Trends in Ecology & Evolution

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Opinion

Dynamic Relationships between Information Transmission and Social Connections

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Understanding the drivers of sociality is a major goal in biology. Individual differences in social connections determine the overall group structure and have consequences for a variety of processes, including if and when individuals acquire information from conspecifics. Effects in the opposite direction, where information acquisition and transmission have consequences for social connections, are also likely to be widespread. However, these effects are typically overlooked. We propose that individuals who successfully learn about their environment become valuable social partners and become highly connected, leading to feedback-based dynamic relationships between social connections and information transmission. These dynamics have the potential to change our understanding of social evolution, including how selection acts on behavior and how sociality influences population-level processes.

Highlights

Animal social relationships are characterized by nonrandom associations and interactions that play a major role in survival and fitness, by influencing foraging decisions, space use, predator avoidance, and mate choice.

Social network analysis, a powerful framework for addressing the causes and the consequences of social variation, is generating substantial evidence for the idea that sociality drives information transmission, where individuals' social connections influence if and when they learn novel information from others.

However, a causal relationship in the other direction, where learning and information transmission influence individuals' social value and thus affect social connections, is rarely addressed.

We need to account for the feedback-based dynamic relationships between learning and social connections when investigating how information spreads through networks.

Social Connections, Valuable Partners, and Information Spread

Exploring how individual variation in behavior is linked to social structure is a major aim in social evolution. Individual differences in social connections, based on nonrandom associations and interactions, form the building blocks of social structure [1,2]. These connections affect diverse functional behaviors ranging from mate choice to competition, from dispersal to predator avoidance, and from **social learning** (see Glossary) to information transmission [1,3–5]. Social connections have important implications for health, survival, and fitness [5–8]. However, we do not yet fully understand the factors that drive social connections [9] and, make some individuals **valuable social partners** [10].

Social network analysis has emerged as a powerful conceptual framework for quantifying individual variation in social connections, allowing robust exploration of how sociality drives population-level processes [1,4,5,8]. The presence and the strength of individuals' connections influence their position in the network. Some individuals are more connected than others and occupy key network positions. These **central individuals** can have increased survival rates and higher fitness [9], but they are also at high risk of acquiring disease and parasites from others [11,12]. Network position also affects the patterns of information transmission by influencing who learns novel information and from whom. Central individuals are more likely than noncentral individuals to learn novel information from their conspecifics [13–20]. Although multiple factors have been demonstrated to affect individual differences in social centrality (Figure 1), the consequences of learning and information transmission on centrality have rarely been explored [21,22].

Here, we propose that the relationships between social connections and information transmission are dynamic, such that successfully acquiring and using novel information influences network position and social connections, in addition to being influenced by them.

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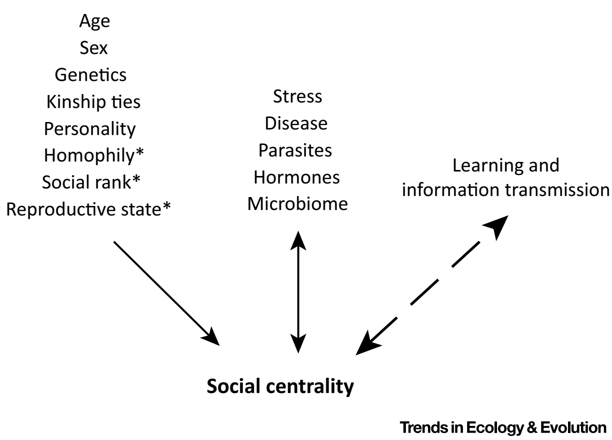

Figure 1. Network Position. Previous studies have demonstrated that network position is influenced by multiple factors, including age, sex, genetics, and personality [1,2,37,44–46,57–60]. Some of these factors have experimentally been shown to rely on feedback-based dynamic relationships, such that they are influenced by centrality, in addition to influencing it (unbroken line, double arrows) [8,12,61–65]. For example, on the one hand, network connections and position predict the patterns of parasite transmission [12,61], while on the other, parasite load and infection influence social behavior and network position [8,62,63]. Likewise, stress is influenced by social connections, and in turn influences not only social connections but also individuals' ability to adjust their social behavior in response to their environment [36,66]. Although there is no experimental evidence yet, it is possible that additional factors (indicated with asterisks), such as social rank and reproductive status, are also influenced by centrality, in addition to influencing it. Importantly, feedback-based relationships are also likely to exist between social centrality and information transmission (broken line).

