

Social networks predict patch discovery in a wild population of songbirds

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Animals use social information in a wide variety of contexts. Its extensive use by individuals to locate food patches has been documented in a number of species, and various mechanisms of discovery have been identified. However, less is known about whether individuals differ in their access to, and use of, social information to find food. We measured the social network of a wild population of three sympatric tit species (family Paridae) and then recorded individual discovery of novel food patches. By using recently developed methods for network-based diffusion analysis, we show that order of arrival at new food patches was predicted by social associations. Models based only on group searching did not explain this relationship. Furthermore, network position was correlated with likelihood of patch discovery, with central individuals more likely to locate and use novel foraging patches than those with limited social connections. These results demonstrate the utility of social network analysis as a method to investigate social information use, and suggest that the greater probability of receiving social information about new foraging patches confers a benefit on more socially connected individuals.

Keywords: social network theory; social information; Paridae; group foraging; scrounging; local enhancement

1. INTRODUCTION

For many animals, food can be difficult to find, with locally abundant but ephemeral foraging sites scattered patchily across the landscape. In these cases, foraging individuals face a challenge they can attempt to overcome through a variety of strategies. Personal information and experience may be used to optimize search patterns, e.g. by re-checking previously successful sites using ‘trap-lining behaviour’ [1]. Alternatively, individuals may use search strategies similar to the Lévy walk model, where clustered searching is alternated with long directional travel [2]. Individuals may also be able to maximize efficiency by searching in groups, particularly if they differ in their personal experience [3–5]. Finally, rather than depending on optimized searching or personal experience, foragers may use social information to locate food.

Social information is a broad concept, encompassing all information resulting from the behaviour of others, whether related to activities as diverse as habitat selection, predator avoidance or mate choice [6–8]. In the context of finding patchy food resources, social information refers to information used by naive individuals to locate resources that they have obtained via the behaviour of successful patch finders [9]. Three such behaviours are generally accepted to occur: recruitment at roosts or colonies, active recruitment to food and local enhancement. The information centre hypothesis proposes that individuals transmit information about food patches when they leave or return to communal roost sites [10]. More commonly,

successful individuals may actively recruit others at the foraging site itself. Here, the signaller pays a cost in producing the signal and increasing competition, but may gain greater benefits from reducing predation risk [11]. Finally, and perhaps most simply, individuals may be attracted to inadvertent cues produced by feeding conspecifics or heterospecifics. Such coarse-level local enhancement has been shown in a wide range of taxa, including invertebrates, fish, mammals and birds [9,12,13], and is thought to be the mechanism by which most animals use social information when searching for food sites [12,14].

While it is generally accepted that many species can use social information of some kind to find food patches, little consideration has been given thus far to between-individual variation in access to information, or that information may spread non-randomly between dyads. Assumptions of free mixing and indiscriminate sharing of information in populations are unrealistic when considering the social processes connected with the spread of information [15,16]; social interactions rarely occur completely at random, and individuals often differ in their number and strength of connections to other individuals [17]. Social network theory seeks to explain this variation by measuring individual contact patterns and incorporating them into a descriptive framework that integrates all levels from individual behaviour to population processes [16]. With recent methodological advances, social network analysis has become a promising new way to investigate the effect of individual and community heterogeneities on information transmission dynamics. Network-based diffusion analysis (NBDA) is one such method, designed to identify social learning processes in animals [18–20]. We propose that if individuals exploit social information in the discovery of food sites, then this information should

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be more likely to be transferred between associating individuals, and thus follow routes through a social network. Following this logic, individuals that occupy different network positions should also differ in the speed and reliability with which they receive information.

NBDA infers social transmission of information if the pattern of behavioural change over time follows association patterns in the relevant social network. It assumes that the rate at which social transmission occurs between a naive-informed dyad is linearly proportional to the association between them [20]. Hoppitt *et al.* [19] successfully retrospectively applied this method to the spread of innovation in a flock of captive starlings [21]. However, the only two studies to test NBDA in the wild (both in small groups of lemurs) obtained ambiguous results [22,23], with no evidence found for social transmission despite obtaining positive results from using a more traditional ‘two-action control’ paradigm.

