Environmental Complexity Influences Association Network Structure and Network-Based Diffusion of Foraging Information in Fish Shoals

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abstract: Socially transmitted information can significantly affect the ways in which animals interact with their environments. We used network-based diffusion analysis, a novel and powerful tool for exploring information transmission, to model the rate at which sticklebacks (*Gasterosteus aculeatus*) discovered prey patches, comparing shoals foraging in open and structured environments. We found that for groups in the open environment, individuals tended to recruit to both the prey patch and empty comparison patches at similar times, suggesting that patch discovery was not greatly affected by direct social transmission. In contrast, in structured environments we found strong evidence that information about prey patch location was socially transmitted and moreover that the pathway of information transmission followed the shoals' association network structures. Our findings highlight the importance of considering habitat structure when investigating the diffusion of information through populations and imply that association networks take on greater ecological significance in structured than open environments.

Keywords: contagion, public information, social information, social learning, social network, social transmission.

Introduction

Social transmission of information plays a major role in determining how animals obtain information about the environment and can influence movement, resource use, and patterns of interaction (Danchin et al. 2004). For a given population, social network structure, which describes the distribution and frequency of interactions between its constituent individuals, is likely to be important in determining the rate and pattern of diffusion of socially transmitted information (Croft et al. 2008). Social network analysis has been used to quantify the social structure of wild populations in a diverse variety animals, revealing nonrandom and temporally persistent orderings of asso-

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ciations and interactions in groups including cetaceans (Lusseau 2003), pinnipeds (Wolf et al. 2007), primates (Sueur et al. 2011), and ungulates (Sundaresan et al. 2007) among mammals, and in passerine birds (Templeton et al. 2012), reptiles (Leu et al. 2010), and fishes (Croft et al. 2004; 2005). Patterns of association or interaction represent potential pathways for the transmission of information, and statistical methods that take account of such network structure potentially allow for predictions about the likelihood and rate of transmission occurring both between individuals and throughout the group as a whole.

Correspondingly, in recent years, a range of network-based methods have been developed with the aim of analyzing the dynamics of the diffusion of information within animal populations and how information flow is affected by social network structure (Franz and Nunn 2009; Hoppitt et al. 2010*a*, 2010*b*; Hoppitt and Laland 2011). Ultimately, if the factors that influence diffusion rates and patterns can be identified, it should be possible to model future information flow through populations with known network characteristics. In order to achieve this, it is necessary to understand how environmental conditions influence the association structure of animal groups and how they might directly or indirectly affect diffusion dynamics. One environmental parameter that can exert substantial influence on social interaction patterns, and conceivably therefore diffusion dynamics, is its physical structural complexity.

The effects of environmental structural complexity on social network dynamics have been explored in several studies, including investigations centring on free-ranging ungulates (Rubenstein et al. 2007; Sundaresan et al. 2007), and in fishes in the laboratory (Orpwood et al. 2008; Edenbrow et al. 2011). Together these studies report that the structure of the environment, acting in concert with factors including demography, phenotype, and predation pressure can play an important role in influencing social network

properties such as subgroup size, stability, and fidelity, and patterns of courtship interactions.

To our knowledge, however, no study to date has addressed the effects of environmental structure, and associated variation in social network metrics, on the diffusion of information through groups. In order to bridge this gap in our understanding, in this study we sought to determine the effect of environmental structural complexity on the association network structure of fish shoals and to identify its effects, via social transmission of information, on the rate and order in which the individuals within these shoals discovered a hidden prey patch. We used the threespine stickleback (*Gasterosteus aculeatus*) as our study species. Threespine sticklebacks are capable of social learning (Coolen et al. 2003) and are known to exhibit complex, nonrandom patterns of social interaction in the wild (Ward et al. 2002; Croft et al. 2005), making them an appropriate study system.

In the first part of the study, we compared association network structure between multiple groups of fish tested in arenas that contained either open water or an arrangement of barriers, designed to simulate natural environmental structure. We predicted that groups tested in open water would form fewer, larger subunits. We reasoned that the structured environment would provide cover, resulting in reduced antipredatory behavior, manifest in smaller group sizes (Villafuerte and Moreno 1997; Rhim and Lee 2003; Orpwood et al. 2008). In the second part of our study, we used network-based diffusion analysis (NBDA; Franz and Nunn 2009) to investigate whether information about the location of a foraging patch diffused through the networks and whether the diffusion dynamics were affected by environmental structure. By comparing the entry times of fish into both prey patches and empty control patches, we aimed to distinguish between social transmission, in which fish acquired and responded to social information produced by others that had discovered the prey patch, and what we call "an untransmitted social effect," in which the discovery of a prey patch by a given individual is a side effect of it associating with and following others at the same time that they enter the patch.

