SOCIAL INTERACTION IN ANIMALS: LINKING EXPERIMENTAL APPROACH AND SOCIAL NETWORK ANALYSIS

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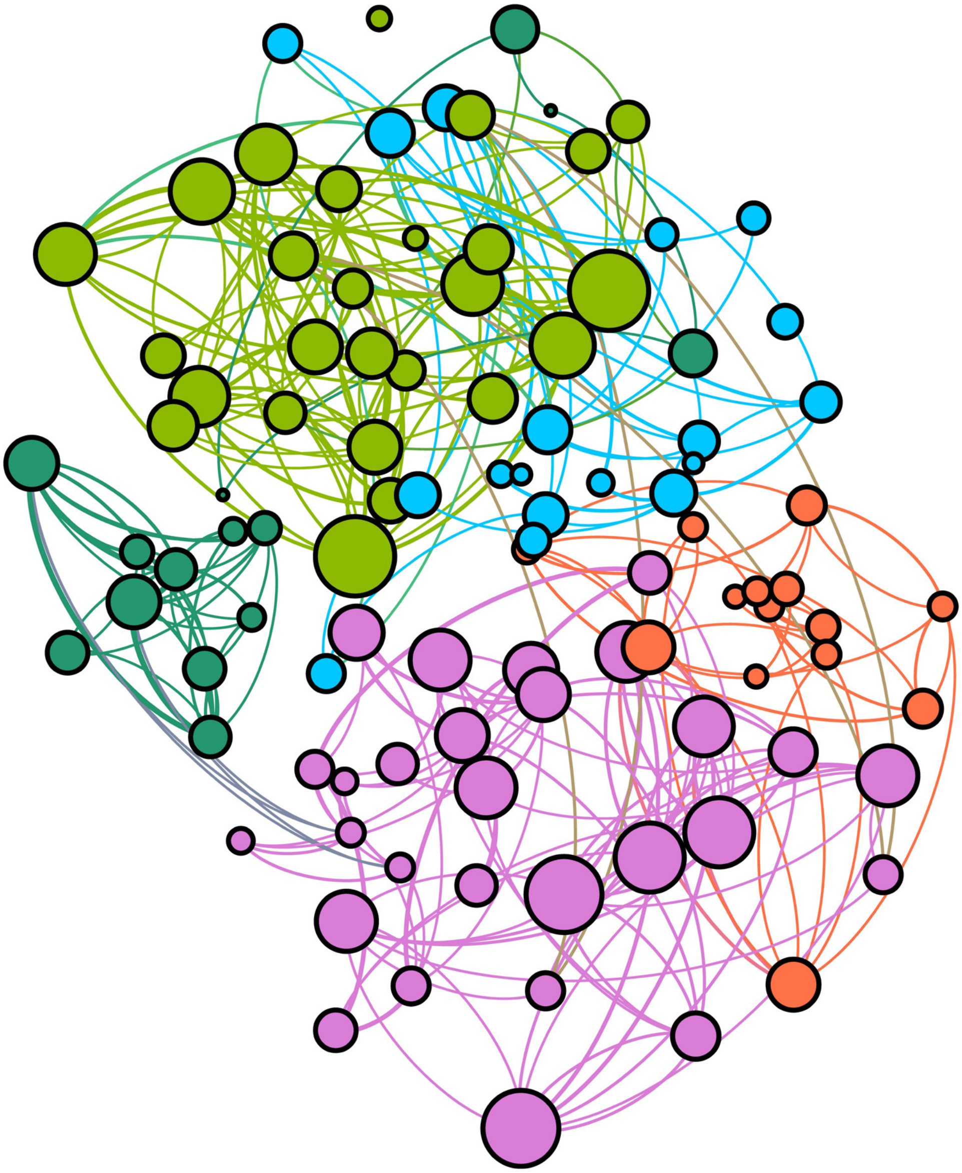

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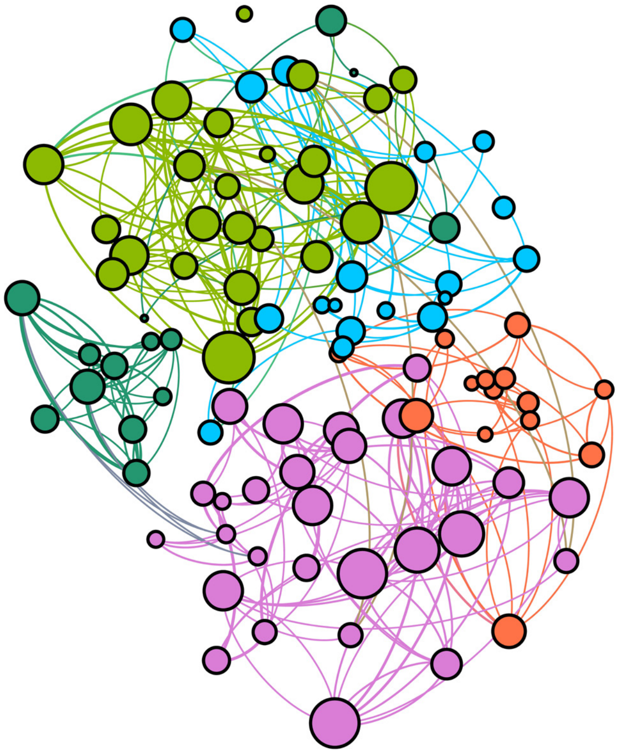
SOCIAL INTERACTION IN ANIMALS: LINKING EXPERIMENTAL APPROACH AND SOCIAL NETWORK ANALYSIS

Topic Editors:
Cédric Sueur, Centre National de la Recherche Scientifique (CNRS), Institut Pluridisciplinaire Hubert Curien UMR 7178, Université de Strasbourg, France
Frédéric Mery, Centre National de la Recherche Scientifique (CNRS), Institut de Recherche pour le Développement (IRD), Université Paris-Sud, Université Paris-Saclay, France



Social network of 100 nodes made in Gephi 0.91
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Understanding the link between individual behaviour and population organization and functioning has long been central to ecology and evolutionary biology. Behaviour is a response to intrinsic and extrinsic factors including individual state, ecological factors or social interactions. Within a group, each individual can be seen as part of a network of social interactions varying in strength, type and dynamic. The structure of this network can deeply impact the ecology and evolution of individuals, populations and species. Within a group social interactions can take many forms and may significantly affect an individual's fitness. These interactions may result in complex systems at the group-level, such as in the case of collective decisions (to migrate, to build nest or to forage). Among them, social transmission of information has been studied mostly in vertebrates: fish, birds and mammals including humans. In insects, social learning has been unambiguously demonstrated in social Hymenoptera but this probably reflects limited research effort and recent evidence show that even non-eusocial insects such as Drosophila, cockroaches and crickets can copy the behaviour of others. Compared to individual learning, which requires a trial and error period every generation, social learning can potentially result in the stable transmission of behaviours across generations, leading to cultural traditions in some species. The study of the processes which may facilitate or prevent this transmission and the analyses of the relationship between social network structure and efficiency of social transmission became these recent years an emerging and promising field of research.

The goal of this research topic is to present the genetic and socio-environmental factors affecting social interaction and information or pathogen transmission with the integration of experimental approaches, social network analyses and modelling. Importantly, we aim to understand whether a relationship between social network structures and dynamics can reflect the efficiency of social transmission, i.e. can we use social network analysis to predict the social transmission of information or of pathogen, collective decision-making and ultimately the evolutionary trajectory of a group?

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EDITORIAL
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Editorial: Social Interaction in Animals: Linking Experimental Approach and Social Network Analysis

Cédric Sueur[1]* *and Frédéric Mery*[2]

[1] *Centre National de la Recherche Scientifique (CNRS), Institut Pluridisciplinaire Hubert Curien UMR 7178, Université de Strasbourg, Strasbourg, France,* [2] *Evolution, Génomes, Comportement and Ecologie, Centre National de la Recherche Scientifique (CNRS), Institut de Recherche pour le Développement (IRD), Université Paris-Sud, Université Paris-Saclay, Gif-sur-Yvette, France*

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Editorial on the Research Topic

Social Interaction in Animals: Linking Experimental Approach and Social Network Analysis

Understanding the link between individual behavior and population organization and functioning has long been central to ecology and evolutionary biology (Krause et al., 2009; Sueur et al., 2011; Kurvers et al., 2014). Behavior is a response to intrinsic and extrinsic factors including individual state, ecological factors, or social interactions. Within a group, each individual can be seen as part of a network of social interactions varying in strength, type, and dynamic. The structure of this network can deeply impact the ecology and evolution of individuals, populations, and species.

Three studies in this present issue tried to understand how group members are socially structured in non-human primates. Borgeaud et al. used a stochastic actor-oriented model (RSiena Package, Snijders, 2001) to test the dynamics of relationships of three groups of wild vervet monkeys. They found that triadic closure was significant in all three groups while degree popularity was significant in only two groups. Moreover, the dynamics of relationships according to the attributes of sex, matriline, and age differed significantly among groups.

In another way, Sosa showed that in Barbary macaques, females are more central, more active, and have a denser ego network in the social network than males; thus, they contribute in a greater way to the cohesive structure of the network. High-ranking individuals are likely to receive fewer agonistic behaviors than low-ranking individuals, and high-ranking females receive more allogrooming. Revealing the positions, the roles, and the interactional behavioral patterns of individuals can help understand the mechanisms that shape the overall structure of a social network.

Naud et al. studied another species of primates, the Mandrills. The objective of their study was to investigate how the group spatial distribution of a semi-free ranging colony of Mandrills in a food competition context relates to its social organization. Their results showed that high-ranking individuals were more observed in proximity of the feeding zone but that affiliative relationships were also associated with individual spatial distributions and explain more the individual distribution than dominance hierarchy.

These studies showed that within a group social interactions can take many forms and may significantly affect an individual's fitness (Silk et al., 2003; Formica et al., 2012; Kurvers et al., 2014). These interactions may result in complex systems at the group-level, such as in the case of collective decisions (Sueur et al., 2012). Among them, social transmission of information has been studied mostly in vertebrates (Whiten and van Schaik, 2007). Duboscq et al. reviewed the context and

Edited by:
Jeffrey R. Stevens,
University of Nebraska–Lincoln, USA

Reviewed by:
Daizaburo Shizuka,
University of Nebraska–Lincoln, USA

***Correspondence:**
Cédric Sueur
cedric.sueur@iphc.cnrs.fr

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the methodology of experiments testing social transmission of information. However, they also discussed the reasons why social transmission sometimes does not occur despite being expected to and spanned a full range of mechanisms and processes including the constraints imposed by the social networks in which animals are embedded.

In a study on zebra finches, Fernandez et al. designed a method analyzing group vocal network semi-automatically. They wanted to test the hypothesis that the social structure of the group influences the parameters of the group vocal network. Using Markov analysis and cross-correlation analyses, they showed that juveniles as well as adults were more likely to respond to individuals of their own age-class.

In insects, social learning has been unambiguously demonstrated in social Hymenoptera but this probably reflects limited research effort and recent evidence show that even non-eusocial insects such as Drosophila, cockroaches, and crickets can copy the behavior of others (Battesti et al., 2012, 2015; Waters and Fewell, 2012). In this way, Pasquaretta et al. also used the RSiena package to analyze the dynamic of the interaction network of the fruit fly *Drosophila melanogaster* during social learning experiments. This work showed the importance of new methodologies in social network analyses to better understand causes and effects of animal social networks properties. The study of the processes which may facilitate or prevent this transmission and the analyses of the relationship between social network structure and efficiency of social transmission became in recent years an emerging and promising field of research (Sueur, 2011; Pasquaretta et al., 2014).

For instance, a number of recent studies have used Network Based Diffusion Analysis (NBDA) to detect the role of social transmission in the spread of a novel behavior through a population (Franz and Nunn, 2009; Hoppitt et al., 2010). Whalen and Hoppitt presented in this special issue a unified framework for performing NBDA in a Bayesian setting, and demonstrated how the Watanabe Akaike Information Criteria (WAIC) can be used for model selection. They performed a large scale simulation study and found that NBDA using WAIC could recover the correct model of social transmission under a wide range of cases, including under the presence of random effects, individual level variables, and alternative models of social transmission.

On another topic, Senior et al. worked on an integrated model approach between social network analysis and nutritional behavior. Animals have evolved complex foraging strategies to obtain a nutritionally balanced diet and associated fitness benefits. This nutritional behavior can also influence animal social interactions and affect group structures. Senior et al. demonstrated how social network analyses can be integrated into such a nutritional modeling framework. They illustrated their approach by examining the case of nutritionally mediated dominance hierarchies and demonstrated how metrics from social network analyses can be used to predict the fitness of agents in these simulations.

Health is a component of fitness also very well studied in Animal Behavioral Sciences (Abbot et al., 2011; MacIntosh et al., 2011; Rico-Uribe et al., 2016). In their study, McCowan et al. argued that nonhuman primate social systems are sufficiently complex to serve as model systems to study links between social life and health as we might observe in Humans. The influence of social contexts influencing health and fitness in non-human primates might help us to improve human health.

Finally, Golemiec et al. used a layer motif approach to understand social networks of kindergarten children and concluded that this method can be applicable on a more general scale to any group of individuals where interactions and identities can be readily observed and scored.

Using different animal species, including humans, this special issue investigated and showed how the structure of a group affects social interaction, information transfer, and collective decisions; but also how individuals treat different sources of information according to their sociality and the latest methodologies used to understand these processes.

AUTHOR CONTRIBUTIONS

All authors listed, have made substantial, direct and intellectual contribution to the work, and approved it for publication.

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ORIGINAL RESEARCH
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Intergroup Variation of Social Relationships in Wild Vervet Monkeys: A Dynamic Network Approach

Christèle Borgeaud [1, 2†], Sebastian Sosa [3†], Redouan Bshary [1, 2], Cédric Sueur [4, 5] and Erica van de Waal [2, 6]*

[1] Laboratory of Eco-Ethology, Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland, [2] Inkawu Vervet Project, Mawana Game Reserve, KwaZulu Natal, South Africa, [3] Adaptive Behavior and Interaction Research Group, University of Barcelona, Barcelona, Spain, [4] Département Ecologie, Physiologie et Ethologie, Centre National de la Recherche Scientifique, Strasbourg, France, [5] Institut Pluridisciplinaire Hubert Curien, Université de Strasbourg, Strasbourg, France, [6] Anthropological Institute and Museum, University of Zurich, Zurich, Switzerland

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Jennifer Vonk,
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***Correspondence:**
Christèle Borgeaud
christele.borgeaud@unine.ch

† These authors have contributed equally to this work.

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Social network analysis is a powerful tool that enables us to describe and quantify relationships between individuals. So far most of the studies rely on the analyses of various network snapshots, but do not capture changes over time. Here we use a stochastic actor-oriented model (SAOM) to test both the structure and the dynamics of relationships of three groups of wild vervet monkeys. We found that triadic closure (i.e., the friend of a friend is a friend) was significant in all three groups while degree popularity (i.e., the willingness to associate with individuals with high degree of connections) was significant in only two groups (AK, BD). The structure and dynamics of relationships according to the attributes of sex, matrilineand age differed significantly among groups. With respect to the structure, when analyzing the likelihood of bonds according to the different attributes, we found that individuals associate themselves preferably to individuals of the same sex only in two groups (AK, NH), while significant results for attachment to individuals of the same matriline were found also in two groups (BD, NH). With respect to the dynamics, i.e., how quickly relationships are modified, we found in two groups (AK, BD) that females' relationships were more prone to variation than males.' In the BD group, relationships within high-ranking matrilines were less stable than low-ranking ones while in the NH group, juveniles' relationships were also less stable than adults' ones. The intergroup variation indicates that establishing species-specific or even population specific characteristics of social networks for later between-species comparisons will be challenging. Although, such variation could also indicate some methodological issue, we are quite confident that data was collected similarly within the different groups. Our study therefore provides a potential new method to quantify social complexity according to natural demographic variation.

Keywords: social network, dynamics of relationships, RSiena, group composition variation, vervet monkeys

INTRODUCTION

Social network analysis is a method that is used to describe and quantify relationship patterns within a group. Such metrics can be applied at an individual, group or species level. During the last decade, social network analysis has become increasingly popular, especially in primatology (Silk et al., 2003, 2010; Flack et al., 2006; Sueur and Petit, 2008; Henzi et al., 2009). However, most previous studies considered a network to be a static structure that does not vary over time. The few studies that integrated temporal variation focused on dyadic relationships or at the group level and compared networks at different periods (Silk et al., 2006a; Henzi et al., 2009). Such a dynamic approach is necessary if we aim at quantifying network instability and hence the need of an individual to monitor and update its knowledge about its own and also third party relationships. One study tested the influence of natural "knock-outs" within the group (Barrett et al., 2012) and measured their effects in term of entropy (i.e., uncertainty reduction). Another one used 20 years of data on a clan of spotted hyenas to understand the effect of rainfall and abundance of prey on the network structure (Ilany et al., 2015). In a parallel publication (Borgeaud et al., in preparation) on wild vervet monkeys, we also made a first step forward toward the analysis of a network dynamics by considering the influence of demographic variation (i.e., the number of individuals entering and leaving the group) on the individual centrality and on the dyadic relationship stability. Results suggested that, despite some intergroup variation, demographic variation of females, and juveniles have a stronger influence than males on both centrality and the relationship stability. This seems logical knowing that, in vervet monkeys, females remain generally in their natal group for their entire life and form strong and long-lasting bonds with their kin, while males migrate throughout their lives (Cheney and Seyfarth, 1990). However, despite the development of new analytical methods, studies that took into consideration changes over time within a network remain scarce (see Pinter-Wollman et al., 2013 for a review).

Explaining cooperative behaviors that benefit the recipient at some cost to the donor (i.e., helping based on investments) has been a great challenge. Both the kin selection (Hamilton, 1964) and the reciprocity (Trivers, 1971) concepts provided an evolutionary explanation to helping, respectively within related and unrelated individuals. Social network analyses have been proposed as a powerful tool to describe how individuals influence each other within a network and how these relationships evolve over time. Ultimately understanding the dynamics of these relationships could help explain how cooperation evolves. For example, triadic closure (i.e., the hypothesis that an individual is more likely to create bonds with the friends of its friends) may facilitate the formation of cohesive sub-/groups and consequently cooperation within a social group (Granovetter, 1973; Lusseau et al., 2006; Easley and Kleinberg, 2010). The process that describes how individuals associate preferably to individuals with high centrality is called degree popularity (Barabási and Albert, 1999) and some studies found that high-ranking individuals are usually more central within a grooming and proximity network (see Schino, 2001 for a meta-analysis; Kanngiesser et al., 2011; Sueur et al., 2011a; Borgeaud et al., in preparation). This supports Seyfarth's theory (1977), which suggests that grooming could be exchanged against coalitionary support and that individuals should compete to associate with high-ranking individuals as they provided better support during conflicts or as tolerance in the vicinity of food resources increase with grooming exchanged. In this way, individuals attracted to central individuals might have a better fitness than other less strategic individuals. Another interesting measurement is the assortativity of relationships based on individual traits which is called homophily (see McPherson et al., 2001 for a review). Examples include space use in sea lions (Wolf et al., 2007), sex and age-related relationships in dolphins (Lusseau and Newman, 2004), and personality in sticklebacks (Pike et al., 2008). Homophily might also increase an individual's fitness. For example, playing behavior between juveniles decreases the risk of injuries (Shimada and Sueur, 2014) and personality or sex segregation increases food research efficiency (Ruckstuhl and Kokko, 2002; Dyer et al., 2009). In primates, some studies report that, except for kin who usually forms the strongest bonds (Chapais, 2001; Silk et al., 2006a,b, 2010, 2012), unrelated individuals of similar rank or age also form long-lasting relationships (Silk et al., 2006a, 2010, 2012). Such bondedness could be explained through familiarity and eventually paternal kinship (Seyfarth and Cheney, 2012) but also personality (Massen and Koski, 2014). It has been reported that the quality of such bonds have an influence of an individual's fitness such as its longevity and offspring survival (Silk et al., 2003, 2009, 2010) resulting in the selection of such social strategies but a lot of studies analyzed such relationships as being part of a static network. Hence it would be important to apply a more dynamic approach to the analyses of relationships quality which evolve naturally over time (Ilany et al., 2015).

One method that has been developed is the Siena model (for Simulation Investigation for Empirical Network Analysis, Snijders, 2001; Blonder et al., 2012; Pinter-Wollman et al., 2013; Ilany et al., 2015; Pasquaretta et al., 2016), available in the R package RSiena. This stochastic actor-based model aims to give a realistic representation of the dependence between the formation and also termination of different network ties. It therefore allowed us to examine how network processes and covariates influence the probability of individuals changing their network ties according to their attributes over time (Burk et al., 2007; Snijders et al., 2010). By applying these analyses on three wild groups of vervet monkeys over a period of 2 years, we aimed at describing the dynamics of their social network (in terms of grooming and proximities relationships) according to the natural demographic variation. Vervet monkeys represent an ideal model as, in addition to natural disappearance, every year a new generation of infants gets integrated. Native sub-adult males leave the group once they have reached sexual maturity and adult males migrate throughout their whole life joining and leaving multiple groups (Cheney and Seyfarth, 1990).

