Information flow through threespine stickleback networks without social transmission

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Social networks can result in directed social transmission of learned information, thus influencing how innovations spread through populations. Here we presented shoals of threespine sticklebacks (*Gasterosteous aculeatus*) with two identical foraging tasks and applied network-based diffusion analysis (NBDA) to determine whether the order in which individuals in a social group contacted and solved the tasks was affected by the group's network structure. We found strong evidence for a social effect on discovery of the foraging tasks with individuals tending to discover a task sooner when others in their group had previously done so, and with the spread of discovery of the foraging tasks influenced by groups' social networks. However, the same patterns of association did not reliably predict spread of solution to the tasks, suggesting that social interactions affected the time at which the tasks were discovered, but not the latency to its solution following discovery. The present analysis, one of the first applications of NBDA to a natural animal system, illustrates how NBDA can lead to insight into the mechanisms supporting behaviour acquisition that more conventional statistical approaches might miss. Importantly, we provide the first compelling evidence that the spread of novel behaviours can result from social learning in the absence of social transmission, a phenomenon that we refer to as an untransmitted social effect on learning.

Keywords: social learning; local enhancement; social networks; threespine sticklebacks; network-based diffusion analysis

1. INTRODUCTION

Innovation can be said to occur when a new behaviour pattern is invented or when an existing behaviour pattern is modified to suit a novel context [1]. Behavioural innovation is an important facet of phenotypic plasticity enabling organisms to exploit new food sources, to improve their efficiency of using a familiar resource or to respond to other changes in their environment [1]. Social learning can lead to the transmission of behavioural innovations, potentially allowing innovations to spread rapidly through populations [2]. Examples of social transmission of behavioural innovations include Japanese macaques, *Macaca fuscata*, washing sweet potatoes [3] and British titmice, *Parus* spp., opening milk bottles [4,5].

Social learning is broadly defined as learning that is influenced by observation of, or interaction with, another individual or the products of its behaviour [6]. Despite extensive recent research into animal social learning [6–9], the social factors influencing learning of innovations by individuals in freely interacting groups remain poorly understood [10–12]. It is commonly supposed that social learning, where it occurs, results in

social transmission, i.e. where performance of a behaviour by one individual makes it more likely that other individuals will add the behaviour to their repertoires. However, in most cases in which the spread of a behavioural innovation has been reported in natural or captive populations, the possibility cannot be excluded that either asocial learning caused the observed change in behaviour, or that the learned behaviour of one individual facilitates acquisition of behaviour by others in more subtle ways than are normally considered [13–15].

Furthermore, many previous theoretical and empirical studies have tended to assume that all members of a population are equally likely to transmit or receive information [11]. Although animals might pay equal attention to the actions of each group member, Coussi-Korbel & Fragaszy [10] suggest that this is unlikely and that, to the contrary, animals within a group are more likely to learn from some individuals than from others. Indeed, this notion of 'directed social learning' suggests that animals either might copy strategically, for instance, by attending to the behaviour of older or more successful individuals [16] or might copy their nearest neighbours [17]. Consistent with the expectation that information flow through animal populations will not be random, results of several studies suggest that captive and wild animal populations (e.g. guppies, *Poecilia reticulata* [18,19], bottlenose dolphins, *Tursiops truncates* [20] and

starlings, *Sturnus vulgaris* [12]) are characterized by non-random social networks [19].

A variety of phenotypic factors have been shown to generate non-random networks within animal groups, including assortment with respect to sex [11], familiarity [21], size [22] and hunger level [23], which may lead to association patterns that shape the route of information transmission. Network-based diffusion analysis (NBDA [24]) is a recently developed method of data analysis of potential use in the field of animal social learning that allows non-random social transmission, as well as other social effects on behaviour, to be detected and quantified. Here we apply NBDA to captive groups of threespined sticklebacks (*Gasterosteus aculeatus*) presented with either one or two foraging tasks, to provide evidence of any non-random patterns of social influence on task discovery and solution within shoals.