As social network analysis is generating substantial evidence for the idea that sociality drives information transmission [13–20], we review this causal relationship briefly before focusing on the rarely explored relationship in the other direction. We argue that, especially in species in which conspecifics repeatedly interact with each other, the **successful individuals** who learn about their environment and apply this knowledge to key behaviors (e.g., foraging, predator avoidance, and mate choice) will be perceived as valuable social partners with whom others would want to socially connect. These successful individuals would then achieve higher social centrality than others. This effect would be most pronounced in networks based on **affiliation** and **association**. We thus suggest that information is an important resource that influences individuals' success and increases their value as social partners. Consequently, successfully learning about the environment, and adjusting key behaviors based on acquired knowledge, is likely to be one of the main drivers of social evolution and structure.

Learning and Social Connections Drive Transmission Patterns

Understanding information transmission in a group requires unraveling how individual differences in learning and social connections interact with each other to affect who learns when and who learns from whom. Individuals vary in the speed and the accuracy with which they acquire, process, and use information about their environment. Such variation is influenced by multiple factors, including learning opportunities, learning ability, social status, age, sex, personality, motivation, persistence, previous experience, genes, and hormones [23–27]. When some individuals learn novel information sooner or more accurately than others, this leads to an unequal distribution of information within the group. As a result, in addition to **individual (asocial) learning**, animals can also socially learn from informed (i.e., knowledgeable)

Glossary

Affiliation networks: networks based on affiliative interactions such as grooming or food sharing. Can be quantified as directed networks.
Association networks: networks based on physical proximity, co-occurrence, or group membership (usually not directed).
Central individuals: central individuals are highly connected or connect the otherwise unconnected conspecifics. They play important social roles due to the number, frequency, or identity of their connections.
Degree: centrality measure based on the number of direct connections. Degree is informative about the number of interaction partners (e.g., number of grooming partners).
Directed networks: in directed networks, the actor and the receiver are, distinguished from each other (e.g., where individual A grooms individual B, A is the actor and B is the receiver).
In-measures: based on incoming ties, in-measures quantify the interactions that an individual receives from others. See indegree and instrength.
Indegree: indicates the number of ties towards a focal individual and describes the number of conspecifics from whom an individual receives an interaction (e.g., number of conspecifics who groom an individual).
Individual (asocial) learning: learning through trial-error and through individual experiences rather than through social learning.
Instrength: the frequency of social interactions that a focal individual receives from conspecifics (e.g., frequency of grooming that an individual receives).
Naïve individuals: individuals who have not yet acquired the information that is being transmitted.
Node: units or entities that make up a network.
Out-measures: based on outgoing ties, out-measures quantify the interactions that an individual initiates towards others. See outdegree and outstrength.
Outdegree: indicates the number of conspecifics towards whom a focal individual initiates an interaction (e.g.,

