strength parameter, and \( a_{ij}^{(t)} \) is the association strength between individuals \( i \) and \( j \) in group \( k \). We used an OADA variant modified to allow between-group comparisons; for additional details, see Hoppitt and Laland (2013).

We tested the explanatory power of 2 network types: 1) association networks, where the association strength between each pair was based on the total number of contact phases between them, and 2) homogeneous networks, where the association strength between each pair was set to 1. The former tests whether the strength of social effects on patch discovery is proportional to the association strength between individuals, whereas the latter tests whether social effects operate homogeneously throughout each group.

Comparison of social effect strength between the real and control patch allowed us to assess the level of support for social transmission relative to that for untransmitted social effects. Social transmission refers to informed individuals increasing the probability of naive individuals becoming informed due to the former’s behavior (Hoppitt and Laland 2013). In contrast, when information or a trait can only be acquired at a specific location—as in our study—individuals who frequently associate together might also be likely to acquire this information at similar times to one another through otherwise asocial means—that is, an untransmitted social effect (Atton et al. 2012; Webster et al. 2013). For example, individuals traveling together could simultaneously encounter a novel food patch. Although social transmission and untransmitted social effects could act together to affect the discovery of a food patch, we assumed that only untransmitted social effects would affect the diffusion of ‘knowledge’ regarding the location of an arbitrary area of gravel—that is, the control patch. Under this assumption, the social effect parameter, \( s \), for the real diffusion is equal to \( s_T + s_{\tau} \), where \( s_T \) is the social effect estimated for the control diffusion and \( s_{\tau} \) estimates the potential strength of social transmission.

We compared the explanatory power of 4 parameterizations that establish how the social effect parameter, \( s \), might vary within and between treatments: 1) social effect strength could vary between treatments—for example, allowing for faster diffusion rates in some treatments—as well as vary between real and control patches; 2) social effect strength could be equal across all treatments, but vary between patch types; 3) social effect strength could vary between treatments, but not between patch types; or 4) social effect strength could be equal across all treatments and patch types. The first 2 alternatives allow for social transmission, whereas the latter 2 suggest that primarily untransmitted social effects may be at work.

We also included several individual-level variables to examine their influence on baseline rates of patch discovery. For each individual, we included its body length and the number of days since its last habituation session. Both variables were first standardized. We also included variables that allowed the discovery rate to vary between patch types, between replicate blocks, and for patch location—that is, the left or right side of the arena. Both additive and multiplicative OADA variants were considered; these specify how individual-level variables interact with social effects. Models were fitted for every combination of network type, OADA variant, social effect parameterization, and individual-level variables. An additional model set was fitted that allowed for only asocial learning but permitted patch discovery rates to differ between treatments. Diffusion data could not be collected for 1 unfamiliar group due to a malfunction with the foraging patch that resulted in the food not being visible; analyses were conducted on 9 familiar, 10 mixed, and 9 unfamiliar groups.

Akaike weights—based on Akaike’s information criterion corrected for sample size—were calculated for each fitted model, indicating the support provided by the data for a model relative to the rest of the model set (Burnham and Anderson 2002). The total support—given as a %—for each network type, OADA variant, social effect parameterization, and individual-level variable was then obtained by summing the Akaike weights for each model in which it was included over the complete model set. Model-averaging approaches were used to calculate parameter estimates and CIs. For the individual-level variables, we calculated 95% Wald CIs adjusted to account for model selection uncertainty (Burnham and Anderson 2002). CIs for social effect parameters are often asymmetric (e.g., Webster et al. 2013); thus, these were obtained using profile likelihood techniques adjusted for model selection uncertainty (Burnham and Anderson 2002; Morgan 2009). CIs were also obtained for the estimated differences in social effect strength between treatments. OADA was conducted in R version 3.2. (R Core Team 2015) using code (version 1.2.11) freely available at http://lalandlab.st-andrews.ac.uk/freeware.

RESULTS

Fission–fusion dynamics and social network structure

Observed fission–fusion dynamics were well reflected by our models as assessed by comparing the observed distributions of the lengths of social contact, of contact with a particular nearest neighbor, and of being alone with simulated distributions generated using the estimated transition probabilities for each treatment (Figure 3). The proportion of familiar individuals within a group did not influence its overall fission–fusion dynamics, as transition probabilities did not significantly differ between treatments (Figure 4).

Social preferences were not expressed in the average duration of contact between 2 individuals (combined \( P \) values: familiar \( = 0.848 \), mixed \( = 0.983 \), and unfamiliar \( = 0.349 \)). When association strength was quantified as the total number of distinct contact phases between a pair, guppies exhibited nonrandom partner selection in familiar (combined \( P = 0.025 \)) and unfamiliar groups (combined \( P = 0.015 \)). Partner selection in mixed groups did not differ from random expectations (combined \( P = 0.162 \)).

