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Original Article

Guppies occupy consistent positions in social networks: mechanisms and consequences

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The social network approach has focused increasing attention on the complex web of relationships found in animal groups and populations. As such, network analysis has been used frequently to identify the role that particular individuals play in their social interactions and this approach has led to the question of whether, and in what context, individuals consistently occupy certain positions within their network. Here we investigated the social networks of guppies, *Poecilia reticulata*, in the wild and tested whether 1) individual fish occupy consistent positions in their network and 2) whether these positions are robust to experimental manipulations to their habitat. Our habitat manipulations involved increasing and decreasing the surface area of their pools as well as translocating an entire pool population between different pools in situ. We found that guppies did indeed consistently occupy positions within their social networks, irrespective of the type of manipulation and that individual network positions vary between individuals. Our results suggest that at least 2 factors contribute to the observed individual variation in network position including 1) the tendency to be social and 2) sex-specific social preferences. Finally, we used a simulation to explore the implications of individuals consistently occupying different network positions regarding the exposure of fish to parasites and predators. The time until infection decreased with increasing rank of individual betweenness and the predation risk increased with decreasing rank of the individual node strength thus illustrating the potential ecological and evolutionary consequences of consistent network positions.

Key words: **network position, social network analysis, habitat manipulation, environmental change**

INTRODUCTION

The social network approach has focused on the complex web of relationships between individuals within groups and populations (Krause et al. 2007; Croft et al. 2008; Wey et al. 2008; Krause et al. 2015). The existence of a fine-scale social structure between individuals has led to a reappraisal of major topics in behavioral biology including cooperation (Ohtsuki et al. 2006; Santos et al. 2006), sexual selection (McDonald et al. 2013), disease transmission (Drewe and Perkins 2015), and information flow (Nightingale et al. 2015) among others. In this context, network analysis has been used frequently to identify the role that particular individuals play in their social environment (Lusseau and Newman 2004; Krause et al. 2010) and this approach has led to the idea that network positions could be a key component in the characterization of social personality types (Wilson et al. 2013, Blumstein et al. 2013). Because social personality types require repeatable individual-level interaction patterns this discussion in turn has led to the investigation of another topic, namely the stability of social structures over time and in the presence of environmental changes (Godfrey et al. 2013; Shizuka et al. 2014; Wilson et al. 2015; Aplin et al. 2015).

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We investigated both the role of social behavioral types and the influence of environmental change for networks using the Trinidadian guppy, *Poecilia reticulata*. Guppies have emerged as a key study system for social networks because these fish can be studied easily in the laboratory as well as in the wild (Croft et al. 2008) and there are many different natural populations (each with different life-histories) which provide a rich test-bed for studying the ecology and evolution of social organization (Magurran 2005). Furthermore, environmental fluctuations such as the dry season or flooding events during the wet season can potentially affect social structure. Such variability in environmental conditions also presents a rarely afforded research opportunity. For example, the small guppy groups that become isolated in small streamside pools during the dry season do not experience the same levels of emigration or immigration (i.e., by transient males, females to a lesser extent; Croft et al. 2003) experienced by other well-connected pools. As such, these isolated groups can form populations that exhibit dynamics similar to larger systems (e.g., fission–fusion) but are actually quite stable in terms of their population members and social processes (Griffiths and Magurran 1997).

Evidence for consistency of individual network positions has been found in a number of species (such as yellow-bellied marmots, *Marmota flaviventris*, Blumstein et al. 2013; rhesus macaques, *Macaca mulatta*, Brent et al. 2013; catsharks, *Syliorhinus canulcula*, Jacoby et al. 2014; great tits, *Parus major*, Aplin et al. 2015). In species that have open fission-fusion groups, the support for repeatable behaviors has come primarily from individual differences in group size choice (Jacoby et al. 2014; Aplin et al. 2015) and also variation in the degree which was used as a measure of gregariousness (Aplin et al. 2015). In contrast, in species with more complex membership control the focus has been on repeatable and heritable differences in network positions regarding grooming and aggressive behaviors (Lea et al. 2010; Brent et al. 2013). Wilson et al. (2013) proposed that in fission-fusion systems consistent network positions are likely to be a result of either preferences for particular individuals or alternatively could be brought about by individual-level variation in the amount of time they spend with others. Therefore we specifically tested whether consistent individual network positions are primarily a result of differences in (a) social preferences and (b) in overall time spent social.

A number of studies have found stable social structures across environmentally variable conditions (lizards: Godfrey et al. 2013; birds: Shizuka et al. 2014; Aplin et al. 2015; fish: Wilson et al. 2015) often in connection with associations between particular individuals (Shizuka et al. 2014; Wilson et al. 2014). In contrast to most previous field studies (but see Firth and Sheldon 2015 for an exception), we experimentally changed the habitat of our study populations to test whether consistent network positions are maintained in the face of environmental variation, with the most extreme manipulations resulting in translocation of the entire social networks from one habitat to another. Specifically we tested whether 1) individual fish occupy consistent, but different, positions in their network and 2) whether these positions are robust to environmental manipulations such as increases and/or decreases in ambient water level and translocation of the entire pool population between independent pools. We used our results to conduct a simulation, which explored the implications of consistent network positions for the exposure of fish to parasites and predators.

