Social learning mechanisms shape transmission pathways through replicate great tit social networks

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Abstract

The emergence and spread of novel behaviours via social learning can lead to rapid population-level changes whereby the social connections between individuals shape information flow. However, behaviours can spread via different mechanisms and little is known about how information flow depends on the underlying social learning rule individuals employ. Here, comparing four different learning mechanisms, we simulated behavioural spread on replicate empirical social networks of wild great tits and explored the relationship between individual sociality and the order of acquisition of seeded behaviours. Our results reveal that, for learning rules dependent on the sum and strength of social connections to informed individuals, social centrality was strongly related to the order of acquisition, with more social individuals adopting new behaviours faster than less social individuals. However, when behavioural adoption depends on the ratio of an individuals' social connections to informed versus uninformed individuals, social centrality was not related to the order of acquisition. Finally, we show how specific learning mechanisms may limit behavioural spread within networks. These findings have important implications for understanding whether and how diverse behaviours are likely to spread across social systems, the relationship between individuals' sociality and behavioural acquisition, and therefore the costs and benefits of sociality.

Introduction

Social learning, in which individuals learn from others, is widespread in the animal kingdom, and enables individuals to acquire novel behaviours facilitating phenotypic change (Heyes 1994; Hoppitt and Laland 2013; Whiten 2021). Socially-induced changes in behaviour can spread through a population and social networks provide the pathways along which behaviour can spread (Hasenjager et al. 2021). Research increasingly shows how the structure of social networks and individual sociality together can influence information flow (Voelkl and Noë 2008; Aplin et al. 2012; Kulahci et al. 2016; Romano et al. 2018). However, information can spread via various social learning mechanisms (Nunn et al. 2009; Firth 2020; Cantor et al. 2021) and we know surprisingly little about how the relationship between sociality and information flow depends on the social learning mechanisms at play.

By definition, the social spread of behaviour to a focal individual requires contact with at least one knowledgeable individual. Frequently, it is intuitively assumed that the extent (i.e. number and duration) of social contacts to knowledgeable others predicts the likelihood of adoption (Hasenjager et al. 2021). In this way, behavioural spread is predicted to follow a similar logic to the transmission

of diseases. However, in contrast to disease spread, individuals may employ 'social learning rules' where they can actively shape how to act on acquired novel information. For example, for more costly behaviours such as the usage of a novel food type, an individual may only change its behaviour after the majority of its social contacts consumes the novel food. Consequently, behavioural spread may require exposure to multiple sources (rather than just one) and depends on the ratio of connections to both informed and uninformed individuals (rather than just the connections to informed others) (Centola and Macy 2007; Guilbeault et al. 2018; Firth et al. 2020). Therefore, the type of behaviour considered and its underlying learning rule can fundamentally influence whether and how behaviour spreads through a social network (Centola and Macy 2007; Firth et al. 2020).

In fact, previous studies have revealed several social learning strategies that suggest a range of different underlying social learning mechanisms (Hoppitt and Laland 2013; Kendal et al. 2018). For instance, an increasingly-reported learning mechanism is conformist learning in which individuals disproportionally adopt the behaviour performed by the majority of their social connections (Pike and Laland 2010; Van de Waal et al. 2013; Aplin et al. 2015; Danchin et al. 2018). Further, individuals often only learn from specific individuals (e.g. depending on status (Canteloup et al. 2020), relatedness (Wild et al. 2019) or conspecifics (Farine et al. 2015)) or adopt behaviours only once the social connections to informed others surpass a certain threshold (Rosenthal et al. 2015).

To date, research on social learning in animals usually assumes that more social individuals (i.e. with more social connections and central network positions) have a higher probability to adopt new behaviours because they are more likely to hold connections to knowledgeable others compared to less social individuals (Aplin et al. 2012; Claidiere et al. 2013; Kulahci and Quinn 2019). This link between individual sociality and behavioural adoption can be expected if the learning rule depends on the sum and strength of social connections to knowledgeable others. However, this relationship may change when learning rules rely on both the connections to informed and uninformed individuals (Firth 2020; Firth et al. 2020). For instance, in the case of conformist learning, we may expect that the most social individuals will be less likely to adopt (because it may take longer until the majority of their social connections becomes informed). Hence, predictions of how individual sociality relates to the probability of acquiring novel behaviour, and the resulting transmission pathways, can change fundamentally depending on the social learning mechanism at play.

Examining and comparing the transmission pathways of behaviours that follow different learning mechanisms in the wild is challenging, if not impossible. Therefore, research investigating the relationship between social structure and information flow often simulates behavioural spread (Voelkl and Noë 2008; Nunn et al. 2009; Cantor et al. 2021; Evans et al. 2021). However, only a handful of studies have considered the impact of different social learning rules (Nunn et al. 2009; Cantor et al. 2021). In addition, behavioural simulations are often performed on artificial social networks with pre-defined structure and size (Voelkl and Noë 2008; Nunn et al. 2009; Cantor et al. 2021; Evans et al. 2021; but see: Naug 2008; Romano et al. 2018), and may thus represent unrealistic social structures, failing to capture the social behaviour observed in real animal social networks. Further, for behavioural spread, an individual's social connections at a relatively small temporal and spatial scale will predict subsequent transmission (Somveille et al. 2018). Thus, it is important to study real animal social networks on a meaningful spatiotemporal scale to better understand whether and how different types of behaviours spread through social networks.

In this study, we explore by simulation how novel behaviours, transmitted according to different social learning mechanisms, spread through replicated empirical social networks of great tits (*Parus major*).