Mantel tests detected no correlation in familiar groups between association strength and phenotypic similarity in terms of body length (2-tailed combined \( P = 0.873 \)), activity level (2-tailed combined \( P = 0.289 \)), or shoaling tendency (2-tailed combined \( P = 0.387 \)). In mixed groups, association strength was correlated with similarity in terms of shoaling tendency (2-tailed combined \( P = 0.002 \) but not body length (2-tailed combined \( P = 0.330 \)) or activity level (2-tailed combined \( P = 0.547 \)). In unfamiliar groups, there was a nonsignificant tendency toward a positive correlation between association strength and similarity in terms of activity level (2-tailed combined \( P = 0.049 \)) but not in terms of shoaling tendency (2-tailed combined \( P = 0.067 \)) or body length (2-tailed combined \( P = 0.941 \)).

Network-based diffusion analysis

Models that included social effects on patch discovery were strongly favored over models that only allowed for asocial learning, with
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the latter receiving virtually no support (Table 1). Association networks based on the total number of contact phases between group members predicted the order in which individuals discovered patch locations (94.7% support). For social effect parameterizations, the greatest support was found for social effects differing between treatments but not between patch types (58.6% support; Table 2). There was strong evidence for no difference in social effect strength between real and control patches (82.1% support), suggesting information flow most likely resulted from untransmitted social effects. There was more support for a difference in social effect strength between treatments than against (63.9% support).

The additive OADA variant that used the association networks received the greatest support (Table 1). Therefore, we used that model subset to obtain model-averaged estimates and CIs (Table 3). All treatments appeared to exhibit social influences on patch discovery, as 95% CIs for the social effect parameters did not overlap with 0 (Table 3). The social effect parameter is interpreted as the linear increase in patch discovery rate per unit of network connection to informed individuals relative to the average asocial rate of discovery (Hoppitt and Laland 2013). Social effects were strongest in mixed groups and weakest in familiar ones, with the difference estimated to be 0.02 (95% CI: 0.01, 0.05). As this 95% CI did not include 0, it provided additional support for the treatment differences in social effect strength suggested by the summed Akaike weights (Table 2). There was less evidence for differences in social effect strength between mixed and unfamiliar groups—estimated difference 0.01 (95% CI: 0, 0.04)—or between unfamiliar and familiar groups—estimated difference 0.01 (95% CI: 0, 0.03)—as the CIs for these estimated differences overlapped with 0. The only individual-level variable that received strong support was the number of days since an individual’s last habituation session (94.9% support). Individuals exhibited a difference in their baseline discovery rate of 0.28 (95% CI: 0.08, 0.48) on the log scale for every elapsed day relative to other individuals; for example, if 3 days had passed for individual A, whereas only 1 day had elapsed for individual B, individual A would have a baseline discovery rate of \( \exp[(3 - 1) \times 0.28] = 1.75 \) times that of B.

**DISCUSSION**

The proportion of familiar individuals within guppy shoals did not influence the mean fission–fusion behavior exhibited by group members—that is, the probability of initiating or ending social contact or of switching between shoaling partners. This is surprising, given that previous studies have found that familiarity influences social decision-making and affects social network structure...
Hasenjager and Dugatkin • Familiarity affects guppy networks and information flow

transition probabilities for Markov chain models of shoaling behavior. Weighted means and 95% confidence intervals are shown. Circles represent the probability, \( p(s,s') \), of starting to shoal after being alone, Xs represent the probability, \( p(s,a) \), of ending social contact to swim alone, and diamonds represent the probability, \( p(\text{switch}) \), of switching between nearest neighbors.

### Table 1

<table>
<thead>
<tr>
<th>Network</th>
<th>Total support (%)</th>
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<tr>
<td>Asocial learning only</td>
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<tr>
<td>Additive</td>
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</tr>
<tr>
<td>Multiplicative</td>
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</tr>
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<td>Association network</td>
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<tr>
<td>OADA variant</td>
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<tr>
<td>Homogeneous network</td>
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<td>0.74%</td>
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### Table 2