We investigate social information use and social networks in three species of sympatric tit (family Paridae) in two relatively isolated sub-populations. The ecology of these species makes them excellent candidates to study food-searching behaviour. Tits and chickadees are a family of passerines that mostly live in open woodland and feed on a mixed opportunistic diet, forming roaming mixed species fission–fusion flocks in the non-breeding season. A long history of captive studies has demonstrated that tits can be attracted to new food patches through local enhancement [24,25]. Recent wild studies have also shown that tits use social information when making habitat selection and dispersal decisions, and that this information use differs between individuals [26,27]. Fewer studies have examined social information and food patch discovery in wild tits and chickadees, but it appears that some species may also actively recruit flock-mates to food sites [28,29].

Here, we report the first application of NBDA to a large-scale experiment in wild animals. By measuring the association matrix of two wild sub-populations of tits and then recording arrival of individuals at novel food patches, we attempt to identify whether these populations use social information to find patchy food sites. We then ask whether individuals with differing network positions vary in their probability of finding new food sites after an initial discovery event, that is, whether some types of individuals differ in their access to information [30,31].

2. MATERIAL AND METHODS

(a) *Study area and population*

The study was conducted in two small areas of broadleaf deciduous woodland near Wytham woods, Oxfordshire (51°46' N, 1°20' W). These areas form part of a long-term project on great tits, and are surrounded by arable land [32]. We included the most common Paridae species in these woodlands: blue tit (*Cyanistes caeruleus*), great tit (*Parus major*) and marsh tit (*Poecile palustris*), all of which commonly forage together [33]. Birds were caught using mist-nets from October 2010 to January 2011, fitted with a unique British Trust for Ornithology metal leg ring, aged as juvenile or adult and sexed based on biometrics. Birds were also fitted with a plastic ring containing a uniquely identifiable passive integrated transponder (PIT) tag. While there was some movement between our study areas and the

main Wytham area, intensive mist-netting of birds throughout the 2010–2011 winter in Wytham woods meant that immigrants were also likely to be ringed and PIT-tagged.

(b) *Association matrix*

Sunflower feeders with two access points were fitted with radio-frequency identification (RFID) antennae (Francis Instruments Ltd., Cambridge) and installed at two locations in each area. The feeders were filled with food for 3 days and left empty for 3 days on a repeated cycle during January 2011 in Higgins Copse and from December to January 2011 in Cammoor/Stimpsons Copse. A data-logger at each feeder recorded the 15-s time block in which each bird visited and the individual's PIT-tag code. Combining the records from both locations at each area resulted in a total of 7790 records at Higgins Copse, and a total of 11 866 records at Cammoor/Stimpsons Copse. The total number of visits each individual made was used as a measure of both individual propensity to visit artificial feeders and overall site residency.

Associations were calculated between individuals using a 75 s moving time window, where an association occurred between two individuals when one individual visited the same feeder within 30 s on either side of the 15 s time block in which the other individual visited. Directionality of interactions could not be inferred, and a gambit of the group approach was used [34]. The results were also analysed using a 135 s time window and were robust to this variation. Twenty-four birds were seen fewer than five times and were excluded from the analysis to avoid a sampling bias that could affect edge weights. An association matrix of all other individuals was then constructed using a simple ratio index [35], whereby edges are scaled between 0 (never associated) and 1 (never observed apart). Two networks were generated (weighted and non-directional), one for Cammoor/Stimpsons and one for Higgins Copse.