METHODS

We caught and individually marked, using fluorescent elastomer (Northwest Marine Inc.), all adult guppies (*P. reticulata*) in selected pools of the upper Turure River, Trinidad. This part of the Turure River has relatively few predators of guppies. Killifish (*Rivulus hartii)* are the likely main predator of juvenile guppies. It should be noted that our location (see GPS coordinates, Table 1) is not the same as the site that Endler (in 1976) used for a translocation of guppies from the Arima River to the Turure River (Magurran 2005).

Experimental work was carried out in March–April in 2013 and 2015. After marking, all individuals were released into their home pool and given 24 h to acclimate prior to the beginning of behavioral observations. We selected the pools on the basis of whether they provided good conditions for pool-side observations of ego-centric networks (see below). Pools 2a and 2b respectively are the same pools but in 2 different years (2013 and 2015; Table 1). However, due to annual flooding events and the short life span of guppies in general, no tagged study fish from the previous year's research were observed.

Data collection

For each of the pools, we recorded the interaction dynamics of the fish by following a given marked focal fish for 2 min and recording the identity of its nearest neighbor every 10 s. If no conspecific was present within 4 body lengths of the focal fish, the focal fish was regarded as having no neighbor for that observation point (Borner et al. 2015). Previous research has shown that this observation frequency/time interval provides ample opportunities for switching partners (Wilson et al. 2014). Upon completion of a 2 min observation period another marked fish was immediately chosen as a focal fish. This process was repeated consecutively until all individuals ($N = 8$–10) in a given pool had been observed and interactions

Table 1

Descriptive details for different aspects of all study pools

Pool	Year	Fish number (♂/♀)	Body size (mm)	Observation days	Treat.	Area (m^2)	Maximum water depth (cm)
1	2015	10 (3/7)	17–23	2	NSA	1.82	30
				2	LSA	2.19	34
				1	NSA	1.82	30
2a	2013	8 (4/4)	17–25	2	NSA	6.84	32
				2	LSA	8.20	37.5
				2	SSA	4.55	25
3				2	TL	2.65	32
2b	2015	8 (4/4)	18–22	2	NSA	2.55	17
				2	LSA	3.91	20
				2	NSA	2.55	17

Treatments: NSA (normal surface area), LSA (large surface area), SSA (small surface area), and TL (translocation to a different pool). The location of the pools was 10°41'8"N, 61°10'22"W.

recorded for that observation session. After completion of an entire observation session, the pool was left undisturbed for a minimum of 10 min prior to beginning data collection for another session. This waiting period was chosen to insure that subsequent observation sessions were independent of the previous session (see Wilson et al. 2014). This process was repeated 5–6 times per day for each pool, occurring between 09:00 and 14:00. The number of observation days for each pool is given in Table 1. We observed the fish from the river bank. Given the almost complete absence of bird predation the fish only weakly respond to overhead stimuli.

Experimental manipulations of pools

First, all interactions between fish in unmanipulated pools were recorded (see Table 1). Second, we increased the surface area of pools by changing water depth. For pool 1 and 2b this increase was then followed by a reduction in surface area back to the original pre-disturbance level. For pool 2a, we reduced the surface area (below the unmanipulated level) and finally translocated all fish to a nearby smaller, but isolated (guppy-free) pool. After each manipulation of surface area and after the translocation all interactions between fish were recorded.

Manipulations of pool surface area were achieved by adding or removing rock substrate from the stream inflow or outflow respectively in the observation pool. Such changes in surface area occur regularly in natural habitats as a result of strong rainfall within and between seasons and are likely to result in significant changes to the environmental parameters of the observation pool (e.g., water flow, salinity, temperature, and refuge availability). However, for the purposes of this experiment, only pool surface area and water depth were quantified in detail. Nonetheless, such manipulations allowed for estimation of network consistency under variable ecologically relevant stimuli as intended. The manipulations of the water level resulted in variable changes in surface area between pools (Table 1). This process could not be entirely standardized under field conditions because the natural features of pools had to be taken into account, which constrained our options regarding such manipulations.

After the experiments were finished, all translocated fish were returned to their point of origin and all pools returned to their original water level. This research was performed in accordance with the laws, guidelines and ethical standards of the country in which they were performed (Trinidad and Tobago).

Consistency of network positions

We constructed composite networks for each observation day of each pool (based on 5 to 6 network sessions, respectively) resulting in a total of 5 networks for pool 1, 8 networks for pool 2a, and 6 networks for pool 2b. We also constructed networks for each treatment of each pool (Table 1) such that we generated 3 networks for pools 1 and 2b and 4 networks for pool 2a (each comprising all observation days of the respective treatment).

We applied the test described in Wilson et al. (2013) to analyze the consistency of individual network positions across the observed networks. This test randomizes the ranks of individual measures for each network and uses as a test statistic the sum of the variances of the individual ranks across the networks. The test requires that the observation probabilities of all individuals in a given network be equal, which was the case in our study. We performed 10^5 randomization steps using the R code available at https://cosa.fh-luebeck.de/download/skrause/.