<table>
<thead>
<tr>
<th>Parameterization</th>
<th>Total support (%)</th>
</tr>
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<tr>
<td>Treatments equal; real patch = control patch</td>
<td>23.51%</td>
</tr>
<tr>
<td>Treatments differ; real patch = control patch</td>
<td>58.57%</td>
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<tr>
<td>Treatments equal; real patch ≠ control patch</td>
<td>12.61%</td>
</tr>
<tr>
<td>Treatments differ; real patch ≠ control patch</td>
<td>5.31%</td>
</tr>
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(e.g., Lachlan et al. 1998; Atton et al. 2014; Kohn et al. 2015). Individual-based models of collective motion have found that stronger social preferences between individuals—mimicking the effects of familiarity—can result in familiar individuals clustering together, forming distinct subgroups within the larger collective (Hemelrijk and Kunz 2005). Furthermore, several studies across a range of taxa have found that individuals are more likely to approach familiar group mates (Lachlan et al. 1998; Keller et al. 2011; Kohn et al. 2015) and associate more frequently with them (Atton et al. 2014).

Our results suggest that variation between groups in terms of the presence and distribution of social preferences may not necessarily translate into group-level differences in fusion–fusion dynamics. This is likely to be particularly the case if strong social preferences are not concentrated within clusters of individuals. Models of collective motion have found that the effect of strong social ties on the size, cohesion, and membership of subgroups critically depends on the distribution of those ties within the overall population and that, in many ways, the dynamics of collective motion in populations with randomly distributed strong social ties greatly resembles those of populations lacking any strong ties at all (Bode et al. 2011). The similarity in fusion–fusion dynamics between our treatments could have consequences for social processes, such as the success of cooperative strategies (Santos et al. 2006), in which outcomes are influenced by the frequency of social encounters and opportunities to switch between partners.

The lack of treatment effects on fusion–fusion behavior might also be explained by several alternative possibilities. First, although familiarity can develop in as little as 12 days in guppies (Griffiths and Magurran 1997) and protocols similar to ours have been successfully used to promote familiarity in both wild and domestic guppies (e.g., Griffiths and Magurran 1997; Lachlan et al. 1998; Swaney et al. 2001; Granroth-Wilding and Magurran 2013), we cannot discount the possibility that our experimental protocol was ineffective in developing familiarity within groups. Another possibility is that because all individuals in our study were fed an identical diet, self-referring strategies based on dietary cues allowed some level of social recognition in all our groups, potentially masking treatment differences in fusion–fusion behavior (Webster et al. 2007; Ward et al. 2009). It may also be the case that the expression of familiarity-based differences in shoaling depends on environmental conditions—for example, the level of predation risk. Groups of familiar fish exhibit greater shoaling cohesion in response to heightened predation risk or potentially threatening novel environments than do unfamiliar groups (Chivers et al. 1995; Granroth-Wilding and Magurran 2013). However, all fish in our study had experience within the arena prior to testing and all groups attempted to feed from the foraging patch, suggesting that the testing procedure was unlikely to have been perceived as especially threatening. Finally, early life experience can influence an individual’s social behavior later in life (Chapman et al. 2008; Lindeyer et al. 2013). At the time females were selected for our experimental groups, the population size within each rearing tank varied to some extent (range: 17–24 individuals). Presumably, the sex ratio within rearing tanks varied as well. Although we find it unlikely that early life experience varied systematically between our treatments, it may still have contributed further variation to our results that obscured differences among treatments.

Randomization tests controlling for the frequency and duration of contact phases with nearest neighbors found that fish in both familiar and unfamiliar groups exhibited nonrandom nearest neighbor preferences, whereas individuals in mixed groups did not. Furthermore, nearest neighbor preferences, when present, were not expressed in the mean duration of contact with specific partners but in the frequency with which individuals were selected as a partner. This is consistent with the work done on wild guppies (Wilson et al. 2014, 2015), though it may be that more data are required to establish whether nearest neighbor preferences were expressed in terms of contact duration because contact phases of longer duration occurred less frequently. Additionally, single bouts of shoaling between two individuals often were broken up into several contact phases due to the fact that only the focal individual’s nearest neighbor—rather than all nearby individuals—was identified at each time point.

Analysis of association networks based on contact phase frequency found that mixed groups were strongly assorted by shoaling...
Table 3  
Model-averaged parameter estimates, confidence intervals, and % support