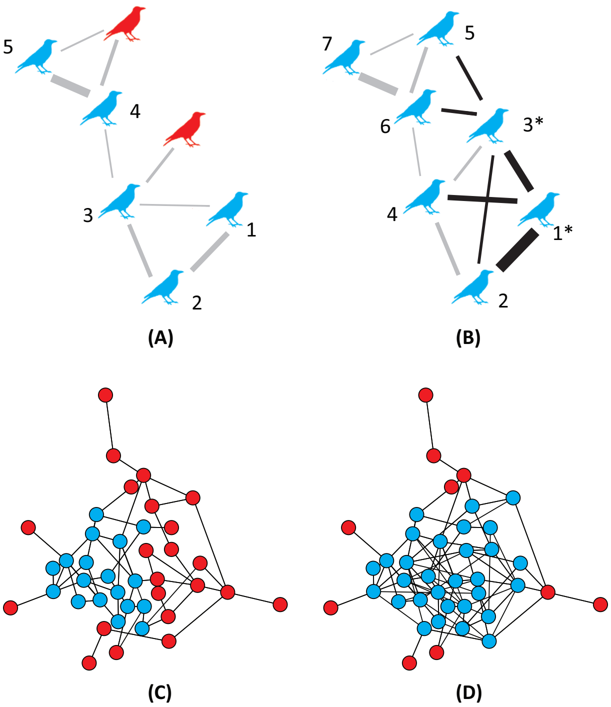

Figure 2. Social Connections and Information Transmission. A hypothetical example demonstrating the patterns of information transmission without (A) and with social adjustments (B), and the consequences at the group level without (C) and with social adjustments (D) is shown. Line thickness is proportional to the connection strength. Numbers next to **nodes** (depicted by birds) indicate the order with which different individuals learn during transmission (red nodes indicate nonlearners). Information is more likely to spread through stronger connections than weak connections, such that if two individuals are connected to the same informed conspecific, the individual with the stronger connection (thicker line) learns sooner than the other. However, it is also possible that animals adjust their connections (black lines in B) based on how reliably conspecifics use novel information and display successful behaviors. Successful individuals (indicated with asterisks in B) can be viewed as valuable partners by observers and become more socially connected as a result. The resulting newly formed or strengthened connections will then influence who has access to the novel information, ultimately affecting the overall transmission patterns and allowing information to spread further. Moreover, information would be more likely to persist within a population when animals adjust their social connections based on conspecifics' success (D) in comparison with when such social adjustments do not take place (C). Bird illustrations: Ipek G. Kulahci.

number of conspecifics that a focal individual grooms).
Outstrength: the frequency of social interactions that an individual initiates towards others (e.g., frequency of grooming that an individual provides).
Social cognition: the ability to successfully keep track of the social environment, learn and remember who is who, and adjust social behavior based on this knowledge.
Social learning: involves gaining information from the behavior of others to increase the probability of learning. Presence of others can become a cue that attracts individuals to a location, or animals can socially learn by observing the behavior of others.
Social network analysis: a framework that allows quantifying the structure and the contents of social patterns. Social networks include ties (e.g., connections) and nodes.
Strength: centrality measure based on the sum of the frequency of interactions of an individual.
Successful individuals: those who learn about their environment and apply this knowledge to key behaviors, leading them to display a novel advantageous behavior (e.g., how to utilize a food resource, avoid a predator, etc.) repeatedly and more reliably than others.
Ties: also called edges or links, ties represent the connections between nodes. Ties are based on interactions (e.g., grooming) or associations (e.g., proximity).
Valuable social partners: individuals with whom conspecifics prefer to associate and interact.

conspecifics who display novel behaviors, leading to transmission of information and behaviors between individuals [28] (Figure 2).

Network-based diffusion analysis (NBDA) allows integrating social network analysis with learning experiments to infer social transmission of a behavior if its spread follows network connections [28,29]. The patterns of information transmission can be predicted by the presence and the strength of connections between individuals [13–20] (Figure 2). In particular, connections in affiliation networks and association networks play critical roles in determining who observes whom and who learns from whom [13–20]. Individuals who are central in these networks are more likely to be connected to at least one informed conspecific they can closely observe, and thus learn from, during transmission [17,30]. Hence, individual differences in social connections have consequences for information acquisition during transmission.

Individuals' Learning Success and Display of Novel Behaviors Can Influence Their Centrality

Individual variation in acquiring information about the environment and applying this knowledge to key behaviors will influence individuals' success. Individual differences in success can affect individuals' value as social partners and thus have major consequences for social connections. For example, animals might preferentially associate and interact with individuals who display novel behaviors (Box 1). Both humans and animals learn from their social connections [13,15–20] and from successful individuals [31]. Being socially connected to successful individuals would provide immediate or future opportunities to observe and learn from them [21,32,33]. Thus, successful individuals are likely to become valuable social partners and receive more social connections from the conspecifics who observe them (Figure 2). Such social changes would lead to an increase in successful individuals' centrality **in-measures** (e.g., **indegree** and **instrength**), especially in affiliation and association networks, while influencing centrality **out-measures** (e.g., **outdegree** and **outstrength**) of the observers who initiate connections towards successful individuals (Box 1). Accordingly, individual variation in knowledge and success, arising from successfully learning about the environment and applying this knowledge to key behaviors, can affect the overall social structure by influencing social connections and network centrality.