The networks were constructed by adding an edge i_1–i_2 between 2 nodes representing the individuals i_1 and i_2, respectively, whenever these individuals were observed to have a common contact phase. In our study, a contact phase of 2 individuals is defined to be a sequence of consecutive time points where one of the 2 individuals was the nearest neighbor of the other one. Due to the fission–fusion behavior of the guppies our networks are almost complete, i.e., each network contains almost all possible edges. This means, there is no information in the mere existence of an edge. Therefore, we used weighted measures to characterize network positions, the node strength, the weighted node betweenness, and the Υ-measure (Boccaletti et al. 2006). The node strength of a node i is the sum of the weights of all edges connected to i. In our case, the node strength measures the number of an individual's social contact phases (which is explained in more detail below). The node betweenness of a node i measures the extent to which shortest paths between other nodes run through i. Note that in a weighted network the shortest path is defined to be the path with the smallest sum of edge weights (in our study, these edge weights are the inverse of the tie strength—see below). This means, the shortest path between 2 nodes may pass through other nodes even if the 2 nodes are directly connected. The node betweenness is a standard measure of centrality and can be used as an indicator of a node's relevance regarding exchange between other nodes (e.g., disease transmission, Krause et al. 2015). The Υ-measure determines the spread of edge weights of a node by computing the sum of squares of the normalized edge weights (i.e., edge weights divided by the node strength). In our study, the Υ-measure expresses the degree to which the individuals have social preferences. The weights attached to the edges of a weighted network have to be chosen according to the meaning of the network measures used. The node strength and the Υ-measure require edge weights that express the tie strengths of pairs of connected nodes, and the weighted betweenness requires edge weights that express distances between pairs of connected nodes. We determined the tie strength of a pair of nodes by counting the number of common contact phases of the respective individuals without taking the lengths of the phases into account. It has been shown that this is an appropriate way to express tie strengths for this study system (Wilson et al. 2014, 2015). As a consequence, in our study system the individuals' node strength is not necessarily correlated with the individuals' overall time spent social. Regarding the distances, we followed a common approach and took the inverse of the tie strengths (Newman 2001).

Social preferences and time spent social

We investigated the roles of sex and body size in structuring social networks in connection with the above measures of consistent network positions. To do this, for each individual we computed the mean and the variance of its ranks across the treatment networks regarding the network measure under consideration. Then, we performed randomization tests (10^4 steps) where we permuted the individual mean ranks in a pool and kept constant the individual sex and body size in order to analyze the influence of sex and body size on the individual network positions. In the same way, we analyzed the influence of these traits on the individual variability in network positions. Here we permuted the variances of individual ranks in a pool (and kept constant the individual sex and body size). To take a possible dependency between body size and sex into account, we additionally performed tests where we permuted the mean ranks (variances of ranks) within each sex, separately. We used 3 different test statistics, two that measure the influence of sex and of body size, separately, and one that combines both traits. To quantify the influence of sex, we computed the absolute difference between the mean of the males' mean ranks (variances of ranks) and the mean of the females' mean ranks (variances of ranks), and this value constituted our test statistic. Large values indicate an effect of sex on the individuals' network positions. To measure the influence of body size, we used as a test statistic Pearson's correlation coefficient between mean rank (variance of ranks) and body size. Additionally, we combined sex and body size by a linear model with the mean rank (variance of ranks) as response variable and used its r^2 as a test statistic. The model also included an interaction term between sex and body size.

Another possible explanation for consistent network positions are individual differences in the percentage of time spent social (Wilson et al. 2013). We quantified this for each individual by computing the overall percentages of time being social (i.e., with some neighbor) for each observation day and for each treatment. We analyzed whether this measure was consistent across the observation days and the treatments by applying the same test method as for the consistency of network positions (10^5 randomization steps). The only difference was that instead of ranked values of certain network measures we used the ranked percentages of time spent social. Given that we found consistent differences in social activity, we computed the individual percentage of social time in the combined data (comprising all observation days) for each pool and tested whether these percentages were correlated with the individual mean ranks across the treatments regarding each of the network measures. We used a randomization test (10^4 steps) where we permuted the individual mean ranks and used Pearson's correlation coefficient as the test statistic. Note that an individual that spends a large percentage of time being social does not necessarily have a high node strength. In our study, the node strength measures the number of contact phases regardless of their lengths rather than the number of time points, where an individual was observed to be social.

Consequences of consistent network positions

Given that we found consistent individual network positions, we quantified potential consequences by simulating the spread of an infectious ectoparasite and the exposure to predation risk for individuals that consistently occupy different positions. As a basis for this investigation we used the stochastic model of Wilson et al. (2014) to simulate the social dynamics of the guppies. Our simulation proceeds in discrete time steps and simultaneously generates the social "states" of all individuals in a group, where a state can be "being alone" or "being neighbor of individual *i*". More details are explained in the results (because some of the results are required for this) and in the supplementary material.

To investigate the spread of an infectious ectoparasite we included a transmission process in this simulation in the following way: an individual is randomly chosen to be initially infected. At each time point, where an infected individual has a neighbor, the parasite is transmitted to this neighbor with a certain probability. To quantify the spread of the parasite, we measured the individual time until infection for different transmission probabilities.

To investigate the predation risk we included predator attacks in our simulation in the following way: a predator appears with a certain probability, randomly chooses an individual, and observes it for a period of n time points. If the chosen individual is alone during this observation period, the predator will attack it. This mechanism is meant to reflect the fact that guppies are known to be more at risk when alone rather than in a group and that stragglers are usually preferred by predators (Krause and Godin 1995; Ioannou et al. 2012). This simple model ignores the fact that some individuals will be easier to detect than others depending on phenotypic characteristics such as body size, coloration, and/or sex. However, here we focus on the role of consistent behavior of the guppies and therefore regard all individuals as being equally detectable. As an indicator of predation risk we counted the number of times an individual was the first to be attacked.