<table>
<thead>
<tr>
<th>Variable</th>
<th>df</th>
<th>Parameter estimate</th>
<th>Unconditional 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Social effect parameters&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Familiar</td>
<td>1</td>
<td>0.03</td>
<td>0.01, 0.06</td>
</tr>
<tr>
<td>Mixed</td>
<td>1</td>
<td>0.05</td>
<td>0.03, 0.09</td>
</tr>
<tr>
<td>Unfamiliar</td>
<td>1</td>
<td>0.04</td>
<td>0.02, 0.07</td>
</tr>
<tr>
<td>Individual-level variables&lt;sup&gt;c&lt;/sup&gt;</td>
<td></td>
<td>Total support</td>
<td></td>
</tr>
<tr>
<td>Body Length (mm.)</td>
<td>1</td>
<td>29.27%</td>
<td>0.003</td>
</tr>
<tr>
<td>Block</td>
<td>1</td>
<td>32.34%</td>
<td>−0.05</td>
</tr>
<tr>
<td>Time since habituation</td>
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<td>94.86%</td>
<td>0.28</td>
</tr>
<tr>
<td>Patch type</td>
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<td>43.66%</td>
<td>−0.10</td>
</tr>
<tr>
<td>Patch Side</td>
<td>1</td>
<td>26.45%</td>
<td>0.003</td>
</tr>
</tbody>
</table>

<sup>a</sup>Total support was based on Akaike weights calculated over the entire model set.

<sup>b</sup>Social effect parameter estimates and their 95% CIs are conditional on the top model from the additive OADA model subset that included the association networks. This model allowed social effects to differ between treatments—but not between patch types—and included an individual’s time since last habituation as an individual-level variable. CIs were constructed using profile likelihood techniques and were adjusted to account for model selection uncertainty as described in Burnham and Anderson (2002).

<sup>c</sup>Individual-level variable parameter estimates and unconditional standard errors were obtained via model averaging over the additive OADA model subset that included the association networks. Unconditional standard errors were used to construct 95% Wald confidence intervals.

...tendency, such that individuals that spent much of their time shoaling were more likely to associate with one another, whereas unfamiliar groups exhibited tendencies toward assortment by activity level. There was no correlation between association strength and phenotypic similarity for any of the traits that we measured in familiar groups. Consistent between-individual variation in both attraction toward conspecifics and activity level has been observed across a range of taxa, including common lizards (*Lacerta vivipara*) (Cote and Clobert 2007), sticklebacks (*Pimephales promelas*) (Laskowski and Bell 2014), and guppies (*Poecilia reticulata*) (Croft et al. 2009; Smith and Blumstein 2010). Such personality traits can be an important driver of group-level social structure and outcomes (Pike et al. 2008; Aplin et al. 2013; Farine et al. 2015), and individuals assorting by behavioral type has been demonstrated in some species (Croft et al. 2009; Aplin et al. 2013). For example, male great tits (*Parus major*) were more likely to associate with other males that scored similarly on the proactive–reactive personality axis (Aplin et al. 2013), whereas wild guppies were assorted by their propensities to shoal with conspecifics and to engage in predator inspection (Croft et al. 2009). In the current study, it is possible that association patterns were influenced to a greater degree by group members’ behavioral type in mixed and unfamiliar groups due to the absence or reduction of familiarity-based social influences. If this is the case, then as familiarity develops between group members, the relationship between an individual’s behavioral type and their social behavior is predicted to shift.

One process by which such a shift could occur is through social niche specialization, which predicts that repeated interactions between group members drive increased between-individual variation and within-individual consistency in behavior in order to reduce social conflict (Bergmüller and Taborsky 2010; Montiglio et al. 2013). Direct support for social niche specialization has been found in social spiders (*Linyphiidae: Tegenaria domingensis*) (Cote and Clobert 2007), sticklebacks (*Pimephales promelas*) (Laskowski and Bell 2014), and guppies (*Poecilia reticulata*) (Carter et al. 2014) and sticklebacks (*Linyphiidae: Tegenaria domingensis*) (Cote and Clobert 2007). However, we did not detect such an effect. Social network analysis provides a framework in which to test the effects of social niche specialization on the consistency of social traits (Wilson et al. 2013). The relative consistency of an individual’s network position may be ecologically relevant, as various network measures have been correlated with individual variation in social learning (Chaidière et al. 2013) and reproductive success (McDonald 2007). Social niche specialization might also be reflected in the distribution of social relationships within a group if consistent between-individual behavioral variation is associated with consistent differences in social preferences. We would then predict that groups composed of unfamiliar individuals would exhibit inconsistent social preferences and/or more evenly distributed network connections. The disruption of nearest neighbor preferences in our mixed groups, presumably due to the introduction of unfamiliar individuals, is consistent with such a process, though similar patterns were not observed in our unfamiliar groups. Future work examining the relationships between the development of familiarity, individual personality, and longitudinal changes in social network structure is likely to be highly informative (Montiglio et al. 2013; Wilson et al. 2013).