RSiena is a powerful program allowing us to answer many questions about the mutually dependent dynamics of networks and attributes (behavior, individual characteristics, etc.) of the individual actors in the network. The RSiena approach allows testing of a great variety of potentially interesting network characteristics such as triadic closure, homophily, and rate effect, which analyses the relationships' stability according to various individual attributes. This approach allowed us to assess how the relationships' quality (i.e., based on grooming and proximity data) evolves in function of the natural demographic variations. First, we tested the effect of triadic closure (**Figure 1A**) and degree popularity as well as the temporal persistence of these effects. As vervet monkeys are a highly social species that shows some level of cooperation (Cheney and Seyfarth, 1990; Borgeaud and Bshary, 2015), we expected triadic closure to be present in all three groups. Specifically, the triadic closure effect will assess whether new incoming individuals developing relationships with specific individuals will also develop relationships with their "friends." Triadic closure is a good model to understand how networks will evolve over time. While simple graph theory tends to analyze networks at one point in time, applying the triadic closure principle can predict the development of ties within a network and shows the progression of connectivity (Easley and Kleinberg, 2010). We also tested the effect of degree popularity (**Figure 1B**): as high-ranking individuals offer better support in case of conflict (Cheney and Seyfarth, 1990) and could also confer some protection when spending time in their proximity (Watts, 2002; Cheney and Seyfarth, 2007) they should be preferred targets for bonding attempts and hence should receive disproportionate amounts of grooming. Therefore, new incomers would challenge existing links between group members and in this case it might result in detectable variation of central/high ranking individuals' position within the network (Cheney and Seyfarth, 1990; Borgeaud et al., in preparation). We also tested homophilic bonds (**Figure 1C**) to know if individuals preferably associate with individuals of similar attributes such as sex, matriline, hierarchy, and age. As females are the philopatric sex and normally remain in their natal group throughout their lives (Cheney and Seyfarth, 1990), we expected them to form stronger bonds with other females rather than with males. As juveniles from the same generation spend at least 4 years within the same group before a potential migration (i.e., for the males) and as adult females have spent many years within the same group (Cheney and Seyfarth, 1990), we expected individuals from similar age to form stronger bonds (Silk et al., 2010). We also expected individuals of similar rank in the hierarchy to form stronger bonds than individuals of distant rank as usually neighboring ranks are more closely related (Cheney and Seyfarth, 1990). Furthermore, as hypothesized by Seyfarth (1977), if high-ranking females are indeed preferred grooming partners, competition may limit the access to high-ranking partners only to neighboring rank individuals (Silk et al., 2006a,b). Finally, we examined how the different group members' relationships according to the same individual attributes are prone to variation over time. As indicated by Silk et al. (2010), adult female baboons form strong and stable bonds with their kin and with females of similar age. We therefore expected the same for female vervet monkeys while males' relationships should be more prone to variation.

METHODS

Study Groups

The study was conducted from January 2012 until December 2013 at the Inkawu Vervet Project, Mawana game reserve (S 28° 00.327; E 031° 12.348), Kwazulu Natal, South Africa. Subjects were three habituated groups of wild vervet monkeys. All individuals were recognized individually through facial and body features. Observers were all requested to pass an identification test and data were collected only if the identity of the individual was certain. We considered females as adults as soon as they had their first infant and males as adults once they migrated from their natal group. Individuals were considered as juveniles (including sub-adults, i.e., generally 3 years old females before they give birth and males before they emigrate) from the age of 1 until adulthood and as infants up to 1 year old. All three groups had been regularly followed since 2010, allowing us to have a good estimation of their age, although for the analyses we considered only two age categories: adult or juvenile while infants were excluded. The size of the Ankhase (AK) group excluding infants varied from 26 to 33 individuals (including from 4 to 7 adult males, 6 to 8 adult females, and 12 to 19 juveniles), Baie Dankie (BD) group varied from 36 to 48 individuals (4 to 5 adult males, 11 to 14 adult females, and 19 to 33 juveniles), and the Noha (NH) group varied from 25 to 41 individuals (2 to 7 adult males, 11 to 12 adult females, and 11 to 25 juveniles) (see **Table 1** for group composition). Hierarchy was assessed by the creation of matrices based on dyadic aggressive interactions (i.e., winner-loser) occurring either in a natural context or around various food experiments. Rank relationships were assessed through the

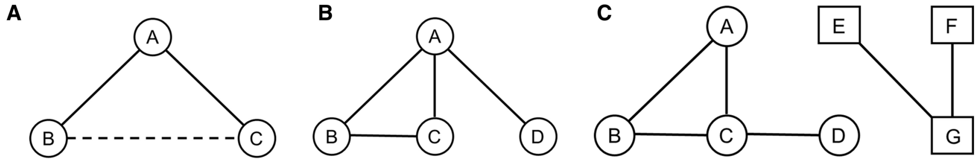

FIGURE 1 | Representations of (A) Triadic closure: If A and B are connected, the probability of B and C being connected is increased; (B) Degree popularity: A being more connected has a higher degree popularity than B, C, and D; (C) Homophily: A, B, C, and D are more connected to each other as they have similar attribute characteristics such as hierarchy for example than they are connected to E, F, and G who themselves have similar attribute characteristics.

TABLE 1 | Group composition.

	Group		
	AK	BD	NH
Adult males	4–7	4–5	2–7
Adult females	6–8	11–14	11–12
Juveniles and subadults	12–19	19–33	11–25
Total	26–33	36–48	25–41

"de Vries" (1998) methodology. The "I&SI" method of de Vries (1998), in which parts of the hierarchy that are unresolved by the "I" method (Slater, 1961, which minimizes the number of inconsistencies) are decided by minimizing the sum of the rank differences between individuals whose ranks are inconsistent, gave us a list of individuals from the most to the less dominant one. The female hierarchy remained stable during the study period, while the male one was highly variable across 3 months periods.

Data Collection

Grooming, 1 and 5 m proximity data were collected through the method of scan sampling (Altmann, 1974) during two full days per week per group. Every 30 min and during a window of 10 min, observers walked within the group to collect the behavior of a maximum number of individuals (except infants). For each scanned individual the identity of all the individuals present within 1 and 5 m of it was also recorded. As data were collected by multiple observers, an inter-observer reliability test was performed for each observer and for each category of data to reduce any bias. The threshold of reliability was set to a minimum of 80%. In total we analyzed 3 months periods over 2 years which equals a total of 8 different periods. In the AK group we collected 31,661 scans, in BD 28,548 and in NH 28,448. Data were collected on handheld computers (Palm Zire 22 or TX, PDA 32 and Pocket pc HP Travel Companion iPAQ rx5935) equipped with the Pendragon 5.1 software.

SIENA Model and Statistical Analyses

SIENA Model (Simulation Investigation for Empirical Network Analysis; Snijders et al., 2010) is a log-linear dynamic model based on Markov processes that allows longitudinal network analysis. It uses an iterative stochastic simulation algorithm in three phases (calculating, updating, and re-calculating) as a Diffusion model updating statistical values after each iteration, making it a powerful method to find significant effects (effects that are greater than expected based on random models) and decreasing probabilities to find false positives (an effect that does really not exist) or false negatives (absence of effect that should be present).

Concerning actors, the model is based on the purposive action. Actors are considered as aware of the state of the network as a whole. They make choices and they can opt for creating, maintaining, or deleting an association in order to optimize their position within the group. These choices are done independently but can be constrained by endogen effects (i.e., relational structuring processes that depend on relational choices made by all the actors but independent from individual characteristics), hexogen effects (i.e., individual attributes such as sex or age), and some random effects.

As for the network, SIENA proposes a statistical model for longitudinal data analysis that requires at least two observations of the state of a network at two consecutive moments. The model supposes that some observations are missing between the two moments and that changes occur on a linear time basis through small steps between the two states observed. Thus, the model is based on Markov chains with linear time in which the future state of the network is linked to the previous state.

Siena only runs on binary matrices (existence or absence of links). In order to turn our valued matrices into binary matrices we used the protocol established by Fedurek et al. (2013) to create a mutual preferred social patterns index based on multiple social indices (i.e., grooming and proximity). The first step of this protocol consists of establishing a threshold for each one of the eight matrices for the three behaviors (grooming, 1 and 5 m proximity). The threshold is based on one-third standard deviation larger than the average for each behavioral matrix. The second and final step consists in considering the dyads as mutual preferred social partners if they were mutual associates for at least two of the three different behavioral matrices at a given time point (Fedurek et al., 2013; Levé et al., 2016). We repeated this protocol for each of the three groups.

The dependent variable here is the change in network relations with an analysis of factors influencing network changes over time. This network modeling aims to explain the network from the links and the actors it is composed of and also to explain the emergence, the pattern, and the evolution of relations within the network. To determine whether effects are significant or not, RSiena applies a stochastic simulation algorithm. The procedure consists of simulating many networks to observe if the value of the effects in these simulated networks is different or not from the observed network. Simulation allows us to obtain two parameters, the estimate and the standard error. To obtain the significance of the effect we performed a Wald-type test (based on the parameter estimate and the covariance matrix). Under the null hypothesis that parameter is zero with approximately a standard normal distribution. See Ripley et al. (2011) for more information about this procedure.

The network evaluation function (analysis of the probability of changes in the links according to some patterns called factors in RSiena) for an actor I is defined by:

$$f_i^{net}(x) = \sum_k \beta_k^{net} s_{ik}^{net}(x) \tag{1}$$

Where β_k^{net} are the parameters and s_{ik}^{net} are the effects chosen by the user (in this research the "TransTrip," " InPop," and "SimX" effects are described above respectively in Equations (2–4).

The analytical protocol consisted in adding the effects one by one, and testing the significance of the effect after each addition. The effect was retained when significant, otherwise it was simply removed from the model.

The first effect tested in the model was one potential structural effects: the "TransTrip," which give information about phenomenon of triadic closure process (TC):

- TransTrip (i.e., TC) effect analyses individuals' transitivity (i.e.,). It is calculated by the number of transitive triplets among relations of *i* (*i* is linked to *j* and *h*, and these are linked to each other). It describes the ≪ friends of my friends are my friends ≫ phenomenon. The TransTrip effect formula is as follows:

$$s_{ik}^{net}(x) = \sum_{j,h} x_{ij}x_{ih}x_{jh} \tag{2}$$

For this effect the contribution of the relation $i \rightarrow j$ is proportional to the total number of transitive triplets formed, which can be ($i \rightarrow j \rightarrow h$; $i \rightarrow h$) or ($i \rightarrow h \rightarrow j$; $i \rightarrow j$).

The second effect tested in the model was another potential structural effects: "InPop," which give information about growth-preferential association (PA).

- The inPop (i.e., PA) effect analyses individuals' ≪ popularity ≫ [i.e., defined by summing relations received by actors *j (degree)* whom *i* is linked to]. In our case as the networks are undirected we can consider this effect as degree popularity. It is calculated by the sum of in-degrees of the individual whom *i* is linked to. Popularity effect discloses individuals' preference to be linked to popular actors (i.e., individuals with highest degrees receive more incoming links). The inPop effect formula is as follows:

$$s_{ik}^{net}(x) = \sum_{i} x_{ij} \sum_{h} x_{hj} \tag{3}$$

Then we investigated the influence of covariate factors one by one by analyzing the "SimX" effects according to sex, matriline hierarchical rank and age, which give information about the tendency of individuals to create relations with individuals with similar attributes. This effect can be seen as an analysis of homophily or heterophily processes. Calculation details of this effect are described above and further information can be found in SIENA manual (Ripley et al., 2011).

- The covariate-related similarity (SimX) effect is the sum of centered similarity scores sim_{ij}^{v} between *i* and the other actors *j* to whom he is tied according to the covariate *v*. The SimX effect formula is as follows:

$$s_{ik}^{net}(x) = \sum_{j} x_{ij}(sim_{ij}^{v} - \widehat{sim}^{v}) \tag{4}$$

Where $\widehat{\mathrm{sim}}^{\mathrm{v}}$ is the mean of all similarity scores.

For each one of this "SimX" effects we added at the same time the "Covariate-ego × alter" effect in order to control unequal ties between groups. The "Covariate-ego × alter" effect is simply the product of I's covariate and sum of his alters. To consider the effect as significant, both "SimX" and "Covariate-ego × alter" effects have to be significant.

Finally, we investigated the rate function effect according to sex, matriline, hierarchy and age one by one. The network rate function analyses how fast interactions change according to individual attributes (e.g., females have higher rate changes than males) for an actor *i*. This function is restricted to positive values as product of exponential elements. It can be defined by:

$$\lambda_i^{net}(\rho, \alpha, x, m) = \lambda_{i1}^{net}\lambda_{i2}^{net}\lambda_{i3}^{net},\ for\ x = x(t),\ t_m \leq t < t_{m+1} \tag{5}$$

With $\lambda_{i1}^{net} = \rho_m^{net}$ representing the dependence of the period, $\lambda_{i2}^{net} = \exp(\sum_h \alpha_h v_{hi})$ representing the effect of actor covariates (v_{hi} as the factor and α_h as the dependence of the degree) and $\lambda_{i3}^{net} = \exp(\alpha_h + x_i)$ representing the contribution of the degree (actor's personal network). Where ρ is the basic rate parameter, α is the dependence of the degree, m is the period (number of observation minus one), and t is the time point.

Models that included all the effects did not provide accurate goodness of fit analyses. For each group, we therefore realized a global model built up step by step by adding and testing the significance of one effect at a time. Once we obtained the final model for each group, we ran a goodness-of-fit test to assess if our model was significantly different from the observational data. We run a one-tailed Monte Carlo Mahalanobis distance test. After controlling for unequal ties between groups, such methodology led to the disappearance of the "hierarchy" attribute effect within the whole model and the "age" effect when testing the presence of homophilic bonds (**Table 2**). We therefore present only significant results below but discuss the absence of these effects within our global model further below. Goodness of fit plots for the degree distribution, the geodesic distribution and the triad census for each group are also presented in the **Supplementary Figure 1**.

RESULTS

First of all, the goodness of fit analyses indicated that our model selection was reasonably accurate for all three groups, AK (MHD = 156.51; $P = 0.054$), BD (MHD = 126.65; $P = 0.425$), and NH (MHD = 77.17; $P = 0.434$).

When analyzing the structure of the network, all three groups showed a significant effect of triadic closure (AK: $\chi^2 = 7.794$; DF = 1; $p = 0.029$; BD: $\chi^2 = 21.573$; DF = 1; $P < 0.001$; NH: $\chi^2 = 53.561$; DF = 1; $P < 0.001$, **Table 2**), while there was a significant effect of degree popularity in only two groups (AK: $\chi^2 = 3.918$; DF = 1; $P = 0.048$; BD: $\chi^2 = 4.228$; DF = 1; $P = 0.039$; **Table 2**).

With respect to the structure, when analyzing the likelihood of homophilic bonds according to the different attributes, we could not find any general pattern across all three groups. Only the AK ($\chi^2 = 8.615$; DF = 1; $P = 0.003$) and the NH ($\chi^2 = 21.719$; DF = 1; $P < 0.001$) group members showed a significant

TABLE 2 | Stochastic actor-oriented model, results summary.

	AK						BD						NH					
	Estimate	**Std error**	***t* ratio**	**X2**	**DF**	***P*-value**	**Estimate**	**Std error**	***t* ratio**	**X2**	**DF**	***P*-value**	**Estimate**	**Std error**	***t* ratio**	**X2**	**DF**	***P* value**
Transitive triplets	0.08	0.04	0.11	4.794	1	**0.029**	0.24	0.05	0.08	21.573	1	**<0.001**	0.27	0.04	−0.02	53.561	1	**<0.001**
Degree popularity	−1.02	0.18	0.12	3.918	1	**0.048**	0.06	0.03	0.09	4.228	1	**0.039**				0.131	1	0.718
Same sex	−0.5	0.17	0.1	8.615	1	**0.003**				0.003	1	0.986	-1.84	0.4	-0.01	21.719	1	**<0.001**
Ego sex effect	1.06	0.28	0.01	14.514	1	**<0.001**				0.002	1	0.963	3.83	0.76	0.03	25.452	*1*	***<0.001***
Same matriline				28.608	1	<0.001	0.83	0.13	0.01	41.833	1	**<0.001**	0.98	0.12	0.03	71.463	1	**<0.001**
Ego matriline effect				1.235	1	0.266	0.01	<0.001	0.05	7.045	1	**0.008**	0.02	0.01	<−0.001	8.309	1	**0.004**
Same hierarchy				2.715	1	0.099				5.486	1	0.019				19.866	1	<0.001
Ego hierarchy effect				0.156	1	0.692				0.017	1	0.898				0.423	1	0.515
Same age				0.029	1	0.864				0.322	1	0.57				4.531	1	0.033
Ego age effect				0.003	1	0.957				0.206	1	0.65				1.762	1	0.184
Rate effect on sex on rate	0.66	0.22	−0.14	9.048	1	**0.003**	0.98	0.23	0.03	17.889	1	**<0.001**				0.406	1	0.524
Rate effect on matriline on rate				2.774	1	0.096	-0.1	0.03	0.08	12.276	1	**<0.001**				1.147	1	0.284
Rate effect on hierarchy on rate				0.716	1	0.397				0.53	1	0.466				0.741	1	0.389
Rate effect on age on rate				1.236	1	0.266				1.001	1	0.317	0.64	0.19	0.03	11.334	1	**<0.001**

Significant effects are represented in bold and the estimate, the standard error and the t ratio are also given for these effects.
For the homophily, the effect is considered as significant only if both main (i.e., sex, matriline, hierarchy, and age) and the ego effects are significant.

preference of association to individuals of the same sex while preference of association with the same matriline was present only in the BD ($\chi^2 = 41.833$; DF = 1; $P < 0.001$) and NH ($\chi^2 = 71.463$; DF = 1; $P < 0.001$; **Table 2**) groups.

Finally, when looking at the network dynamics with relationships variation over time, results indicated a strong intergroup variation. In the AK groups, we found that females experience a greater and quicker relationships' variation than males do ($\chi^2 = 9.048$; DF = 1; $P = 0.003$) while for the BD group there was a significant effect of sex and matriline, suggesting that males' relationships are more prone to variation than females' ($\chi^2 = 17.889$; DF = 1; $P < 0.001$) and that high-ranking matrilines also experience a greater variation in their relationships stability ($\chi^2 = 12.276$; DF = 1; $P < 0.001$). Only in the NH group, we found that juveniles' relationships were more prone to variation than adults' ($\chi^2 = 11.334$; DF = 1; $P < 0.001$; **Table 2**).

DISCUSSION

In this study we tried to understand the dynamics of a social network through detailed analysis of the creation and destruction of relationships over time according to the following individual attributes: sex, matriline, hierarchy, and age. Main results indicate that individuals associate themselves with friends of their friends but many differences exist between the three groups. To our knowledge, this is the first study that uses a SAOM to analyze such dynamics on multiple and non-experimental groups. Indeed, another study (Ilany et al., 2015) already used such a model, but focused on only one group of hyenas and the effects of ecological variables. RSiena package was also used to understand social information transmission in experimental groups of drosophila (Pasquaretta et al., 2016). Our results show the importance of observing multiple groups when we want to assess the effect of different social variables on the temporal evolution of a network structure.

The analyses on triadic closure (which represents the likelihood of two individuals to be associated if they have a mutual third party associate) indicated that such effect was present in all three groups. According to some hypotheses, triadic closure might facilitate the evolution of cooperation (Banks and Carley, 1996; Davidsen et al., 2002; Righi and Takacs, 2014). For example, someone might be more likely to become friends with and potentially help a friend of a friend. This suggests that vervet monkeys' social system met the conditions for the emergence of triadic closure (Lusseau et al., 2006). In animals, only one study focused on how the triadic associations influence a social network structure (Ilany et al., 2013). However, what remains unknown with such theory is if triadic closure is the evolutionary consequence or the prerequisite of cooperation. More studies are needed to understand whether triadic closure is a by-product of social network or relatedness or is a social strategy leading to better cooperation between multiple partners. The degree popularity results, which represent the preferred association to highly central individuals, indicate that individuals try to bond with individuals that are central within a network, but this effect was found only in two groups. This pattern results in more centralized networks having great impact on information and disease transmission and several researches are done to understand whether and how natural selection might impact these social network properties (Pasquaretta et al., 2014; Duboscq et al., 2016; Romano et al., 2016). As multiple previous studies found a positive correlation between rank and/or matriline and centrality (Schino, 2001; Kanngiesser et al., 2011; Sueur et al., 2011a; Borgeaud et al., in preparation), our results partially support the generality of Seyfarth's model (1977). This model also suggests that grooming can be exchanged against tolerance among food resources or coalitionary support, which seems to exist in vervet monkeys (Borgeaud and Bshary, 2015). Central individuals are either high-ranking individuals, either close relatives or experienced individuals (Sueur et al., 2011b). In this way we can easily understand how preferred association to central individuals might be selected as a social strategy increasing fitness but still, we can observe that this effect is dependent on group composition. However, it should be noted that some studies fail to provide evidence for degree popularity, including in vervet monkeys (Henzi et al., 2013), as we do for one of the study groups.