Methods

Fish Collection and Housing

Threespine sticklebacks were collected from a small tidal stream in St. Andrews, United Kinigdom (56°20′06″N, 2°47′23″W), in October 2007 (part 1) and October 2009 (part 2). In our laboratory they were held in groups of 40 in 90-L aquaria containing a layer of coarse sand, plastic vegetation, and an internal filter. The photoperiod was 12L : 12D, and the temperature was held at 8°C. The fish were fed daily with frozen bloodworm. Part 1 was conducted between December 2007 and February 2008 and part 2 between December 2009 and February 2010. No individual was used more than once.

Part 1: Association Network Structure

We quantified the association network structure groups of eight fish in the open and structured environment treatments. We tested 16 groups in total, eight in each environment. Each group was formed by drawing a single fish from each of eight different holding tanks, in order to control for effects of familiarity on association preferences (Ward and Hart 2003). We used fish measuring between 35 and 40 mm standard length, and within each group all fish were size matched to within 2 mm. Individual fish were identified by a 5-mm-diameter disk tag placed over the first dorsal spine. A previous study determined that these tags do not affect fish shoaling preferences (Webster and Laland 2009). We avoided using red or orange tags, since these colors are associated with male nuptial coloration (Smith et al. 2004) and may affect shoaling behavior. We used black, white, blue, green, brown, yellow, black/yellow, and blue/white tags. The fish were tagged 3 h before the experiments commenced. Only fish showing no signs of entering reproductive state were used, since this is known to influence social behavior in related species (Webster and Laland 2011).

Experimental Arena

Each group was tested within an arena measuring 80 cm × 60 cm (base) and 30 cm tall. The base of the arena was covered with a 3-cm-deep layer of pale gray gravel. The depth of the water above the substrate was 5 cm. The open environment arena contained no other structure, while the structured environment contained 24 10-cm-long, 0.3-cm-wide black plastic barriers arranged in a grid of four rows of six along the longest axis of the tank. These were spaced evenly across the floor of the arena and positioned so that each was perpendicular to the previous one. These ran from beneath the substrate to the surface of the water and produced a structurally complex environment. The experimental arena was surrounded by a shelter constructed from a black plastic frame with walls and ceiling covered with diffusion filter paper (white diffusion 216, Lee Filters, Andover, UK). Illumination was provided by a ceiling-mounted strip light directly above the test arena. A camera (Canon HG20, high resolution) was placed 150 cm above the arena and filmed it through a small aperture in the diffusion filter that formed the ceiling of the shelter. The diffusion filter ensured an even distribution of light over the surface of the test arena.

Experimental Procedure

Fish were deprived of food for 24 h before testing. One trial was conducted per day. The fish were tagged at 10 a.m. on the day of testing and held in a 30-L aquarium with black-screened walls and a coarse sand substrate for three further hours. Following this they were netted out and placed in the center of the test arena, from where they were allowed to move around freely for 30 min until the start of the experiment. At the commencement of the experiment the camera was switched on by remote control and the arena and group of fish was filmed for 2 h. Following this the fish were removed and placed in a separate aquarium. The test arena and substrate were then thoroughly cleaned in preparation for the next trial.