In NBDA, the rate that individuals move from a naive to an informed state (having solved a task) is modelled as a function of the total of their network connections to informed individuals. Thus, NBDA implicitly assumes that social learning will be manifest as social transmission. However, in a foraging task, social influences other than social transmission might operate independently to decrease either the latency with which naive individuals discover the task or the latency with which they subsequently solve it. Furthermore, a fully informed individual who has solved a task might exert more influence on the naive than an individual who has merely discovered that task. To investigate such possibilities, we extend the NBDA model to multiple states, analysing the process of task solution as comprising two identifiable stages, discovery and solution, thus allowing specific types of social influence on each to be both detected and quantified.

Fish are well suited to the study of social diffusions in the laboratory. Both the processes of social learning and the contexts in which it occurs have been well studied in fishes (for review, see [25–27]), which offer several practical advantages for the study of directed social learning. The diffusion of innovations and animal traditions are group-level phenomena and, accordingly, their study is facilitated not only by using replicate animals, but by using replicate populations as well [27]. Populations of small fishes are easy to maintain in the laboratory and fishes are frequent subjects in experiments on social learning.

2. MATERIAL AND METHODS

(a) *Subjects and apparatus*
Subjects were 160 threespined sticklebacks maintained in 16 groups of 10, with eight groups used in each experiment. We used no individuals displaying signs of nuptial coloration or gravidity as reproductive state has been shown to affect an individual's reliance on social learning in sticklebacks [28].

To encourage size-assortative shoaling [23], and thereby to promote heterogeneity of social network structures, we deliberately generated variation in body size within groups. Individuals ranged from 38 to 71 mm in length with an overall mean within-group range of 14.8 mm.

We captured subjects using mesh cage traps from the Kinnessburn, St Andrews, UK (56.33.4925 N, −2.78.8151 W) between June and September, 2010 and held them in groups of 40 in 60 l tanks at a temperature of 8°C, and fed them daily with frozen chironomid (*Chironomus* sp.) larvae for a minimum of two weeks before testing (July to October, 2010).

We tested groups of 10 individually marked fish [29] in a rectangular black test tank measuring 60 × 80 cm. To ensure that vertical distance within the water column between individuals did not confound estimates of inter-individual distances, we filled the test tank with filtered tap water to a depth of only 5 cm. The test tank had a gravel substrate 1 cm in depth, and 10 black, pyramid-shaped obstacles (measuring 10 cm diameter at the base and 6 cm high) placed at regular intervals throughout the tank (see the electronic supplementary material), allowing only associating individuals to see one another while allowing the experimenter to view all fish. We filmed each test trial using a Canon HG20 video camera held 1.2 m above the test tank.

We conducted both one-task and two-task experiments, involving identical foraging tasks, comprising a transparent cylindrical tube measuring 24 cm in length and 7 cm in height placed horizontally on the gravel substrate at each end of the test tank. We inserted 15 ml of defrosted chironomid larvae suspended in water into one end of the tubes, which had 15 small holes (2 mm diameter) allowing olfactory cues from larvae to escape. The other end of each tube was open and its circumference clearly marked with black electrical tape. Consequently, although fish could see and smell food at both ends of each tube, they could gain access to food only at one end.

We predicted that diffusion of information regarding both the location of food and the solution to the tasks would be influenced by the social network, with individuals that had a high level of association with one another being more likely to discover and solve the tasks in succession and with more similar latencies than individuals that had a low level of association.

(b) *Procedure*
(i) *Determining the network structure*
To describe social networks, for each experiment we individually placed each of eight groups of 10 fish into the test tank and allowed each group to settle and explore the tank for a period of 15 min before filming for 2 h. We subsequently took point samples from the film at 6 min intervals, giving a total of 20 observations for each group.

We defined individuals as associating if they were within four body lengths (defined as the mean body length of a group's members) of one another from head to head, a distance generally accepted as indicative of shoaling in fishes [30]. We then created an association matrix based upon the proportion of point samples that each fish was observed to be within four body lengths of each of the other fish in its group.

(ii) *Testing for social learning*
At the end of the 2 h filming of a group, we introduced the foraging tasks and filmed the group for a further 45 min, after which the trial ended and we removed all fish from the experiment. We recorded both the latency with which each individual first discovered each task (defined as occurring when an individual was seen striking at food through the transparent tube) and the latency with which each individual first solved each task (defined as consuming food within the tube). We scored only the first 20 min of video footage after the first fish in each group solved each task at which time food items were still visible inside the tube in all trials.