We also tested if individuals associated preferably with individuals of similar attributes. After controlling for the differences in sex ratio (Female ratio: AK: 44; BD: 56; NH: 50%), our results surprisingly indicate that females form stronger bonds between themselves rather than with males only in the AK and NH groups. These results confirm that individuals of the philopatric sex, which normally remain in their natal group throughout their lives form strong and long-lasting bonds with each other (Cheney and Seyfarth, 1990; Silk et al., 2010). However, it remains challenging to explain the absence of significant results in the BD group. One explanation could rely on the presence of multiple adult males who, in contrary to the other groups were already present within the group at the beginning of the project in 2010 and remained within the group for a large part of the study. In this situation and at least on the time period of our study, females might have developed strong and long lasting relationships with these males. Similarly, our results suggest that members from the same matriline form stronger bonds than members of different matrilines, but only in the BD and NH groups. The positive results fit predictions by kin selection (Hamilton, 1964), while it remains unclear why such an effect should be absent in the AK group. In contrary to these two groups, the AK group is generally more tolerant and females of distant ranks regularly groom each other (Borgeaud and Bshary, 2015), which could reflect the results of this study. Tolerance between non kin was shown to be an advantage to decrease risk injuries, energy costs to maintain social relationships, or increase food research efficiency (Sueur et al., 2011a,b; Fushing et al., 2013; Pasquaretta et al., 2014). Preliminary results on genetics indicate that the average relatedness from the AK group members is 0.25 while both BD and NH are related at the level of 0.15 (Schnider et al., unpublished data). These results support previous results indicating that kin form stronger bonds than non kin individuals (Silk et al., 2010). We did not find any effect of hierarchy on bonds' strength. This suggests that individuals of close ranks either do not have stronger bonds than individuals of distant ranks or they have stronger bonds but this effect is undone by the more important effects of sex and matriline. As our analyses include both males and females, another explanation could be that high-ranking males may bond as much with high-ranking than with low-ranking females, canceling a potential rank effect. Finally, our lack of results about association between individuals of similar age is rather surprising as this difference cannot really be explained by a difference in age ratio (Adult age ratio: AK: 43; BD: 31; NH: 42%). Previous studies suggested the importance of bonds with individuals of similar age. For example juveniles' play-fights allow the development of the social techniques necessary to acquire a central position in a society (Shimada and Sueur, 2014). On the other hand it might simply reflect that, despite the age difference, bonds between a mother and her offspring are the strongest of all associations, which has also been found in baboons (Silk et al., 2010). Another explanation could rely on the fact that our juvenile age category included 1–4 years olds and it is likely that they form stronger bonds within rather than across generations.

Finally, when testing how quickly relationships are modified according to the individual attributes, we found no patterns that were consistent among our three groups. In both AK and BD groups, females' relationships are more prone to variation than the males' and in BD the relationships of individuals belonging to high-ranking matrilines were also less stable. This supports the Seyfarth's model (1977) which implies a potential instability of higher ranking individuals' relationships due to social competition. The BD group was the only one where the high-ranking matrilines had a significant influence on how quickly relationships were modified. Similarly, previous studies found differences between populations in their relationships management (Silk et al., 1999; Henzi et al., 2013). Finally, in the NH group, our results suggest that adults' relationships are more stable than those of juveniles. These results support previous studies in baboons (Silk et al., 2006a,b, 2010, 2012), which indicate stable relationships within adult females. Female juveniles in vervet monkeys form strong and rather stable relationships with adult females while male juveniles' relationships are more prone to variation (Fairbanks, 2002; juvenile vervet monkeys). However, the fact that such results are significant only in one group is rather puzzling but could be due to group differences in relationships management and group composition (Cronin et al., 2014a,b).

We based our evaluation of effect size entirely on the distinction "significant effect" vs. "non-significant effect" and the size of the estimate. In the future, it would be interesting to test multiple groups simultaneously following the "multilevel" SAOM method that has been recently developed (Snijders et al., 2013). To our knowledge this is the first time that a study focuses on the social network dynamics of three different groups of monkeys. Interestingly, our results indicate substantial intergroup variation. This variation might be due to (1) real intergroup difference, (2) problem in methodology, (3) non powerful statistical analyses. However, we made considerable efforts to apply the same scoring methods on the three groups. Despite this effort, various *p*-values were either non-significant or so very small (<0.001) and seems to indicate that groups differed indeed with respect to various variables. However, we currently cannot test how much intergroup variation could be due to differences in genetic relatedness. On the other hand, a purely ecological explanation seems unlikely as all three groups live in overlapping home ranges. In part, the differences could also be due to different individual strategies and/or personalities, which could have various impacts on the network variation depending of their position within this network (Cronin et al., 2014a,b). Such a cause of variation would indeed be interesting. In any case, our results suggest that studies on multiple groups are necessary to build up any hypothesis concerning network features and dynamics within a species.

Most primates live in closely related and bonded social groups in which individuals have to deal with many social challenges and opportunities (Humphrey, 1976; Harcourt, 1988). Famously, Humphrey (1976) proposed that large brains evolved in primates primarily to cope with the social environment as it is less predictable than the physical environment. This idea has been developed further in the Machiavellian intelligence and social brain hypotheses (Byrne and Whiten, 1988; Dunbar, 1992; Whiten and Byrne, 1997). Therefore, the complexity of a species' social network may be a good indicator for the cognitive demands that individuals face and be reflected in the complexity of the species' brain. To be able to test this hypothesis, we first need to establish methods on how to measure different aspects of network complexity (Lehmann and Dunbar, 2009). The methods we used rely on quantifying the dynamics of relationships patterns according to individual attributes while considering changes in group composition. These analyses could be applied to a variety of species. Ultimately such measures should allow a comparison between species to assess how network dynamics is correlated with brain complexity. In this context, the observed variation among group network structures may turn out to be an indicator of great social flexibility that demands a social brain.

ETHICS STATEMENT

The study was approved by the relevant authority, Ezemvelo KZN Wildlife and by the University of Cape Town, South Africa.

AUTHOR CONTRIBUTIONS

Data collection: CB and Ev; writing: first version by CB, then all authors contributed; statistical analyses: SS and CS; funding for data collection by SNF Sinergia grant to RB.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fpsyg.2016.00915

Supplementary Figure 1 | Goodness of fit plots for the degree distribution, the geodesic distribution, and the triad census for each group.

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The Influence of Gender, Age, Matriline and Hierarchical Rank on Individual Social Position, Role and Interactional Patterns in *Macaca sylvanus* at 'La Forêt des Singes': A Multilevel Social Network Approach

Sebastian Sosa*

Formerly affiliated with Grupo de Conducta Adaptativa e Interacción, Psychology Faculty, University of Barcelona, Barcelona, Spain

Edited by:
Cédric Sueur,
Institut Pluridisciplinaire Hubert Curien, France

Reviewed by:
Ikki Matsuda,
Kyoto University, Japan
Borbala Foris,
Leibniz Institute for Farm Animal Biology, Germany

Correspondence:
Sebastian Sosa
s.sosa@live.fr

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A society is a complex system composed of individuals that can be characterized by their own attributes that influence their behaviors. In this study, a specific analytical protocol based on social network analysis was adopted to investigate the influence of four attributes (gender, age, matriline, and hierarchical rank) on affiliative (allogrooming) and agonistic networks in a non-human primate species, *Macaca sylvanus*, at the park La Forêt des Singes in France. The results show significant differences with respect to the position (i.e., centric, peripheral) and role (i.e., implication in the network cohesiveness) of an individual within a social network and hence interactional patterns. Females are more central, more active, and have a denser ego network in the affiliative social network tan males; thus, they contribute in a greater way to the cohesive structure of the network. High-ranking individuals are likely to receive fewer agonistic behaviors than low-ranking individuals, and high-ranking females receive more allogrooming. I also observe homophily for affiliative interactions regarding all attributes and homophily for agonistic interactions regarding gender and age. Revealing the positions, the roles, and the interactional behavioral patterns of individuals can help understand the mechanisms that shape the overall structure of a social network.

Keywords: social network analysis, multilevel analysis, non-human primate, allogrooming, antagonism, individual attributes, homophily

INTRODUCTION

Animal societies are complex systems in which individuals have non-random and complex interactions, and are likely to develop behavioral strategies (Dunbar, 1989). This leads to the formation of a multilayered and multi-behavioral structure. However, questions persist about the fundamental evolutionary process by which a society emerges, stabilizes, and adapts.

Previous studies of animal species, including human and non-human primates, have investigated the behavioral differences and interactions among individuals according to attributes such as gender (Fedigan, 1982), age (Wey and Blumstein, 2010), body size (Archie et al., 2006), social status (Bergman and Moore, 2003), reproductive state (Cavigelli and Pereira, 2000), and kinship (Widdig et al., 2001). This study focuses on four specific attributes: gender, age, matriline (matrilineal kinship), and hierarchical rank.

Differences in gender lead to contrasting reproductive (Fragaszy and Mitchell, 1974; Fedigan and Baxter, 1984; Pereira, 1988; Cords, 2002) and behavioral strategies (Fedigan, 1982), and in particular, the expression of aggressiveness and allogrooming.

Age, or more precisely, ontogenesis (i.e., the development of an organism), influences the evolution and development of social relations and species-specific behaviors that are largely affected by interactional experiences with congeners (Harlow and Suomi, 1974; Hinde, 1974; Wilson, 1980; Shimada and Sueur, 2014). For example, hierarchical rank acquisition appears to be closely related to age (Borries et al., 1991) and the early experiences of juveniles (Mitchell et al., 1967; Olds et al., 1997). However, this influence differs according to species and gender (Sosa, 2015). Additionally, older individuals and females in particular are more likely to experience social exclusion (i.e., decrease in social interactions) (Hauser and Tyrrell, 1984).

One major kinship phenomenon among the animal kingdom is the matrilineal rank inheritance (MRI) (Kawamura, 1958) observed in macaques. It consists of the transmission of hierarchical rank from mother to daughter; the latter acquires the hierarchical rank directly below that of her mother. In addition, as according to the youngest ascendancy rule, young females outrank their older sisters (Thierry et al., 2004). The MRI process is made possible by nepotism, in that related females support each other during conflicts against non-kin females and help juvenile females outrank their older sisters (Cheney, 1977; Datta, 1983; Chapais and Gauthier, 1993). Furthermore, an adult female can outrank her mother when she is old and subsequently lacks kin support and has limited physical ability (Chapais and Berman, 2004). See Chapais and Berman (2004) and Hepper (2005) for an overview.

Social network analysis (SNA) is one approach used to analyze systems (Sueur et al., 2011) as complex as animal societies. SNA was first applied in psychological studies and, for a few decades, in animal social research (see Prell, 2011 and Brent et al., 2011 for an overview of SNA epistemology). However, certain methodological precautions must be taken when using any of the various analytical techniques based on SNA (Wasserman and Faust, 1994; Krause et al., 2009; Brent et al., 2011). In this study, I describe an analytical protocol based on SNA tools that compensates for the intrinsic limitations of animal behavioral data (i.e., dependency of data) and allows the analysis of weighted networks (network with weighted links).

Several studies have used SNA tools to examine the position and role of group members in non-human primates and other animal species. Lusseau and Newman (2004) revealed that central individuals are key players in maintaining social cohesion and have greater knowledge of their environment. In some non-human primate societies, central individuals are high-ranking animals (Kanngiesser et al., 2011). Using an interspecific comparative approach, several studies have analyzed network metric variations and succeeded in linking them to variability in social structure and dominance style (Sade, 1972; Voelkl and Noe, 2008; Sueur et al., 2011). Previous studies have also found that individuals from the philopatric gender are more central within a network (Smuts, 1985; Matsuda et al., 2012). In this way, central individuals play an important role in group cohesion and their position depends on several individual characteristics. Thus, identifying these central individuals according to their attributes could allow us to better understand how a social structure is shaped.

SNA research also addresses the principles of homophily and heterophily that refer to preferential interactions between similar (homophily) or dissimilar (heterophily) individuals (Lazarsfeld and Merton, 1954). These phenomena have been observed in many animal species: cetaceans (Lusseau and Newman, 2004), fishes (Croft et al., 2005), marmots (Wey and Blumstein, 2010), and human (McPherson et al., 2001) and non-human primates (Silk, 2001; Cords, 2002; Carter et al., 2015). However, animal research has generally disclosed the existence of homophily for one behavior as related to a single attribute. In this study, I examine the existence and level of homophily as related to a variety of behaviors and attributes. Moreover, revealing such a phenomenon may help us understand how individuals build their networks depending on the attributes of other individuals.

Macaca (*Macaca* sp.) societies are characterized by their common social organization, but they are also known for their different social styles. Extensive research has shown that dominance hierarchies vary greatly in the macaque genus (i.e., dominance styles) (De Waal and Luttrell, 1989; Thierry et al., 2000; Sueur et al., 2011). Furthermore, the hierarchical structure of females in the *Macaca* taxon is a well-studied phenomenon that appears to be entirely dependent on the MRI (Thierry et al., 2000). In contrast, each *Macaca* species has stable multi-male, multi-female, and multi-generational social groups in which females are philopatric and males migrate. These common characteristics allow the elucidation of the influence of individual attributes on the interactions between individuals and represents an excellent biological model for this study.

In this study, I use SNA tools to determine individual positions and interactional patterns according to four specific attributes (age, gender, matriline, and hierarchical rank) in affiliative and agonistic networks in *M. sylvanus*. Based on previous studies, several assumptions can be made in response to the following questions:

(1) Who are the most central individuals? As in many cercopithecines, *M. sylvanus* females are the philopatric gender, which should increase their ability to form denser, stronger, and more perennial networks than males (Smuts, 1985). Thus, they can be expected to be the most active and central individuals in the affiliative network. Exploring such functions could reveal the significance of their role in facilitating group cohesion. Males are generally the more aggressive individuals (Gray, 1971), and therefore should be particularly active and central in the agonistic network.

(2) How age and gender influence the positions and roles of individuals? According to our extensive knowledge of the MRI process, we can expect to observe age-related behavioral variations in females that are highly correlated with their reproductive status (Borries et al., 1991; Chapais, 2004)

and matriline. The social activity of young females would therefore be more intense (affiliatively and agonistically), with a decrease in activity during their latter ontogenesis, which in some cases may lead to social exclusion at an advanced age. In males, a minimum hierarchical level for older individuals may exist that enables them to maintain a certain ranking (Sosa, 2015). Such kinetics among males reduces their chances of experiencing social exclusion and thus they may face only a minor decrease in social activity, position, and role.

(3) Do common interactional patterns exist among individuals according to their attributes? One sociological model predicts attractiveness to high-ranking females (Seyfarth, 1977). However, this model appears subject to variability. It is mainly observed in despotic societies, and attractiveness to low-ranking individuals has been reported in other species (Schino, 2001; Sueur and Petit, 2008). According to these findings, Seyfarth's model should not apply to *M. sylvanus*. I also expect to observe homophily related patterns such as allogrooming that target same-gender and same-age individuals and kin (Hirsch et al., 2012). As for agonistic behaviors, it is difficult to form any hypothesis, but heterophily can be suspected.

Responding to these questions allows to reveal how individual attributes and social structure (gender philopatry) produce behavioral divergences that lead to different positions and roles within the group (question 1), how these deviations evolve with the ontogenesis of an individual (question 2), and by which mechanisms individuals interact among themselves (question 3). This multilevel approach allows for a better understanding of how these different levels shape the overall structure of the society in *M. sylvanus*.

MATERIALS AND METHODS

Study Site and Subjects

The current study was conducted over a period of 4 months (July to October 2011) in the park *La Forêt des singes*, in Rocamadour, France. The 141 *M. sylvanus* individuals in the park are divided into three groups and live in semi-free ranging conditions (Sugiyama, 2015) in a 20 hectare forest. They are fed in foraging areas twice per day and have water *ad libitum*. For more details on the management of the park, refer to de Turckheim and Merz (1984). The demographic data (gender, age, and matriline) were provided by the scientific director of the park, Ms. Ellen Merz. The study focused on one of the three groups. Four newborns were excluded from the observations (three males and one female), so that the number of individuals observed was $N = 52$. The group had a balanced gender ratio of 25 females and 27 males, with an age range between 1 and 25 years old. The individuals were previously identified during 1 month through their tattoos. The observations were conducted with the approval of the park management, an agreement that was subject to the specific condition that I would not directly contact nor handle individuals. As I performed simple observations without any type of intervention, I did not require authorization from the French National Advisory Ethics Committee.

Behavioral Observations

Observations were conducted by repeated focal samplings of 30 min per individual. Each individual was observed approximately 30 times (15 ± 2 h), for 786 observation hours of 52 individuals. Focal sampling time was determined after 2 months of pre-observation. To trade with bias of observation in time of day and feeding time, individuals were observed randomly from 8 am to 5 pm over the 4 months. During the observations, I registered allogrooming and agonistic behaviors (threatening face or growl, charge, avoidance, attack, chase, and aggressive slap, grab, or bite). A complete description of the ethogram of *M. sylvanus* can be found in Hesler and Fischer (2007). An iPad 1 tablet (Inc, 1976) computer and the WhatISee2.0 application (Inc, 2009) were used to register the individuals involved, and the direction, frequency, and duration of the behaviors. Directed and weighted agonistic and allogrooming matrices were built using the obtained behavioral frequencies (**Figure 1**). The overall observation yields a total of 5867 agonistic interactions and 1281 grooming interactions. The agonistic matrices allow us to calculate the hierarchical rank of each individual using David's Score (David, 1987) with R 3.0.1 (Ihaka and Gentleman, 1996) package steepness (de Vries et al., 2006).

Social Network Analyses

Building Matriline Categories

Kinship bonds among individuals were determined using two methods. First, data were provided by the park officials who, along with scientists, have been monitoring the population in the park. Second, matrilines were determined through genetic analyses of mitochondrial DNA using eight microsatellite markers. The collection and analysis of DNA samples were performed by the park authorities. The poor quality of DNA samples made some DNA results uncertain. For this reason, matriline groups were built only with individuals whose relatedness was confirmed based on direct observations and genetic analyses. To conserve only close kinship relationships, only the individuals with the same mother were considered related for each mitochondrial haplotype (**Figure 2**). Thus, individuals whose matrilines were uncertain did not belong to any matriline group (eight males and one female). In addition, matriline results must be carefully considered, as not all individuals were taken into account owing to a lack of information on their kinship bonds.

Data Consideration before Analysis

Collecting data from all members of the same social group led us to the construction of two social networks (agonistic and affiliative) through the existence of multiple interactions. The intrinsic nature of the collected data (interactions between same-group individuals) underlies the non-independence of the data required by inferential statistical techniques (Wasserman and Faust, 1994; Krause et al., 2009; Brent et al., 2011). Several possibilities exist to deal with this fact. Link filtering is commonly

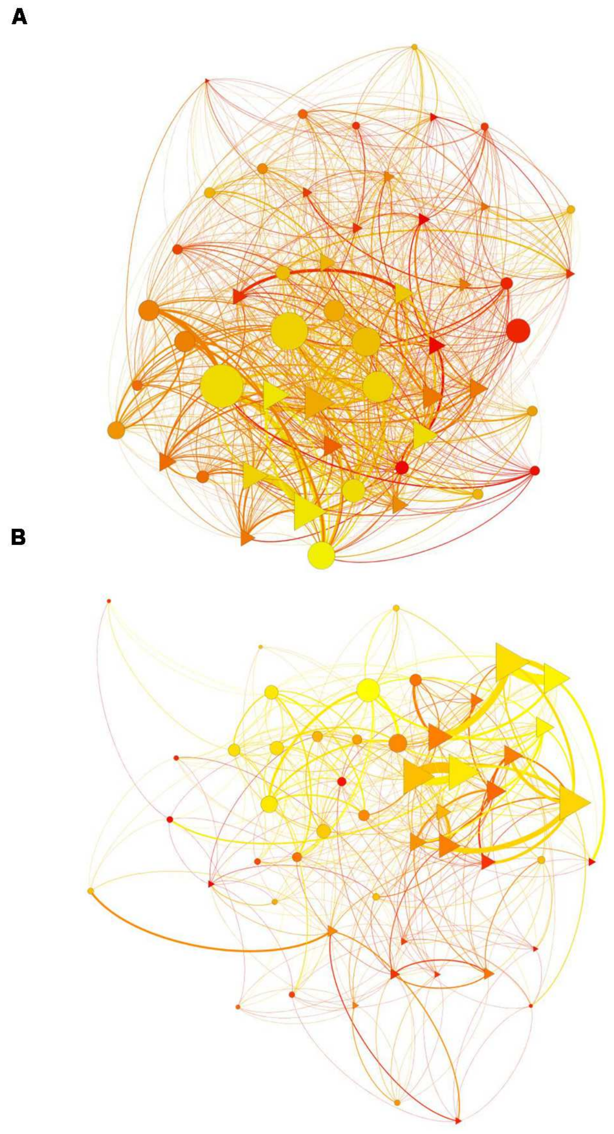

FIGURE 1 | Social networks: (A) agonistic network, (B) allogrooming network. Yifan Hu layout. Gradient color of vertices (from yellow to red) represents individuals' age (from youngest to oldest). Shape of vertices represents individuals' gender (females: triangles; males: circles). Size of vertices represents individuals' degree. Size of edges represents the strength of interactions and the color is in accordance with the age of the individual that gives the behavior.

used in animal SNA to delete interactions that can be attributed to random or "chance" events (Croft et al., 2008). However, at present, this filtering process has not been submitted to any formal methodology and has two major limitations: (1) the non-consideration of weak ties (Granovetter, 1973) and thus the loss of important information (Croft et al., 2011); and (2) the sensitivity to data errors such as misidentification.

The approach adopted in this study is based on permutation tests and may help standardize the analysis of animal behavioral data obtained using SNA. In this study, I assumed an approach that allows analysis without the need to filter the links. To this end, the weight of the links must be taken into consideration, which can be done by using weighted social network metrics (Opsahl, 2009; Brent et al., 2011). Frequency-based data are less prone to sampling biases, yet by themselves, they do not solve the issue of data dependency. Therefore, I used weighted network metrics with Null Hypothesis Significant Tests (NHST) involving a permutation-based approach (Manly, 2006). This method generates a set of random values based on the real data set and creates the null hypothesis that the real structural measure X is not different from the random one. This hypothesis is accepted or rejected by comparing the observed value X to the random one. If the observed value is greater than the random one from 95%, then the null hypothesis is rejected. The use of permutation tests in the study of animal societies is discussed in details by Whitehead (2008) and Croft et al. (2011).

The following analyses were performed on both weighted allogrooming and agonistic matrices with 10000 permutations.