Great tits are small songbirds that forage in mixed-species flocks during winter (Ekman 1989) and frequently use social information (e.g. to find novel food (Aplin et al. 2012; Firth et al. 2016), to access novel food (Aplin et al. 2015), prey avoidance (Thorogood et al. 2018; Hämäläinen et al. 2020)) which makes them an ideal study species. Here, we create weekly social networks from the birds' foraging associations at distinct locations to capture the social structure at a relatively small spatiotemporal scale. Subsequently, we simulate behavioural spread on these weekly, local, networks using four different social learning mechanisms. The first learning mechanism follows the omnipresent concept which assumes that the probability of adopting depends on the number and strength of connections to informed individuals (i.e. simple adoption rule). The other three learning mechanisms imply more complex adoption rules: (i) a threshold rule, (ii) a proportion rule, and (iii) a conformity adoption rule. Here, the probability of adopting the novel behaviour depends on: (i) the connections to informed individuals surpassing a given threshold; (ii) the proportion of connections to informed individuals (rather than the sum); and (iii), the behaviour that the majority of connections performs. We then investigate the transmission pathways by comparing how the social behaviour of individual great tits relates to the order in which they acquire novel behaviour under the four different social learning rules.

Individual variation in sociality - the number of social connections and centrality within the network - may influence the access to information and thus behavioural adoption. We infer individuals' sociality by extracting three commonly used weighted social network metrics: the weighted degree (i.e. sum of their social connections to others), weighted clustering coefficient (propensity for their associates to be associated with one-another), and weighted betweenness (propensity to act as a 'bridge' within the network). We predicted that the relationship between individual sociality and behavioural adoption would differ depending on the social learning mechanism. Specifically, if the likelihood to adopt a behaviour depends on the number and strength of connections to informed individuals such as in the case for the simple and threshold rule, we predicted that more social individuals (i.e. high degree and betweenness and low clustering coefficient) should be faster in adopting the novel behaviour due to being more likely to be connected to at least one informed conspecific. In contrast, if the likelihood of adopting a behaviour depends on the ratio of an individual's informed and uninformed connections, such as in the case for the proportion or conformity rule, we expected that less social individuals (i.e. low degree and betweenness and high clustering coefficient) should be faster in adopting the novel behaviour because the majority of their social connections should become informed faster.

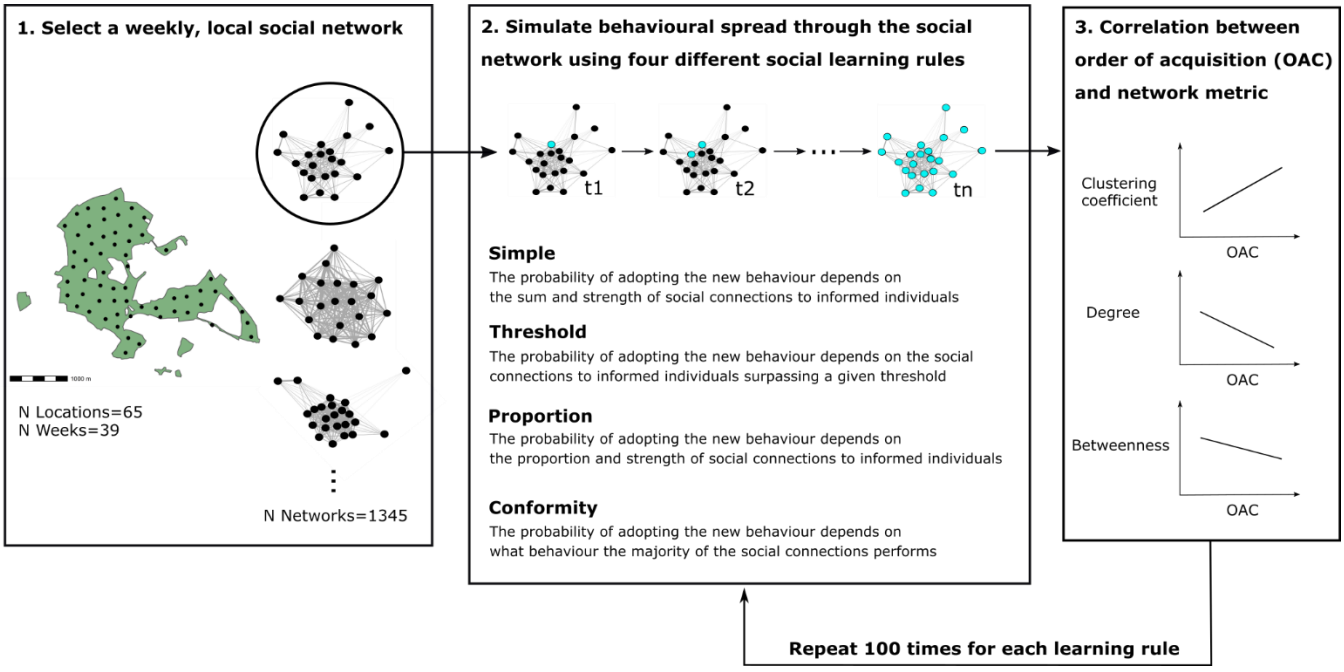

Figure 1. Overview of the simulation procedure. First, a weekly social network of one of the 65 locations (shown as black dots) in the study site was selected. Second, behavioural spread was simulated on the selected network using four different social learning rules (i.e. simple, threshold, proportion, conformity). The starting point (i.e. the first individual performing the new behaviour) was randomly chosen. Then, at each timestep (t1-tn), a naïve individual became knowledgeable with a given probability of the adoption event being from social learning (dependent on the social learning rule at play; see methods for further details) until all individuals in the network were knowledgeable. Third, we calculated a correlation coefficient (Spearman's rank correlation coefficient) between three individual social network metrics (i.e. weighted clustering coefficient, weighted degree and weighted betweenness) and the order (i.e. timestep) in which individuals acquired the novel behaviour. Finally, we repeated this process 100 times for each of our 1345 weekly, local social networks.