In addition to recording the latency for discovery and solution of the tasks, we also recorded the latency with which each fish entered an arbitrary area (measuring 20×10 cm) within the tank. This control location contained no food and no distinctive topographical features. In our analysis, we compared inter-individual latencies to 'discover' the control location with similar latencies to discover the tasks. This comparison allowed us to distinguish between effects of affiliation and effects of exposure to individuals in the vicinity of tasks.

(iii) Network-based diffusion analysis

We used NBDA [2,24] to determine whether the sequence with which subjects discovered and/or solved the tasks was correlated with the pattern of association observed between individuals in a group (i.e. the social network). NBDA was designed to reveal social learning when non-random patterns of association are detected. Inference of social learning using NBDA results from comparing models that include social learning with models with only asocial learning to see whether 'social-learning' models provide a better fit to the observed data than 'asocial-learning' models. When social learning is included in an NBDA model, the rate of social transmission between 'informed' and 'naive' individuals is assumed to be proportional to the strength of the network connection between them.

We used the order of acquisition diffusion analysis (OADA) variant of NBDA [2], which is sensitive only to the order in which individuals acquire a trait, not to latencies of acquisition (see the electronic supplementary material for justification). We analysed order of acquisition across all groups, treating the data from all eight groups as a single diffusion network, with zero network connections between individuals in different groups. This treatment of the data renders the OADA sensitive to between-group differences. If consecutive discoverers/solvers tend to be from the same group, this is consistent with the hypothesis that they are learning from each other.

We also modified the OADA model to allow for multiple states (see the electronic supplementary material for details). Existing NBDA approaches assume that individuals move directly from a 'naive' to 'informed' state when they first solve a task [31]. Here we wished to tease apart social effects influencing the rate at which individuals discovered and solved the task (cf. [12]). We assumed that at any given time an individual could be in one of three states: 'naive' (has not discovered the task), 'discovered' (has discovered the task) and assumed further that discovered individuals could be either a 'non-solver' (has not solved the task) or 'solver' (has solved the task). Each task was treated separately, for example, an individual classed as a 'solver' for the left-hand task could still be 'naive' for the right-hand task.

We fitted separate OADA models for: (i) the rate at which naive individuals discovered the task, and (ii) the rate at which 'discovered' individuals solved the task (see the electronic supplementary material). We allowed for the fact that both rate of discovery and rate of solving might be affected by network connections to individuals that: (i) had discovered the task or (ii) had solved the task.

We also included body length as an individual-level variable (entered as a difference from group mean body length) and treated 'group' as a factor, to allow for the possibility that groups might differ in their rates of asocial discovery or solving. We considered social learning and group differences in asocial rates of learning as alternative explanations for differences between groups and consequently did not include both

variables in the same model although we considered models including all other possible combinations of variables.

Instead of using a model-selection procedure to choose a best model, we used a model averaging approach, using Akaike's information criterion, corrected for sample size (AICc) [32]. Inferences based on model averaging take into account uncertainty as to which model is best. AICc estimates the Kullback–Leibler (K–L) information for a model (i.e. the extent to which the predicted distribution for the dependent variable approximates its true distribution). The AICc allows us to calculate an Akaike weight for each model that gives the probability that the model is the actual best K–L model (that with the lowest K–L information) out of those considered, allowing for sampling variation. By summing Akaike weights for all models that include a specific variable, we obtain the probability that a variable is in the best K–L model, thus quantifying support the data give for an effect of a variable [32].

This approach is preferable to calculating a *p*-value to quantify the strength of evidence for each effect, because: (i) the *p*-value depends on which model is chosen and consequently does not account for model uncertainty, and (ii) a large *p*-value tells us little about the strength of evidence against an effect (i.e. while statistical power can be calculated, the power has to be for a specified, usually arbitrary effect sizes [33]). Therefore, for each variable considered, we give its total Akaike weight (as a %) and model-averaged estimate [32]. We also provide unconditional 95% confidence intervals using Burnham & Anderson's [32] method for adjusting profile likelihood confidence intervals for model selection uncertainty.