RESULTS

Consistency of network positions

We found that guppies occupied consistent network positions in all 3 pools regarding the node strength (all $P < 0.009$) and the node betweenness (all $P < 0.037$) across the networks per day as well as per treatment. Regarding the Υ-measure the guppies occupied consistent network positions in pools 1 and 2a (all $P < 0.012$) but not in pool 2b. Figure 1 shows the treatment networks for the 3 pools and Table 2 contains all P values of the tests for consistency of network positions. The individuals' values and ranks for each of the 3 network measures can be found in Table 3 (for pool 2a) and Supplementary Table 1 in the Supplementary Material (for pools 1 and 2b).

Using a permutation test we additionally analyzed possible correlations between the individual mean ranks regarding the 3 network measures. We found a correlation between the node strength ranks and the node betweenness ranks in all 3 pools ($P < 0.01$ for each of the 3 pools), but neither between the node strength ranks and the Υ-measure ranks ($P = 0.79$ for pool 1, $P = 0.87$ for pool 2a, and $P = 0.73$ for pool 2b), nor between the node betweenness ranks and the Υ-measure ranks, ($P = 0.95$ for pool 1, $P = 0.90$ for pool 2a, and $P = 0.76$ for pool 2b, 2-tailed tests). The negative result regarding node strength and Υ-measure is important for our interpretation of the Υ-measure, because individual differences in the Υ-measure could in the absence of individual preferences also be caused by individual differences in the total numbers of contact phases. Individuals with small numbers of contact phases would then tend to have higher values regarding the Υ-measure. The fact that we did not find a correlation between node strength ranks and Υ-measure ranks suggests that in our study system the values of the Υ-measure are mainly caused by individual preferences. To further investigate this issue we performed an additional test where for each pool we randomized the identities of the individuals' contact partners in each session of each treatment. From each of the randomizations (10^4 steps) we constructed a single network comprising all sessions and computed the sum of individual values of the Υ-measure. We found that for each pool the sum of the observed Υ-measure values was significantly greater than expected under the null hypothesis of randomly chosen contact partners ($P < 0.01$ for each of the 3 pools), which confirms our assumption that in our study system the Υ-measure values are mainly caused by individual preferences.

Social preferences

Neither sex nor body size had an influence on the network positions regarding node strength and node betweenness. The mean ranks of males and females did not differ significantly ($P = 0.17$ for pool 1, $P = 0.25$ for pool 2a, and $P = 0.93$ for pool 2b regarding node betweenness; $P = 0.94$ for pool 1, $P = 0.35$ for pool 2a, and $P = 0.45$