From the 2-h recording of the trial we constructed an association network for the group. To do this we point sampled the shoaling behavior of the fish at 6-min intervals, giving a total of 20 point samples per trial, recording for every individual which other individuals it was shoaling with. This allowed us to construct a pairwise association matrix for each group. The 6-min interval was chosen because, during pilot observations, 3–4 min was seen to be sufficient time for any given individual to associate with (by the criteria described below) and then move away from all of its group mates at least once, in both experimental conditions. By selecting a sampling interval greater than this we were able to be confident that pairwise shoaling associations recorded at $t2$ were not dependent on associations occurring at $t1$. Fish were deemed to be shoaling if they were within 2 body lengths of each other. This corresponds to the interindividual distances seen in shoals of sticklebacks described in Webster et al. (2007*a*). We used a gambit of the group approach (Croft et al. 2008), such that if a cluster of individuals shoaling within 2 body lengths or less were recorded together, then all were assumed to be associating with each other, even if the distance between the outermost individuals in the cluster exceeded 2 body lengths. In the structured environment treatment, fish that were within 2 body lengths but that were separated by a barrier were deemed to be associated with one another. While the barriers prevented the transmission of visual cues between fish that were either side of them, the groups of fish were typically mobile, and individuals from the same groups often passed either side of the barriers, while continuing on the same trajectory. The barriers were short enough for the fish to regain contact rapidly after passing the barrier. Furthermore, vision is not the only sensory modality involved in social recognition and group maintenance in this species, with chemical cues being at least as important (Ward et al. 2004, 2005, 2007; Webster et al. 2007*a*). The design of the barriers did not prevent the transmission of chemical information between individuals, and other information, such as acoustic cues, may also have been transmitted. Finally, we did not wish to impose different shoaling criteria on fish in the two different treatments. One of the aims of this study was to quantify the effects of environmental structural complexity on shoal structure, and using different shoal criteria between treatments confounds this aim.

Network Metrics and Statistical Analysis

In all but one of the association networks obtained for our groups, all fish were seen to associate with all others in their group at least once (fig. 1*D*). For this reason, many of the standard network metrics, such as path length, betweenness, and clustering coefficient, which are commonly used to describe networks with incomplete connectedness, were unnecessary or inapplicable here (see Croft et al. 2008). Instead, we focused on just three metrics: mean subgroup size, network density, and network differentiation.

Subgroup size was determined by calculating the mean number of individuals within each subgroup (groups where individuals were connected by 2 body lengths or less) at each sampling instant and from this calculating a mean for each group. Network density describes the proportion of observed pairwise interactions, that is, the number of pairwise interactions observed divided by the maximum possible number of pairwise interactions. For a network containing eight individuals, where interactions are reciprocal, the maximum possible number of pairwise interactions is 28. As with subgroup size, we calculated the network density at each sampling point for each group and from that determined the group mean. Subgroup size and network density are related, since the size of the subgroups determines the number of pairwise interactions observed. Finally, we calculated network differentiation, essentially a measure of the evenness of the distribution of the total pairwise interactions between individuals within an association matrix (Edenbrow 2011), derived from the coefficient of variation (standard deviation of observed interactions per pair for the group/mean number of interactions per pair for the group). A lower network differentiation score is indicative of lower variation in the extent to which individuals associate with one another. We compared these three metrics between the open and structured environment treatments using independent samples *t*-tests.