Social Cognition Skills Can Also Influence Centrality

Some individuals excel at acquiring up-to-date information about their social environment, which requires assessing social signals and tracking social changes [34,35]. These **social cognition** skills (also known as social competence [36]) allow animals to gain social knowledge and to adjust their social behavior [35,36]. Individuals who are better able to attend to their social environment when making social decisions, such as deciding with whom to associate, mate, fight, or cooperate, will respond more appropriately to social situations. As such, individual variation in social cognition skills can directly affect which individuals identify successful conspecifics and initiate affiliation towards them (Box 1).

Animals gain more reliable social knowledge when conspecifics' social behavior is consistent through time and across contexts. These consistencies reflect social preferences, such as the tendency to be socially connected, and have been demonstrated in multiple taxa [37–41]. Social individuals are more likely than less social individuals to initiate social interactions towards conspecifics. Thus, individual differences in social cognition skills and in social preferences can interact with each other to directly influence who initiates affiliative behaviors towards whom.

Box 1. How Does Learning Influence Centrality?

Individual differences in knowledge state (e.g., informed versus **naïve**), which arises from variation in learning about the environment and applying this knowledge to key behaviors, leads to individual differences in success. For example, individuals who learn about novel food resources and use this information while foraging (Figure I; left side, blue text) could be perceived as reliable information sources and as successful foragers from whom others can learn. This could then attract the attention of the naïve conspecifics (Figure I; right side, red text) who have not yet learned about these resources. As one of the social learning strategies that animals use is to learn from successful individuals [31], naïve individuals would benefit from staying in proximity to or affiliating with successful conspecifics [21,32,33], which would provide immediate or future opportunities to observe and learn from them. Thus, learning success can influence successful individuals' centrality if the naïve individuals who observe them preferentially associate or affiliate with them.

Among the naïve individuals, those who acquire up-to-date social information and adjust their social behavior accordingly (Figure I; right side, red text) would be more likely to initiate affiliative behaviors towards successful conspecifics. Some network centrality measures, such as **degree** and **strength** [5,45] can be used as directed measures to differentiate between initiated connections (based on outgoing **ties**; outdegree and outstrength) and received connections (based on incoming ties; indegree and instrength) [5]. If naïve individuals initiate connections towards successful individuals, this would lead to a change in their outdegree and outstrength, while affecting the indegree and instrength of the successful individuals. Thus, out-measures can be more informative than in-measures at predicting who learns novel information when, during transmission [21]. Additionally, long-term social bonds can form through repeated interactions and have a knock-on effect on transmission patterns (Figure I; center).