An important concept in social network analysis is centrality, with measures reflecting the extent and manner to which individual nodes are connected to others. Here, we concentrate on two measures of centrality most appropriate to local enhancement [30]. ‘Eigenvector centrality’ extends the concept of degree centrality (the number and strength of a node's connections) by also measuring the relative connectedness of an individual's associates. ‘Betweenness centrality’ (unweighted) is a measure of an individual's role in connecting otherwise distinct groups of individuals, and is calculated by counting the number of shortest paths between nodes that pass through the focal node. Both centrality measures were calculated in the SNA package (v. 2.2-0) in the software program R (v. 2.12.2) [36].

(c) *Patch-discovery experiment*

Fourteen days after the end of the association matrix data collection, one sunflower feeder fitted with two RFID antennae was placed at a random location within each area to function as a new artificial food ‘patch’. A data-logger recorded patch arrival times for each individual. The same feeder design as that used for the social network was used to reduce any effect of neophobia, and feeder installation was undertaken at night to avoid inadvertently producing information about the site [37]. The artificial food patch was removed after 3 days, and the process repeated at a new randomly chosen site, with 7 days between trials. Four trials were completed at the Cammoor/Stimpsons Copse and three at Higgins Copse. In each of the seven trials,

different individuals first located the food patch; initial discovery appeared to show a trend towards great tits (four of seven) and first-years (six of seven).

In summary, the association matrix measured undirected relationships from multiple observations of flock composition, and the discovery experiment recorded individual order of arrivals to the food site (with no implied sociality)—the two should only be related if social behaviour is involved in patch discovery. While the methods of data collection for the association matrix and patch-discovery trials were superficially similar, they differed in two important ways. First, the association matrix was measured over a period of one to two months at four set locations, with the feeders as well-established food resources. For the patch discovery, one feeder was installed at a completely novel location such that no individual had any pre-existing knowledge. Second, visits were recorded for the association matrix over an extended period, with individual dyadic feeding co-occurrences accumulated over numerous feeding bouts. Timing of arrival was not differentiated, nor directionality implied. In the patch-discovery experiment, only the time of first discovery for each individual was measured, and group arrival was controlled for in the NBDA.

(d) Data analysis

Two alternative methods were used to ask whether the measured network predicted the pattern of patch discovery observed. NBDA seeks to identify social transmission by assuming that if social transmission is occurring, then the spread of behaviour should follow the patterns of associations between individuals, with the rate of social transmission being linearly proportional to the strength of association [18–20]. Second, network centrality parameters were used to try and identify individuals with a higher probability of both finding foraging patches and arriving at patches earlier (after the initial discovery).

Data were inputted using the NBDA code v. 1.2 [19] in R [36]. The time of first arrival at the artificial food patch for each individual was entered using the ‘time of acquisition diffusion analysis’ function. All individuals that discovered patches but were not in the social network were excluded from the analysis; this equated to 23 individuals at Higgins and 21 at Cammoor/Stimpsons. To allow for the possibility that some individuals were more effective ‘transmitters’ than others, weights were assigned to each individual of its total number of visits in each trial. This assumes that the rate of social transmission from individual A is proportional to the number of times they visited in the trial. Additionally, individuals who arrive at the new food patch together close in time may be recorded as transferring information, while actually simultaneously acquiring the knowledge as a group. This was accounted for by adding ‘ties’ between all individuals who first arrived at the food patch less than 10 min apart, with no possible information transfer permitted between tied individuals—this should provide a conservative but robust estimate [19].

Within one area, all trials were assumed to have similar rates of transmission and analysed together on the same network, though we allowed the asocial rate of acquisition to vary between each. Five individual-level variables were incorporated into the models: sex, age (first year per adult), species (marsh tit per great tit per blue tit), site where the individual was first caught (either of the two study plots, or two adjacent areas that are part of the Wytham woods

area) and propensity to use feeders (total number of visits by each individual at network feeders). All possible models were fitted.

Individual network centrality measures were analysed in two ways. First, a binomial family-generalized linear model in R was used to compare individuals who did or did not discover any food patches (where all trials were combined), in terms of sex, age, species, propensity to use feeders per site fidelity, eigenvector centrality and betweenness centrality. Second, a linear-mixed model in R was used to determine whether the order of first arrival of all individuals to the novel patches was predicted by the same explanatory variables detailed earlier. Individual identity and trial were included as random intercepts.