Network Metrics

For each individual, I calculated the following weighted network metrics: indegree, outdegree, degree, eigenvector centrality, and clustering coefficient with Ucinet 6.375 (Borgatti et al., 2002). Briefly, the degree corresponds to the total number of individuals that directly interact with one given individual (Freeman, 1979). The weighted version takes into account the weight of the links. I also differentiated between indegree (incoming ties) and outdegree (outgoing ties). This metric is historically the first and conceptually the simplest centrality network metric, and in this case, can also be considered as the activity, or "involvement," of an individual. The eigenvector centrality index is the sum of the connections to neighbors weighted by their degree. This index provides a metric that determines the individual centrality relative to the rest of the network and the "influence" of an individual on the network (i.e., connection to high-degree nodes) and thus, on the social structure. Additionally, it would appear to be a more pertinent centrality metric for non-human primate groups (Kasper and Voelkl, 2009). The weighted clustering coefficient gives weight to the neighborhood densities proportionate to their size and indicates the contribution of each individual in the connectivity and thus, in the cohesion of the network structure (Watts, 2003; Hanneman and Riddle, 2005). For an overview of the weighted network metrics and calculations, see: Wasserman and Faust (1994), Croft et al. (2008) and Whitehead (2008).

Statistical Analyses

Individual Level

For the first analysis, I aimed to study gender, matriline, hierarchical rank, and age-related changes in each network metric. To this end, I used general linear mixed models (GLMM) in which weighted degrees, indegrees, outdegrees, eigenvectors, and clustering coefficients are the dependent variables in separate models. Exact ages, genders, hierarchical ranks, and matrilines are the independent variables.

To offset the non-independence of these data, I realized GLMM with permutation. The consequent biological null

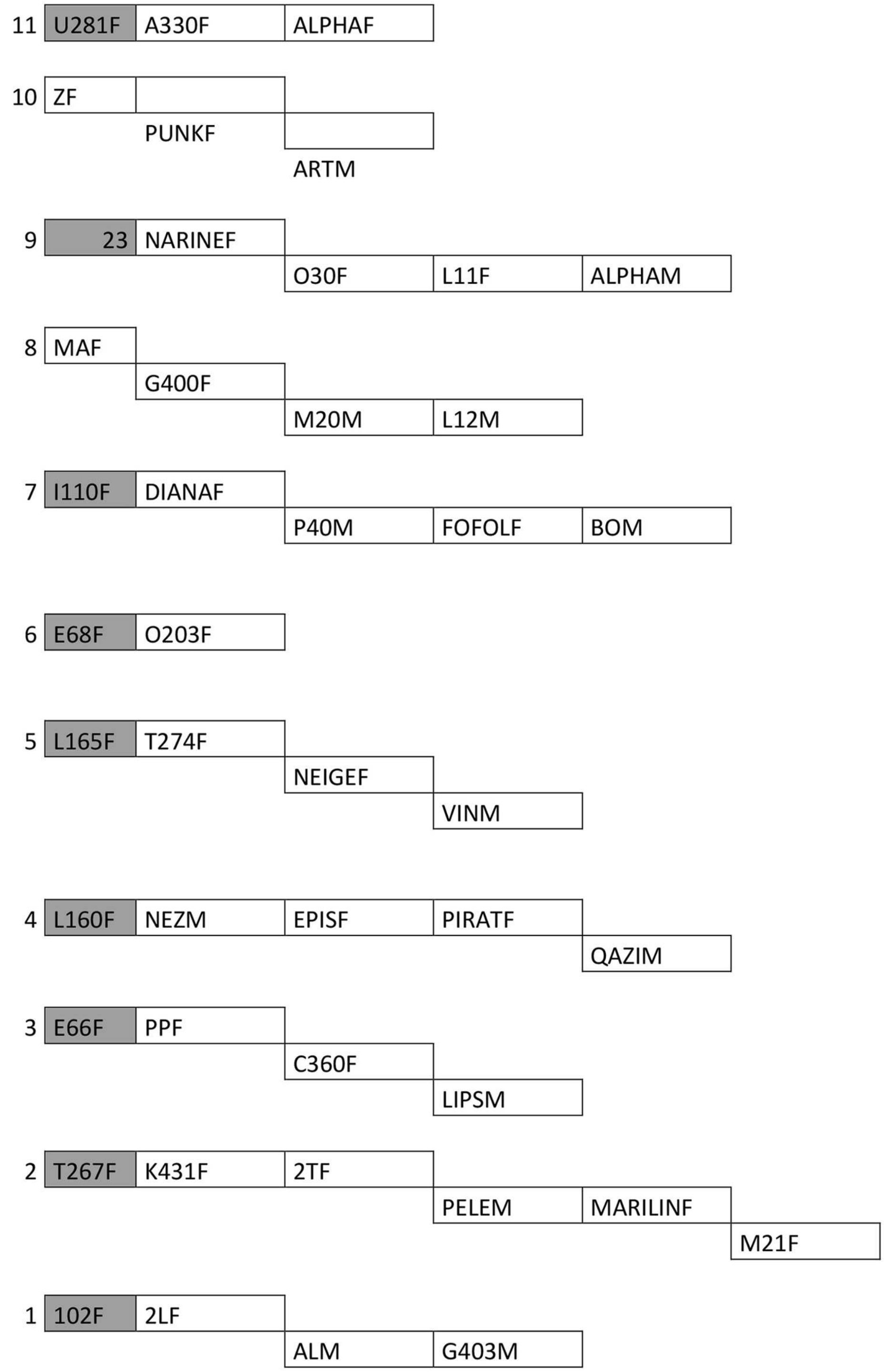

FIGURE 2 | Matrilines. This scheme represents individuals which were kept for kinship analysis. Gray cells are dead individuals. Numbers represent the different matrilines. Each subline represents an offspring of the corresponding mother.

hypothesis was that any individual could have any network metric value. Opting for this method has several advantages. First, it takes into account the non-independency of the data; second, it is a better option than multiple *t*-tests and ANOVA (which both need discrete variables and would increase the number of tests) with permutation or simple correlations; and finally, it facilitates the analysis of the interactions between factors.

Initially, I created two types of models: those with no interactions with the dependent variables and those with gender interacting with other individual attributes to examine whether age, matriline, and hierarchical rank dissimilarly influence individuals according to their gender. Only factors estimated higher than 0.009 were considered significant. This threshold is arbitrary and aims to consider only significant effects with sufficient weight. These analyses were performed using SPSS 17 (SPSS, 2008) GLM Procedure with Bootstrap option of p-value $= 0.05$.

Group Level

The aim of the second analysis was to examine homophily and heterophily, for which I used NHST (Stephens et al., 2007) with permutation.

The principle of homophily, or the preferential interactions between same-attribute individuals, consequently determines whether the links within a same-attribute group have greater frequencies than the links between groups. Thus, to study homophily between genders, I used a simple t-test with permutation for comparing the mean of the links between and within the groups depending on gender.

To study homophily according to age (a continuous attribute), I used the Moran statistic which indexes the differences between the score of an actor and the mean, and then weights the cross products (Moran, 1950). Permutations are used to create a sampling distribution in which scores on the attribute are randomly assigned to actors. As for any permutation test, the real structural measure (the Moran statistic in this case) is compared to the random one (Hanneman and Riddle, 2005). The Moran "I" statistic of autocorrelation ranges from -1.0 (perfect negative correlation) through 0 (no correlation) to $+1.0$ (perfect positive correlation). These analyses were performed using Ucinet 6.375 (Borgatti et al., 2002).

RESULTS

Individual Level

In the agonistic social network, results show that the higher the matriline, the more central (eigenvector: 0.015, $p < 0.05$) and active (degree: 17.866, $p < 0.05$) its members, and the more they receive agonistic behaviors (indegree: 9.857, $p < 0.05$) and contribute to network cohesion (clustering coefficient: 0.077, $p < 0.01$). The results also reveal that the higher the hierarchical rank of an individual, the more it gives agonistic behaviors (outdegree: 6.075, $p < 0.05$), but the less it receives them (indegree: -14.698, $p < 0.01$). Finally, we observe that with age, individuals are less active (degree: -12.529, $p < 0.01$), give less (outdegree: -3.568, $p < 0.05$) and receive fewer (indegree: -8.961, $p < 0.01$) agonistic behaviors. These results are synthetized in **Table 1**.

The results of the agonistic social network model for gender interactions with other individual attributes are as follows (synthetized in **Table 2**, **Figure 3**, Appendix 2 and 3):

TABLE 1 | General linear mixed models (GLMM) for agonistic network metrics.

GLM with Bootstrap for estimates of fixed effects on agonistic network

Network metrics	Factor	Estimate	Standard error	p
Eigenvector	Intercept	0.277	0.065	0.000
	Gender	−0.015	0.026	0.560
	Age	−0.008	0.001	0.000
	Matriline	**0.015**	**0.005**	**0.013**
	Hierarchy	−0.006	0.002	0.035
Clustering coefficient	Intercept	1.767	0.464	0.001
	Gender	0.181	0.183	0.330
	Age	**−0.037**	**0.009**	**0.001**
	Matriline	**0.077**	**0.022**	**0.001**
	Hierarchy	0.021	0.014	0.142
Degree	Intercept	501.027	126.637	0.001
	Gender	−10.413	47.543	0.826
	Age	**−12.529**	**2.219**	**0.000**
	Matriline	**17.866**	**7.515**	**0.049**
	Hierarchy	−8.624	4.056	0.052
Outdegree	Intercept	−52.915	76.476	0.492
	Gender	13.104	31.082	0.674
	Age	**−3.568**	**1.411**	**0.022**
	Matriline	8.010	4.463	0.103
	Hierarchy	**6.075**	**2.547**	**0.040**
Indegree	Intercept	553.942	68.172	0.000
	Gender	−23.517	27.990	0.415
	Age	**−8.961**	**1.529**	**0.000**
	Matriline	**9.857**	**4.129**	**0.039**
	Hierarchy	**−14.698**	**2.052**	**0.000**

In bold, singnificant attributes.

- The eigenvector model shows that for females, the higher the matriline, the more central the individual (0.023, $p < 0.01$). Furthermore, the centrality of females also decreases with their individual hierarchical rank (-0.010, $p < 0.01$).
- The degree model shows that degree significantly decreases with age for females (-12.269, $p < 0.01$), but not for males. Individual degree increases with matriline (30.332, $p < 0.01$) and decreases with hierarchical rank for females only (-14.824, $p < 0.05$).
- The outdegree model shows that outdegree significantly decreases with age (-3.474, $p < 0.05$) for females only. Individual outdegree increases with hierarchical rank for females (7.989, $p < 0.05$).
- The indegree model shows that indegree significantly decreases with age for females (-8.795, $p < 0.01$). Individual indegree increases with matriline (23.783, $p < 0.05$) for females. However, indegree decreases with hierarchical rank for both males and females (males: -18.430, $p < 0.01$; females: -22.813, $p < 0.01$).
- The clustering coefficient model shows that clustering coefficient significantly decreases with age (-0.038, $p < 0.01$) and increases with matriline (0.106, $p < 0.01$) for females only.

TABLE 2 | General linear mixed models for agonistic network metrics for interactions between gender and other individual attributes.

GLM with Bootstrap for estimates of fixed effects on agonistic network				
Network metrics	**Factor**	**Estimate**	**Standard error**	***p***
Eigenvector	Intercept	0.281	0.044	0.000
	Males*Age	−0.009	0.040	0.555
	Females*Age	−0.008	0.001	0.000
	Males*Matriline	0.010	0.012	0.305
	Females*Matriline	**0.023**	**0.005**	**0.000**
	Males*Hierarchy	−0.005	0.011	0.393
	Females*Hierarchy	**−0.010**	**0.003**	**0.004**
Clustering coefficient	Intercept	2.300	0.273	0.000
	Males*Age	0.036	0.162	0.706
	Females*Age	**−0.038**	**0.010**	**0.001**
	Males*Matriline	0.059	0.043	0.111
	Females*Matriline	**0.106**	**0.038**	**0.007**
	Males*Hierarchy	−0.008	0.045	0.792
	Females*Hierarchy	0.005	0.022	0.814
Degree	Intercept	529.526	85.390	0.000
	Males*Age	−12.999	42.661	0.512
	Females*Age	**−12.269**	**2.154**	**0.001**
	Males*Matriline	9.245	17.587	0.527
	Females*Matriline	**30.332**	**8.212**	**0.003**
	Males*Hierarchy	−8.301	13.377	0.349
	Females*Hierarchy	**−14.824**	**5.719**	**0.014**
Outdegree	Intercept	−56.542	52.424	0.242
	Males*Age	−15.798	23.689	0.222
	Females*Age	**−3.474**	**1.375**	**0.031**
	Males*Matriline	5.964	10.263	0.468
	Females*Matriline	6.549	5.537	0.201
	Males*Hierarchy	10.129	7.676	0.087
	Females*Hierarchy	**7.989**	**3.708**	**0.047**
Indegree	Intercept	586.068	48.560	0.000
	Males*Age	2.799	23.371	0.786
	Females*Age	**−8.795**	**1.359**	**0.000**
	Males*Matriline	3.281	9.362	0.666
	Females*Matriline	**23.783**	**4.906**	**0.000**
	Males*Hierarchy	**−18.430**	**7.197**	**0.009**
	Females*Hierarchy	**−22.813**	**3.248**	**0.000**

In bold, significant attributes.

The allogrooming social network is primarily influenced by gender and age, with matriline having no significant effect. We also observe that the higher the hierarchical rank, the more an individual receives allogrooming (indegree: 1.366, $p < 0.05$). Furthermore, with age, individuals are less central (eigenvector: −0.014, $p < 0.01$), less active (degree: −5.625, $p < 0.01$), and give (outdegree: −3.082, $p < 0.01$) and receive (indegree: −2.064, $p < 0.01$) less allogrooming. Interestingly, whereas no significant difference was observed between males and females in the agonistic network, in the allogrooming network, females are more central (eigenvector: 0.231, $p < 0.01$) and more active (degree: 71.708, $p < 0.01$) than males. Allogrooming behaviors are mostly given (outdegree: 32.018, $p < 0.01$) and received by females (indegree: 39.691, $p < 0.01$). These results are synthetized in **Table 3**.

The results of the allogrooming social network model for gender interactions with other individual attributes are as follows (synthetized in **Table 4**, Appendix 4 and 5):

- The eigenvector model shows that eigenvector significantly decreases with age for females (−0.014, $p < 0.01$), but not for males.
- The degree model shows that degree significantly decreases with age for females (−5.836, $p < 0.01$).
- The outdegree model shows that outdegree significantly decreases with age for females (−3.724, $p < 0.01$).
- The indegree model shows that for females, indegree significantly decreases with age (−2.112, $p < 0.01$) and increases with hierarchical rank (2.719, $p < 0.05$).
- The clustering coefficient model shows non-significant results with any individual attribute.

Group Level

With respect to agonistic behaviors, we obtain homophily for gender (difference in means: −1.651, $p < 0.05$) and for age ($I = 0.273$, $p < 0.05$). Testing genders separately, we obtain homophily by age for females ($I = 0.336$, $p < 0.05$) and for males ($I = 0.211$, $p < 0.05$). The results for matriline and individual hierarchical rank were non-significant.

For allogrooming, homophily is observable for gender (difference in means: −1.942, $p < 0.05$) and for age ($I = 0.318$, $p < 0.05$). Testing genders separately to analyze if there are homophilic differences between genders according to age, we obtain homophily by age for females ($I = 0.565$, $p < 0.05$), but we do not obtain significant results for males according to age ($I = 0.100$, $p = 0.106$). Homophily is also observed by matriline ($I = 0.321$, $p < 0.05$) Testing genders separately, we

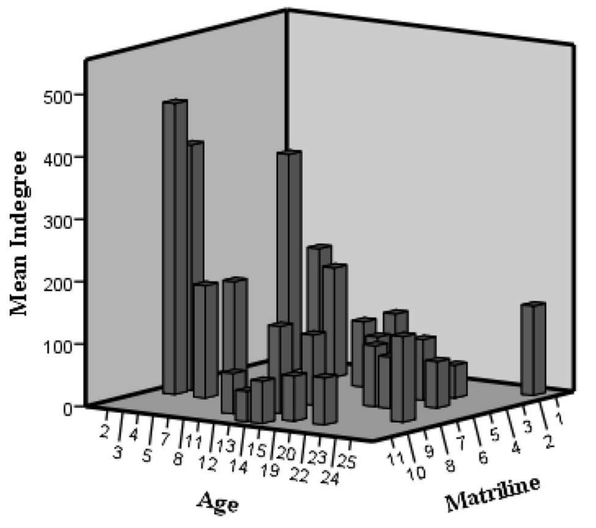

FIGURE 3 | 3D histogram of indegree variation according to age and matriline in the agonistic network.

TABLE 3 | General linear mixed models for allogrooming network metrics.

GLM with Bootstrap for estimates of fixed effects on allogrooming network				
Network metrics	**Factor**	**Estimate**	**Standard error**	***p***
Eigenvector	Intercept	−0.230	0.085	0.015
	Gender	**0.231**	**0.045**	**0.001**
	Age	**−0.014**	**0.003**	**0.002**
	Matriline	0.003	0.004	0.404
	Hierarchy	0.004	0.003	0.122
Clustering	Intercept	−0.007	0.607	0.990
	Gender	0.681	0.321	0.056
	Age	−0.035	0.032	0.362
	Matriline	0.061	0.045	0.206
	Hierarchy	−0.009	0.027	0.734
Degree	Intercept	−12.075	26.373	0.638
	Gender	**71.708**	**14.753**	**0.001**
	Age	**−5.625**	**0.947**	**0.000**
	Matriline	1.210	1.675	0.457
	Hierarchy	0.393	0.840	0.624
Outdegree	Intercept	37.450	12.688	0.007
	Gender	**32.018**	**7.777**	**0.004**
	Age	**−3.560**	**0.475**	**0.000**
	Matriline	0.524	0.907	0.545
	Hierarchy	−0.973	0.425	0.027
Indegree	Intercept	−49.525	18.027	0.011
	Gender	**39.691**	**8.388**	**0.001**
	Age	**−2.064**	**0.518**	**0.002**
	Matriline	0.686	0.931	0.437
	Hierarchy	**1.366**	**0.522**	**0.012**

In bold, significant attributes.

TABLE 4 | General linear mixed models for allogrooming network metrics for interactions between gender and other individual attributes.

GLM with Bootstrap for estimates of fixed effects on allogrooming network				
Network metrics	**Factor**	**Estimate**	**Standard error**	***p***
Eigenvector	Intercept	0.215	0.095	0.036
	Males*Age	0.017	0.018	0.148
	Females*Age	**−0.014**	**0.004**	**0.005**
	Males*Matriline	−0.002	0.007	0.722
	Females*Matriline	0.005	0.012	0.669
	Males*Hierarchy	−0.011	0.007	0.074
	Females*Hierarchy	0.004	0.007	0.620
Clustering coefficient	Intercept	2.055	0.632	0.019
	Males*Age	0.152	0.129	0.114
	Females*Age	−0.024	0.029	0.500
	Males*Matriline	−0.031	0.050	0.454
	Females*Matriline	0.230	0.118	0.119
	Males*Hierarchy	−0.087	0.050	0.079
	Females*Hierarchy	−0.103	0.066	0.187
Degree	Intercept	108.684	24.574	0.001
	Males*Age	2.393	6.459	0.612
	Females*Age	**−5.836**	**1.010**	**0.001**
	Males*Matriline	1.526	2.400	0.495
	Females*Matriline	−2.140	3.934	0.583
	Males*Hierarchy	−3.576	2.393	0.073
	Females*Hierarchy	2.626	2.048	0.210
Outdegree	Intercept	95.139	11.878	0.000
	Males*Age	2.467	3.206	0.272
	Females*Age	**−3.724**	**0.514**	**0.000**
	Males*Matriline	1.099	1.360	0.382
	Females*Matriline	−1.061	2.134	0.607
	Males*Hierarchy	−3.593	1.247	**0.002**
	Females*Hierarchy	−0.093	1.040	0.927
Indegree	Intercept	13.546	16.413	0.378
	Males*Age	−0.075	3.757	0.978
	Females*Age	**−2.112**	**0.579**	**0.003**
	Males*Matriline	0.427	1.203	0.678
	Females*Matriline	−1.080	2.201	0.608
	Males*Hierarchy	0.018	1.350	0.989
	Females*Hierarchy	**2.719**	**1.236**	**0.034**

In bold, significant attributes.

observe significant homophily by matriline for females (0.458, $p < 0.01$), but not for males. Finally, we also observe homophily by hierarchical rank ($I = 0.228$, $p < 0.05$), yet testing genders separately, we do not observe significant results in either gender.

DISCUSSION

In this study, I established an analytical protocol that balances the inter-dependency of the data without filtering the links and that considers the weight of the links, and I analyzed the effects of several factors (gender, age, matriline, and hierarchical rank) at different levels of social organization in a non-human primate species, *M. sylvanus*. These findings reveal to what extent SNA facilitates the investigation of various aspects of animal societies by studying: (1) the position and influence of individuals according to their attributes; (2) the attribute-related network; and (3) the interactional dynamics reflected by homophily. In this way, I demonstrated that the sociogenesis process (rank acquisition) is intimately linked to ontogenesis (i.e., it is age-related), and differs between genders. Hence, individuals with common attributes have similar positions and roles in the group. I also stressed the existence of homophily in several behaviors, reflecting common individual behavioral patterns, including: (1) the acquisition of status within an age-related category, leading to intra-generational conflicts; (2) high-ranking individuals preferably groom similar-rank and opposite-gender individuals to secure better protection and support; and (3) the existence of homophily in grooming behaviors by gender, age, hierarchical rank, and matriline. The results suggest six main findings.

First, we observe that variations in individual attributes have a greater impact on the position, role, and interactional patterns of females than on males. In most cases, these dissimilarities result from the social structure of females in *M. sylvanus* that is based on philopatry and MRI. Additionally, we observe significant disparities in activity and centrality between males and females.