Results

The data in this study were simulated across 1345 empirically-derived social networks, inferred from recordings of 1764 individual great tits at 62 feeder locations across 39 weekends and 3 years. Social networks varied in size (right skewed distribution towards smaller networks, see Figure S1) and consisted of an average of 21.7 individuals (min:10, max:77, sd=10.0).

Relationship between individual social behaviour and order of acquisition

Simulating behavioural spread under four different social learning rules revealed different transmission pathways across social networks. For both the simple and the threshold rule, the weighted clustering coefficient was positively related to the order of acquisition, with more clustered

individuals adopting the seeded behaviour later than less clustered individuals (Figure 2). Weighted degree and betweenness were negatively related to the order of acquisition. Thus, individuals with higher weighted degree and weighted betweenness adopted the novel behaviour faster than individuals with a lower weighted degree and betweenness (Figure 2).

In addition, we show the relationship between mean individual network metrics and the standardized order of acquisition across all network sizes (Figure S2). For the simple learning rule, the relationship between network metric and order of acquisition only changed when the majority of individuals in a network had already adopted the behaviour (with approximately 75% of individuals knowledgeable; Figure S2). Behavioural spread under the threshold rule showed a small 'hump' shortly after the start of behavioural spread (Figure 2, S2), before the relationship between mean network metric and order of acquisition increased (for weighted clustering coefficient) or decreased (for weighted degree and betweenness, Figure 2, S2). This 'hump' indicates that initially more social individuals (i.e. lower weighted clustering coefficient, higher weighted degree and betweenness) adopted the behaviour first, before the relationship between mean network metric and order of acquisition turned (Figure 2, S2). In contrast to the simple and threshold rules, there was little or no relationship between individual social network metrics and the order of acquisition under both the proportion and conformity learning rules (Figure 2, S2).

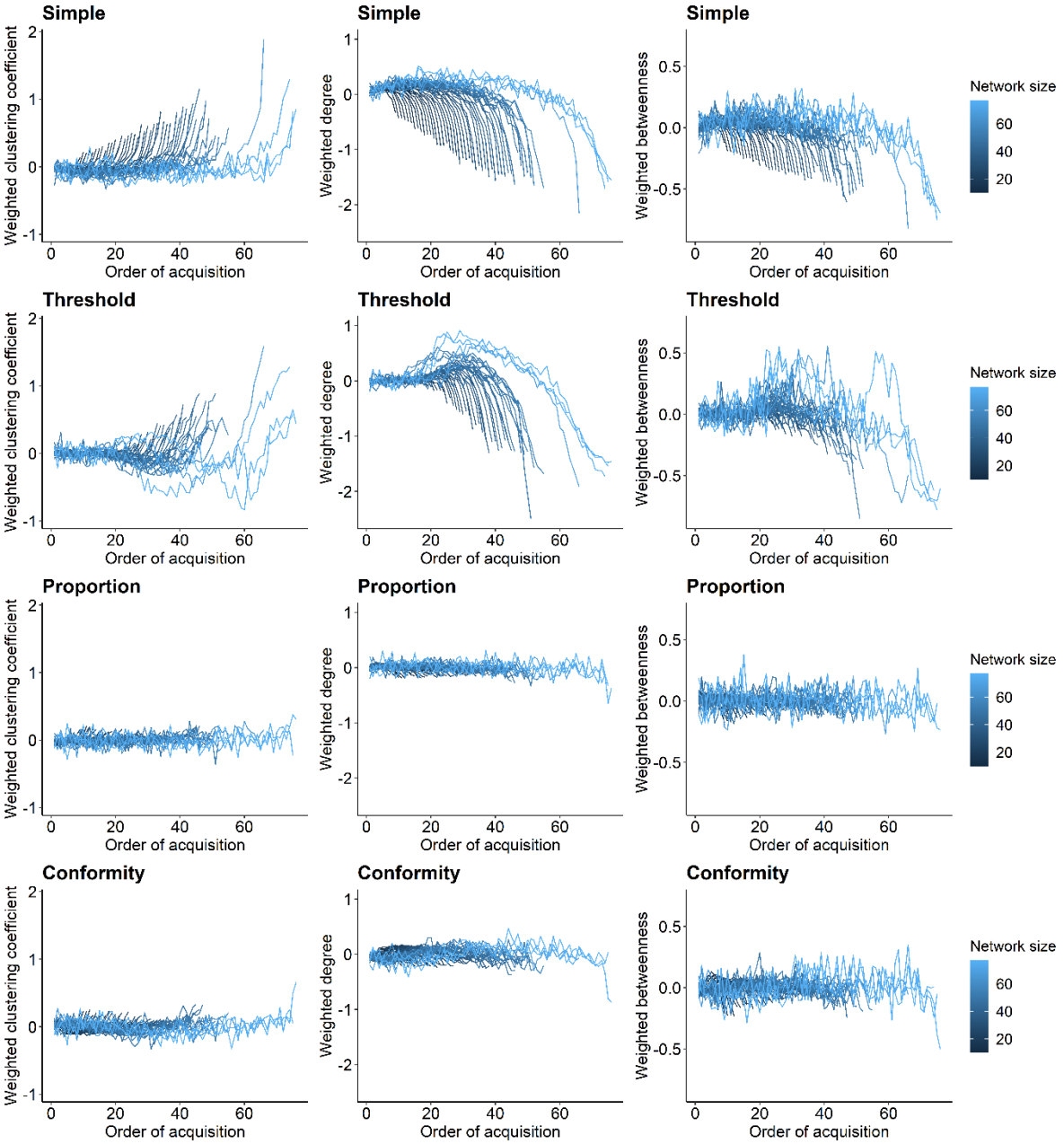

Figure 2. Relationship between individual network metric and the order of acquisition for each social learning rule. Each column shows a different network metric (left to right: weighted clustering coefficient, weighted degree and weighted betweenness). Each row represents one of the four spreading rules (top to bottom: simple, threshold, proportion and conformity). Lines plot the average network metric for each order of acquisition and network size from the 100 simulations of each network. Colour represents network size with darker colour indicating smaller networks.