Part 2: Diffusion Task

In this experiment we set out to determine whether the association patterns seen within groups in open and struc-
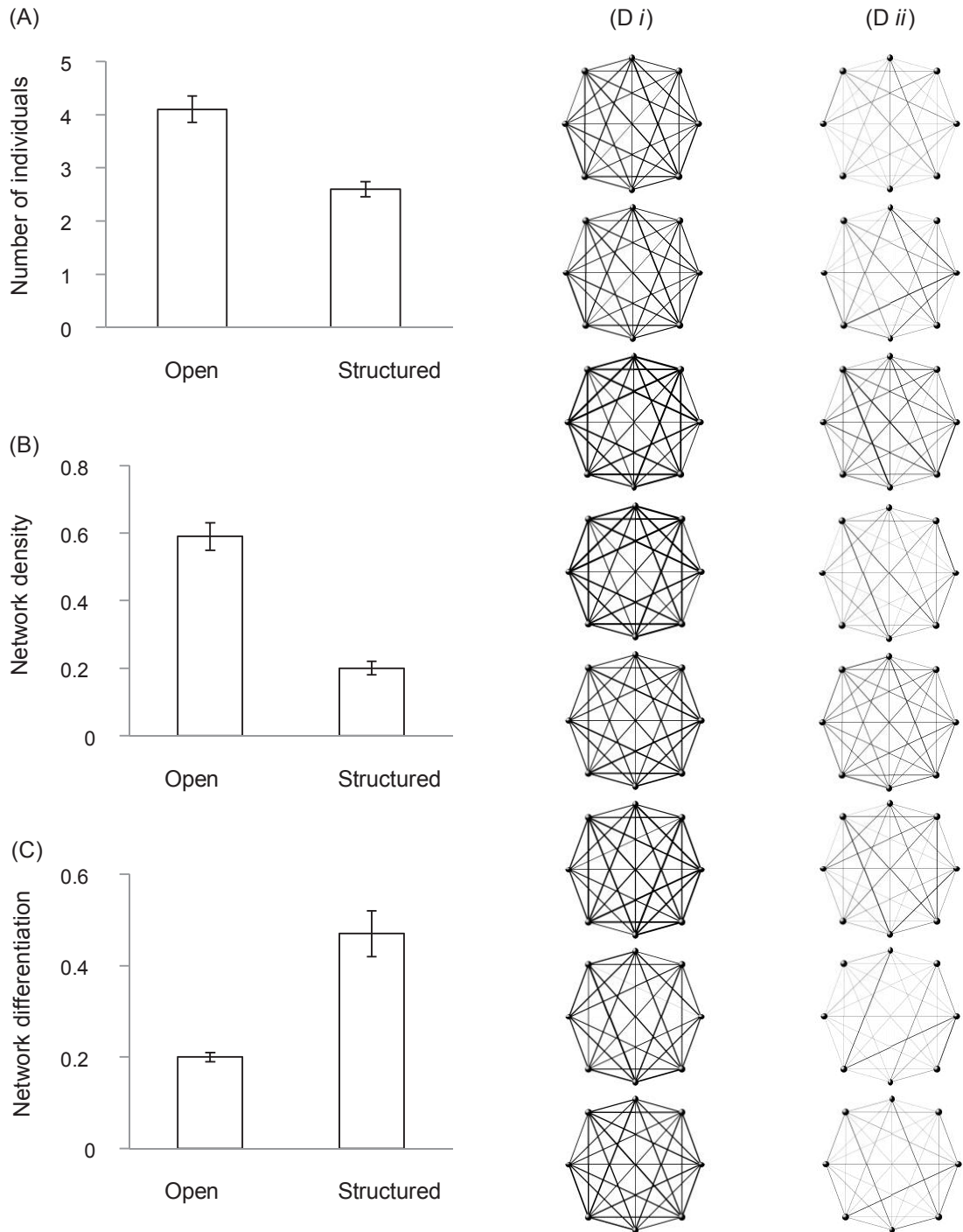
Figure 1: Network metrics describing the association network structures seen in the open and structured treatments in experiment 1 (means ± SE): *A*, subgroup size; *B*, network density; *C*, network differentiation. Network plots are shown for the open and structured treatments (D*i* and D*ii*, respectively). Each circle represents one individual. The lines connecting them indicate the strength of the interactions observed between them; thicker lines indicate that individuals were recorded together more frequently. The network plots were produced using NodeXL (Smith et al. 2010).

tured environments predicted arrival times at a hidden prey patch within the arena. To do this we quantified the association network structure for each of several groups in each treatment before uncovering a previously hidden prey patch and recording the discovery times by each individual.

Experimental groups were established exactly as described above, and the tagging and settling procedures were identical. We tested five groups of eight fish in each of the treatments. We used a modified version of the experimental arena, described in part 1. A prey patch was placed in the center of the arena, buried within the gravel substrate. This consisted of a Perspex container measuring 4 cm × 2 cm × 1 cm containing water and 25 blood-worms. The container was sealed, preventing prey chemical cues from entering the water of the test arena. Because the container was set within the substrate, the fish could not see the prey inside it until they passed over it. For the first 90 min of the trial the prey patch was hidden beneath an opaque cylinder, preventing the fish from locating or interacting with it.

We recorded association patterns at 6-min sampling points as described above for the first 90 min of the trial, giving a total of 15 sampling points. Following this, the cylinder covering the prey patch was carefully removed, so as not to startle the fish, revealing the prey patch. The trial ran for a further 30 min.

Using the point samples from the first 90 minutes of the trial we constructed association matrices for each group. In the remaining 30 min we recorded the identity of each fish as it passed over the prey patch and the time at which its first visit took place. During the same 30-min period we also recorded entry times into a control patch, an unmarked patch of substrate of equivalent area to that of the prey patch, located 20 cm away from the prey patch. There were no barriers between these patches in the structured environment treatment. The use of a control patch enabled us to infer whether the location of the prey patch was socially transmitted between individuals via social cues related to discovery of the prey patch, such as feeding strikes (which we observed, in the prey patch), increased activity, or changes in posture (Krause 1992) or whether individuals that had previously associated closely were simply more likely to enter the same areas at similar times, regardless of what those areas contained (more details below).