(e) Model selection procedures

For all analyses, Akaike’s information criterion (AICc; corrected for sample size) was used to select the best predictive model from a set of *a priori* models constructed from initial data exploration. The Δ AICc values were used to compare competing models with all models within Δ AICc of 2 having good evidence of fit [38]. AICc weights were also calculated to assess the probability that each model is the one with best K-L information (predictive power) [38]. For the general linear model of patch finding probability, we assessed the severity of any multicollinearity between coefficients by calculating the variance inflation factors using the car library in R. As all $\sqrt{\text{GVIF}}$ values were less than 2, we considered that there was no evidence for multicollinearity [39].

3. RESULTS

At Higgins Copse, 81 birds were included in the social network (a median of 40 records per bird, maximum of 294 records). At Cammoor/Stimpsons Copse, 73 birds were included in the network, with a median of 78 records per individual and a maximum of 1440 records. Eleven birds (7.1%) were observed in both study areas. Over both areas, 102 individuals were blue tits, 43 great tits and seven marsh tits (summary network statistics are detailed in the electronic supplementary material, table S1). At Higgins Copse, 68 per cent of individuals in the social network found at least food patches (median = 2 patches). In Cammoor/Stimpsons Copse, 59 per cent of individuals found one or more food patches (median = 2 patches; figure 1) (see the electronic supplementary material, figure S3 for Higgins Copse).

(a) Network-based diffusion analysis

A full model-fitting procedure was carried out on the network and all patch-discovery trials for each area. The most parsimonious models for each area contained social transmission and had a non-constant, declining rate of acquisition. Two models had good support at Higgins Copse, an additive model with no individual-level variables (AICcWgt = 0.37), and a multiplicative model incorporating site and species (AICcWgt = 0.30). The best model for Cammoor/Stimpsons Copse was multiplicative and included age, site and species (AICcWgt = 0.89). In both areas, there was little or no support for models containing purely asocial acquisition mechanisms (table 1). Parameter estimates are reported in the electronic supplementary material. In the top multiplicative