Females are more central and active (for both received and given behaviors) in the allogrooming network. More specifically, they give and receive more allogrooming, mainly with individuals who have similar characteristics, namely females according to homophily results. These findings are in line with the literature that stresses that the philopatric gender plays a key role in affiliative behaviors (Aureli and de Waal, 2000; Silk, 2001). From a biological perspective, the philopatric gender has more time to develop a denser, stronger, and perennial network than the non-philopatric gender. In addition, female matriline homophily results emphasize the relevance of kinship bonds among females in affiliative behaviors. Individuals with high centrality and activity thus preferentially contribute to the establishment of the global network structure (Lusseau and Newman, 2004; Sosa, 2014) and cohesion of the group. In *M. sylvanus*, these key individuals are unquestionably the females.

Second, we observe that for female *M. sylvanus*, network metrics decrease with age in the agonistic and allogrooming networks. In the agonistic network, older females are less active (degree, indegree, and outdegree) and less involved in the cohesion of the network (clustering coefficient). In the allogrooming network, older females are less active (degree, indegree, and outdegree) and less central (eigenvector). During the early years, high centrality and activity for allogrooming behaviors is likely related to a long period of mother–infant and kin-related preferential interactions (which is supported by the results of matriline homophily for allogrooming behaviors) that generates kin recognition and later, kin-biased affiliative interactions (Pereira and Fairbanks, 1993). Furthermore, juveniles learn how to interact by relating to their close relatives. The observed decrease of allogrooming centrality and activity with age is likely related to the progressive stabilization of the affiliative networks of females. In addition, the decline with progressing age in the agonistic network (as related to activity and the role in the cohesion of the network) is probably a result of the stabilization of the hierarchical ranks of females when sexual maturity is attained (Chapais, 2004). These results show that the sociogenesis process, or rank acquisition, is intimately linked to ontogenesis (i.e., it is age-related), with the latter being closely related to the reproductive status of females (menarche and postmenopause) (Borries et al., 1991). This ontogenetic process can be characterized into three stages. The first occurs before sexual maturity, when the female has numerous social interactions in order to establish her position within the group. Second, once the female is mature, she has fewer social interactions, which indicates a period of stabilization of her position. The final stage corresponds to the postmenopausal period, which can lead to even fewer social interactions resulting from exclusion (Borries et al., 1991; Sosa, 2015). Unlike females, males are not subject to the phenomenon of declining social interactions, as none of their network metrics significantly decreases with age.

Third, the frequency of given agonistic behaviors increases with the hierarchical rank of a female. More specifically, the higher her hierarchical position, the greater number of submissive individuals with whom to ensure her rank a female has (Tokuda and Jensen, 1969) and the more she intervenes in conflicts to provide support (De Waal and Roosmalen, 1979; Seyfarth and Cheney, 1984; De Waal, 1997). This does not appear to be a response to received agonistic behaviors as the indegree would also increase, which is not the case. Instead, the agonistic indegree, together with the eigenvector, decreases with the hierarchical rank of a female. This decline in agonistic indegree is also observed in males, stressing that high-ranking individuals, regardless of gender, receive fewer agonistic behaviors than low-ranking ones. This reveals the benefits of dominant positions, with the reduction of associated risks (Gartlan, 1968; Bernstein, 1976; Chapais, 1991). Additionally, a significant relationship between the frequency of received allogrooming behaviors and hierarchical rank is observed in females. The absence of such phenomenon among males can be attributed to the fact that attractiveness to high-ranking individuals in allogrooming for males seems species-specific (Watts, 2000). Nonetheless, this phenomenon is observed among females according to GLMM results, which is in accordance with the theory advanced by Seyfarth (1977) in which dominant females should be preferred allogrooming partners as they can provide better protection (Watts, 2000; Cheney and Seyfarth, 2008) and support (Cheney and Seyfarth, 1990).

The fourth finding is that, similar to the hierarchy results, females within the same matriline have similar centralities and activities, and the higher the matriline, the more central and active the female is in the agonistic network. This trend can be attributed to the fact that in the genus *Macaca*, the hierarchical ranks of females are intimately linked to their matrilines. Furthermore, a closer examination of the previously discussed high agonistic activity of immature females shows that the indegree is more intense for high-born ones (**Figure 3**). Before sexual maturity, females must settle their dominance relations with lower matriline-ranking females through agonistic interactions (Chapais (2004). Thus, in their early years, females compete to establish their hierarchical rank on multiple fronts: (1) within their own matriline (as supported by the MRI phenomenon); (2) within their age category (in accordance with age homophily results for agonistic behaviors); and (3) toward older lower-ranking females.

Fifth point is that homophily results for the agonistic network show that agonistic interactions are mainly directed within the same age and gender. These findings, combined with GLMM results, yield interesting biological interpretations. Higher activity and connections in the agonistic ego network among young individuals (GLMM results) can be interpreted as a phenomenon of hierarchical rank acquisition. Homophily results highlight that this rank acquisition occurs mainly between same-age and same-gender individuals (Chapais, 1988; Holekamp and Smale, 1991), stressing the existence of a particular phenomenon that we could call the intra-generational conflict. Furthermore, the fact that affiliative behaviors are also primarily directed toward same-age individuals (age homophily results for allogrooming behaviors) underlines the trend of individuals to build their affiliative network within their age category.

Sixth, we observe homophily in allogrooming behaviors according to hierarchical rank, but only when both genders are taken into account. In other words, opposite-gender individuals with similar hierarchical ranks have preferential affiliative interactions. Allogrooming behaviors facilitate the creation of affiliative bonds and potential support in future conflicts (De Waal and Roosmalen, 1979; Seyfarth and Cheney, 1984; De Waal, 1997). Subsequently, this behavioral pattern can explain the decrease of agonistic behaviors received by high-ranking individuals (observed in GLMM results) owing to the high-ranking support of a third party.

Homophily has previously been reported in many species (McPherson et al., 2001; Lusseau and Newman, 2004; Massen and Koski, 2013). Extensive research on human homophily stressed that it is a major mechanism in stranger cooperation (Haun and Over, 2015), social learning (Buttelmann et al., 2013), and cultural and norms transmission (Chudek and Henrich, 2011). Recent studies argue that homophilic preferences may explain the gap between animals and humans regarding these abilities (Haun and Over, 2015). Revealing homophily in several behaviors and as it is influenced by different attributes highlights the importance of these mechanisms in a non-human primate species. However, many methods exist to evaluate the presence or absence of homophily (E-I index, ERGM, assortativity, Moran I statistic), each one of them with inherent pros and cons that would need to be evaluated before determining which of these approaches is more relevant for studying animal societies.

This analytical protocol can be used to study other animal societies and might enable interspecific comparisons. I believe that the important findings of this study might help understand the global patterning of a non-human primate society, and likely other animal societies, from an evolutionary perspective.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and approved it for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fpsyg.2016.00529

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Relations between Spatial Distribution, Social Affiliations and Dominance Hierarchy in a Semi-Free Mandrill Population

Alexandre Naud[1, 2, 3], Eloise Chailleux[4], Yan Kestens[2], Céline Bret[5], Dominic Desjardins[6], Odile Petit[1, 3], Barthélémy Ngoubangoye[7] and Cédric Sueur[1, 3]*

[1] Centre National de la Recherche Scientifique, Département Ecologie, Physiologie, et Ethologie, Strasbourg, France, [2] Département de Médecine Sociale et Préventive, École de Santé Publique, Université de Montréal, Montréal, QC, Canada, [3] Institut Pluridisciplinaire Hubert Curien, Université de Strasbourg, Strasbourg, France, [4] École Nationale Vétérinaire d'Alfort, Maison-Alfort, France, [5] Jr Research Group "Sexual Selection," German Primate Center, Göttingen, Germany, [6] Départements des Sciences Biologiques, Institut de Recherche en Biologie Végétale, Université de Montréal, Montréal, QC, Canada, [7] Centre International de Recherches Médicales de Franceville, Franceville, Gabon

Edited by:
Thomas Bugnyar,
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***Correspondence:**
Cédric Sueur
cedric.sueur@iphc.cnrs.fr

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Although there exist advantages to group-living in comparison to a solitary lifestyle, costs and gains of group-living may be unequally distributed among group members. Predation risk, vigilance levels and food intake may be unevenly distributed across group spatial geometry and certain within-group spatial positions may be more or less advantageous depending on the spatial distribution of these factors. In species characterized with dominance hierarchy, high-ranking individuals are commonly observed in advantageous spatial position. However, in complex social systems, individuals can develop affiliative relationships that may balance the effect of dominance relationships in individual's spatial distribution. The objective of the present study is to investigate how the group spatial distribution of a semi-free ranging colony of Mandrills relates to its social organization. Using spatial observations in an area surrounding the feeding zone, we tested the three following hypothesis: (1) does dominance hierarchy explain being observed in proximity or far from a food patch? (2) Do affiliative associations also explain being observed in proximity or far from a food patch? (3) Do the differences in rank in the group hierarchy explain being co-observed in proximity of a food patch? Our results showed that high-ranking individuals were more observed in proximity of the feeding zone while low-ranking individuals were more observed at the boundaries of the observation area. Furthermore, we observed that affiliative relationships were also associated with individual spatial distributions and explain more of the total variance of the spatial distribution in comparison with dominance hierarchy. Finally, we found that individuals observed at a same moment in proximity of the feeding zone were more likely to be distant in the hierarchy while controlling for maternal kinship, age and sex similarity. This study brings some elements about how affiliative networks and dominance hierarchy are related to spatial positions in primates.

Keywords: mandrill, spatial distribution, feeding competition, dominance, affiliative relationships, social network

INTRODUCTION

Group living is a common social pattern among primates (Alexander, 1974; Wrangham, 1987). Although there exist advantages of group-living in comparison to a solitary lifestyle (Krause and Ruxton, 2002), a growing body of evidence indicates that costs and benefits of group living may be unequally distributed and spatially determined (Viscido and Wethey, 2002; Quinn and Cresswell, 2006; Hirsch, 2007; Tkaczynski et al., 2014). Research suggests that predation risk, vigilance levels, and food intake may depend on an individual's position within a group spatial geometry. This implies that certain within-group spatial positions may be more or less advantageous than others (Janson, 1990; Krause, 1994; Motro et al., 1996; Hall and Fedigan, 1997; Hirsch, 2007) and that individuals may compete for certain spatial positions (Motro et al., 1996) or adopt particular spatial behaviors (De Vos and O'Riain, 2010) in order to maximize their fitness. Furthermore, in species characterized by a dominance hierarchy, high-ranking individuals are commonly observed in more advantageous spatial positions (i.e., a position that reduces costs and maximize the gains of group-living; van Noordwijk and van Schaik, 1987; Janson, 1990; Hall and Fedigan, 1997; Murray et al., 2007).

(Hamilton, 1971) selfish herd theory suggests that individuals mainly located at the edge of a group should experience higher risk of predation in comparison to their central counterparts. This "marginal effect" is well-supported by empirical evidence on different taxa, which demonstrates that predation risk (Krause, 1994; Stankowich, 2003) and vigilance levels (Petit and Bildstein, 1987; Janson, 1990; Burger et al., 2000) tend to be higher among peripheral individuals. Even when predators have relatively equal access to all group members—i.e., when predators move into a 3 dimensional space while prey move in a 2 dimensional space—they are more likely to attack peripheral animals (Romey et al., 2008). This means that in order to reduce one's risk of predation, individuals will compete for a central group position (Couzin and Krause, 2003) resulting in group aggregation (Hamilton, 1971). In addition, studies on inter-individual spacing have shown that groups tend to become more tightly spaced after an encounter with a predator (van Schaik and Mitrasetia, 1990; De Vos and O'Riain, 2010) or in high predation risk areas (Quinn and Cresswell, 2006; Kelley et al., 2011).

Food gain has also been found to be related to spatial position (Hirsch, 2007). When food is dispersed, spread, and thus not monopolized (scramble competition), foraging gains may increase for peripheral group members as spacing between them reduces feeding competition (Morrell and Romey, 2008). Conversely, when food patches are limited and defendable (i.e., contest competition; van Schaik and van Noordwijk, 1988), individuals may aggressively compete over food (Grant et al., 2002) resulting in a spatial distribution where high-ranking individuals are in the center, occupying food patches, while low-ranking individuals are distributed in peripheral positions (Hirsch, 2007). This spatial distribution, characterized by dominant and tolerated individuals in central positions having high food intake, is observed in different primate species (Robinson, 1981; Janson, 1990; Barton, 1993; Motro et al., 1996). When we consider group mobility, the most advantageous position in species following a producer-scrounger model (i.e., individuals found their own food—produce—or join the food discoveries of others—scrounger–) should be in the center-front during group foraging (Hirsch, 2007) which has been observed in white-faced capuchins (*Cebus capucinus*; Robinson, 1981; Hall and Fedigan, 1997).

Dominance hierarchy may not be the only social variable that explains within group spatial distributions among primate species that live in relatively stable groups (i.e., where relationships persist over months or even years). In complex social systems (Whitehead, 2008), individuals might develop affiliative relationships that shape social organization (Pasquaretta et al., 2014). These affiliations may therefore balance the effect of dominance relationships in individual's spatial distribution. Indeed, subordinate individuals tend to groom high ranked individuals (Schino, 2001; Nakamichi and Shizawa, 2003; Silk et al., 2003) presumably to develop alliances and tolerance in order to increase access to resources and to get potential allies in agonistic interaction (Seyfarth, 1977). This might change the ranks of these subordinate individuals or give them access to an advantageous spatial position without changing ranks. Additionally, Robinson (1981) has shown that an individual's spatial location is best predicted when affiliative relationships are considered during agonistic interactions. These strategies and social preferences make the emergent group social network more complex. At a population level, association preferences between multiple individuals may divide the community into subgroups where individuals in a subgroup interact more among themselves than with the rest of the community (Krause et al., 2007; Sueur et al., 2011a). Such community divisions, or clusterisations, potentially resulting in fission-fusion dynamics (Sueur et al., 2011c), have been observed in different primate species (Mandrills, *Mandrillus sphinx*: (Bret et al., 2013); Rhesus macaques, *Macaca mulatta* and Japanese macaques, *Macaca fuscata*: (Sueur et al., 2011d); Howling Monkeys, *Alouatta palliata*: (Bezanson et al., 2008); Human, *Homo sapiens*: Newman, 2004) and other non-primate social species (Bottlenose dolphin, *Delphinidea Tursiops*: (Lusseau et al., 2006); Columbian ground squirrel, *Spermophilus columbianus*: Manno, 2008). Clusterisations may play a role in competition for a certain spatial location—low-ranking individuals in a subgroup with high-ranking individuals may access food patches more easily—or may help to decrease food competition by spreading individuals across different resources (Sueur et al., 2011b).

The present study investigates how the group spatial distribution of a semi-free ranging colony of Mandrills (*M. sphinx*) relates to its social organization. Mandrills are highly social primates found in large groups (i.e., hordes) comprised of several hundred individuals in a natural context (Rogers et al., 1996; Abernethy et al., 2002). Social organization of the Mandrill in a natural context is poorly understood (Setchell and Wickings, 2005). Abernethy et al. (2002) has described Mandrill groups as stable and possessing a social organization consisting of adult females and their dependent offspring. Less than 2% of the group is constituted of adult males, while other adults and sub-adult males are present only during the mating season. Only the alpha male is 100% permanently associated with the social group (Setchell and Dixson, 2001). Previous studies of a semi-free-ranging colony showed that male Mandrills exhibit a strong linear dominance hierarchy and that affiliative behavior is extremely rare among males (Setchell and Wickings, 2005; Setchell et al., 2006). On the other side, females seem to be organized in matrilines (Setchell, 1999) and kin related females fraternize together more than unrelated females (Bret et al., 2013). A more recent study using social network analyses has shown that semi-free mandrills are organized in subgroups of preferential relationships, which are not related to kinship, age, or dominance rank of group members (Bret et al., 2013). The absence of a correlation between kinship and subgroup organization in this study may be explained by group composition (i.e., some females were the only representatives of their matriline). However, it may suggest that affiliative relationships also shape the social organization of Mandrill living in semi-free conditions.

In our study, we aim to examine, in a semi-free mandrill population, how individual's spatial position during food competition is explained by group social organization. Previous studies have shown that dominance relationships may explain the spatial distribution of individuals according to food distribution pattern, with dominant individuals monopolizing resources. Our objective is to evaluate whether affiliative relationships also explain individual spatial distribution in this situation. Our research questions are: (1) does dominance hierarchy explain observed proximity or distance from a food patch? (2) Do affiliative associations also explain observed proximity or distance from a food patch? (3) Do rank differences in the group hierarchy explain being co-observed in proximity of a food patch?

Our expected findings are that high-ranking individuals will be observed in proximity of the food patch more often, while low-ranking individuals will remain distant from the food patch. We also expect that belonging to certain subgroups of affiliative relationships will also explain spatial observations within different distances of the food patch, while controlling for dominance ranking. This would suggest that affiliative relationships are another aspect of social organization that may explain access to advantageous spatial positions. Finally, we have two opposite hypotheses for our third research question. Individuals of similar rank in the hierarchy may form stronger bonds than individuals of distant rank, as usually individuals of neighboring ranks are more closely related (Cheney and Seyfarth, 1990) and are more tolerant of each other. In this case, individuals of a similar rank should be co-observed more often in close proximity of the food patch. In contrast, previous studies found that proximity (or distance) within the dominance hierarchy does not explain affiliation in semi-free Mandrills (Bret et al., 2013) and they seem to be characterized by a more relaxed dominance hierarchy in comparison to other primate populations (Bout and Thierry, 2005). Therefore, it is possible that distant individuals within the hierarchy may tolerate each other in proximity of the feeding area.

METHODS

Ethical Statement

Our methodological approach solely involved observations. Animals were not handled, and no invasive experiments were carried out on the mandrills. Animals were already accustomed to human presence in their enclosure. Our protocol followed the ethical guidelines of the CNRS (Centre National de Recherche Scientifique) and the recommendations of the Gabonese government. This study was conducted with the approval of the International Medical Research Center (CIRMF) scientific committee in Gabon via a research agreement (nu045/2011/CNRS). All occurrences of injuries or illness in the observed animals were reported to veterinary staff at the CIRMF primatological center.

Study Group and Environment

The study was comprised of 39 mandrills from a group of 75 individuals born in captivity and living in a large, naturally rainforested enclosure (6.5 ha), at the CIRMF in Franceville, Gabon. Mandrills were free to forage in the enclosure and were supplemented by a provision of homemade soya-cake and local seasonal fruits twice a day. Water was available *ad libitum*. Juveniles (<5 years old) were excluded from the study population because they spent all their time with their mothers and because of the instability of their relationships with other group members (Sueur et al., 2011d). Remaining individuals were aged between 5 and 26 years (mean = 10.42; SD = 4.09) and comprised of 18 females and 21 males. Dates of birth and matrilineage were recorded for all individuals. Kinship was computed from matrilineage by recording motherhood. All subjects were identified using morphological differences and/or ear tags.

Spatial Observations and Data Recording

Data was collected from April to June 2012. One of the researchers (E.C.) observed the group 6 h per day (09:00–12:00 and 15:00–18:00) from a tower located behind the feeding zone. Observations were recorded in front of the feeding zone in a 30 × 30 m area covered with grass and small trees allowing good visibility (see **Figure 1**). At the beginning of each observation period (i.e., a.m. and p.m.), a food supplement was placed in a

FIGURE 1 | Photograph of the observation area from the tower where observations were realized. Credit Chailleux E.

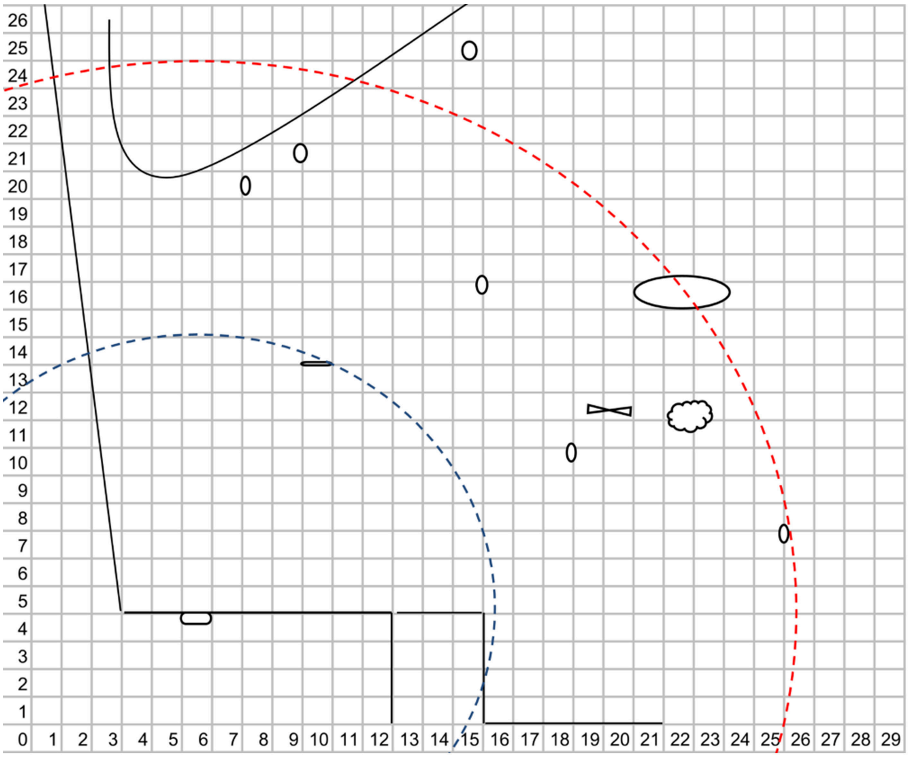

FIGURE 2 | Schema used to record individuals' spatial position. The scale of this schema is 1 m^2. Circles, ellipses, and polygons represent trees and bushes where the mandrill could get covered. The line on the upper side represents the beginning of the forest area. The feeding zone is contained to X = 12–15 and Y = 0–4 and the door is represented by the polygon in X = 5–6 and Y = 3–4. The two circular buffers are characterized by the 10 m (blue) and the 20 m (red) areas used to calculate frequencies of observation.

closed section, visible but not accessible to the mandrills during the whole observation period. At the end of each observation period (i.e., after 12:00 and 18:00), the door giving access to the food supplement was opened. This situation resulted in an artificial food patch, an advantageous spatial position for which the Mandrills could compete for. We used instantaneous scan sampling (Altmann, 1974) with a 15 min sampling frequency (total of 26 scans per day) to record individual spatial positions within the observation area. Individuals observed during a scan were positioned on a map representing the 30 × 30 m area in front of the feeding zone door using 1 m spaced vertical and horizontal grid lines (**Figure 2**). A total of 631 scans were completed, representing 157.75 h of observations. All individuals were not observed at each scan (mean frequency of scans = 145.2; SD = 73.35).