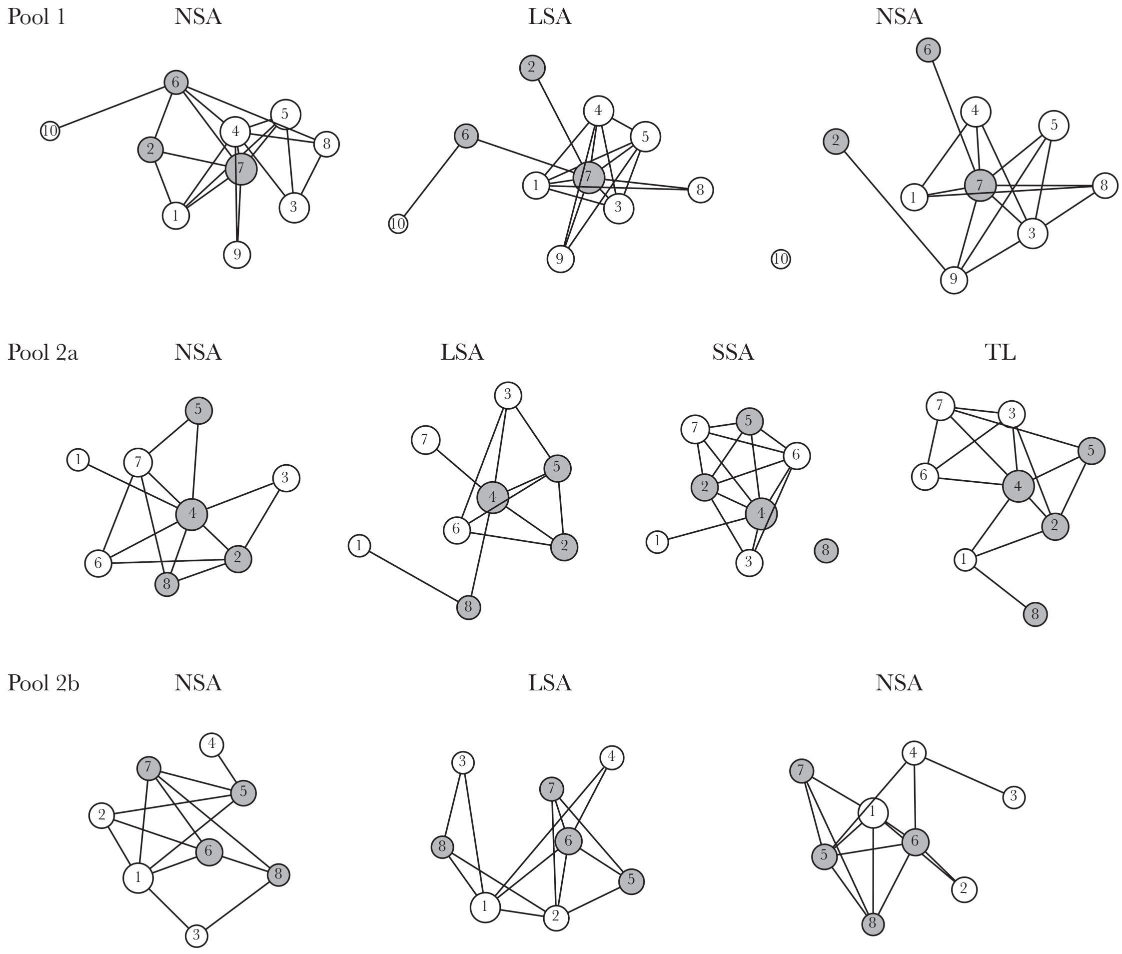

Figure 1

Networks for each treatment of the 3 pools. Treatments: NSA (normal surface area), LSA (large surface area), SSA (small surface area), and TL (translocation to a different pool). The tie strength was defined by the number of common contact phases. The gray nodes represent the males. The area of each node is proportional to the percentage of time spent social in the combined data for each pool. Each of the observed networks contained almost all possible edges. To make the structure clearer, only edges with weights greater than the median weight of each treatment are shown. However, the spring layouts were computed taking all edges into account. The networks were drawn using Graphviz version 2.38 (http://graphviz.org).

Table 2

***P* values of the tests for consistency of network positions**

	Across the treatments			Across the observation days		
Pool	Node strength	Υ-measure	Node betweenness	Node strength	Υ-measure	Node betweenness
1	**0.000**	**0.009**	**0.027**	**0.000**	**0.006**	**0.000**
2a	**0.003**	**0.009**	**0.002**	**0.000**	**0.012**	**0.003**
2b	**0.009**	0.441	**0.028**	**0.002**	0.399	**0.037**

Significance ($P < 0.05$) is indicated in bold.

for pool 2b regarding node strength) and the mean ranks were not significantly correlated with body size regardless of whether the permutations were performed on all individuals in a pool ($P = 0.45$ for pool 1, $P = 0.30$ for pool 2a, and $P = 0.37$ for pool 2b regarding node betweenness; $P = 0.93$ for pool 1, $P = 0.70$ for pool 2a, and $P = 0.73$ for pool 2b regarding node strength) or only within individuals of the same sex ($P = 0.79$ for pool 1, $P = 0.46$ for pool 2a, and $P = 0.33$ for pool 2b regarding node betweenness; $P = 0.96$ for pool 1, $P = 0.94$ for pool 2a, and $P = 0.58$ for pool 2b regarding node strength). Also, the combination of sex and body size using a linear model could not explain the network positions regarding node strength and node betweenness ($P = 0.49$ for pool 1, $P = 0.56$ for pool 2a, and $P = 0.65$ for pool 2b regarding node betweenness; $P = 0.26$ for pool 1, $P = 0.50$ for pool 2a, and $P = 0.26$ for pool 2b regarding node strength). However, sex could (partly) explain the network positions regarding the Υ-measure for pools 1 and 2a ($P < 0.01$ for pool 1, $P = 0.02$ for pool 2a, but $P = 0.56$ for pool 2b). As mentioned above, pools 1 and 2a were also the pools where we observed consistent network positions regarding the Υ-measure. In both pools the males had smaller mean values of the Υ-measure than all females.

Table 3

Values and ranks of the individuals in the 4 treatment networks of pool 2a regarding a) node strength, b) weighted node betweenness, and c) *Υ*-measure

a)

			Node strength				Rank				
ID	Sex	Size	NSA	LSA	SSA	TL	NSA	LSA	SSA	TL	Mean
1	F	17	25	19	42	54	8	8	7	4	6.8
2	M	20	48	41	91	57	2	3.5	2	3	2.6
3	F	22	28	41	68	60	7	3.5	6	2	4.6
4	M	20	58	68	115	79	1	1	1	1	1.0
5	M	21	38	47	70	43	5.5	2	5	7	4.9
6	F	25	38	35	85	49	5.5	6	3	5.5	5.0
7	F	25	46	39	76	49	3	5	4	5.5	4.4
8	M	18	43	30	37	27	4	7	8	8	6.8

b)

			Node betweenness				Rank				
ID	Sex	Size	NSA	LSA	SSA	TL	NSA	LSA	SSA	TL	Mean
1	F	17	0	0	0	7.5	6	6	5.5	2	4.9
2	M	20	1	1	2	2	2.5	3	2	4	2.9
3	F	22	0	0	0	3.5	6	6	5.5	3	5.1
4	M	20	6	11	6	8.5	1	1	1	1	1.0
5	M	21	0	2	0	0	6	2	5.5	6.5	5.0
6	F	25	0	0	0	0	6	6	5.5	6.5	6.0
7	F	25	1	0	0	0	2.5	6	5.5	6.5	5.1
8	M	18	0	0	0	0	6	6	5.5	6.5	6.0

c)