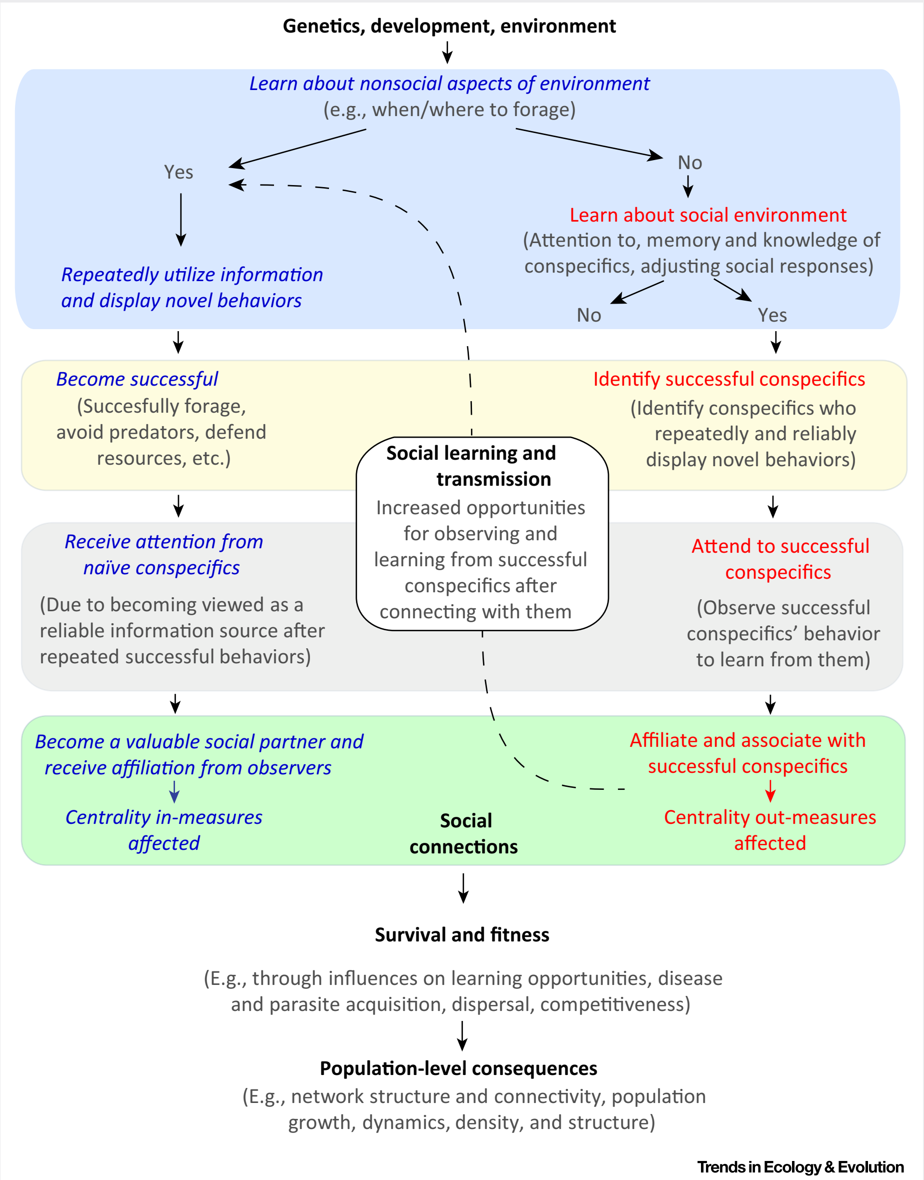

Figure I. A Framework Outlining the Processes Through Which Dynamics Arise. Individuals who acquire novel information and frequently use it to display novel behaviors can be perceived as successful individuals who are reliable information sources (blue text), which leads to becoming valuable social partners and receiving more social attention from others. Individuals' social cognition skills (red text) are likely to affect whether or not they preferentially attend to and initiate affiliation towards successful individuals. Together, these social changes will have consequences for network position, survival, and fitness.

Intriguingly, we know relatively little about how individual variation in cognition shapes individual differences in social connections [22] (see Outstanding Questions). For example, if learning about social stimuli (e.g., conspecifics) and nonsocial stimuli (e.g., food or predators) utilize the same cognitive skills and neural processes [35,36,42,43], then individual variation in cognition tests should be linked to each other. Alternatively, if trade-offs exist between acquiring social and nonsocial information, then some individuals will be more attentive to their social environment and excel at gaining knowledge about their social environment, while others will excel at gaining knowledge about their physical environment. We currently lack experimental evidence to assess these possibilities. Therefore, detailed studies of cognition, including social cognition, are now needed to understand how cognitive variation influences social connections and centrality.

Experimental Approaches to Identify the Direction of Causal Relationships

Determining the causal direction of the underlying relationships between social connections and information transmission requires making a distinction between when social connections are affecting learning versus when learning is affecting social connections. Distinguishing between these two possibilities is difficult to do with correlational studies, because the factors that influence both learning [23,24,30] and centrality [1,2,37,44–46] can confound our understanding of the causal directions. Carefully designed experiments are therefore necessary.

One promising approach involves utilizing social transmission studies to determine whether individuals' social connections and centrality change after they acquire information and display novel behaviors [21,22] (Box 2). This approach can then be coupled with experiments in which perceived success of individuals are manipulated by allowing only certain individuals access to novel information. These manipulations would allow us to detect if individuals adjust their social responses towards the conspecifics they perceive as successful.

For instance, a single individual from a group could be trained on a complicated task before the task is introduced to the group [32]. Alternatively, task-access could be restricted to certain individuals using remote controlled [33] or radio-frequency identification (RFID)-controlled automated devices. For example, if a noncentral individual, who is presented as the only group member who possesses and repeatedly uses novel information, achieves higher indegree or instrength after being observed, then this would suggest that this centrality increase is due to conspecifics' social responses to that individual's success [21]. Alternatively, socially central individuals can be presented as nonsuccessful individuals, by preventing them from acquiring and using novel information, to determine if their centrality is reduced as a result.