Social network size and behavioural spreading

Assessing the relationship between each individual's network metric and the order of acquisition across all social networks and simulation runs, revealed substantial variation in relationship strength (Figure 3). Across network metrics, there were on average the strongest correlations under the simple

rule (Figure 3), and coefficients for the threshold, proportion and conformity model were lower. The mean average network metric for later adopters (i.e. larger values for the order of acquisition) increased (for weighted clustering coefficient) and decreased (for weighted degree and betweenness) with increasing network size under the simple and threshold rule (Figure 2). The correlation between individual sociality and their order of acquisition were predicted by network size (Figure 4, Table S1). For the simple and threshold model, behavioural spread on larger networks led to more positive (for weighted clustering coefficient) and negative correlations (for weighted degree and betweenness) between individual network metric and order of acquisition (Figure 4, Table S1). The predicted effects of network size on mean correlation coefficient inferred under the proportion and conformity rule suggest contrasting directions (Figure 4, Table S1).

Social spread under the threshold rule may be limited in smaller networks (see also section on *'Probability of social* spread') causing the reduced correlations between individual network metrics and order of acquisition. Repeating the simulations under the threshold rule, but with a threshold location proportional to network size (in contrast to a fixed threshold location across all networks, see methods), revealed no strong change in the mean individual network metric and order of acquisition with increasing network size (Figure S3). Similar patterns were detected when repeating simulations under the threshold model, with a threshold location smaller (a=3, Figure S4) and larger (a=7, Figure S4) than the location set for the main analyses. When using a smaller threshold, the negative relationship between mean network metric and order of acquisition was already evident in smaller networks (Figure S4). However, when setting a larger threshold, the relationship between network metric and order of acquisition did not reveal a distinct direction (Figure S4). Further, for the threshold rule, the limited ability of social spread and the prominent 'hump' at the initial stages of the spread, may have led to overall low correlation coefficients between individual network metrics and order of acquisition (Figure 3), even though the relationship between mean network metric and order of acquisition (Figure 2) indicated otherwise.

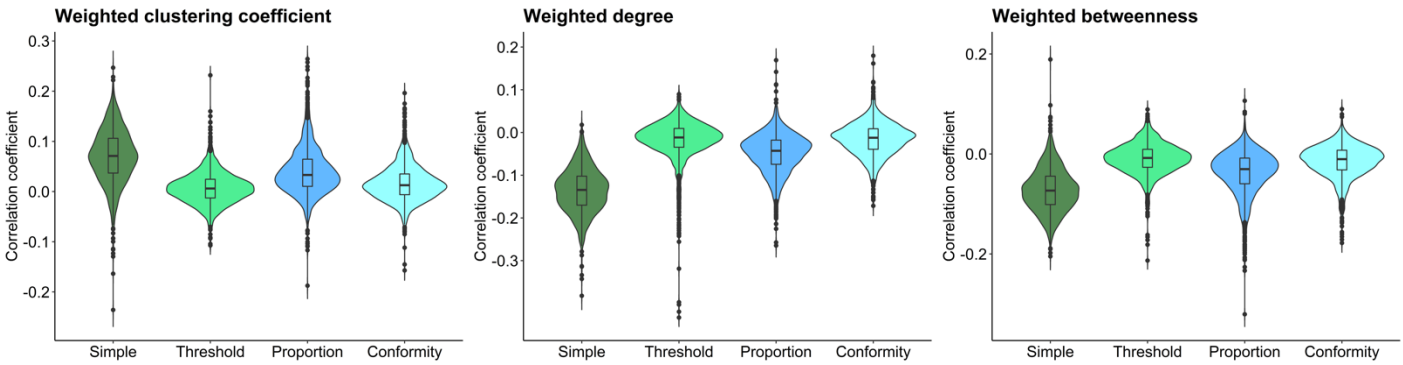

Figure 3. **Distribution of average correlation coefficients for each social learning rule and network metric.** Violin and boxplots show the distribution of the average correlation coefficients across 100 simulations from each network for each of the four social learning rules (i.e. simple, proportion, conformity and threshold). Each plot shows one of the individual network metrics (weighted clustering coefficient, weighted degree, weighted betweenness).

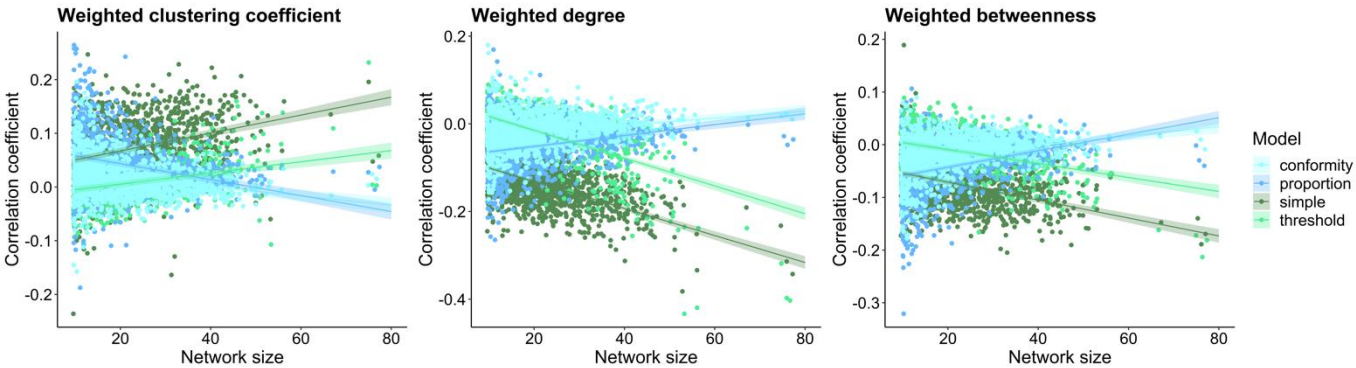

Figure 4. **Relationship between correlation coefficient and network size across the four social learning rules.** Each plot shows one of the individual network metrics. Average correlation coefficients across each 100 simulations per network are plotted as dots, lines represent the effects generated from linear mixed-effect models (LMM) and ribbon represents the 95% CI (see Table S1 for model results).