(iv) Comparison of network-specific and homogeneous effects

Our OADA analysis is sensitive to between-group differences in discovery and solving times. Consequently, evidence of an effect of network connections to other 'discovered' and/or 'solved' individuals might reflect an effect that operates equally among all individuals in each group, rather than an effect that follows the social network. To tease apart network-specific and homogeneous (i.e. non-network-specific) effects, we fitted alternative versions of models for rate of discovery and for solving. To reduce the set of models to be fitted, we constrained all models to include effects for which there was more support for than there was against (greater than 50%). To assess whether each social effect operated homogeneously within groups (i.e. independent of patterns of association), we replaced the social network with a homogeneous network (connection of strength 1 for individuals in the same group, 0 for those in a different group) for each effect. We also allowed for the possibility of network-specific and homogeneous components to each effect (electronic supplementary material, §7).

(v) Social transmission versus an untransmitted social effect

NBDA was designed such that evidence for $s > 0$ could be used to infer social transmission of a trait. However, an $s > 0$ need not indicate social transmission of discovery of a food patch. Closely associated 'undiscovered' individuals might discover the food source at a similar time simply because they tend to move about together, and movement in a group is distinct from social transmission. In social transmission, one individual discovering a food patch causes associated individuals to discover the food patch sooner than they otherwise would. In contrast, we refer to the simultaneous discovery of

Table 1. Two-option NBDA results for naive → discovered and discovered non-solver → solver. Italic font indicates there was more support for an effect than against (greater than 50%).

variable	d.f.	support (sum of Akaike weights) (%)	model-averaged effect estimate[a]	unconditional 95% confidence interval[b]
(a) Two option NBDA results for naive → discovered				
total network connection to discoverers: option specific	*1*	*97.8*	*1.4*	*[0.32, 4.4]*
total network connection to discoverers: cross option	1	5.6	0.007	—
total network connection to solvers: option specific[c]	1	24.2	0.094	—
total network connection to solvers: cross option[c]	*1*	*75.4*	*1.4*	*[0.20,6.5]*
body length (mm)	*1*	*91.3*	*0.048*	*[0.016,0.096]*
bias towards right option	1	26.3	1.0×	
group	7	1.1	1.0×	—
discovered other option	*1*	*81.8*	*0.29×*	*[0×, 0.78×]*
solved other option[c]	1	32.7	0.02×	
(b) two-option NBDA results for discovered non-solver → solver				
total network connection to discoverers: option specific	*1*	*79.9*	*3.9*	*[0.334, 590]*
total network connection to discoverers: cross option	1	26.5	0.38	—
total network connection to solvers: option specific	1	6.8	0.048	—
total network connection to solvers: cross option	1	12.6	0.087	—
body length (mm)	*1*	*82.4*	*−0.171*	*[−0.94,−0.0049]*
bias towards right option	1	28.6	1.1×	
group	7	<0.1	1.0×	—
discovered other option	1	30.3	1.2×	
solved other option[c]	1	47.2	1.9×	

[a]Social effects are estimated relative to the mean rate of asocial discovery, e.g. the value 1.4 in table 1*a* signifies that an average individual with one unit of total association to discoverers of an option is 2.4 times faster to discover the same option than an average individual with no connections to discoverers of that option. The effect of body length is estimated as the logarithm of the multiplicative difference per millimetre in body size (standard in modelling rates), e.g. in table 1*a*, 0.048 indicates that the asocial rate of discovery for a fish of 50 mm would be exp $(5 \times 0.048) = 1.27$ times greater than that for a fish of 45 mm. For all other effects, we give the estimated multiplicative difference in rate, for group this is for the most extreme groups.
[b]Unconditional 95% confidence intervals were calculated using a computationally intensive profile likelihood procedure (see the electronic supplementary material, §4) so we only calculated these for variables with support greater than 50%.
[c]The effect of association to solvers is estimated as the effect over and above that of their effect as discoverers. Likewise the effect of having solved the other option is estimated as the effect over and above the effect of having discovered the other option.

a food patch by naive individuals moving in a group as an 'untransmitted' social effect. The key distinction here is that, in the case of social transmission, knowledgeable individuals pass on some of their knowledge to others, whereas with an untransmitted social effect, the individuals that facilitate learning in others are uniformed. Perhaps slightly confusingly, such untransmitted social effects often meet accepted definitions of social learning [6], which encompass any social process that facilitates learning in others. Note that simple movement in a group can account only for an apparent social transmission effect on the rate of discovery, not on the rate of solving.