Network Metrics and Statistical Analyses

We calculated, and compared between treatments, the same network metrics as described in part 1. We then went on to (i) test for social transmission of the prey patch location, (ii) estimate the strength of social transmission

in each environment, and (iii) infer whether the time at which individuals first fed at the food source followed the group's social network, using network based diffusion analysis (Franz and Nunn 2009; Hoppitt et al. 2010a). NBDA fits a model in which the rate at which a behavioral trait is acquired is a linear function of a naive individual's total network connection with informed individuals. We used the time of acquisition diffusion analysis (TADA) variant of NBDA, where the times of acquisition are used to fit the model. For multiple groups of individuals, the NBDA model can be expressed as

$$\lambda_{ik}(t) = \lambda_0(t)\left(s\sum_{j=1}^{N_k}\alpha_{ijk}z_{jk}(t) + 1\right)(1 - z_{ik}(t)), \quad (1)$$

where $\lambda_{ik}(t)$ is individual i in group k's rate of acquisition of the trait at time t, $\lambda_0(t)$ is a baseline rate function, common to all individuals, which we assumed to be constant: $\lambda_0(t) = \lambda_0$ (see appendix, available online), $s \geq 0$ is a parameter determining the rate of social transmission between individuals per unit of network connection, where $s = 0$ indicates that all acquisition is by asocial means, α_{ijk} is the network connection leading from individual j to i, z_{jk} is the status of i at time t, where 1 indicates informed and 0 indicates naive, and N_k is the number of individuals in group k.

We extended the analysis in two ways: (i) to investigate whether the rate of social transmission per unit of network connection was influenced by environmental structure and (ii) to distinguish social transmission from other processes that might result in a superficially similar pattern of acquisition. Although NBDA was designed such that a positive result ($s > 0$) could be used to infer social transmission of a trait, this is not necessarily the case with spatially specific traits, such as discovery of the location of a food patch. The problem is that closely associated individuals might discover the food source at a similar time, purely because they tend to move around together. This is logically distinct from social transmission, where one individual's discovery of the food patch causes another associated individual to discover the food patch sooner. In the former case, one individual discovering the food source at time t merely provides researchers with the information that associated individuals are also likely to be close to the patch at time t, and so more likely to discover the patch sooner. We refer to this process as an "untransmitted" social effect, referring to the fact that the first individual's discovery of the food patch does not cause the second individual to do so. This is not say that individuals do not causally influence one another under the untransmitted social effect hypothesis: the position of an individual A is likely to exert a causal influence on the position of a naive individual B (and vice versa), but critically, the status of

individual A (naive or informed) is causally irrelevant for B's rate of discovery. Conversely, in the case of social transmission, discovery of the food patch causes the discoverer to act in a way that attracts others to the patch, through perhaps increased feeding strikes, increased activity, or changed posture, or merely through a tendency to remain at, or return to, the patch. For both processes, total network connection with informed individuals will predict rate of acquisition.

To separate the two processes, we reasoned that the former process would apply on occasions where individuals first entered any arbitrary area within the test arena. Conversely, there is no reason why social transmission would operate for an arbitrary patch, since there is no reason why "discovery" of such a patch would cause that individual to behave in a way that caused other individuals to visit that location. Therefore, we identified a control patch in each arena, 20 cm from the prey patch, and recorded the time at which each individual first entered the control patch. We then treated these data as an additional set of diffusions and replaced the s parameter for the real patch with the term $s_T + s_U$ (≥ 0) and the s parameter for the control patch with s_U (≥ 0). Here s_U quantifies the "untransmitted" effect, common to both patches, and s_T the transmitted effect, which operates (if at all) only the real patch. Evidence for $s_T > 0$ constitutes evidence for social transmission. We estimated these parameters separately for each environment and estimated the difference in social transmission between the two environments. We obtained 95% confidence intervals (CIs) using the profile likelihood technique.