These experiments can be coupled with dynamic social network analysis to address if individuals' centrality changes after they acquire and use novel information [21]. If data on the timing of social interactions is available, then relational event models can be used to model the history of interactions and to assess changes [47,48]. Stochastic actor-oriented models (SAOM) can also be useful for detecting gradual changes. However, SAOM will not be suitable for all questions and species, as they do not allow inclusion of information on the strength of social connections [49].

Directed networks will be highly informative when uncovering the direction of these causal relationships (Box 1). However, directed network data are challenging to obtain in most species. Instead, undirected networks, such as those based on physical proximity, are frequently used to quantify connections [50]. The advancement of technologies such as accelerometers, animal-borne cameras, and automated tracking methods should improve our ability to collect directed data [51]. Furthermore, using a multinetwork approach to include different social contexts will provide valuable insights into the pathways of transmission [17]. Multilayer social networks, in particular, are highly promising, as they allow integration of social behavior through time and across contexts [52].

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Box 2. A Case Study for Detecting Social Changes.

Social consequences of learning can be addressed by quantifying changes in social connections after information transmission. We illustrate this approach with a recent study on ring-tailed lemurs (*Lemur catta*) [21]. Although the free-ranging population in this study was provisioned daily, a previous study has demonstrated that the foraging behavior, activity budgets, and social interactions of lemurs in this population are comparable with those of wild lemurs in Madagascar [67]. Lemurs use affiliative behaviors to form and reinforce differentiated social bonds [37,68,69] (Figure I). To address the possibility that conspecifics' reliable use of information and perceived success influence these bonds, Kulahci *et al*. [21] compared networks before and after a task-learning experiment. The lemurs who learned to solve the foraging task sooner than conspecifics, and solved it frequently while being observed by others, received more affiliative behaviors after the experiment than they did before, and had higher centrality (indegree and instrength) in affiliation networks after the experiment.

The increased affiliation that the frequently observed lemurs received was not caused by a change in their own social behavior, as their out-measures (indicating initiated interactions) had not changed after the experiment. Notably, out-measures but not in-measures (indicating received interactions) predicted whether lemurs learned the task solution from others; lemurs who frequently approached informed conspecifics and initiated affiliation were more likely to learn during transmission. This suggests that network data that differentiates between received and initiated connections is highly informative about transmission patterns [21].

Animals can initiate affiliation to gain benefits such as food access. For example, when multiple food items are available, individuals in close proximity to informed conspecifics can benefit from their actions [32,33,70]. However, the task in the lemur study was designed to minimize scrounging and food sharing. As only the solvers were able to obtain the reward, leading to a direct correlation between learning the task solution and retrieving the food reward, solvers could have been perceived as successful individuals [21]. Consequently, individual differences in learning and success can lead to long-lasting changes in social bonds and social structure.

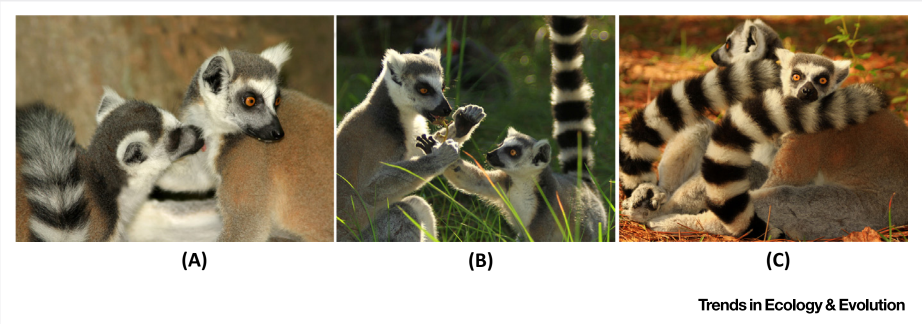

Figure I. Lemurs Form Strong Social Bonds that are Reinforced by Affiliative Behaviors such as (A) Grooming, (B) Food Sharing, and (C) Close Physical Contact. These bonds influence how new information and behaviors spread in the group. In turn, successfully learning and using information shapes social bonds, when individuals preferentially affiliate with successful conspecifics. Photos: Ipek G. Kulahci.

Social Consequences and Population-Level Implications

The dynamic processes between social connections and information transmission can shed light on the persistence of novel behaviors in populations [53]. Transmission of information between individuals depends on the presence and the strength of social connections, and forms the foundations of cultural evolution. Changes in social connections during and after information transmission will thus influence the pathways through which novel information and behaviors propagate. It is predicted that central individuals are more influential than noncentral individuals as information spreaders [1]. When individuals who display novel behaviors become more central, more group members would have opportunities to observe and learn these behaviors. As a result, information would propagate further and possibly even faster, ultimately providing a pathway for behaviors to evolve and persist in a population.