To separate untransmitted and transmitted social effects, we reasoned that untransmitted social effects would be seen whenever individuals first entered any arbitrary area within the test arena. As mentioned in §2, we identified an arbitrary control patch that contained no food in the test arena and recorded the time at which each individual in each group first entered the control patch. We then treated these data as an additional set of diffusions, and estimated the *s* parameter for both control and real patches, i.e. s_R and s_C, respectively. We then estimated the strength of social transmission as the difference in *s* parameters between real and control patches ($s_R - s_C$). We included only body length as an additional covariate in this analysis since body length was strongly supported by the Akaike weights (table 1*a*).

3. RESULTS
As the one-task and two-task experiments generate consistent findings, we present only the two-task experiment

results, but emphasize that the key findings are replicated in the one-task experiment (see the electronic supplementary material).

(a) *First discovery*
There were no trials in which all individuals within a group discovered both options, with the number of discoverers of each option ranging from three to eight. A minimum of seven individuals discovered one or the other of the options with 112 first discoveries across both individuals and options (figure 1*a*). Diffusion curves for discovery time (figure 1*a*) generally reveal a rapid increase in number of individuals discovering one or both options after initial discovery by one individual.

Both estimates from the NBDA and support for each variable are shown in table 1*a*. There was strong evidence (total Akaike weight = 97.8%) that being well connected to others who had already discovered an option increased the probability that a naive individual would be the next to discover that option, providing clear evidence of social learning. The magnitude of this effect was estimated to be a linear increase of 1.5 times (95% CI = [0.32, 4.4]) the average asocial rate of discovery for every unit of network strength. However, there was no evidence for social transmission of the patch location, with the contrast between real and control food patches ($s_R - s_C$) estimated at −2.48 (95% CI: [−11.0,1.4]), a result in the opposite direction to that expected if social transmission were occurring. The present finding that
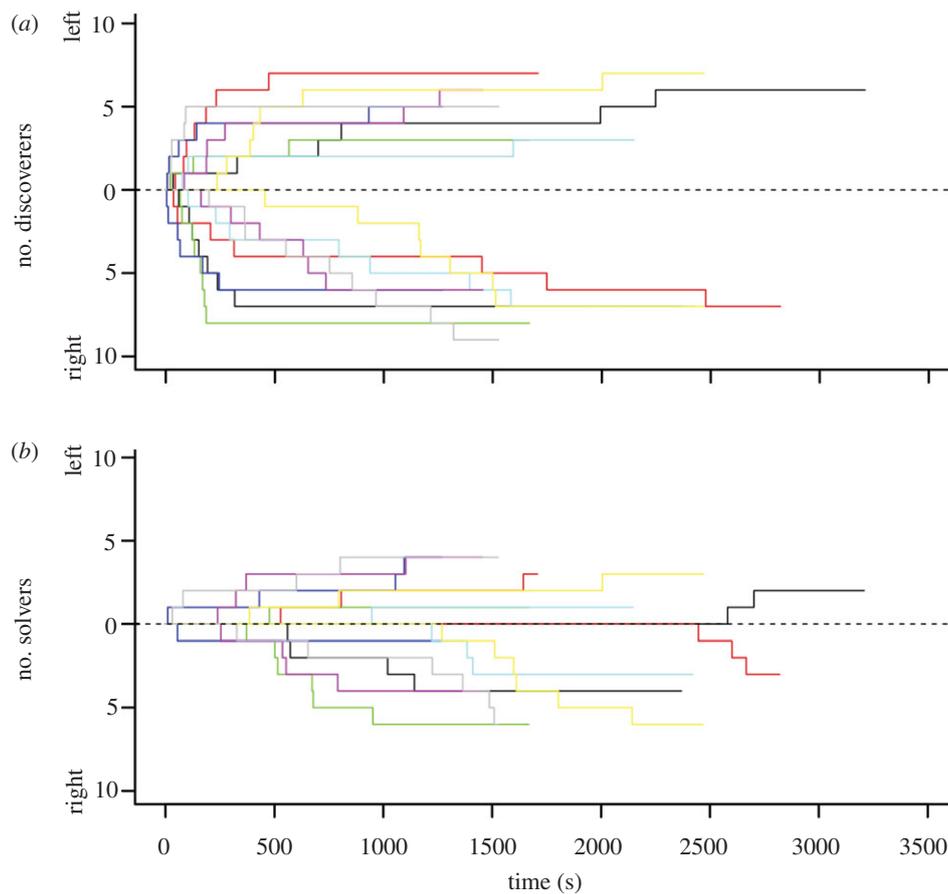
Figure 1. The diffusion curves for the times of (*a*) first discovery, and (*b*) first solving, showing times for both the left- and right-hand options. Each colour represents a different group.