Probability of social spread

For each spreading simulation, an initial random individual was seeded with the behaviour, and then at each timestep a new individual adopted the seeded behaviour, whereby each time each individual has a probability of adopting the behaviour through either asocial learning (which is constant across all individuals with no connections to informed individuals) or through social learning which ranges from 0 (asocial acquisition only, i.e. an individual has no connections to informed individuals and cannot socially learn the behaviour under the set learning rule) to 1 (obligate social learning, i.e. when an individual is well connected to informed individuals so the individual will only learn under the set learning rule).

Across the different social learning mechanisms, the average probability that an individual socially adopted the seeded behaviour increased with increasing timestep (i.e. order of acquisition). This is because with an increasing number of individuals becoming knowledgeable, the probability to be connected to informed others and thus to reach the set learning criterion increased (Figure 5). However, under certain spreading processes, social learning was limited (Figure 5). This was particularly the case for smaller networks when transmission followed the threshold rule. For instance, in networks consisting of less than approximately 20 individuals, the set threshold for socially adopting the behaviour was almost never met (average probability of social learning is close to 0; Figure 5 Threshold). Repeating the simulations under the threshold rule, but with a threshold location proportional to network size, removed these patterns (Figure S5). For the conformity rule, larger networks limited social spread, but only at the initial phase of transmission (Figure 5 Conformity). In larger social networks, individuals have on average more social connections and thus at the initial stages of behavioural spread, it is less likely that the majority of an individual's social connections are already informed.

Behaviours spreading under the simple and proportion rule, on average always had a non-zero probability to socially spread (Figure 5). This is the case because both the simple and proportion rule, did not require to surpass a given threshold (such as set for the threshold rule or reaching the majority

of an individual's connections as set for the conformity rule). Therefore, one connection to an informed conspecific was sufficient for the seeded behaviour to spread socially.

For both the simple and threshold model, the mean probability of social spread initially increased but then dropped towards the later adoptions (Figure 5). This may be caused by a few individuals that are not well connected in the social network, and thus have in general a low probability to socially learn under the simple and threshold rule. For instance, some great tits may only be connected to one other individual and thus, even if the number of knowledgeable individuals in the social network increases over time, it is very unlikely to reach the required threshold for social learning. For the proportion and conformity rule, the average probability of social learning peaked after a given percentage of individuals being knowledgeable (Figure 5).

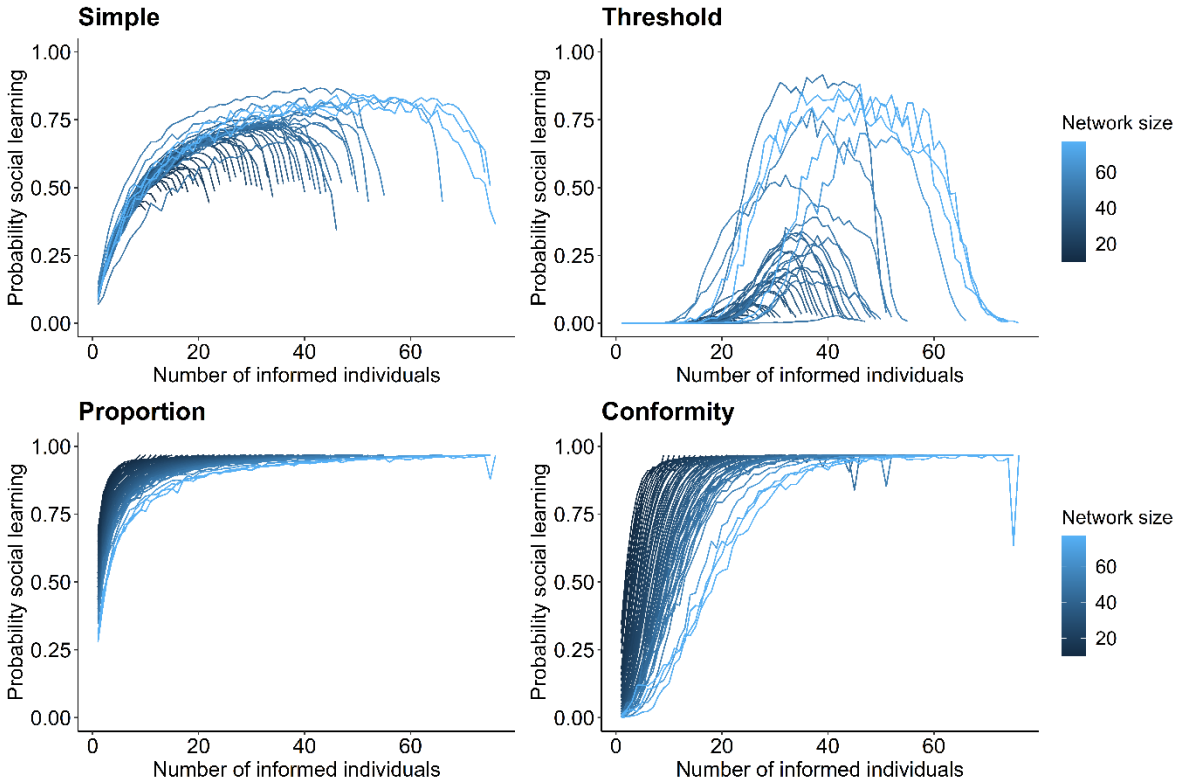

Figure 5. Relationship between the probability of an individual socially adopting the seeded behaviour and the number of informed individuals within the network. Panels show the results for each of the four social learning rules (simple, threshold, proportion, conformity). The x-axis describes the number of informed individuals within a social network. The simulations are set so that at each timestep one individual changes its status from 'uninformed' to 'informed'. At each timestep a new individual adopted the seeded behaviour, whereby each time each individual has a probability of adopting the behaviour through social learning (y-axis) given the set learning rule. Lines plot the average probability for each timestep and network size from the 100 simulations. Colour represents network size with darker colour indicating smaller networks.