			Υ-measure				Rank				
ID	Sex	Size	NSA	LSA	SSA	TL	NSA	LSA	SSA	TL	Mean
1	F	17	0.187	0.219	0.188	0.260	3	2	3	1	2.3
2	M	20	0.165	0.186	0.159	0.202	6	5	6	4	5.3
3	F	22	0.171	0.265	0.196	0.214	5	1	2	3	2.8
4	M	20	0.147	0.177	0.159	0.179	8	6	7	8	7.3
5	M	21	0.195	0.165	0.161	0.216	1	8	5	2	4.0
6	F	25	0.193	0.197	0.183	0.200	2	3	4	5	3.5
7	F	25	0.186	0.190	0.199	0.197	4	4	1	7	4.0
8	M	18	0.160	0.171	0.154	0.199	7	7	8	6	7.0

Body size is given in mm and NSA indicates normal surface area, LSA large surface area, SSA small surface area, and TL translocation to a different pool. M = male; F = female.

This means the contact phases of males were distributed more evenly over the other individuals than that of females. Like for the other measures, body size did not have influence on the *Υ*-measure regardless of whether the permutations were performed on all individuals in a pool ($P = 0.69$ for pool 1, $P = 0.73$ for pool 2a, and $P = 0.34$ for pool 2b) or only within individuals of the same sex ($P = 0.14$ for pool 1, $P = 0.28$ for pool 2a, and $P = 0.45$ for pool 2b). The combination of sex and body size yielded results that are very similar to those of sex alone ($P < 0.01$ for pool 1, $P = 0.03$ for pool 2a, and $P = 0.94$ for pool 2b).

We additionally tested whether body size influenced the network positions regarding the node strength, if only mixed-sex contacts are taken into account (i.e., we constructed a network where edges only exist between nodes representing individuals of opposite sexes). We found that in all 3 pools the guppies occupied consistent network positions regarding this measure (all $P < 0.02$) across the networks per day as well as per treatment. However, again body size did not have an effect on the network position in any of the 3 pools ($P = 0.60$ for pool 1, $P = 0.86$ for pool 2a, and $P = 0.57$ for pool 2b).

Neither sex nor body size nor the combination of both had an influence on the individual variability in network positions regarding node strength, node betweenness, or the *Υ*-measure. The *P*-values can be found in Supplementary Table 3 in the Supplementary Material.

Time spent social

The individuals' ranks regarding the percentage of time spent with other individuals were consistent across the observation days for all 3 pools ($P < 0.01$ for pools 1 and 2a, and $P = 0.03$ for pool 2b), and across the treatments for pools 1 and 2a ($P < 0.01$ for pools 1 and 2a, but $P = 0.07$ for pool 2b). The non-significant *P*-value for pool 2b was probably caused by low test power (8 individuals, 3 networks). Supplementary Table 2 in the supplementary material contains the individual values and ranks regarding the percentage of time spent social for all 3 pools.

For all 3 pools the individual percentage of time spent social was positively correlated with the individual network position (mean rank across the treatment networks) regarding the node strength and the node betweenness (all *P*-values < 0.01). However, we did not find a correlation regarding the *Υ*-measure ($P = 0.76$ for pool 1, $P = 0.79$ for pool 2a, and $P = 0.85$ for pool 2b). This suggests that a high percentage of time spent social is not achieved by extending the duration of individual contact phases but by having many contact phases, where the spread of the distribution of these contact phases over the other individuals does not differ between individuals with high and with low percentages of social time. To understand what differences in social activity caused the observed consistency in network positions, it is necessary to investigate the underlying dynamics of social activity. Wilson et al. (2014) showed that a model consisting of 3 probabilities can explain a number of aspects of guppy social dynamics, including the percentage of time the individuals are social (or alone) and the number of contact phases between the individuals. This model can be characterized by specifying the probabilities of leaving the current nearest neighbor ($P_{\text{leave\_nn}}$), of ending social contact in general ($P_{\text{s}\to\text{a}}$), and of ending being alone ($P_{\text{a}\to\text{s}}$). The reciprocal values of theses probabilities are proportional to the mean lengths of contact phases (with the same neighbor), of phases of being social (with any neighbor), and of phases of being alone, respectively.

For a description of the overall social dynamics of a population it is sufficient to use the same probabilities for all individuals (Wilson et al. 2014). However, this does not necessarily mean that the social behavior of all individuals is identical. There may be small but consistent individual differences that can lead to consistent network positions. To analyze these potential differences we estimated individual-specific values of the probabilities $P_{\text{leave\_nn}}$, $P_{\text{s}\to\text{a}}$, and $P_{\text{a}\to\text{s}}$ for each individual *i* by taking into account only those observation sequences where *i* was the focal individual. For each of these probabilities we tested whether the ranks of the individual estimates were consistent across the treatments. We used the same test as for the consistency of network positions (see above). We found that the individuals differed consistently regarding the probability $P_{\text{a}\to\text{s}}$ in all 3 pools ($P < 0.01$ for pool 1, $P = 0.03$ for pool 2a, and $P = 0.04$ for pool 2b), while there was no consistent difference regarding $P_{\text{leave\_nn}}$ in any of the pools ($P = 0.66$ for pool 1, $P = 0.06$ for pool 2a, and $P = 0.61$ for pool 2b). Regarding $P_{\text{s}\to\text{a}}$ the individuals had consistent differences only in pool 1 ($P < 0.01$ for pool 1, $P = 0.31$ for pool 2a, and $P = 0.47$ for pool 2b). The probabilities $P_{\text{a}\to\text{s}}$ and $P_{\text{s}\to\text{a}}$ were negatively correlated for pool 1 ($P = 0.02$ in a permutation test with 10^4 steps and Pearson's correlation coefficient as test statistic). This means that in all 3 pools the individuals differed consistently across the treatments regarding the length of phases of being alone, while there were no consistent differences in the length of contact phases. The individuals in pool 1 also had consistent differences regarding the length of phases of being social. These results suggest that the guppies achieve the consistent differences in their social activity mainly by controlling the lengths of phases of being alone. In pool 1, the guppies with shorter phases of being alone additionally had longer social phases.