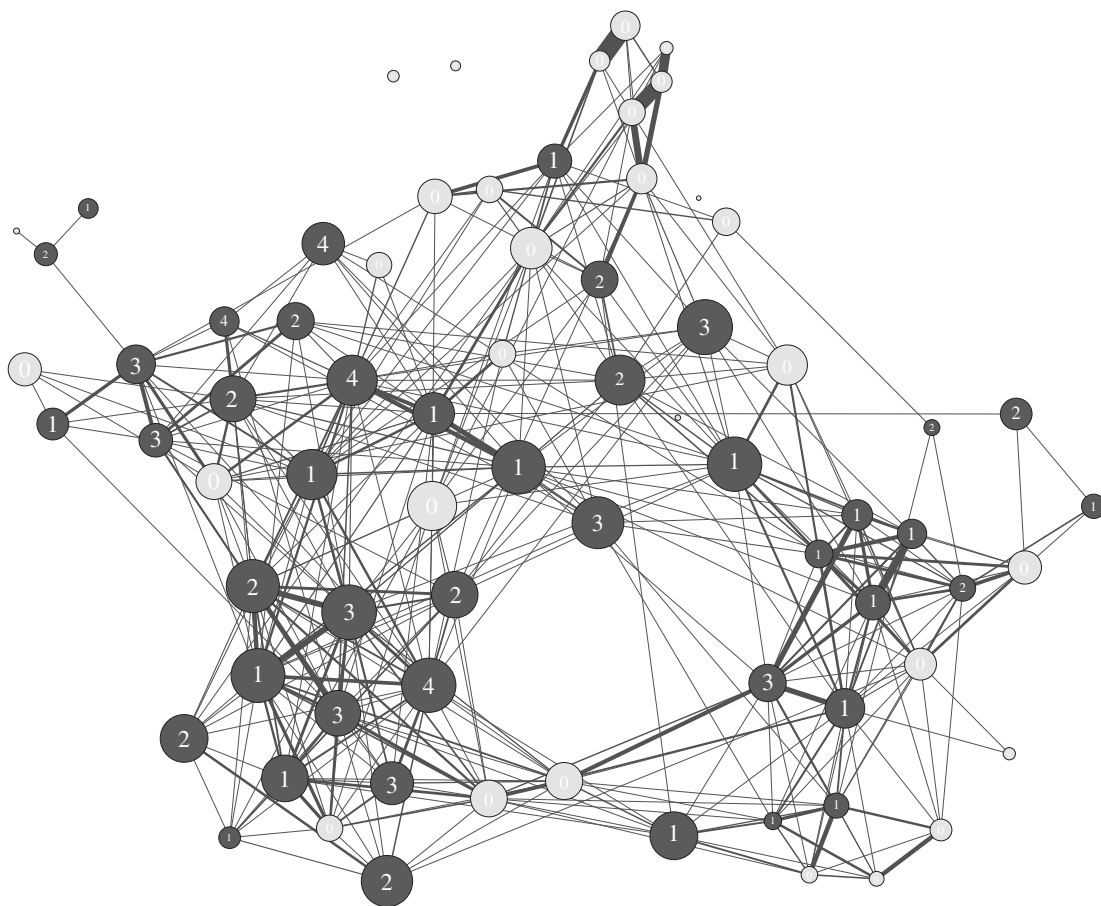


Figure 1. Social network for Cammoor/Stimpsons Copse, contrasting the network positions of individuals with differing patch-discovery success. Dark nodes represent individuals who found food patches; numbers inside nodes indicate how many patches found. Increasing node size indicates increasing eigenvector centrality, and edge (line) weight indicates association strength. Edges are thresholded to weights above 0.02.

Table 1. Summary of model selection statistics for NBDA performed in both areas. *si*, site of first capture; *sp*, species; *a*, age; *v*, feeder use; *se*, sex. Average association strength for Higgins = 0.027, Cammoor = 0.022. Additive models assume individual-level variables affect only asocial rate, in multiplicative models differences also influence social transmission [19]. Constant (*c*) baseline rate denotes rate of asocial discovery constant over time; non-constant (*n-c*) denotes systematic increases/decreases in rate of asocial discovery [20]. Transmission rate(s) denote rate estimate of social transmission per unit of connection relative to rate of asocial learning.

model type and rate	parameters	S.T. effect (s)	ΔAICc	AICcWt	cum. wt
<i>Higgins Copse—models with social transmission and asocial learning</i>					
additive, n-c, declining		0.01	0	0.37	0.37
multiplicative, n-c, declining	$P_{si} + P_{sp}$	0.01	0.33	0.30	0.67
<i>Higgins Copse—top asocial model</i>					
constant	$P_v + P_{si} + P_{sp}$	0	2.76	0.08	0.75
<i>Cammoor/Stimpsons Copse—models with social transmission and asocial learning</i>					
multiplicative, n-c, declining	$P_a + P_{si} + P_{sp}$	0.27	0	0.89	0.89
multiplicative, n-c, declining	$P_a + P_v + P_{si} + P_{sp}$	0.1	6.38	0.04	0.93
<i>Cammoor/Stimpsons Copse—top asocial model</i>					
n-c, declining	$P_a + P_{se} + P_{si} + P_{sp}$	0	23.39	0	1

model, great tits discovered patches at a rate of 1.01 higher than blue tits at Higgins Copse, and 1.65 times higher at Cammoor/Stimpsons Copse. Adults also discovered at a higher rate than first years at Cammoor.