By applying NBDA to multiple groups, the analysis becomes sensitive to differences in the time of acquisition between groups: that is, if individuals in the same group learn at a similar time, a large s parameter is estimated. Consequently, evidence for $s_T > 0$ does not necessarily constitute evidence that social transmission follows the network within each group; it could be that information spreads homogeneously within groups. To investigate this alternative explanation, we considered models in which the measured network was replaced with a homogenous network, in which connections between all individuals in each group were set to 1. We used Akaike weights (Burnham and Anderson 2002) to assess the relative strength of evidence for social transmission following the network, homogeneous social transmission, and no social effects (see appendix).

We also considered three other variables influencing the rate at which individuals acquire the trait: group, environment (open vs. structured), and patch (prey vs. control). The latter two factors were included to control for differences in asocial rate of discovery, which might otherwise be mistaken for differences in the s parameters,

though there was little evidence any had an effect (see appendix).

NBDA analyses were performed in R 2.14.1 (R Development Core Team 2011) using code provided on our website (NBDA code V1.2; http://lalandlab.st-andrews.ac.uk/freeware.html).

Results

Part 1: Network Metrics

Mean group sizes were larger in the open water treatment compared to the structured environment (independent samples t-test: $t = 8.05$, df $= 14$, $P < .001$; fig. 1*A*). Network density is directly related to group size and was therefore also higher in the open water treatment ($t = 9.06$, df $= 14$, $P < .001$; fig. 1*B*). Finally, network differentiation was lower in the open water than the structured environment treatment (independent samples t-test: $t = -5.31$, df $= 14$, $P < .001$; fig. 1*C*).

Part 2: Diffusion Task

Network metrics observed for the first 90 min (15 sampling points) were comparable to those seen in part 1 (see fig. fig. 2*A*i and 2*B*i for network plots). Mean group sizes and network densities were larger in the open water compared to the structured environment treatment (independent samples t-test: $t = 7.80$, df $= 8$, $P < .001$ and $t = 4.60$, df $= 14$, $P = .002$, respectively). Network differentiation was lower in the open water than structured environment treatment ($t = -3.06$, df $= 14$, $P = .007$).

The data provide much more support for NBDA models in which social effects follow the network (support [total Akaike weight] $= 97.9\%$) than either those in which social effects operate homogeneously within each group (support $= 2.1\%$) or a model with no social effects (support $= 0.0\%$). Further investigation suggested that the time of discovery follows the network predominantly in the structured environment. We refitted the best model, replacing only the networks for the structured environment with homogeneous networks and found an increase in the corrected Akaike Information Criterion (AIC$_c$) of 10.1 (a 160-fold decrease in support). Conversely, when we replaced the networks for the open environment with homogeneous networks, we found an increase in AIC$_c$ of only 0.7 (a 1.4-fold decrease in support), indicating that the network is an important predictor of time of discovery only in structured environments.