The order in which fish discovered a novel foraging site was predicted by their social networks. This result matches similar findings reported in a range of species, indicating that social networks can influence the diffusion of information through social groups (Claidière et al. 2013; Webster et al. 2013; Aplin et al. 2015). However, there was less support for social transmission of information in our study. Instead, it is likely that information diffusion occurred primarily due to untransmitted social effects. Social transmission occurs when the behavior of informed individuals—for example, feeding strikes, knowledgeable individuals acting as leaders—increases the probability of naïve individuals becoming informed (Hoppitt and Laland 2013). Conversely, closely associated individuals might acquire the same information through individual learning at similar times to one another due to their tendency to remain in close proximity—that is, an untransmitted social effect. This mechanism is consistent with learning via local enhancement, where individuals are attracted to a site due to the presence of other individuals and may thus be more likely to acquire information about that site (Thorpe 1956; Hoppitt and Laland 2013).

In our study, social effect strength was equivalent when comparing diffusions regarding the real patch to those of the control. Although this does not eliminate the possibility of social transmission, it does suggest that if a social transmission effect is present, it is no stronger than the more parsimonious explanation of information flow occurring primarily via untransmitted social effects (Atton et al. 2012). Conversely, if social effect strength was greater for the real patch relative to the control, this would point to a role for social transmission in addition to any untransmitted social effects at
work. However, the precise mechanism underlying social transmission would still need to be determined.

The strength of social effects on patch discovery differed between treatments, with mixed groups experiencing the fastest diffusion rates and familiar groups the slowest. Familiarity between shoal mates has been demonstrated to enhance the diffusion of foraging information in fish as a result of an increased tendency to follow familiar individuals (Lachlan et al. 1998; Swaney et al. 2001; Atton et al. 2014). However, our results point to an additional role for group composition in terms of familiarity in determining the speed of information flow through social groups. Group phenotypic composition has been shown to have wide-ranging effects on group-level outcomes (Farine et al. 2015), including collective foraging success (Dyer et al. 2009; Aplin et al. 2014), group exploration (Hui and Pinter-Wollman 2014), and information flow (Morrell et al. 2008; Atton et al. 2014). Benefits of within-group behavioral diversity can arise through mechanisms such as negative frequency dependence (Maynard Smith 1982)—that is, behavioral strategies receive lower payouts as they become more common—or social heterosis (Nonacs and Kapheim 2007), where the presence of alternative behavioral types within a group can be mutually beneficial.

Although information is predicted to flow most readily between familiar fish, novel information may be more likely to originate from unfamiliar individuals if those individuals are also more likely to occupy different habitats or exhibit different diet preferences. Such an effect might underlie preferences for unfamiliar individuals observed in some contexts (Morrell et al. 2007; Galef and Whiskin 2008). Furthermore, the introduction of unfamiliar individuals into our mixed groups might have facilitated information diffusion throughout the network as a whole by promoting greater mixing and a more homogeneous social organization. Simulation studies of disease transmission using models of fusion–fusion dynamics found that individuals became infected more rapidly in the absence of individual-specific social preferences (Wilson et al. 2014). Similarly, simulations of social learning over real-life primate networks have found that greater homogeneity in both structural patterns and association strength increases the rate at which information spreads through a group (Voelkl and Noe 2010). Another alternative involves the presence of dense, interconnected clusters of social individuals in mixed groups, resulting from strong assortment by shoaling tendency. Within such clusters, information would be predicted to flow especially rapidly. These clusters might also potentially act as information hubs for the rest of the network. Likewise, highly interconnected individuals within heterogeneously structured networks facilitate the diffusion of information or disease by bridging the gap between otherwise weakly connected individuals (e.g., Pinter-Wollman et al. 2011).

Increasing recognition is being given to the importance of group phenotypic composition in influencing individual fitness and driving group-level outcomes (Farine et al. 2015; Kurvers et al. 2014). Our study adds to this literature by demonstrating that variation in the proportion of familiar individuals within a group can influence its social network structure and the speed at which information flows through it, even in the absence of differences in fusion–fusion dynamics. An important next step is to determine the robustness of our results and the extent to which these patterns may act in natural populations. Future work could also examine shifts in network structure as familiarity between group members develops as well as the role of social niche specialization and individual personalities in shaping these processes (Montiglio et al. 2013; Wilson et al. 2013). Social networks mediate a wide swath of animal behavior, including mating, transmission dynamics, and cooperation (Hasenjager and Dugatkin 2015; Krause et al. 2015), as well as play an important role in shaping evolutionary outcomes (Kurvers et al. 2014). A better understanding of the links between group composition and the emergent structure and properties of social networks will prove highly beneficial to our understanding of behavioral ecology.

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Data Accessibility: Analyses reported in this article can be reproduced using the data provided by Hasenjager and Dugatkin (2016).

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