When calculating the mean number of observed individuals by observation period (e.g., 9:00, 9:15), we noticed that more individuals were observed during the afternoon (i.e., 15:00–18:00) compared to the morning (i.e., 09:00–12:00; see **Figure 3**). In practice, the food was not always made available by the CIRMF at 12:00 but systematically at 18:00. Therefore, mandrills had possibly learned this pattern and food competition was probably more important during the afternoon. Consequently, we used only observations from the afternoon period to calculate spatial positions of individuals within different distances of the feeding zone (see Section Hierarchal Dominance).

Spatial Distribution

First, we calculate the Euclidian distance (Legendre and Legendre, 2012) between the center of the feeding zone door and the Cartesian coordinates of all observations (**Figure 2**). We used the door as the centroid of the food patch because this location was the most coveted since it is the only access to the feeding zone. Then, the frequency of observations within 10 m and over 20 m distances of the food patch were computed from the Euclidian distances. We did not use observations between 10 and 20 m because we wanted to contrast spatial observations in proximity and distant from the feeding zone door. We used a 10 m scale in order to get sufficient observations for statistical analysis. For observations within 10 m of the feeding door, we calculated the relative frequencies to adjust for the number of scans during which individuals were observed. For observations over 20 m of the feeding door, individuals that were out of sight (i.e., in the forest area) were included in the measure. Two variables were created: (1) the relative frequency of observation within 10 m of the feeding door (F10M) and (2) the frequency of observations over 20 m of the feeding door (F20M).

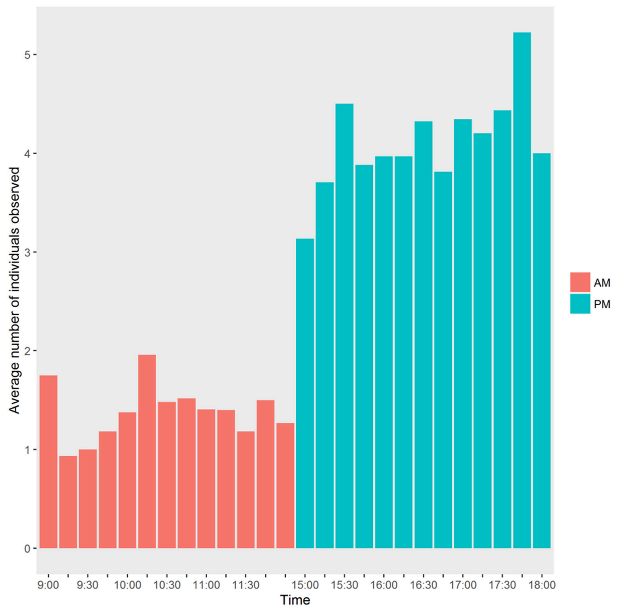

FIGURE 3 | Histogram of the average number of individuals observed during each period. 12:00 is considered in the morning period (am) in this figure. The bar plot was realized with the ggplot2 package (Wickham, 2009).

Hierarchal Dominance

Agonistic interactions were recorded *ad libitum* during both observation periods (i.e., a.m. and p.m.). According to previous studies (Setchell, 1999), a list of 13 behaviors was chosen and described in a catalog. Actor, receivers, behavior, date, and time were recorded for each aggressive event. When interactions included a series of behaviors, only the last behavior (causing the submission of the other mandrill) was recorded. Also, only unidirectional aggression with a clear issue was used to calculate the hierarchy. Since dominance hierarchy is only based on dyadic interactions, interactions between more than two individuals were discarded. Linearity of the hierarchy was measured with de Vries' *h*' index (de Vries, 1995). Individual dominance indices were calculated with de Vries' modification of David's score (MDS) (David, 1987; de Vries et al., 2006). These measures were calculated with SOCPROG 2.4 (Whitehead, 2009).

Affiliative Relationships and Co-Occurrence within 5 m of the Feeding Zone

To measure the social network of affiliative relationship (i.e., affiliative network), we used spatial proximity (i.e., association measures) between individuals as a proxy of social preferences in our group (Whitehead, 2008). Two individuals (i.e., a dyad) were considered to be in association when they were seen within a distance of 1 m from each other during a scan. We assumed that a distance close to the average body length of adult mandrills represented a situation where touch interactions (e.g., grooming) may take place. The average body length of adult mandrills is 80 cm for males and 60 cm for females (Wickings and Dixson, 1992). We were, however, limited to 1 m because it was the smallest distance measured from the previous spatial observations (the data were already collected when the analyses were planned). For each pair of individuals, we calculated a half-weight association index (HWI) with the number of associations. Since we did not observe the whole group at each scan, all individuals were not observed at the same total frequency. HWI allow to control for the non-observation of all group members at each scan (Whitehead, 2008). Then, we tested if individuals associated in a non-random way by permuting associations within each scan (*H0* = no preferred or avoided relationship for any dyad; Whitehead et al., 2005). We used the coefficient of variation of association indices as the test statistic for significance level. To measure if our population could be usefully divided into subgroups, we used the modularity test of Newman (Newman, 2004, 2006) which measures the difference between the proportion of the total associations in the subgroups and the summed associations of the whole group. Eigenvalues were used to determine the level of certainty through which individuals were assigned to subgroups. These three measures were computed with SOCPROG 2.6 (Whitehead, 2009).

Finally, we created a second association matrix where every individual observed within 5 m of the feeding zone door in a same scan were considered associated (i.e., co-occurrence network). We used HWI to control for non-observation of group members. We used a smaller radius than for spatial proximity to the feeding zone door (5 m instead of 10 m) because we assumed that competition would be stronger in a limited space and therefore co-occurrence would indicate tolerance among individuals.

Statistical Analyses

To evaluate homoscedasticity assumptions, we used Spread-Location plots of standardized residuals against fitted values, Bartlett test, and the Breusch-Pagan test (Greene, 2003; Scherrer, 2007). We used square root transformations on the relative frequency within 10 m (SRF10M) in order to obtain homoscedasticity and reduce the skewness of the distribution. We had two missing values for the variable age. We replaced those values by the means of their respective age group (e.g., sub adults' mean ages = 6.8). We had one missing data for MDS and removed the individual from further analysis. All significance levels were obtained through permutations because our observations did not represent a sample from a larger statistical population with a known distribution and permutations allow parametric statistical methods to be used when distributional assumptions are not satisfied (Legendre and Legendre, 2012). We used 10,000 permutations in each analysis.

First, we aimed to test how hierarchy is structured by age and sex by testing bivariate relationships between hierarchy, sex, and age. Relationship between dominance rank (MDS) and sex was tested using a student test (one-tailed). Relationships between dominance rank and age were tested on the full sample and stratified by sex using Pearson correlation tests (one-tailed). We used one-tailed tests because our hypothesis was that males were more dominant than females and there is a positive correlation between age and dominance ranking. Second, we tested the relationship between the explanatory variables (1) age, (2) sex, (3) dominance rank, and (4) matrilineage (i.e., kinship) and affiliative associations. Age, dominance rank, and sex variables were first transformed into three distance matrices. Distances for age and dominance ranking were calculated with Euclidian distance and sex was calculated with a binary coefficient (same sex = 1; different sex = 0). We then used a multiple regression quadratic assignment procedure (MRQAP) test (Whitehead, 2008) with the "double-semi-partialing" technique of Dekker et al. (2007). This analysis aimed to better understand how social relationships are distributed according to animal characteristics.

To test our first research question—does dominance hierarchy explain observed proximity or distance from a food patch?—we used Pearson correlations (one-tailed) between dominance rank and frequency of observations within distances of the feeding door (SRF10M and F20M). To test our second research question—do affiliative associations also explain observed proximity or distance from a food patch?—we used partial regression to test the relationships between SRF10M or F20M as outcomes, and dominance rank and subgroups (found with modularity method as described above) as explanatory variables. Finally, to test our third hypothesis—do rank differences in the group hierarchy explain being co-observed in proximity of a food patch?—we tested the correlation between the co-occurrence network and the dominance distance matrix while controlling for kinship, age, and sex with the MRQAP test using the "double-semi-partialing" technique. Correlation were run between the co-occurrence network and the affiliative network (recalculated without observation within 5 m of the feeding zone) with a Mantel test to see if the co-occurrence within 5 m of the feeding door was related to the observed associations in the whole area.

All statistics were performed in R 3.1.2. (CRAN, 2014) and SOCPROG 2.6. (Whitehead, 2009). We used Bartlett-test (stats library) and ncvTest (car package) functions for Bartlett and Breusch-Pagan tests, corPerm3 and t.perm (available from Pierre Legendre website) functions for bivariate relationships, mantel.test (ape package) function for mantel test, varpart and rda (vegan package) functions for partial regressions (Paradis et al., 2004; Fox and Weisberg, 2010; Legendre, 2015; Oksanen et al., 2016). MRQAP tests were performed in SOCPROG 2.6.

RESULTS

Dominance Hierarchy

Linearity of the dominance hierarchy was significant [p(perm) $<$ 0.0001] but not perfectly consistent [De Vries h' = 0.253]. Dominance index (MDS) was correlated to sex [p(perm) = 0.02053] where males had greater dominance indices in comparison to females. The correlation between dominance index and age was not significant for the whole group [r = 0.24924; p(perm) = 0.07069] but significant when stratified by sex. Stratified linear correlation showed that this relationship is stronger for males [r = 0.88461; p(perm) $<$ 0.00001] than for females [r = 0.41382; p(perm) = 0.03548; **Figure 4**].

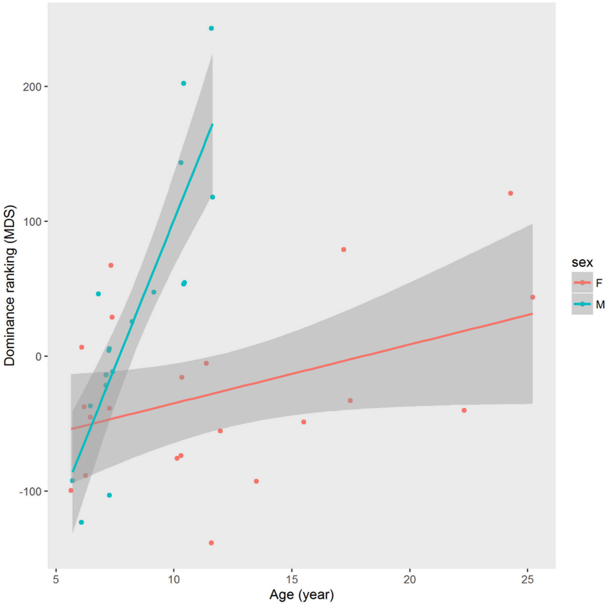

FIGURE 4 | Linear regression between dominance rank (MDS) and age (years) in semi-free ranging group of mandrills (*Mandrillus sphynx*) stratified by sex. The line represents the curve estimated by the linear model and the gray shape represents the standard error. The scatter plot was realized with the ggplot2 package (Wickham, 2009).

Affiliative Relationships

The estimated affiliative associations (**Figure 5**) were found to be non-random [p(perm) $<$ 0.001]. Affiliative associations were not correlated with age differences [partial r = 0.0525; p(perm) = 0.1119] or with MDS differences [partial r = 0.0359; p(perm) = 0.1919], but were correlated with sex [partial r = 0.0858; p(perm) = 0.0099] and matrilineage [partial r = 0.3081; p(perm) $<$ 0.0001] where individuals of the same sex and kin associate more often. Newman modularity tests gave us eight subgroups composed of 3–9 individuals. Modularity for this test was 0.590, and a modularity score $>$ 0.3 indicates a useful subdivision of the group (Whitehead, 2008; Sueur et al., 2011b).

Spatial Positions According to Dominance Hierarchy and Affiliative Network (H1 and H2)

Proximity to the feeding zone was correlated with dominance hierarchy: SRF10M was positively correlated with MDS [one-tailed Pearson correlation; r = 0.36385; p(perm) = 0.01190] and F20M was negatively correlated with MDS [one-tailed Pearson correlation; $r = -0.45755$; p(perm) = 0.00155].

In the multivariate linear model with SRF10M as an outcome (**Table 1**), the fraction of variance explained by MDS [semipartial r^2 = 0.089658; p(perm) = 0.015] and subgroups [semipartial r^2 = 0.450367 p(perm) = 0.002] are both significant [adjusted R^2 = 0.48853; p(perm) = 0.002]. In the multivariate linear model with F20M as an outcome, the fraction of variance explained by MDS [semipartial r^2 = 0.15267; p(perm) = 0.003] and the fraction of variance explained by subgroups [semiparial r^2 = 0.28086; p(perm) = 0.005] are both significant [adjusted R^2 = 0.37510; p(perm) = 0.001; **Table 1**]. These results indicate that both MDS

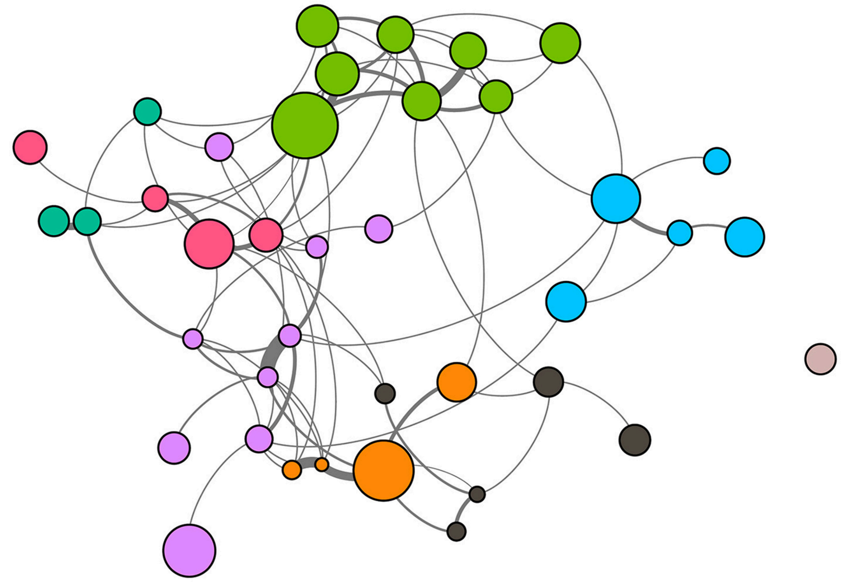

FIGURE 5 | One meter proximity network of a semi-free ranging group of mandrills (*Mandrillus sphynx*). This network was generated from the matrix of associations. Node size represents variation in hierarchical dominance rank (MDS). Node color shades characterize subgroup membership and edge thickness represents the strength of the connection between two nodes; the thicker the edge, the stronger the association. Individuals are positioned in 2D according to their social relationships using the Force Atlas 2 spatialization option in Gephi 0.9 (Bastian et al., 2009).

TABLE 1 | Partial regressions between each spatial observation variables (SRF10M, F20M) as outcomes and dominance hierarchy (MDS) and subgroups as explanatory variables.

	Df	Semipartial r^2	Adjusted R^2	p(perm)
SRF10M				
MDS	1	0.089658		0.015
Subgroups	6	0.450367		0.002
MDS + Subgroup	7		0.48853	0.002
F20M				
MDS	1	0.15267		0.003
Subgroups	6	0.28086		0.005
MDS + Subgroup	7		0.3751	0.001

and subgroups predict being observed in SR10M and F20M when controlling for the other predictor, but that subgroups explain more of the total variance in both cases.

Co-Occurrence Network and Dominance Hierarchy (H3)

The co-occurrence network (individuals co-observed within 5 m of the feeding zone) was correlated to a second affiliative network calculated without associations within 5 m of the feeding zone [Mantel test; $r = 0.2169$; $p(perm) < 0.0001$]. When using binary descriptors ($1 =$ affiliation; $0 =$ no affiliation), 76% of the affiliative associations found within 5 m of the feeding zone were observed in the rest of the area (i.e., second affiliative network). We found a positive correlation between the co-occurrence network and the dominance distance matrix [partial $r = 0.2046$; $p(perm) = 0.0007$] while controlling for kinship [partial $r = 0.0751$; $p(perm) = 0.0449$], age distance [partial $r = -0.0061$, $p(perm) = 0.4489$], and sex similarity [partial $r = 0.0928$; $p(perm) = 0.0117$], which indicates that individuals that are co-observed more often around the feeding zone door have greater differences in their respective dominance status while controlling for the other descriptors.

DISCUSSION

In this study, we aimed to understand how the spatial position of individuals in a feeding context was influenced by social organization.

We first found that dominance hierarchy was correlated with sex, where males were more dominant than females within the group. We also found linear correlations between dominance and age within male and female individuals. These results are coherent with previous studies on the same study population and from a captive population (Holt, 1980; Setchell et al., 2006). Studies on mandrills remain rare and these results are important to understand the social organization of this species. The distribution of relationships within our affiliative network was correlated with sex and kinship but not to age and dominance. In comparison with a previous study on a different Mandrill group living in the same semi-free context (CIRMF colonies), the correlations with age and dominance were found to be consistent, while correlations with sex and kinship were found to be inconsistent (Bret et al., 2013). A possible explanation for this difference comes from the composition of our study population. Few females were related in the previous study, whereas more females were from the same matriline in our study population. Our ability to compare this population to other semi-free populations is limited, since most of our knowledge on Mandrill behavior comes from the CIRMF colonies.

High-ranking individuals were more often observed in proximity of the feeding-zone area, while low-ranking individuals were more observed at the boundaries of the observation area. In our case, the food patch was limited in space and was only available for a fixed time. This encourages contest competition resulting in a spatial distribution where high-ranking individuals control the food patch and low-ranking individuals are in peripheral positions. This behavior has been observed in different primate species (Long-Tailed Macaques, *Macaca fascicularis*: van Schaik and van Noordwijk, 1988; Wild chimpanzees, *Pan troglodytes*: Murray et al., 2007; White-faced capuchins, *Cebus capuccinus*: Hall and Fedigan, 1997; Brown capuchin *Cebus apella*: Janson, 1990) and other taxa (Convict cichlids, *Archocentrus nigrofasciatum*: Grant et al., 2002). Furthermore, frequencies of the presence of observations, either in proximity or far from the feeding zone, were also explained by the affiliative network. Division of the affiliative network into subgroups of preferential associations explained ∼45 and 28% of the total variation of observations within 10 m (SRF10M) and over 20 m (F20M) of the feeding zone, respectively. In comparison, dominance explained ∼9 and 15% of the total variation of SRF10M and F20M, respectively [these percentages are the rounded semipartial r^2 calculated in Section Spatial Positions According to Dominance Hierarchy and Affiliative Network (H1 and H2)]. These results do not only indicate that affiliative relationships are associated with individual spatial distributions, but that the subgroup associations explain more of the total variance in both cases. Therefore, spatial distribution in a feeding context seems to be more strongly associated with the affiliation than dominance hierarchy within the social organization. In this way, affiliative relationships may allow individuals to be tolerated by high-ranking individuals at the feeding zone and the resulting affiliative advantage for low-ranking individuals may explain the observed competition to groom dominant individuals (Sade, 1972; Chapais et al., 1995; Schino, 2001).

The analysis of the co-occurrence network showed that individuals observed within 5 m of the feeding zone at the same moment were more likely to be distant within the hierarchy, while controlling for maternal kinship, age differences, and sex similarity. Furthermore, the co-occurrence network was correlated with the affiliative network, which indicates that associations in the feeding zone area were consistent with associations observed in the whole area. A possible explanation for these results is that low-ranking individuals use their preferential associations with high-ranking non-kin individuals in order to gain access to the feeding-zone area. This would be consistent with results from another study on the wedge-capped capuchin monkeys (*Cebus nigrivittatus*), which found that food patches were controlled by the most dominant individuals, their siblings, and tolerated individuals (Robinson, 1981).

Dominance may be an important factor for accessing food when one is at the top of the hierarchy, but for mid and lower ranked individuals, affiliation through alliances with high-ranked individuals seems to be a more effective way of reaching food than relying strictly on one's own dominance status. A possible explanation for these results is the existence of a biological market between associated individuals of different dominance ranking (Barrett et al., 1999). Among wild tufted capuchin monkeys (*Cebus abella*) and wild Japanese macaques (*M. fuscata*), during feeding, high-ranking individuals are more likely to tolerate low-ranking individuals that groom them the most, after controlling for kinship (Ventura et al., 2006; Tiddi et al., 2011). Moreover, high-ranking individuals tend to be groomed more than their low-ranking counterparts, a phenomenon that is observed in adult females of different primate species (Schino, 2001). However, other studies on *C. abella* and *M. fuscata* found no correlation between dominance distances and grooming behaviors (Nakamichi and Shizawa, 2003; Schino et al., 2009). Tolerance is a currency that primates may exchange against affiliative behaviors (Janson, 1985), and therefore, low-ranking individuals may tend to groom high-ranking individuals so as to improve their fitness by gaining access to resources that are monopolizable (Fruteau et al., 2009). Furthermore, market exchange between allogrooming and agonistic support has also been observed among different primate species (Schino, 2007).