The fact that the lengths of contact phases (with the same neighbor) did not differ consistently between the individuals suggests that the number of contact phases is proportional to the overall time being social. We tested this and found that in all 3 pools the number of contact phases was positively correlated with the time being social (all $P < 0.01$ in a permutation test with 10^4 steps and Pearson's correlation coefficient as test statistic). This explains why the overall percentage of time being social is positively correlated with the node strength.

Consequences of consistent network positions

To quantify the consequences of consistent individual network positions, we simulated the spread of an infectious ectoparasite and the exposure to predation risk for individuals that occupy different positions. We expect that individuals with higher node betweenness will be infected earlier than others given that node betweenness is a good measure for transmission processes (see Methods above) and that individuals with higher node strength will have a smaller predation risk than others (here we used node strength as a proxy for time spent social, see results above). For our investigation we chose individuals 7, 1, and 10 of pool 1, which have consistently high, medium, and low ranks, respectively, regarding node strength and node betweenness (Supplementary Table 1).

As a basis for this investigation we used the above described stochastic model based on the 3 probabilities $P_{\text{leave\_nn}}$, $P_{\text{s}\to\text{a}}$, and $P_{\text{a}\to\text{s}}$. We estimated the model probabilities from our observations of pool 1 and additionally included individual preferences (see supplementary material for details). From "observations" of the simulated social dynamics, performed in the same way as our real observations, we constructed networks. For the 3 individuals under consideration the simulated values as well as the ranks of both the node strength and the node betweenness were very similar to the empirically observed values (Supplementary Table 4). The simulated mean ranks for the node strength were 1.3, 5.0, and 10.0 (empirically observed values 1.3, 4.7, and 10.0), and for the node betweenness 1.3, 4.7, and 10.0 (observed values 1.7, 5.5, and 7.3). This shows that the simulation generates realistic networks with the same characteristics regarding node strength and node betweenness as the ones observed in the wild.

As expected, the time until infection decreased with increasing rank of individual betweenness regardless of the transmission probability and the individual with the highest rank encountered parasites twice as fast as the individual with the lowest rank (Table 4a).

Also, as expected, the predation risk increased with decreasing rank of the individual node strength and the individual with the lowest rank was at least twice as likely to be the selected prey item compared to the individual with the highest rank (Table 4b). The differences between individuals become bigger with increasing observation time of the predator, because guppies with smaller node strength have longer phases of being alone.

In the absence of consistent positions, i.e., if all individuals on average behaved equally and different network positions were only short-term effects caused by random fluctuations, both the exposure to predation risk and the time until infection would on average be the same for all individuals. We simulated such a scenario by excluding individual preferences and using the same values of the 3 model probabilities for all individuals (estimated from the combined data). The results did not differ between the individuals and were similar to those of the observed individual 1, which had a consistently medium ranked network position. The mean percentage of cases, where an individual was the first to be attacked was always 10% and the mean times until infection with an ectoparasite were 6% smaller than for the observed individual 1. The smaller times are probably caused by the absence of individual preferences (Wilson et al. 2014).

DISCUSSION

We found stable network positions in guppies across different days and treatments (including translocation to a new pool). Our results

Table 4

Results from a simulation (10^5 repetitions) based on a model of the social dynamics of the 10 observed individuals in pool 1

a)

ID	Betweenness mean rank	Time until infection (s)		
		Transmission probability		
		0.05	0.1	0.2
7	1.7	1265	647	338
1	5.5	1527	782	405
10	7.3	2889	1469	762

b)

ID	Node strength mean rank	% attacked first		
		Length of observation period		
		10 s	20 s	30 s
7	1.3	7%	6%	5%
1	4.7	10%	10%	10%
10	10.0	14%	16%	19%

a) Mean time until infection with an ectoparasite for selected individuals. At the beginning of each simulation one of the 10 individuals was randomly picked to be initially infected. The transmission probability specifies the probability of a parasite being transmitted from an infected individual to a non-infected one, if both stay together for 10 s. b) Mean percentage of cases, where the individual was the first to be attacked by a predator in the group of 10 individuals. The length of observation period specifies the time for which an individual needs to be alone to be potentially attacked by the predator.

suggest that individual consistency in both social activity and social preferences had an influence on the individual network positions. Node strength and node betweenness, but not the Υ-measure, in guppies could be explained by variation in social activity. The Υ-measure indicates how social time was allocated and differed significantly between males and females with the contact phases of males being distributed more evenly over the other individuals than those of females.