(b) Network centrality

A generalized linear model was run using patch discovery (yes or no) as the binary response variable. At Higgins

Copse, the variable with the highest predictive power was betweenness centrality (AICcWgt = 0.13; figure 2a). However, there was also good support for total feeder visits, betweenness + eigenvector centrality, betweenness + sex and betweenness + age ($\Delta\text{AICc} = 1.00, 1.47, 1.62, 1.81$). Although the magnitude of difference between the best model and competing models was small, betweenness centrality was present in four of the five top models. At the Cammoor/Stimpsons Copse study area, the

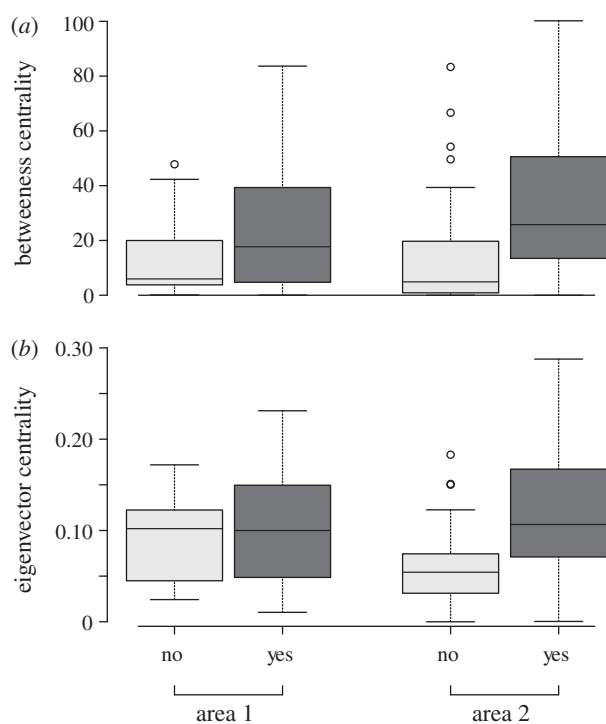


Figure 2. The relationship between two measures of network centrality and the patch-discovery success (no or yes) in area 1 (Higgins Copse); and area 2 (Cammoor/Stimpsons Copse). For a comparison of the observed and expected average network measures for each area, see the electronic supplementary material, table S1 and figure S2.

best model was eigenvector centrality ($AICcWgt = 0.21$; figure 2b). There was also good evidence for models containing eigenvector centrality + age ($\Delta AICc = 1.35$) and eigenvector centrality + betweenness centrality ($\Delta AICc = 1.89$), but eigenvector centrality was present in all of the top five models. The set of models with $\Delta AICc$ weights collectively totalling 95 per cent are detailed in the electronic supplementary material, table S6.

There was no relationship between network measures and the relative patch arrival time of individuals. Rather the total number of visits to the network feeder was the best predictor of arrival time ($AICcWgt = 0.27$ for Higgins Copse, $AICcWgt = 0.28$ for Cammoor/Stimpsons Copse). Models containing species + feeder visitations and age + feeder visitations also had strong support at both study areas (Higgins Copse: $\Delta AICc = 0.27$, 1.30, Cammoor/Stimpsons Copse: $\Delta AICc = 0.68$, 1.06). Therefore, birds that visited the initial network feeders more frequently were more likely to discover novel food patches earlier. Adults tended to arrive at patches earlier than birds in their first year, and marsh tits and great tits were earlier than blue tits.

4. DISCUSSION

Our study population of tits, as with many parid species, form loose roaming flocks of unrelated individuals in the non-breeding season, during which time they depend on clumped ephemeral food resources such as beech mast (seeds of *Fagus sylvatica*) [32]. Such resources vary in time and space, and while individuals may benefit from optimized search patterns and personal experience, we offer evidence using a novel social networks approach

that tits also use social information to locate new foraging resources in the wild. This is consistent with a long history of accumulated evidence from captive studies [24,25], and related studies on food-associated communication in Parids [28,29]. However, our results are novel because they demonstrate that the flow of this information is not random between individuals, but rather that it flows in accordance with the structure of the social network of the population.