effects of group membership at real patches were not greater than those at control patches suggests that the social effect on discovery may be a result of associated individuals encountering the task at approximately the same time because of their influence on each other's movements. There was little evidence that being well-connected to solvers of an option facilitated discovery of that option, and strong evidence against an effect of connectedness to discoverers generalizing across options, implying that discovery was a location-specific effect.

Surprisingly, there was some support for the hypothesis that individuals were more likely to discover an option next if they were well connected to individuals who had solved the other option than if they were not so connected. This effect was estimated to be similar in magnitude to the option-specific effect of discoverers (1.4, 95% CI = [0.20,6.5]). There is also support for an effect of body length, with larger individuals being more likely than smaller individuals to discover an option first, as well as evidence that individuals that had discovered one option were less likely to discover the other (see table 1*a* for estimated effects and confidence intervals).

(b) First solve
In all eight trials, each option was solved by at least one individual within the allotted time with six individuals solving the task in three of the groups and a total of 39 first solves across all individuals and options. Again, discoverers did not move food items outside of the tube.

As confirmed by the NBDA analysis, diffusion curves for the solving times of the foraging tasks (figure 1*b*)

show individuals solving both options at fairly regular intervals rather than in collective bursts, suggesting that solvers were not influenced by other solvers.

Both estimates from the NBDA and support for each variable are shown in table 1*b*. Probably as a result of the low number of total solvers (39 of 80 subjects), there is no strong support for any one effect. However, total support for models in which at least one social effect is operating is high (93.3%), and there is little support for the alternative hypothesis of underlying group differences in rate of discovery of the two options. A likely explanation for the pattern of data is that individuals that had already discovered one option and were closely connected to other discoverers of that option were more likely to solve that option than other individuals (support = 77.9%), with the effect estimated at 3.9 (95% CI = [0.334, 590]). There is also some evidence for an effect of body size on solving, with smaller individuals who had already discovered an option tending to solve it sooner than larger discoverers.

(c) Comparison of network-specific and homogeneous effects
Support for models that included social effects on learning, either specific to the social network and/or non-network-based group effects, is shown in the electronic supplementary material, table S2. There is a fairly clear indication that, if there is a social effect on the rate at which discoverers first solve the task, it follows the social network (support = 88.5%). Effects of the social network are less clear on the rate at which naive

individuals discover the task. Possibly, individuals are attracted to an option by strongly connected individuals that have already solved an option, and consequently, are more likely to return to that option and/or remain near it than individuals weakly connected to solvers, making it likely that they will solve that option more rapidly than individuals only weakly connected to solvers. Counteracting this effect is evidence for a second process whereby, when many individuals in a group have solved an option, those group members that had not yet discovered the alternative option are more likely to do so, perhaps because the popular option becomes too crowded to solve. In either case, there is clear evidence of social learning.