Information regarding differences in network positions in animals has been growing in recent years (Pike et al. 2008; Krause et al. 2010; Blumstein et al. 2013; Brent et al. 2013; Wilson et al. 2014; Aplin et al. 2015; Firth and Sheldon 2016; Formica et al. 2016). Jacoby et al. (2014), for example, reported consistent network positions in catsharks, *S. canulcula*. A detailed analysis of the observed patterns revealed that differences in individual network positions were potentially driven by variation in group size preferences (i.e., shoaling/aggregation tendency) by individuals. Strong individual-level differences in group size choice were also reported from great tits by Aplin et al. (2015). Detailed comparisons of our results with those of Jacoby et al. (2014) and Aplin et al. (2015) are made difficult by the fact that we measured time spent social rather than group size for the simple reason that most of our fish are either alone or with one other fish (i.e., group sizes of 3 or larger are not very common). Aplin et al. (2015) also reported high repeatability in individual great tits regarding the association strength and the betweenness in networks based on observations of gathering events at feeding stations.

We know from Wilson et al. (2015) that guppies can maintain their fission-fusion dynamics despite environmental manipulations which requires the fish to counteract the strong and automatic effect of changing densities on their encounter rates such as differences in density. Here we show that fish also maintain their network positions. The broader question of how individuals buffer environmental change in social networks is an interesting challenge for many study systems (Godfrey et al. 2013; Shizuka et al. 2014, Wilson et al. 2015) and requires a detailed study of the interaction dynamics. Density independence in the context of social responses has been reported from flocks of starlings, *Sturnus vulgaris*, where individuals respond to a fixed number of close neighbors regardless of distance (Ballerini et al. 2008). It remains to be tested whether a similar mechanism is at work in our system.

In contrast to our manipulations of the physical environment, which did not change the network positions of individual guppies, other studies have more commonly shown that the interaction dynamics of a group can be altered by causing changes directly in the social composition. For example, such changes might result from the addition of new individuals (Darden et al. 2009; Jacoby et al. 2010; Wilson et al. 2015) or perhaps, from manipulations of group dynamics based on behavioral type (Sih and Watters 2005). As such, manipulations of social dynamics might be more likely to result in changes to consistency in network position than environmental manipulation alone, even in cases of dramatic disturbance. This might particularly be the case in populations that undergo significant changes in their membership or perhaps in systems where there are great differences in social ranking between members. For example, in species that exhibit strong dominance hierarchies (Shizuka and McDonald 2012) such as cichlid fishes (Schurch and Heg 2010; Schurch et al. 2010; Riebli et al. 2011) or primates (Crofoot et al. 2011). In these systems, the addition or removal of individuals can have dramatic consequences for consistency in network position as individual positions within the network shift to higher or lower positions in the social hierarchy. This delineation between effects of change in the ambient versus social environment is a potentially exciting as well as important area of future research.

Network structure is known to have a strong effect on disease transmission (Newman 2003; Beisner and McCowan 2015; Drewe and Perkins 2015). Clustering and modularity are network characteristics that can reduce the probability of disease transmission because diseases are more likely to spread within clusters and modules than between them (Salathe and Jones 2010; Griffin and Nunn 2012). Individual social preferences can lead to strong bonds between unrelated individuals (birds: Shizuka et al. 2014; fish: Wilson et al. 2014; mammals: Wolf et al. 2007; lizards: Godfrey 2015). Such preference structures are expected to slow down transmission processes because social preferences create modular structures within networks that have a tendency to contain outbreaks. We found no influence of body size on network positions (which is consistent with previous studies, Krause et al. 2000) but sex was found to have an effect on the Υ-measure with males spreading their contacts more evenly than females. This finding is consistent with the fact that females are known to form strong cooperative ties with other females in contrast to males (Croft et al. 2006, 2009) and suggest that it is the females which are primarily responsible for the modularity of social structures in guppies. The consequences of such modularity for transmission processes remain to be experimentally tested.

Our simulations explored the implications of individual fish consistently occupying network positions regarding the exposure to parasites and predators. Higher node betweenness had the expected effect of increasing parasite transmission. The transmission might, of course, follow more complex probabilities than the simple binomial probability we used. However, since the mean durations of contact with a specific neighbor do not differ between the individuals, this choice should not have much impact on our results. The fact that we can simulate the social dynamics of our fission-fusion system opens up unusual options. Not only can we study and predict how fish at different network positions should be affected by an ectoparasite. We should also be able to investigate what challenges a parasite is faced with when adapting to our fish population because we know how much time is spent alone and social and how frequently individuals change partners. This should be an interesting field for future research.

Higher node strength resulted in relatively lower exposure to predation in our simulation. Our study was carried out on guppies in the Upper Turure, a low-predation population, and it would be informative to investigate whether there is indeed a shift towards individuals with higher node strength and increased $P_{a\rightarrow s}$ (thereby specifically reducing the mean time spent alone) in high-predation populations. So far comparative studies on fish populations have only considered the overall time budget of time spent shoaling (e.g., guppy: Magurran 2005; Botham et al. 2008) whereas an assessment of the detailed fission-fusion dynamics can potentially offer much deeper insights into the ways in which selection has shaped social behavior.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Krause et al. (2016).

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