This study fulfilled its objective of better understanding the spatial position of mandrill group members under a feeding context but met some limitations. Whilst the study of captive populations might allow us to gain a better understanding of the social factors affecting behavior, our first limitation was that the phenomenon observed in a semi-free context may not be representative of the natural context of behavior. An example of this situation is found in the group clusterization: subgroup number three that consisted of five low-ranking adult males with five of the seven lowest positions in the male hierarchical ranking. These individuals would probably have left the population in a natural context since only dominant individuals remain in the population outside the mating season (Abernethy et al., 2002). In this semi-free context, they associated themselves with other mandrills and remained in the periphery of the group, mimicking males' migration observed in the wild (Abernethy et al., 2002). A second limitation was that we had no information on associations and tolerance when the feeding zone door was open. Thus, it is possible that high-ranking individuals became intolerant with low-ranking individuals when food was accessible. Another way of measuring food accessibility would have been by co-feeding in the feeding zone. Thirdly, we had no measures of grooming interactions and therefore, the association network may not be fully representative of the real occurrences of affiliative interactions. However, body contact and close proximity networks were correlated in the study of another group in the CIRMF, validating the use of close proximity (within 1 m) as a relevant variable to represent social relationships (Bret, personal comm.). Fourthly, the spatial distribution (Section Spatial Distribution) and social association (Section Affiliative Relationships and Co-Occurrence within 5 m of the Feeding Zone) measures were both derived from the same dataset (i.e., Cartesian coordinates within the 30 × 30 m area; Section Spatial Observations and Data Recording). This could have created dependence between our variables and thus may influence our results. For observations within 10 m of the food patch, Cartesian coordinates of dyadic associations during the afternoon period and within 10 m of the food patch were comprised in both measures (SF20M and affiliative relationship). These dyadic associations represented 12.7% of all observed dyadic associations. We performed sensitivity analysis with subgroups of preferential associations (Section Affiliative Relationships and Co-Occurrence within 5 m of the Feeding Zone) recalculated without these dyadic associations and found that relationships between spatial distribution, dominance index and subgroups [Section Spatial Positions According to Dominance Hierarchy and Affiliative Network (H1 and H2)] were consistent with our previous findings. We also found our results to be consistent with those of a sensitivity analysis performed with the observations that were over 20 m away from the food patch. Finally, even if we restricted our spatial distribution measures to the afternoon period, it is impossible to know whether mandrills maintained interest in an inaccessible food source for 3 h. Thus, not all these measures of spatial distribution may have been taken in a feeding competition context.

This study gives us a better understanding of how affiliative networks and dominance hierarchy are related to the spatial positions of primates. These results were obtained by combining social network analysis with spatial analysis. A next step would be to better understand the temporal dimension of this process. This would result in determining how aspects of social organization co-influence animal behavior and explain within group spatial distribution.

AUTHOR CONTRIBUTIONS

AN is the main author of this article. He developed the hypothesis, conduct the analysis, and wrote the article. EC collected the data and assisted AN in the elaboration of the hypotheses, the analysis and the writing of this paper. DD and CB contributed to the analysis and the work drafting. YK and CS supervised the analysis and revised the work critically. OP and BN made possible the acquisition of the data used in this article. All authors agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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Social Information Transmission in Animals: Lessons from Studies of Diffusion

Julie Duboscq[1,2,3]*, **Valéria Romano**[1,2], **Andrew MacIntosh**[3,4] **and Cédric Sueur**[1,2]

[1] *Département Ecologie, Physiologie et Ethologie, Centre National de la Recherche Scientifique, Strasbourg, France,* [2] *Institut Pluridisciplinaire Hubert Curien, Université de Strasbourg, Strasbourg, France,* [3] *Wildlife Research Centre, Kyoto University, Kyoto, Japan,* [4] *Primate Research Institute, Kyoto University, Inuyama, Japan*

The capacity to use information provided by others to guide behavior is a widespread phenomenon in animal societies. A standard paradigm to test if and/or how animals use and transfer social information is through social diffusion experiments, by which researchers observe how information spreads within a group, sometimes by seeding new behavior in the population. In this article, we review the context, methodology and products of such social diffusion experiments. Our major focus is the transmission of information from an individual (or group thereof) to another, and the factors that can enhance or, more interestingly, inhibit it. We therefore also discuss reasons why social transmission sometimes does not occur despite being expected to. We span a full range of mechanisms and processes, from the nature of social information itself and the cognitive abilities of various species, to the idea of social competency and the constraints imposed by the social networks in which animals are embedded. We ultimately aim at a broad reflection on practical and theoretical issues arising when studying how social information spreads within animal groups.

Keywords: information, sociality, experimental design, social cognition, social network, social competency

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***Correspondence:**
Julie Duboscq
julie.a.m.duboscq@gmail.com

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INTRODUCTION TO SOCIAL DIFFUSION THEORY AND EXPERIMENTS

Many organisms, from plants to social animals, have the capacity to use information provided by others to guide their own behavior or decision (Morand-Ferron et al., 2010). Such information, the behavior of others or its product, constitutes social information. It can be advertently (a signal) or inadvertently (a cue) produced and may complement personal information acquired through trial and error and direct interactions with the environment (Bonnie and Earley, 2007). The use of social information is thought to allow individuals to adapt to their environment faster and/or better than through collecting personal information alone. Use of social information thus provides tremendous evolutionary advantages and is known to occur in many contexts, e.g., regarding food location, availability and palatability, predator threats, and finding and choosing mates (Danchin et al., 2004; Laland, 2004; Dall et al., 2005; Kendal et al., 2005; Bonnie and Earley, 2007; Taborsky and Oliveira, 2012). Even when the information or behavior appears non-adaptive, such as many of the behavioral traditions observed in non-human primates [e.g., hand-clasp grooming (McGrew and Tutin, 1978) or stone-handling (Leca et al., 2012)], such traditions may still be adaptive by preserving group cohesion or reinforcing group membership/identity through conformity for example. In any case, the transmission of such traditions can be under the same social influences as that concerning more obviously adaptive social information. In this review, our main focus is on the transmission pathways of information between one individual (or group thereof) and another, regardless of its ultimate function/adaptive value. However, it must be kept in mind that low adaptive value may in itself partly explain a lack of diffusion of a given behavior, tradition or piece of information, and conversely that high adaptive value may facilitate and even enhance the diffusion process.

Within animal societies, an individual's ability to use social information and the properties governing its diffusion among group members or conspecifics have been studied under diverse frameworks, from evolutionary psychology (culture, social learning, and communication) and behavioral ecology (public information, eavesdropping) to neuroethology and economics of decision-making (information processing, social influences; Danchin et al., 2004; Dall et al., 2005; Kendal et al., 2005; Bonnie and Earley, 2007; Taborsky and Oliveira, 2012). The common threads binding all of these studies are twofold: (1) the source of information is the behavior of others and (2) the outcome of interest is the change in behavior associated with the acquisition and use of social information (Bonnie and Earley, 2007). Social information is thus a type of biological information, i.e., a property of some source that elicits a change in the state of the receiver in a (usually) functional manner. Differences between fields rest in the information content (who, what, and how) and packaging (signal vs. cue), as well as in the payoffs of using social information (Bonnie and Earley, 2007). For example, an animal's choice of a feeding site can be influenced by whether or not conspecifics are already feeding there (social influence or social learning), by the conspecifics' feeding behaviors that may be indicative of resource quality (public information), by how many other animals one can outcompete around the resource (eavesdropping), or by all of the above.

The acquisition and use of social information seems to be inherently adaptive, although some theoretical and empirical examples show that it could also be neutral (e.g., symbolic/arbitrary) and sometimes maladaptive (Rogers, 1988; Giraldeau et al., 2002). A maladaptive decision might also be defined as an inevitable by-products of an adaptive strategy that has evolved under strong selective pressures (Rieucau and Giraldeau, 2011; Pelé and Sueur, 2013). This probably relates to the existence of a trade-off between acquiring costly but accurate information through personal experience and using cheap but potentially less reliable information from others (Barnard and Sibly, 1981; Giraldeau et al., 2002; Laland, 2004; Kendal et al., 2005). Animals must thus adjust the weight they give to both sources of information depending on circumstance. Individuals may rely on social information when personal information is difficult to acquire or unreliable, and when they are uncertain about how to behave. They may instead rely on personally acquired information when the available social information conflicts with it or is incomplete, and/or when individuals are confident in the quality of their own information (Giraldeau et al., 2002; Laland, 2004; Kendal et al., 2005; Rieucau and Giraldeau, 2011). Most likely, decisions involve taking into account a combination of social and personal information and the diffusion of information is thus a function of the cost-benefit ratio of the different strategies available (Rieucau and Giraldeau, 2011). Yellow-bellied marmot (*Marmota flaviventris*) alarm calls, which are given to signal the presence of a predator, provide an opportunity to exemplify this because the caller's reliability in signaling danger is directly linked to the amount of time others allocate to personally assessing the threat: when the caller is judged unreliable, other marmots spend more time being vigilant (i.e., gathering personal information) before acting (or not) upon the threat (Blumstein et al., 2004). In species establishing recurrent and/or enduring social relationships between group members, reliability of social information also concerns these social relationships. For example, a middle-ranked female rhesus macaque (*Macaca mulatta*) will be more assertive toward an unfamiliar individual if she has seen a familiar subordinate individual defeating it in some competitive interaction (reliable social information), in contrast to conditions in which the interaction involved a familiar dominant or an unfamiliar individual (unreliable social information; cue reliability approach, Dewar, 2003).

Ways of testing functional and mechanistic hypotheses about social information and its use include: observing animals throughout their ontogeny, observing different populations of the same species with different behavioral traditions, or carrying out so-called social diffusion experiments in the lab or in the field. Social diffusion experiments investigate the transmission of social information from one individual (or group) to the next, seeding experimentally controlled innovations in behavior into groups of naïve individuals and tracking and documenting the spread (or otherwise) of the innovation (Whiten and Mesoudi, 2008; Whiten et al., 2016). A traditional experimental paradigm is to have two groups of subjects, an experimental group with a knowledgeable, proficient model that others can observe performing an action, and a control group without such an opportunity to observe. Alternatively, one of several new behaviors is seeded in one or few so-called informed individuals in a group of naïve individuals in order to artificially create behavioral variation amongst groups or populations. The aim is then to track the progressive acquisition of the new behavior in terms of pathways (from whom to whom the behavior is transmitted), speed, accuracy, and characteristics of individuals involved as compared to controls or variants (Whiten and Mesoudi, 2008; Whiten et al., 2016).

In this article, we first review such social diffusion studies and their goals, methods and outputs. We take a broad perspective on such studies, whether observational or experimental, with paired individuals or open groups, in a social learning or public information framework, but try to focus on salient research fitting our aims. We make no attempt to discuss what does or what does not constitute social learning (for comprehensive discussions of this see Galef and Laland, 2005; Hoppitt and Laland, 2008, 2013; Leadbeater, 2015, amongst others), nor to distinguish the mechanisms by which this particular use of social information occurs (see Laland, 2004; Hoppitt and Laland, 2013, amongst others), nor to debate whether the use of social information is adaptive (see Rogers, 1988; Giraldeau et al., 2002; Kendal et al., 2005, amongst others). Hereafter, we instead focus exclusively on the possible pathways for information transmission within groups or aggregations of individuals, and the factors that may enhance or, more interestingly for us, inhibit information transmission. We pay special attention to studies in which the goals and outputs did not necessarily coincide because these studies tell us as much as do studies presenting "positive" results about how animals use, or do not use, social information. In the second part of this article, we return to essential concepts and expand our review on the nature of social information itself, the putative cognitive abilities of various species, the idea of social competency, and the influence of social networks on the use of social information in animal societies (**Table 1**). To paraphrase Bonnie and Earley (2007), our intention here is not to revolutionize the field, but rather to continue stimulating discussions about the abilities of animals to extract, use, and produce information from the social environment, and their influence on information diffusion.

SOCIAL DIFFUSION EXPERIMENTS: GOALS, METHODS, AND OUTPUTS

One of the earliest known accounts of social transmission of behavior is milk bottle opening among tits (*Parus major*, *Periparus ater*, and *Cyanistes caeruleus*) in England, where birds learned to pierce the lid of milk bottles left on doorsteps to drink the cream within (Fisher and Hinde, 1949; Aplin et al., 2013). Although this innovative behavior started in several places independently, once present in a population it would spread extensively, suggesting the influence of social processes (Fisher and Hinde, 1949; Lefebvre, 1995; Aplin et al., 2013). Another known example of social transmission among animals comes from Japanese macaques (*Macaca fuscata*) washing sweet potatoes in water, a behavior that spread gradually through the group (Kawai, 1965). In the years following the start of this seminal study, several other newly acquired behaviors (e.g., begging, stone-handling) emerged and spread through different groups of macaques in different regions of Japan following rules of acquisition dependent mainly on age, sex, and kinship (Kawai, 1965; Huffman et al., 2008). Since then, almost all published experimental or natural studies of social information transmission show that given the possibility to observe knowledgeable individuals performing a task, the majority of naïve, non-knowledgeable individuals subsequently use the same technique to accomplish the same task (Morand-Ferron et al., 2010). The non-random process of task acquisition is generally demonstrated if it occurs either above chance or above the proportion of naïve individuals performing the same task in a control group without knowledgeable demonstrators or in a group seeded with a different technique (Whiten and Mesoudi, 2008; Whiten et al., 2016). These results seem to be taxon-independent and pertain to insects, birds and mammals, demonstrating the overwhelming generality of social information use by animals (Laland, 2004; Chittka and Leadbeater, 2005; Galef and Laland, 2005; Whiten and Mesoudi, 2008; Rieucau and Giraldeau, 2011; Whiten et al., 2016). We can nevertheless distinguish these studies into three, non-exclusive categories: (1) those relating to the presence/absence of diffusion of the behavior; (2) those regarding individual characteristics and their influence on transmission; and (3) those interested in the pathways and characteristics of diffusion (e.g., persistence of transmission). Complementary to the ideas presented here, Whiten and Mesoudi (2008) and then Whiten et al. (2016) also provide extensive and updated reviews of diffusion studies in animals and humans.

Presence/Absence of Diffusion

A first step in studies of social diffusion is to show that information is actually transferred amongst animals in some way. The literature is vast and spans contexts such as foraging, breeding, anti-predation strategies, and social interactions. Examples range from bumblebees (*Bombus impatiens*) choosing the same-colored flowers as those chosen by conspecifics they previously observed (e.g., Leadbeater and Chittka, 2005; Worden and Papaj, 2005), to client fish (*Scolopsis bilineatus*) spending more time near cooperative cleaner fish (*Labroides dimidiatus*) than cleaner fish of unknown cooperative level after observing other clients' interactions with these cleaner fish (e.g., Bshary and Grutter, 2006), to flycatchers (*Ficedula albicollis*) using others' breeding outcomes (offspring quantity and/or quality) to select a breeding habitat (e.g., Doligez et al., 2002).

The interest here lies in where transmission apparently did not occur, because looking at how, why, and in what context animals do not use social information is just as telling as when they do. For instance, wild keas (*Nestor notabilis*), a mountain parrot, failed to solve a foraging task despite having the opportunity to observe proficient individuals solving the same task and to engage with the experimental setup immediately thereafter (Gajdon et al., 2004). When the experiment was repeated with captive keas, a majority of the birds solved the task after observing a proficient model (Huber et al., 2001; Gajdon et al., 2004). This indicates that the absence of social information transmission was independent of the task's level of difficulty. It could be that wild keas have the capacity to learn socially but some constraints prevent them to express it – maybe a question of opportunity or utility. This is similar to what is found in spotted hyenas (*Crocuta crocuta*), a social carnivore, where individuals in captivity seem more proficient at solving foraging tasks than those in the wild. This difference was attributed to personality rather than more trivial factors such as time-energy threshold, inasmuch as captive hyenas are more exploratory and less neophobic than their wild counterparts (Benson-Amram et al., 2013). In contrast, a novel foraging behavior (piercing a lid to access food) spread more quickly amongst groups of free ranging urban pigeons (*Columba livia*) than amongst captive groups. This was explained by the fact that urban pigeon groups are open to migrants which could enhance the degree of innovation and diffusion (Lefebvre, 1986).

Looking in more details at the hyena example, whether in captivity or in the wild, individuals presented with a box containing meat were more likely to approach and manipulate the box when they had seen others do it but were not more

TABLE 1 | Summary of points examined in this review.

Transmission process	Known influential factors	Directions for further studies
Initiation	– Producer characteristics (sex, age, dominance rank, and personality, motivation), – Environment (complexity, stability), – Type of innovation	– Competing solutions to the same problem – Suboptimal demonstrator characteristics – Seeding of information to individuals with different characteristics simultaneously
Pathway	– Producer/receiver characteristics – Producer/receiver relationships (kinship, dominance difference, "friendship") – Cognitive abilities (sensory output and processing) – Social network (openness, connectedness, tolerance) – Adaptive value – Information characteristics	As above, and: – Several information of varied types (e.g., social/asocial), qualities, relevance, or congruence presented at the same time – Social structure disturbance/manipulation (e.g., alone/in a social setting) – Same type of experiments to many different species/groups (including interspecies) – Different task complexity/difficulty concurrently
Establishment/ termination	– Cost/benefit ratio, – Conservatism level – Social network structure	– Comparison between initial transmission and long-term transmission patterns

Additional aspects:

- Technological equipment to track non-invasively: individuals' movements (GPS, accelerometer), physical states (heart rate monitor, blood glucose or glucocorticoid level monitor, infrared imaging), social proximities [radio-frequency identification (RFID) tags]
- Test apparatus version 2.0 with touch screens or panels, automated feeders, eye-trackers, face recognition
- Long-term population studies
- Heritability/evolution/environmental changes studies
- Taking inspiration in other diffusion domains such as epidemiology, informatics, or social media
- Building a database of protocols, pre-print, and published studies

likely to succeed in opening it (Benson-Amram et al., 2014). In this case, social information is used indirectly to enhance extraction of personal information but not directly to solve an environmental problem. This could be explained by the simplicity of the task (solvable by trial and error), or the characteristics of the demonstrator (not relevant or reliable). It could also be that social constraints, such as a rather competitive environment, affects the cost/benefit ratio of social information vs. personal information: hyenas are very good at solving goal-oriented cooperative tasks (Drea and Carter, 2009), which may be necessary to hunt large prey, but when they already have access to food, they may instead pay more attention to avoiding aggression than to new ways of obtaining the food *per se*. A lack of diffusion and establishment of a behavioral pattern can also occur when two alternatives are equally profitable. In meerkats (*Suricata suricatta*), individuals were at first more likely to feed on the same feeder as a demonstrator, but the more they explored the experimental apparatus, the more they realized they could easily get food at two "locations," making it less likely they would continue to use the demonstrator's feeder more frequently (Thornton and Malapert, 2009). In this example, although there was social transmission from one demonstrator to one observer, there was no establishment of behavioral tradition such that the behavior spread within the whole group according to individual's assortativity.

In other cases, the task presented seems too difficult, not appropriate or not ecologically relevant for the tested animals. For instance, laboratory-reared rhesus monkeys learned to fear snakes from watching videos of wild-reared conspecifics' reactions to snakes, but never learned to fear a flower on the same basis (Cook and Mineka, 1989). In a two-step foraging task, vervet monkeys (*Cercocebus aethiops*) had to remove a rope blocking a door before opening that door to retrieve food. Although the trained model was ultimately successful at the task, other individuals failed to master it although they were exposed to a successful model, suggesting that the link between one gesture and the next in a several-steps task was not evident (van de Waal and Bshary, 2011). Another example of a behavior, this time naturally occurring, that failed to spread is dental flossing in Japanese macaques (Leca et al., 2010). In their study, the authors reported several factors likely to constrain the diffusion of innovation such as belonging to a small grooming cluster relative to group size or having few close kin in the group, and the form, function and context of the behavior. The most interesting point that the authors made here is that the low adaptive value of dental flossing, a "comfort" innovation with such a "narrow window of applicability," may also account for its lack of diffusion (Leca et al., 2010).

Influence of Individual Characteristics on Diffusion

Because social groups are often mixed groups of individuals of different sexes, ages, and/or personalities, individuals' interest in, and experience and knowledge of, their environments vary. Thus, some individuals are potentially more likely to discover resources in the environment, to start innovating, or to correctly assess dangers than others, creating a differentiation in the availability and reliability of the social information produced within a group/aggregation of animals. On the other hand, some individuals are also more likely to learn from their conspecifics because they are more social (in general terms), i.e., they are more often in proximity to others, they pay more attention to others, or they are more often engaged in social activities.

For instance, only 54% of naïve blue tits exposed to a proficient demonstrator solved a new foraging task (Aplin et al., 2013). Investigation of the variables that could explain this percentage showed that young females and subordinate males with higher innovative problem-solving capabilities were more likely to solve the task than others, whereas the characteristics of the demonstrator had no influence on the performance of naïve birds, i.e., there was no preferential attention to certain models (Aplin et al., 2013). On the other hand, studies on vervet monkeys demonstrated that social transmission is often influenced by kin relationships, i.e., vertical, from mother to offspring (van de Waal et al., 2014). When transmission is horizontal, from peer to peer, or oblique, from adults other than parents, vervet monkeys are more likely to copy the new foraging technique of an adult female compared to an adult/subadult male (van de Waal et al., 2010). Adult females of this species are philopatric and live their entire lives in the group in which they were born. This potentially makes them more reputable concerning food acquisition and processing because they have more experience and are the more familiar individuals in the group. They could also occupy more central positions in the social network of the group and may be more tolerant of individuals in proximity, all of which could potentially enhance social information transmission.