For the structured environment, we estimated social transmission to be $s_T = 0.16$ (95% CI $= 0.017$–0.29), indicating evidence for social transmission after accounting for the possible "untransmitted" effect. This coefficient can
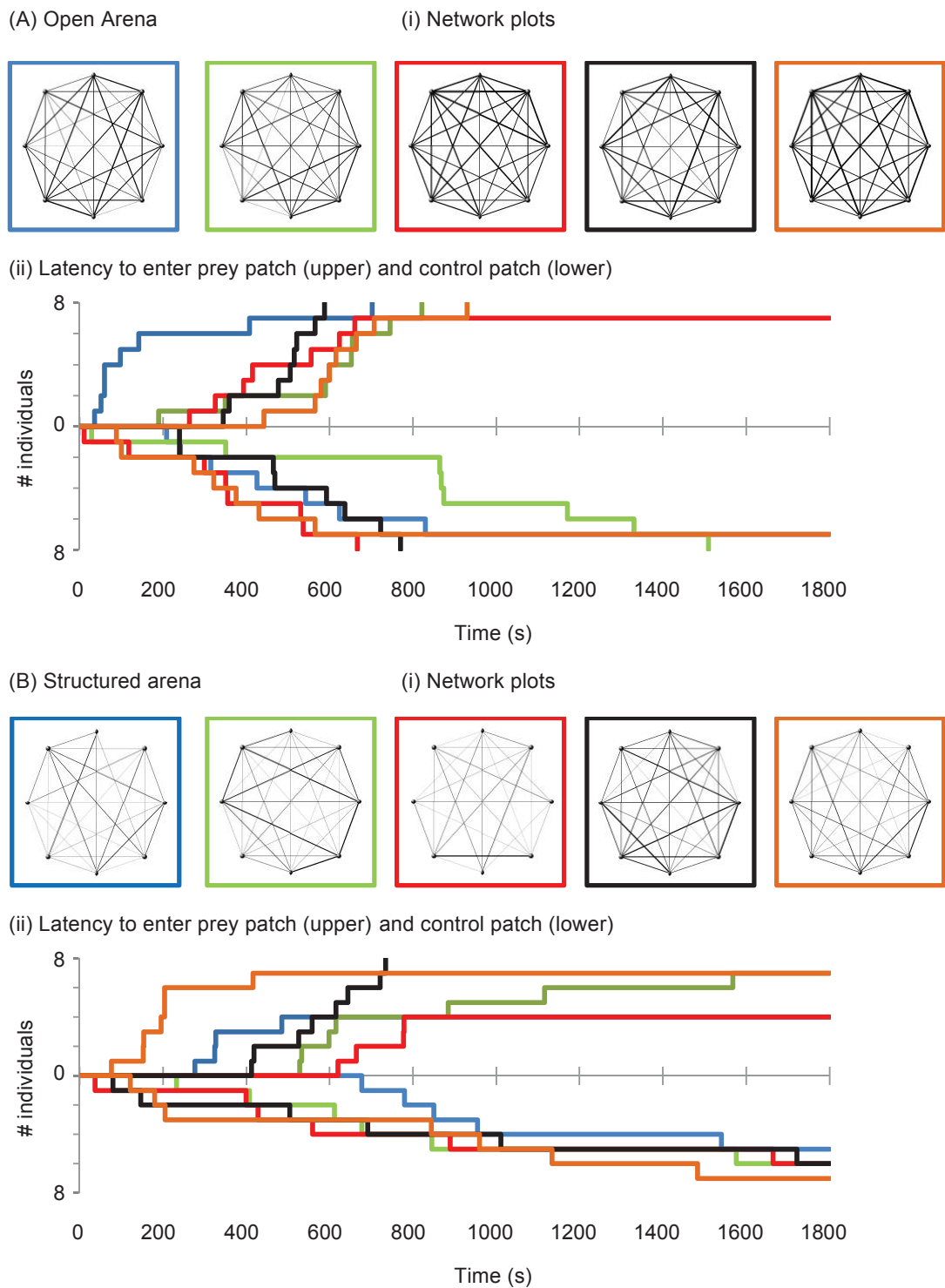
Figure 2: Network plots are shown for the open (Ai) and structured (Bi) treatments in experiment 2. Each circle represents one individual. The lines connecting them indicate the strength of the interactions observed between them; thicker lines indicate that individuals were recorded together more frequently. The network plots were produced using NodeXL (Smith et al. 2010). The diffusion curves show the

be interpreted as the rate at which naive individuals discover each patch by social transmission, per unit of network connection to informed individuals, relative to the baseline rate of asocial discovery. For example, a naive individual with 5 units of network connection to informed individuals in a structured environment is expected to discover the real food patch at a rate of $1 + 5 \times 0.16 = 2.2 \times$ (95% CI = 1.1–4.3) greater than an individual not connected to informed individuals. In contrast, for the open environment, there is little evidence of social transmission: $s_T = 0.01$ (95% CI = -0.13–0.10), suggesting there is only an untransmitted social effect. Correspondingly, there is reasonable evidence that social transmission is greater in the structured than the open environment (difference estimated at 0.15, 95% CI = 0.024, 0.324; fig. 2).

We estimated the untransmitted social effect to be $s_U = 0.046$ (95% CI = 0–0.16) in the structured environment and $s_U = 0.25$ (95% CI = 0.15–0.49) in the open environment.

Discussion

In open environments, fish formed larger groups and interacted more equally with their group mates, compared to those in the structured environment treatments. These differences were seen to affect the dynamics of information transfer through the groups. In both open and structured environments, the time for an individual to first visit the hidden prey patch was strongly predicted by the times at which other individuals in their group first visited the patch. However, in the structured environment, there was also strong evidence that information flow followed the network structure, as models assuming a homogeneous within-group network structure had considerably less support. This was not the case for the open environment, probably because of the different, more homogenous network structure, meaning that any small departures from a homogeneous network were not meaningful with regard to the flow of information between individuals. This implies that association networks may take on far greater ecological significance in structured than in open environments.