Discussion

We show how the underlying social learning rules individuals employ strongly influences the transmission pathways of behaviours across social networks derived from real-world data. Under learning rules that rely purely on the extent of social connections to informed others, we found that more social individual great tits were likely to adopt the seeded behaviour faster, in line with common expectations of the benefits of sociality for gaining information. However, if the likelihood of adopting a behaviour depended on the ratio of connections to informed and uninformed others, such as conformist learning, social network centrality was not strongly related to the order in which individuals acquired the seeded behaviour. Notably, this contrasts with the widely proposed prediction that more social individuals may be more likely to adopt new information. Thus, our results show how the relationship between individual sociality and information acquisition can change fundamentally with the type of social learning mechanism at play. Finally, we reveal that the probability of social spread under certain social learning rules is predicted to be limited in certain real-world settings, particularly in networks of a very small or large size.

Individuals differ in the quantity and quality of social connections to others which impacts several aspects of life history (McDonald 2007; Formica et al. 2012; MacIntosh et al. 2012; Farine and Sheldon 2015; Alberts 2019; Beck et al. 2021), including the social transmission of information (Aplin et al. 2012; Kulahci and Quinn 2019). Generally, individuals that hold many social connections to others, and occupy central network positions, are expected to be more likely to acquire information (Hoppitt and Laland 2011; Aplin et al. 2012; Claidiere et al. 2013; Kulahci et al. 2016). In line with these assumptions, we find that more social great tits (i.e. with a lower clustering coefficient, higher degree and betweenness) were more likely to adopt the seeded behaviour faster when the underlying spreading mechanism depended on the extent of connections to knowledgeable others (Figure 2). However, when rules were more complex, for example when behavioural adoption depended on the ratio of connections to knowledgeable and naïve individuals, sociality was not strongly related to the order of acquisition (Figure 2), matching the expectations from studies on complex contagions in humans (Guilbeault et al. 2018). These findings suggest that under certain spreading mechanisms, the extent of social connections can reduce social spread. Thus, the concept that more social and central individuals are especially important in acquiring and subsequently spreading information (Kulahci and Quinn 2019) cannot be generalized across different types of behaviours, and may even lead to erroneous conclusions. For instance, if no evidence is found that individual sociality is related to the probability of behavioural adoption, one might be led to conclude the absence of social learning where, in fact more complex social learning rules may be in operation. Therefore, our findings have important consequences for our understanding of the relationship between sociality and behavioural acquisition, and also for what may constitute an 'optimal' social structure for efficient social transmission (Pasquaretta et al. 2014; Romano et al. 2018).

Furthermore, our results have implications for our understanding of the costs and benefits of individual sociality. While increased access to information is one of the postulated key benefits of sociality, simply holding more connections to others may in fact hinder the adoption of novel behaviours under certain social learning rules. For instance, if a novel behaviour follows a conformist learning mechanism, highly social individuals with lots of connections may be exposed to the new behaviour sooner than less social individuals because they are more likely to be connected to at least

one informed conspecific, but despite this will be less likely to adopt the novel behaviour if it requires the majority of their social connections to become informed first. Hence, considering the social learning mechanism at play, and differentiating between access to information and behavioural adoption (Carter et al. 2016), are crucial for our understanding of the potential costs and benefits of individual sociality.

Examining behavioural innovation and its subsequent spread in nature is challenging (Whiten and Mesoudi 2008; Klump et al. 2021). This is because new behaviours are often only detected once the majority of individuals in a population are already knowledgeable. Alternatively, behavioural innovations may occur much more frequently but remain undetected if the behaviour does not spread far (e.g. because the behaviour is mechanically challenging for individuals (Gajdon et al. 2006) or when the carryover of older, outdated behaviour hinders the spread of novel and more adaptive behaviours (Aplin et al. 2017; Barrett et al. 2019)). Here we used simulations on real-world empirical networks, and demonstrate that the ability of a behaviour to socially spread depends on its underlying social learning mechanism, which is consistent with other studies that investigated different spreading processes (Nunn et al. 2009; Cantor et al. 2021). Across the four models, the probability that individual great tits socially adopted the seeded behaviour increased with increasing timestep (Figure 5). This is expected as at each timestep in simulations a new individual becomes knowledgeable and remains in this state thereby increasing the number of knowledgeable individuals within the network. However, social transmission under certain social learning mechanisms was limited. For instance, behaviours that needed to surpass a given threshold of social connections to informed others (i.e. threshold or conformity rule) required more asocial learning events in the initial spreading phase to be able to subsequently transmit via social learning (Figure 5). In contrast, for the simple and proportion rules, social transmission was always possible, even in the initial spreading phase (Figure 5). This demonstrates that some behaviours may have a much higher likelihood to spread socially, whereas other behaviours, following more complex processes, may rely on a larger extent of asocial learning events or social reinforcement. Therefore, the majority of empirical research on behavioural spread in animals may in fact examine more simple social transmission processes (because they are easier to detect and observe) which may bias our picture of the existing social learning mechanisms of animals and behavioural innovations.