We also carried out a single-task experiment, on different individuals of the same species, which we have described in detail in electronic supplementary material, §8. This experiment followed the exact same procedure as the one discussed here, except for the use of only one foraging task instead of two. The results of this experiment are consistent with that described above. There was again strong support across groups for the hypothesis that naive individuals well connected to others who had discovered the task were more likely than individuals weakly associated with discoverers to be the next to discover the task themselves (total Akaike weight = 99.8%), providing clear evidence of social learning. There was also no strong evidence for social transmission of patch location, with the contrast between real and control food patches ($s_R - s_C$) estimated at 1.84 (95% CI: [−3.9,11.3]). These findings, like those of the present experiment, suggest an untransmitted social effect underpinning the observed diffusions of task discovery. Social transmission also did not influence the rate at which individuals solved the task, either individually or as a group.

4. DISCUSSION

We present one of the first examples of NBDA of the behaviour of non-human animals. By breaking the processes of task solution into identifiable stages, specific types of social influence were both characterized and quantified.

(a) *Discovery*

We found strong evidence for a social effect of the discovery of the novel foraging tasks, with individuals tending to discover a task sooner when others in their group had previously done so. However, overall we find no evidence that this effect is the result of the task location being socially transmitted between individuals, since the social effect on 'discovery' of an arbitrary empty control patch appeared as strong as discovery of a patch where foraging was possible. These findings suggest that an untransmitted social effect underlies the observed diffusions—almost certainly the influence of fish on one another's movements.

We note that, in the absence of NBDA, most researchers would have interpreted the evidence of diffusion along a social network as indicative of social transmission, although the possibility of asocial learning underlying diffusions has long been recognized [2,14,34]. Here, use of NBDA provided evidence for a third possibility: the social learning of task location in the absence of social transmission. There is unambiguous evidence for both learning and a social influence on latencies to learn, but

no evidence of social transmission. The social effect on 'discovery' of an arbitrary empty control patch appeared as strong as the social effect on discovery of the tasks.

A number of previous studies of social learning in fish report social effects consistent with local enhancement but equally consistent with the hypothesis of a mutually reinforcing tendency of individuals that have discovered a potential food source to remain near that food source and eventually learn to exploit it [35–38]. The present findings are of particular significance in that they draw attention to the possibility that many natural diffusions may similarly result from untransmitted social effects rather than from either social transmission or asocial learning.

(b) *Solution*

Our findings also provide little evidence of social transmission of solution to the task. A higher level of association with previous solvers did not predict a higher rate of solving the task and gaining access to food. Social transmission would require that association with those that had solved the task leads to a higher rate of transition from a naive to an informed state: either increasing the rate of discovery or the subsequent rate of solving. Here we find evidence of neither. Nonetheless, we did find evidence of a social effect on solving the task; a higher degree of association with those that had previously discovered the task predicted a higher rate of solving it.

Unexpectedly, we found that associating with others that have previously solved one option leads to an increased rate of discovery of the remaining option. Two processes, stimulus enhancement and competition, provide plausible explanations. Stimulus enhancement [39] is a process similar to local enhancement. However, in cases of stimulus enhancement, individuals attract the attention of others not to a particular location but to a class of objects. Because the two tasks were identical, stimulus enhancement of one task would have led to increased attention to the other. Alternatively, when one of the tasks had attracted many foragers, remaining individuals may have sought an alternative foraging location where there was less competition for food.

5. CONCLUSION

Our results suggest that social influences on learning can be strong, even without direct transmission of information (e.g. patch locations or task solutions) between individuals. Individuals within each group tended to discover a food patch sooner when others in their group had previously done so, but this temporal pattern of discovery did not appear to be a result of social transmission *per se*. Rather, the tendency of fish to travel in groups resulted in increased simultaneity of discovery, followed by individual learning of the solution. Knowledge as to how to solve a task and acquire food did not spread from informed to uninformed individuals; rather uniformed individuals learned together, but nonetheless benefited from the elevated rate of patch discovery associated with social foraging. Our results are replicated in another experiment using only one foraging task (electronic supplementary material, §8), giving significant strength to our arguments. The methods of analysis employed here could be widely used by those studying diffusion of social information through populations to provide

finer characterization of the nature of social influences on diffusion of innovations through social groups.

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