Through their impact on social connections, learning and success can also have knock-on effects on multiple population-level processes. For example, central individuals are less likely to disperse than noncentral individuals [54]. If successful individuals become central, they can delay dispersal, which would then have consequences for group composition as well as for population structure, stability, dynamics, and density. Furthermore, although central individuals have been shown to have higher survival and fitness, they are also at greater risk of acquiring parasites and diseases from conspecifics [9,11,12]. An additional cost of being central is being subject to information and resource scrounging. Concealing information about novel resources from others would be advantageous to reduce competition. However, central individuals are more likely to be in proximity to others, resulting in inevitably sharing information or resources with them. These potential costs can be offset if successful individuals become attractive as preferred mates [55]. Hence, understanding the dynamics between learning, success, and social connections is essential for understanding behavioral evolution, for improving conservation, and for reducing the spread of contagious diseases and parasites.

If learning success influences social connections, then the proximate and ultimate factors that influence individual differences in learning (e.g., age, sex, personality, maternal effects, genes, and hormones) [23–27,31] are likely to have knock-on effects on centrality. For example, personalities influence both learning [56] and dispersal patterns [54]. By dispersing into a new population, explorative individuals can introduce novel behaviors and information, and thus have a disproportionate effect on the information available in the population. If conspecifics preferentially interact with these explorative individuals, such adjustments would provide a process through which personalities can affect both transmission and social structure.

Furthermore, social changes can significantly confound how we interpret transmission patterns across a wide range of species. Multiple studies have demonstrated that central individuals are more likely than noncentral individuals to socially learn from conspecifics [17,30]. However, it would be essential to determine whether social adjustments are partially responsible for these patterns. This could happen, for example, if some central individuals have become central only after they learn and display novel behaviors (e.g., after conspecifics have observed their behavior and socially connected with them). This possibility can be addressed by analyzing changes during and after transmission [21].

Concluding Remarks

We propose that successfully learning about the social and the physical environment, and using this knowledge to adjust key behaviors, is one of the major drivers of individual variation in social connections and network position. We suggest that information is an important resource that increases the social value of the individuals who successfully acquire and use it. As such, individual differences in learning and success will have consequences for who receives affiliation from whom, ultimately influencing social connections and centrality.

Surprisingly, the feedbacks between learning and social connections are rarely acknowledged in information transmission studies. This is quite unexpected, given the exciting increase in both the breadth and the number of studies that integrate social network analysis with animal cognition experiments to investigate how information spreads in groups. We suggest that the dynamic relationships between learning and social connections offer multiple intriguing directions for understanding the network-based processes and the links between social and cognitive variation (see Outstanding Questions). We thus hope that our paper will inspire a close investigation of this currently unexplored topic.

Outstanding Questions

How do animals decide with whom to form social bonds? Which individuals are perceived as valuable social partners? How does variation in learning and success drive social bonds?

What factors drive individual variation in sociality and thus affect social network position? Which factors interact with each other and which factors form feedback-based relationships with network position?

Do animals use similar cognitive skills in social and nonsocial situations? Are some individuals more likely to learn about their social environment than their nonsocial environment? Are there trade-offs, or, do some individuals equally succeed at both?

What are the population-level implications of the interplay between social connections, centrality, learning, and information transmission? In which social systems does this interplay feature the most important role?

What consequences do social adjustments have for survival and fitness?

How do we reliably identify the causal direction of the relationships between social connections and learning?

Does the nature of the information that is being transmitted influence whether transmission has consequences for social connections? For instance, if information that is difficult to learn is more likely to spread through social transmission, then such information can be more likely to result in a change in the centrality of the successful individuals.

At what stage during information transmission does the centrality of the successful individuals start to change? Are these changes long-lasting? Are they frequency-dependent, such that the presence or the extent of social changes depends on the number of successful individuals?

Do social network and transmission studies in captivity predict what happens in wild or free-ranging populations?

How can we best acquire directed network data? What are the challenges we need to overcome to develop technologies such as accelerometers, animal-borne cameras, and automated tracking methods?

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