We found that network size impacted behavioural spread across the four transmission models. The strength of the relationship between individual network metric and the order of acquisition increased with increasing network size under the simple and threshold rule (Figure 4). The weaker correlation between individual sociality and order of acquisition in smaller networks might be caused by the relatively reduced likelihood of social spread (Figure 5). For instance, for the threshold rule, individuals in larger networks have an overall higher number of social connections (compared to individuals in smaller networks) which facilitates reaching the set threshold for social learning and thus increases the likelihood of social spread. This is supported by our results when simulating spread using different threshold values (see Figure S4). Past studies have investigated behavioural spread on relatively large networks (using simulations: (Voelkl and Noë 2008; Nunn et al. 2009; Cantor et al. 2021; Evans et al. 2021) or natural observations: (Allen et al. 2013; Aplin et al. 2015)). However, for behavioural spread, social connections at a relatively small spatiotemporal scale may predict an individual's decision to adopt a novel behaviour. Our findings that network size can impact behavioural spread thus have important consequences for our understanding of the influence of wider society structure on when and where behaviours may emerge, and how to interpret empirical results. As such, it is important to

improve our understanding of the factors that give rise to different social network sizes and shapes and subsequently influence information flow. For instance, spatiotemporal variation in environmental features (such as the availability and distribution of resources) may influence population densities and subsequently local social network size, and as such facilitating or hindering social spread.

Our study suggests further questions for future research. First, our models assume that each individual adopts a seeded behaviour under the same 'learning rule'. However, individuals may differ in the extent of social information use, which is often context and state-dependent (Rendell et al. 2011; Penndorf and Aplin 2020). For instance, dominance rank (Krueger et al. 2014) and sex (Aplin et al. 2013) have been shown to be related to variation in social information use. Further, individuals may only copy behaviour from certain individuals, based on familiarity or kin (Kavaliers et al. 2005; Boogert et al. 2018). Thus, future simulation or empirical studies could explore how heterogeneity in learning rules impacts information flow. Second, using simulations did not allow us to test changes in the social network resulting from behavioural adoption: individuals may occupy more central social network positions once performing a new behaviour (Kulahci et al. 2018; Kulahci and Quinn 2019). This can be the case if individuals preferentially associate with knowledgeable others (Kulahci et al. 2018), or if individuals change their behaviour in response to information acquisition which can also lead to an increased in social connections (Kulahci and Quinn 2019). Such dynamics are not reflected in our study, and would require the investigation of natural behavioural spread ideally under experimental conditions in the wild. Third, our models assume that once individuals become 'informed', they cannot return to an 'uninformed' state. In natural conditions, however, individuals may return again to an 'uninformed' state if the novel behaviour was not rewarding. Future studies incorporating these aspects could provide further new insights into the patterns of social transmission and its link to sociality.

From copying the majority (Van de Waal et al. 2013; Aplin et al. 2015; Danchin et al. 2018) to learning from specific tutors (Wild et al. 2019; Canteloup et al. 2020), individuals use a large range of different learning strategies (Hoppitt and Laland 2013; Kendal et al. 2018). While, an increasing number of studies show how social network structure can influence social transmission (using simulations: (Voelkl and Noë 2008; Romano et al. 2018; Evans et al. 2021) and empirical data: (Naug 2008; Firth et al. 2016; Romano et al. 2018)), our research highlights the importance of the underlying social learning mechanism in shaping the transmission pathways across social networks. We demonstrate that the common assumption that sociality is linked to a higher likelihood in acquiring information and adopting new behaviours cannot be generalized for behavioural spread in real world networks. This also sheds new light on our current understanding of the costs and benefits of individuals sociality and asks to focus more on the social learning mechanism at play, and to differentiate between access to information and behavioural adoption. In addition, we reveal that social transmission can be limited under certain adoption rules (such as the threshold rule), and social networks of particular size. Our findings thus have important consequences for our understanding of whether and how behaviours spread across different social networks, and subsequently the establishment of traditions and cultures. Further, differences in spreading mechanisms alter predictions of what may constitute optimal social structures for the transmission of information, and how selection may act on sociality.

Materials and methods

Study system

The empirical data used in this study were collected over three years (December 2011 – March 2014) in a population of great tits located in Wytham Woods, Oxfordshire, UK (51° 46' N, 01° 20' W, approx. 385ha). Great tits are hole-nesting songbirds that form socially monogamous pairs, and establish territories during the breeding season (March – June). During the non-breeding season (September – February), great tits forage with other species in loose foraging flocks (Hinde 1952; Ekman 1989) and frequently use social information (Aplin et al. 2012; Farine et al. 2015; Firth et al. 2016).

The woodland contains 1017 nest-boxes hosting breeding great tits and 65 bird feeders that were deployed during the winter months in an evenly spaced grid (see Figure 1). Each feeder contained two access holes of which both were equipped with radio-frequency identification (RFID) antennas. For the duration of the study, the feeders collected data on the bird visits from pre-dawn Saturday morning until after dusk on Sunday evening. In each of the three winters, the feeders were in place from December to February and the location of each feeder was consistent.

All birds were caught in either a nest-box or a mist-net and were fitted with a uniquely numbered metal leg ring (British Trust for Ornithology). In addition, each bird was also fitted with a uniquely coded passive integrated transponder (PIT) tag enclosed in a plastic ring fitted to the other leg. This allowed us to record each visit of a PIT-tagged bird when it came close to the RFID antenna of a feeder (approximately 3 cm). At every detection, the bird's unique PIT tag code, and the date and time were saved to a data logger.

Social networks

We created social networks based on the foraging associations of PIT-tagged great tits at each feeder and each of the 13 weekends across the three years. We created temporal and locally restricted networks because we wanted to generate a large number of different social networks (rather than just one network from the whole population) and because we expect networks from such a small time-window (i.e. one weekend) to be most meaningful in capturing the social connections relevant for the spread of a novel behaviour (i.e. social networks spanning a large time-window may contain many connections not relevant at the time a novel behaviour was introduced).