Furthermore, in the open water environment, there was

little evidence of a difference between the social effect on the time of first visit to the prey patch and that on the time of first visit to the empty control patch. Consequently, the data here provide no evidence social transmission of the prey patch location. Rather, individuals that associate more frequently may simply be more likely to enter areas of habitat at the same time compared to individuals that associate more weakly, regardless of what those areas contain (Lachlan et al. 1998). In contrast, in the structured environment, we saw a substantial difference in the effect between the prey and control patches, indicating strong evidence of social transmission about the location of the prey patch. As the fish in the open environment tended to swim in fewer, larger groups, they were likely to encounter the prey patch at much the same time, leaving little role for social transmission of information about the food patch. In contrast, in the structured environment, it was more likely that only one or a few fish would encounter the prey or control patch at once.

Plausibly, the location of the prey patch could be socially transmitted by the discoverers to nearby individuals via feeding attempts or related behavior performed by the discoverers (Krause 1992; Gill and Hart 1994; Coolen et al. 2001). The experimental design employed in this study presented fish that had entered the prey patch with visual prey cues only, and consequently they were unable to actually consume the prey. However, the fish were observed to attempt to feed by performing "feeding strikes," lunges or pecks directed at the substrate where the prey were concealed. In contrast, in the control patch where no prey were present, no such feeding attempts were observed. Individuals that disproportionately associate with one another will be more likely to be closer to each other should one of them discover prey and therefore more likely to detect any cues associated with feeding produced by the discover. If they are attracted to and move toward individuals producing such cues, then they will be consequently more likely to enter the prey patch. In the control patch, where discovers did not produce feeding cues, such social attraction would not be expected. This effect may be enhanced further in structurally complex environments, since structure may prevent more distant individuals from obtaining information by blocking such cues, further strengthening the correlation between individuals' net-

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latency of individuals within each treatment group to enter the prey patch (upper half of the panel) and control patch (lower half of each panel in the open [Aii] and structured [Bii] treatments in experiment 2). Each line represents one group. Each group on the diffusion curve is represented by the network plot with the corresponding colored border. Note the steepness of the diffusion curves: in the open environment (Aii), the curves for first entry times into the prey and control patches are of similar steepness, while in the structured habitat (Bii), the diffusion curves showing first entry times into the prey patch are generally steeper compared to those for the control patch. This is consistent with the data providing more support for models in which the social effect differed between the real and control patches in the structured environment, but not in the open environment (see main text for further discussion).

work association strength and time of discovering the prey patch. The statistical methods employed in this study did not take into account behavior that might provide further cues about the location of the prey patch to observers, by individuals that had already found the prey patch. It is likely that such cues have some influence on the behavior of observers, since previous studies have shown that threespine sticklebacks are strongly attracted to areas where they can see others feeding (Krause 1992; Coolen et al. 2003; Webster and Hart 2006; Webster et al. 2007*b*). A natural extension to our study is therefore to incorporate discoverer behaviors into weighted NBDAs in order to determine their importance in social transmission of information about patch location.

We have shown that environmental structural complexity exerts a strong effect on social network structure, which in turn influences patterns of prey patch discovery through social transmission and social facilitation. This work has also revealed that individual-level social transmission dynamics vary, depending on social network structure. These findings have implications for comparative work investigating variation in diffusion dynamics and social learning between different groups, or among multiple populations of the same species. Our findings imply that the role of variation in social structure and its underlying causes, including variation in environmental structural complexity, may need to be accounted for if researchers are to understand interpopulation behavioral variation. Finally, if researchers are to use association network structure to make longer-term predictions about resource encounter rates in wild populations, then they will need to incorporate information about network stability over time and in response to demographic, seasonal, and environmental perturbations. Information on network stability exists for relatively few study systems. In wild meerkats (*Suricata suricatta*), for example, social structure and interaction patterns were reported to be relatively stable over a 24-mo period, but with short-term variation in response to seasonal variation in ecological conditions (Drewe et al. 2009). Ultimately, by incorporating ecological parameters along with estimates of network structure change over time into network-based diffusion models, it may be possible to forecast, within reasonable margins of error, the rates and pattern of the spread of information through animal groups.

Acknowledgments

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Threespine sticklebacks *Gasterosteus aculeatus*. Photo by K. N. Laland.