NBDA found strong evidence for social transmission. Under this model of patch discovery, the first individual to find the food patch did so by chance (mediated by individual differences in searching behaviour), and subsequently arriving individuals discovered the patch by a combination of chance and receiving social information from connected individuals. Which set of individuals eventually found and exploited the patch therefore largely depended on the identity of those that were first to discover it.

While the study of the movement of information in social networks is rapidly growing in human studies, it is still in its infancy in the field of animal behaviour. NBDA [18–20] offers the most comprehensive model to date to identify information transmission in animal populations. This model uses the theory of directed social learning, i.e. that information is transmitted at different rates depending on association patterns [22,40]. Although supported by simulations and theoretical work [18,41,42], there has been very little empirical evidence for either NBDA or directed social learning. We suggest that the successful application of NBDA may depend on two factors: (i) a large enough sample size for there to be sufficient variation in association strengths and (ii) a social network of sufficient relevance to the type of information transferred [42]. Our study had both these factors, with two networks of 73 and 81 nodes and a network built using foraging associations.

In both our study areas, marked individual variation in patch discovery was observed. On average, 60 per cent of individuals found the novel foraging patches, and of the individuals who found new patches, most only found one or two. None of the morphological or behavioural characteristics we measured, including sex, species, age or site fidelity explained this variation, either in patch-discovery probability or in the number of patches found. Rather at both areas the best model for patch discovery identified was a network characteristic—eigenvector centrality at Cammoor/Stimpsons, and betweenness centrality at Higgins. These two network centrality measures are considered related to information and disease transmission [30,31], with central individuals having a ‘high susceptibility risk’. Few empirical studies have tested these hypotheses in animals, although Godfrey *et al.* [43] found that Gidgee skinks (*Egernia stokesii*) with a higher degree had a higher parasite load. Christley *et al.* [31] simulated epidemics on networks, and similarly found that centrality measures predicted risk of infection. Our study appears to extend this pattern to the transfer of social information.

It is interesting to speculate why the two areas appeared to highlight different centrality measures as important in social information transfer. Perhaps the differing topography of the two areas is implicated; in Higgins, birds appeared to roam freely, whereas in Cammoor (a long strip of woodland), birds might be more

restricted in their movements. In this case, information may be more likely to pass ‘grapevine’ style along immediate associates [30]. There was also evidence of a higher social transmission rate for Cammoor using NBDA. However, the exact mechanisms by which individuals transfer information in this study system are unknown. We suggest that basic mechanisms such as local enhancement (resulting from auditory and visual cues produced during feeding) would be sufficient to produce these patterns; yet, if deliberate food-contact calls occur, this could add an intriguing complexity to the relationship between the social network and patch discovery.

Finally, there was no relationship in this study between social network measures and the order of arrival of individuals at an artificial food patch, despite NBDA finding that the order and timing of arrival reflected associations between individuals. While these results are not necessarily contradictory (network centrality cannot predict a discovery order so highly dependent on the identity of first discoverer), centrality measures may be further obscured by additional factors. The NBDA model suggests that species and age differences in social information use may influence discovery rate. Another such factor may be personality; previous studies on parids have found a correlation between personality and patch discovery, with bold individuals arriving faster to new feeders [37,44]. Our study did not measure personality, so the effect of this variable is unknown. However, there is some evidence that personality is correlated with social information use in tits [45], and that personality may affect an individual’s social network position [46]. If so, social network position in our study may be correlated with both personality and patch discovery—this merits further study.

In conclusion, we report the successful use of NBDA to detect social information transfer in the wild, with closely associating individuals being more likely to transfer information about new food sites. Furthermore, we found that individuals with higher social network centrality measures have a higher probability of finding new food patches. Thus far, the weight of evidence in social network research has highlighted the negative impacts to being well connected (between and within communities), with such individuals suffering greater parasite loads and a higher risk of disease infection [31,43,47]. In contrast, our study suggests that the greater probability of receiving social information about new foraging patches may rather confer a benefit on better socially connected individuals.

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