An "association" was defined as two birds foraging together within the same flock. Flock membership was identified using Gaussian Mixture Models (Psorakis et al. 2012; Psorakis et al. 2015) from the R package "asnipe" (Farine 2013). This method detects events of increased feeding activity in the spatio-temporal data, clusters these into non-overlapping gathering events (i.e. flocking events), and assigns each individual detection to the event it most likely belonged to. This provided us with information about which individuals co-occurred in the same flock (Psorakis et al. 2012; Psorakis et al. 2015). From the pattern of co-occurrences, we then inferred the strength of associations for each dyad. We calculated association strength using the simple ratio index (SRI, (Cairns and Schwager 1987)). The SRI describes the proportion of observations of two individuals in which they were seen together, ranging from 0 (never observed in the same flock) to 1 (always observed in the same flock). We created undirected social networks with edges weighted by the SRI for each sampling weekend (in total: 39 weekends across 3 years) and feeder location (in total: 65).

For each of the weekly, local networks, we then inferred for each individual three social network metrics: the weighted clustering coefficient (following (Barrat et al. 2004)), the weighted degree and the weighted betweenness. Network metrics were calculated using the R package 'igraph' (Csardi and Nepusz 2006) and describe respectively: how tightly a focal individual is clustered to form distinct cliques, the total interaction rate for a foal individual with all other individuals, and the number of shortest paths from all individuals to all other individuals that pass through the focal individual. Last, we standardized the individual metrics within each network to allow comparisons between networks. Social networks including less than ten individuals and exhibiting no variation in individual network metrics were excluded from further analyses resulting in the final sample size of 1345 social networks (generated from 62 locations).

Simulations

On each network, we simulated behavioural spread using four different social learning rules, as described in (Firth et al. 2020), using the R package 'complexNBDA'. A brief explanation is provided below but full detailed description of each can be found in Firth et al. 2020 and all resources are freely available at https://github.com/whoppitt/complexNBDA.

(1) Simple rule. This transmission rule follows the logic of the classic NBDA framework. Here, the probability that an uninformed individual adopts a new behaviour is directly dependent on the number and strength of connections to informed others that are currently displaying the behaviour. Consequently, the more connections to informed individuals, the more likely an individual is to adopt the behaviour. The social transmission strength s was set to 1.

(2) Threshold rule: This transmission rule assumes that the probability of adopting a new behaviour remains low until an individual's social connections to informed individuals reaches a given threshold. We set the threshold value a to 5 for all networks. We set the sharpness of the threshold effect, b, to 3 (reflecting a sharp threshold). The social transmission strength s was set to 30. In addition, we repeated simulations by setting a threshold in relation to the network size, a threshold of 3 and a threshold of 7 (see supplementary material).

(3) Proportion rule: This transmission rule defines the learning rate to be proportional to the ratio of connections that an individual holds to informed others. As such, the individual with the highest proportion is most likely to learn and assumes additional influence from individuals' uninformed connections rather than just considering the sum of connections to informed individuals. The social transmission strength s was set to 30.

(4) Conformity rule: Finally, the fourth transmission rule assumes that individuals are disproportionately more likely to copy the majority of the population (i.e. frequency dependent). Thus, an individual is expected to adopt a new behaviour if it is perceived as being performed by the majority of its' social connections. Similar to the proportional rule, the conformity rule considers an individual's informed and uninformed connections. The value f describes the probability of adopting the new behaviour, whereby $f>1$ means that the individual adopts the behaviour performed by the majority. For our simulations, we set f to 3 and the social transmission strength s to 30.

For each simulation the individual 'initiating' the behaviour (i.e. the demonstrator) was randomly chosen but was consistent across the four transmission models. We simulated behavioural spread

across the entire network. At each timestep within each simulation, a new individual was chosen to acquire the behaviour, which is dependent on the likelihoods of acquisition assigned to each uninformed individual at that timestep based on the probability of any individual 'asocially' acquiring the behaviour, and the probability of each individual socially acquiring the behaviour which is derived from their social connections' status (informed or uninformed) and the learning rule at play. Full details for this method, and associated tests, are available in the complexNBDA package (Firth et al. 2020) and follows the principles of NBDA transmissions (Hasenjager et al. 2021). Once individuals adopted the novel behaviour, they remained 'informed' within each simulation run. For each network, we repeated the simulations 100 times to minimize the influence of the identity of the randomly selected demonstrator on the subsequent transmission pathways. We selected 100 simulation runs because this was enough in acquiring a relatively stable mean correlation coefficient between network metric and order of acquisition (Figure S6). As such, as total of 538000 simulations (1345 weekly networks x 4 different learning rules x 100 simulation runs) were carried out across all the variations of the reported analyses.

Data summary statistics

To assess the relationship between each individual's network metric and the order of acquisition, we calculated Spearman's rank correlation coefficients. After every simulation, for each of the networks and transmission models, we calculated the Spearman's rank correlation coefficient between the order in which individuals adopted the behaviour (always excluding the demonstrator) and each of the three individual network metrics (i.e. the weighted clustering coefficient, the weighted degree and the weighted betweenness). For an overview of the transmission process, see Figure 1. For each network and model, we then calculated the average correlation coefficient for each network metric across the 100 simulations (Figure 3). To additionally assess the relationships between the size of the network, and the correlation coefficient between individuals' centralities and their acquisition order, we used linear mixed-effect models (LMM). We set the average correlation coefficient as the dependent variable and network size in interaction with the learning rule as the predictor variable. Location identity and week nested in year were set as random effects to factor in these differences when assessing this relationship (see Table S1 for results).

Acknowledgments

We thank the large number of contributors to the data collection. The study has been supported by grants from NERC (NE/S010335/1) and BBSRC (BB/S009752/1).

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