Similarly, it has been experimentally shown that, visually, monkeys do attend more to higher-ranking individuals than to lower-ranking individuals (e.g., McNelis and Boatright-Horowitz, 1998; Deaner et al., 2005), and to strong affiliates compared to average affiliates (Bonnie and de Waal, 2006; Micheletta et al., 2012). This pattern is interpreted as being more salient in terms of acquiring social information. As another case in point, the oldest living female in a group of African elephants (*Loxodonta africana*), the matriarch, often leads the group from one place to another and initiates group defense behavior (for example when encountering signs of unfamiliar individuals or of predators), potentially because she has enhanced local knowledge of the environment and group members defer the decision of travel/action to this informed individual (McComb et al., 2001, 2011; Mutinda et al., 2011). However, the best innovators, i.e., individuals more likely to start using a novel behavior, are not necessarily the best models for information transmission. For example, although male canaries (*Serinus canaria*) were better at solving a foraging task and thus could have been selected as demonstrators, their aggressive tendencies toward others prevented them from being good models (Cadieu et al., 2010). In this case, females constituted the best demonstrators because they tolerated individuals around them, so social transmission of an innovation mainly rested on females.

Diffusion Pathways

When social information is transmitted, determining the pathways taken by this information within a group of individuals as well as how fast and far it travels can give insights into the mechanisms of social information use. Indeed, animals living in groups or aggregations do not interact or associate randomly with one another, but have preferred associates or affiliates which are reflected in the heterogeneous structure of the social network of the group/aggregation. As such, the flow of social information is not random between individuals, but is in accordance with the structure of the social network of the population (Krause and Ruxton, 2002; Krause et al., 2007; Croft et al., 2008). Social transmission of information can thus fail not only because of some characteristics of demonstrators and/or naïve individuals, but also because the link between knowledgeable and naïve individuals may be suboptimal, e.g., the pair is not often together, not strongly affiliated or even avoids association, whatever the underlying causes. "Where" [i.e., with which individual(s)] to seed the social information diffusion within a network of individuals is thus as crucial as how connected the individuals are.

In brown capuchins (now *Sapajus apella*) for example, transmission during diffusion chain experiments was controlled in that pairs of demonstrators-observers were chosen amongst affiliates and the demonstrator was the higher-ranking of the two, which may have facilitated transmission (Dindo et al., 2008). In contrast, in a group of squirrel monkeys (*Saimiri sciureus*), where the chosen demonstrator of a new foraging technique was the alpha male, the open diffusion experiment demonstrated that more central individuals in the social network (those well connected and integrated in the group) were more successful at mastering the technique and quicker at using it than less central individuals (Claidière et al., 2013). Central individuals indeed may have more opportunity to observe the demonstrator and/or to manipulate the apparatus, especially if the demonstrator is itself central, which would enhance the use of social information. In a more natural setting, Brown (1986) showed that cliff swallows (*Hirundo pyrrhonota*) that were unsuccessful at bringing food back to the nest for nestlings were more likely to follow a successful individual on their next foraging trip than were successful foragers. Unsuccessful foragers were also more likely to follow their nest neighbors on subsequent trips, especially those within 1 to 5 nests away than further away in the colony. As there was intra-individual variation in foraging success, any bird could be a successful or unsuccessful forager and thus a follower or a leader to a foraging patch. This led Brown to coin the swallow colonies as "information centers" and is one of the earliest examples of diffusion analysis in a foraging context, albeit in a crude way (Brown, 1986).

A major step forward in the study of social diffusion is the development of network-based diffusion analysis (NBDA). NBDA is a tool now commonly used to demonstrate that the expression of a behavior by an individual is the result of it being associated with animals that themselves express this behavior with an increased probability compared to a model not including social effects (Franz and Nunn, 2009; Hoppitt et al., 2010). The model specifically illustrates directed social learning, in which information is transmitted at different rates depending on association patterns between individuals (Coussi-Korbel and Fragaszy, 1995). Such social effects explain variance in lobtail feeding in whales (Allen et al., 2013) or food patch discovery in tits (Aplin et al., 2012). The latter study not only demonstrated that tits use social information to locate new food patches but also that the discovery success was linked to individual centrality in the flock association network: more central individuals were more likely to locate and use novel foraging patches than those with limited social connections. By looking at an animal or human group as a network of connected individuals, social network analysis has facilitated great progress in diffusion studies, and as a result, in the understanding of animal and human culture. Because culture is fundamentally based on the exchange of social information, social structure and culture are indeed linked (Cantor and Whitehead, 2013). In this perspective, diffusion studies, whether experimental or observational, coupled with social-network-based analysis brought substantial advances to our understanding of how animals use social information.

FURTHER PERSPECTIVES ON SOCIAL DIFFUSION STUDIES

Questions regarding the acquisition and use of social information are typically concerned with when to copy (e.g., when resources are easy or difficult to exploit/find, or when the environment is stable or unstable), who to copy (e.g., successful or reputable or familiar or genetically related individuals), what is copied (i.e., what kind of information is remembered and transmitted) and how individuals copy (i.e., the mechanisms or supports by which the information is reproduced; Laland, 2004; Bonnie and Earley, 2007; Whiten and Mesoudi, 2008; Whiten et al., 2016). The literature covering each of these aspects is vast and continues to expand almost exponentially (Galef, 2012; Whiten et al., 2016). The challenge that remains even today is to examine those questions in more integrative ways and to find the right experimental, empirical, and statistical paradigm to do so (Whiten et al., 2016).

Important aspects of diffusion that we feel deserve more attention include social information characteristics, what makes an animal a producer and/or a user of information, the cognitive capacities involved in acquiring, processing, and using social information, and finally the social competency of animals. We also think that future work could pay more attention to quantifying the rate at which information spreads, how far this information can spread in a network, and the factors that influence the flow of information. This means that an additional focus to factors favoring social transmission could be on those explaining an absence thereof. We now turn to these topics in a humble attempt to participate in advancing the field of social information use in animal societies.

Social Information Characteristics

The characteristics of social cues, i.e., information that is inadvertently produced through interaction with the environment, can greatly influence their transmission inasmuch as acquiring and using social information is directly related to the cost of acquiring and using asocial or personal information (Boyd and Richerson, 1988). These characteristics can be experimentally modified to assess which are important to the animals. For example, is the number of conspecifics performing a task sufficient, or are subtler cues necessary to decide to use social information? For instance, experiments of social transmission in fruit flies (*Drosophila megalonaster*) showed that within an aggregation, the number of informed individuals needed to be about twice the number of uninformed individuals in order to observe transmission of information from informed to uninformed individuals (Battesti et al., 2015). Experiments with fish and birds demonstrate that individuals without *a priori* information on environmental resources are more likely to follow a large group of conspecifics to a food location compared to a small group. But as soon as individuals can observe others actually feeding, they would rather follow few individuals feeding than many individuals not feeding (Kendal, 2004; Coolen et al., 2005; Rieucau and Giraldeau, 2011). This suggests that observing a direct link between a task and a reward is more salient than just observing a task. Similarly, individuals with *a priori* personal (or asocial) information are less influenced by their companions' behavior than those without. In an experiment with nutmeg mannikins (*Lonchura punctulata*), individuals without prior personal information consistently chose the feeder associated with previously acquired social information regardless of whether it was the mere numbers of companions present or the numbers of companions feeding. Individuals with prior personal information, however, did stick to their initial choice and switch feeders only if they observed companions actually feeding (Rieucau and Giraldeau, 2009). More subtly, homing pigeons were shown to adjust their flight routes, to which they generally show high fidelity, depending on those followed by conspecifics (Biro et al., 2006). When the pre-established routes of two pigeons did not differ greatly, a pair would converge on an average path, supporting the "many-wrong" hypothesis arising from a compromise between personal and social information. However, as soon as the routes diverged beyond a distance threshold, one individual became the leader, usually the pigeon most faithful to its own pre-established route, supporting the leadership hypothesis in which the most insistent, "confident," or less flexible individual imposes a social choice on the group. In other cases, both pigeons defaulted to their established routes and thus no use of social information was observed, again usually when the routes diverged beyond a distance threshold (Biro et al., 2006; Freeman et al., 2011).

Another characteristic of information that is likely to influence its transmission is complexity or difficulty. A one-step task may thus be acquired and spread faster between individuals than a task requiring four steps to be completed. For example, callitrichid monkeys used social information to solve a challenging foraging task involving pulling a door toward oneself and retrieving food inside a box, whereas they solved an easier foraging task involving pushing a door and reaching inside to retrieve food without using social information (Kendal et al., 2009). Similarly, vervet monkeys easily solved a simple foraging task such as pushing/pulling a door (van de Waal et al., 2013), but failed to solve a two-action foraging task, even when being provided with social information (van de Waal and Bshary, 2011). Information complexity or stability can also emerge from the environment. For example, the structure of the environment (open vs. closed, arboreal vs. terrestrial) can influence how communication signals can be perceived (Maciej et al., 2011). Starlings (*Sturnus vulgaris*) in an unpredictable environment are better at foraging when in the presence of an informative demonstrator (who consistently indicated the same food location) than in the presence of an uninformative demonstrator, whereas individuals in a predictable environment performed equally well with or without an informative demonstrator (Rafacz and Templeton, 2003). The extent to which the complexity or stability of the environment affects the transmission speed, accuracy, and reach of social information is still not very clear, however. Ecological and social environments may very well interact to affect social information transmission inasmuch as an individual's perception and action are tightly linked to both (e.g., Barrett, 2011).

Some types of information are also more salient or relevant than others, which will influence their social transmission. For example, humans recall and repeat social information such as gossip involving third-parties with greater accuracy and in greater quantity than non-social information such as the geographical description of a city (e.g., Bartlett, 1932; Mesoudi et al., 2006). In animals, several studies hint that individuals would probably also pay more attention to information relating to social events as opposed to non-social events. For example, fish choose to take a long circuitous route with their mates rather than a shorter more direct route alone to access food. This preference persists over several generations even when founder demonstrators have disappeared from the population (Laland and Williams, 1998). Similarly, in a two-choice test paradigm where male rhesus macaques had to choose between receiving a fruit juice reward or receiving a fruit juice reward and seeing an image of a conspecific, they not only chose the latter option but sacrificed a bit of the amount of juice they could have received to do so (Deaner et al., 2005). This choice demonstrated that monkeys were ready to sacrifice a food reward to gather social information.

Another characteristic we briefly mentioned before concerns the adaptive value of a given piece of social information. If social information that is obviously adaptive, e.g., use of a tool to extract food among primates and corvids, versus that which is not-so-obviously adaptive, e.g., stone-handling among Japanese macaques, were to be seeded in the same group or aggregation, would the spread, speed and reach of diffusion of the former be more important than the latter? The relevance of the former compared to the latter would intuitively lead us to predict a positive relationship between adaptive value and these diffusion properties. However, if these not-so-obviously adaptive socially transmitted behaviors play a role in increasing group cohesion through conformity for example, the answer may not be so straightforward.

So, in general, although animals can display great interest in an experimental apparatus or a given situation, perform a task or a behavior to perfection, and readily observe and copy others, we still know too little about the nature of social information and its influence on transmission dynamics to predict when these behavioral aspects will coincide and result in diffusion. Is it about quality, quantity, complexity, congruence, relevance, or a mixture of all of these traits? Determining this requires long and patient trial-and-error tests, massive undertakings of experiments encompassing varied conditions, contexts, and characteristics, mathematical models and efforts in complex systems science and, importantly, although the information can sometimes be extracted from the study itself, a systematic report or test of the kind of information that is tested/used. Experiments combining tests of asocial and social information simultaneously are also important in determining characteristics of diffusion as it is likely that animals use a combination of both at every instant (Rieucau and Giraldeau, 2011).

Animals as Information Processors and Users

Each step of the transmission process requires individuals to "innovate" on a personal level, that is, they are not necessarily the first to express the behavior but this is the first time that they themselves express it. In this sense, understanding limits to innovation helps understanding constrains on social diffusion (Brosnan and Hopper, 2014). One of these limits is within the animals themselves, related either to individual characteristics – explored in this section – or to cognitive abilities – explored in the next section (for limits concerning the social environment, see "The social competency of animals or the social network effect").

Characteristics of the information producers, such as relative status, age, or sex, cannot only influence the performance of an individual in its environment but can also condition another animal's decision to observe such producers and to use the information gathered. Similarly, characteristics of the information receiver determine its processing and use of information and, as such, the speed, accuracy and extent of information transmission. Individual constraints on social diffusion (here, of innovations) stem from the propensity of individuals to be conservative, that is, individuals tend to persist with existing behaviors, or the existing uses of behaviors, rather than explore novel options (Brosnan and Hopper, 2014). As a case in point, bolder and less neophobic individuals are more likely to produce information and to innovate than shy and neophobic individuals because they tend to take more risks and explore their environments more (Wilson, 1998). Lower-ranking chimpanzees tend to be more innovative, probably because they are more constrained in their access to food and have to find an alternative solution more often than higher-ranking individuals (Reader and Laland, 2001). In great tits, variation in spontaneous problem-solving performance was unrelated to individual state (e.g., body condition) and not even associated with behavioral traits (e.g., neophobia), but most likely reflected inherent individual differences in the propensity to forage innovatively (Cole et al., 2011). In starlings, less neophobic and higher-ranking individuals were more likely to approach the experimental novel foraging tasks. Group mates of these first "contactors" approached the experimental apparatus more quickly as well if they themselves had a propensity to feed in a novel environment (Boogert et al., 2008).

Nevertheless, although some studies have determined which individuals tend to learn or innovate faster or better (see references in previous paragraph), we are still at risk of making a lot of assumptions about who those individuals might be instead of testing who they actually are. When studying animals living in group, especially in natural conditions, researchers are indeed often constrained in the choice of knowledgeable demonstrator(s) vs. naïve observer(s), because high-ranking individuals monopolize the resources for example, or because bolder individuals are more explorative. It is also very difficult to disentangle which individual characteristics can have the most influence, as high-ranking individuals for instance can also be bolder than low-ranking individuals. Studies conducted with wild animals must keep these sociodemographic constraints in mind when being discussed or reported. Finding ecological validity in diffusion studies is a much needed challenge (Whiten et al., 2016).

Overall, what makes a producer and/or a user of information varies greatly according to ecological, social, and individual circumstances. What we need to be more aware of is that not all individuals will produce or use social information, in relative and absolute terms. Optimizing our knowledge and understanding of the speed, accuracy, and spread of social information transmission requires that the profiles of producers and users be more systematically reported. We also need studies that can select producers and users with suboptimal characteristics, for example a high-ranking individual with a lower-than-expected network centrality compared to a low-ranking individual with a higher-than-expected network centrality, or a lower-ranking individual with a higher-than-expected boldness profile compared to a high-ranking individual with a lower-than-expected boldness profile. For instance, in several groups of vervet monkeys tested in an experimentally induced coordination problem, dominant individuals naïve to a foraging task learnt to wait outside of an imaginary forbidden circle that the proficient but low-ranking individual approached and solved the task and allowed food access to the whole group (Fruteau et al., 2013). What is also needed is the assessment of the effects of individual characteristics on diffusion in naturally or spontaneously occurring innovations, observed from their birth to their establishment or disappearance, in a population where individuals are identifiable and their characteristics *a priori* known [e.g., dental flossing (Leca et al., 2010) and louse egg-removal techniques (Tanaka, 1998) in Japanese macaques, lobtail feeding in humpback whales (Weinrich et al., 1992; Allen et al., 2013), or moss-sponging in chimpanzees (Hobaiter et al., 2014)].

Cognitive Abilities

The social brain hypothesis states that increasing social complexity drives the evolution of large brains with more cognitive capacities, in the sense of information-processing, because of the challenges of managing complex social relationships (Whiten and Byrne, 1997; Dunbar, 1998; Pérez-Barbería et al., 2007). However, the use of social information is so widespread in the animal kingdom that one could contend that information-processing capabilities do not relate only to brain size (Barton, 2006; Morand-Ferron et al., 2010; Lihoreau et al., 2012). The fact that invertebrates such as wasps and bees are capable of memory and learning demonstrates how complex cognitive processes are possible even with a limited number of neurons (Lihoreau et al., 2012; Avarguès-Weber and Giurfa, 2013; Grüter and Leadbeater, 2014). Paper wasps (*Polistes fuscatus*) can recognize individuals and remember the identity of social partners, even after a succession of interactions with other individuals (Sheehan and Tibbetts, 2008). Honey bees (*Apis mellifera*) are well known for their symbolic “dance language,” which they use to build consensus about relocating to a new home: the swarm integrates the different information given by different explorative scouts through their dancing and make a decision about a single location (Seeley, 2010). In the field of social learning, it has been argued that social learning does not depend on “advanced” cognitive adaptations, and that social and asocial learning alike depend on the same mechanisms (Heyes, 2012). This hypothesis is supported by the facts that social and asocial learning abilities covary across and within species (Bouchard et al., 2007; Reader et al., 2011), that social learning occurs also in solitary animals (Fiorito and Scotto, 1992; Wilkinson et al., 2010), and that social learning has the same key features in diverse species, including humans (Heyes, 1994, 2012). Heyes (1994, 2012) therefore argues that social and asocial learning depend on a common set of associative learning mechanisms and that social learning merely reflects the case in which the information is provided through a social channel (Heyes, 2012). This illustrates how the use of social information may in fact require relatively simple and computationally inexpensive forms of cognition (Lihoreau et al., 2012).

However, the use of social information also involves perceptual, attentional, and motivational processes specific to information coming from other individuals (Heyes, 2012). Acquiring and using social information requires animals to link other individuals’ actions to environmental and/or social reactions or patterns. Feedback from the social domain also requires that individuals integrate and process stimuli not only related to the external (e.g., sex, size) but also to the internal (e.g., “emotional”) states of other interacting agents, to the current social context, and to what this information means to the individual at that moment in time in order to respond with the appropriate behavior (Trimmer et al., 2008; Clutton-Brock, 2009; Taborsky and Oliveira, 2012). Throughout the evolutionary history of social species, these social-specific processes may have been selected for and may have further coevolved with the complexity of social life (Heyes, 2012; Leadbeater, 2015). For instance, Pinyon jays (*Gymnorhinus cyanocephalus*), a social corvid species, perform a social learning task better than an asocial learning task whereas Clark’s nutcrackers (*Nucifraga columbiana*), a less social corvid, perform equally well in both tasks (Templeton et al., 1999). Based on these differences, social learning capabilities were interpreted as being adaptations to social life (Templeton et al., 1999; Heyes, 2012). This is essentially one of the tenants of the cultural intelligence hypothesis (Whiten and van Schaik, 2007; van Schaik and Burkart, 2011), which examines links between asocial and social learning and the development and maintenance of learned skills both horizontally and longitudinally in an effort to better understand the emergence and maintenance of cultures and traditions.

From a neuroethological perspective, some parts of the brain are specifically dedicated to social stimuli, such as face recognition and processing, social approval (i.e., individuals tend to conform to social norms to "fit in"), selective social attention (e.g., individuals pay more attention to higher-ranking individuals), or recognizing and responding to socio-emotional signals such as fear and anger (Brothers, 1999; Insel and Fernald, 2004; Phelps and LeDoux, 2005; Barton, 2006; Adolphs, 2008; Rilling and Sanfey, 2011). Mirror neurons are specifically activated both when one performs an action such as reaching for food and when one observes someone else performing that same action (Gallese, 2007; Caggiano et al., 2009). In the broadest sense, emotions are "an evaluative response of the organism involving physiological arousal and expressive behavior," and "interfacing between sensory inputs and motor outputs in a way that allows flexibility in the response (to a stimulus)" (Aureli and Schino, 2004 for one definition amongst many). They function as adaptive responses to environmental demands, preparing individuals to cope with challenges (Aureli and Whiten, 2003; Aureli and Schino, 2004; Phelps and LeDoux, 2005; Naqvi et al., 2006; van den Bos et al., 2013). As shown in many (natural or induced) experiments of brain lesions/malfunctions in humans and animals (e.g., in the case of autism or brain damage due to an accident), individuals that are physiologically or neurologically stressed or impaired have difficulties making decisions in the social domain and may thus be poor users of social information, which would ultimately constrain social information diffusion without giving any indication about their cognitive abilities. For example, individuals with a damaged ventromedial prefrontal cortex have normal intellect and problem-solving abilities under test conditions in the lab, but make unfortunate decisions in real-life situations and do not learn from their mistakes. This is due to the fact that they have a generally "flat affect" and are thus unable to use emotions to aid in decision-making (Damasio, 1994; Naqvi et al., 2006).

From these perspectives, focusing social cognition research on sensory information, computational challenges, and neural networks, i.e., brain functioning, would be a rewarding way of looking at animal cognitive abilities in the social domain (Chittka and Niven, 2009; Barrett, 2011; Lihoreau et al., 2012). Designing experiments and observations where animals' motivational, emotional and perceptual capabilities concerning their social worlds are accounted for could give important insights into how social information is transferred within a group.

The Social Competency of Animals or the Social Network Effect

Ingenious mathematical models and experimental designs show that efficient transfer of information and decision-making can occur within animal groups in the absence of individual recognition, advanced cognitive abilities or complex mechanisms of transfer, and that individuals can respond spontaneously to others that possess information. All that is needed is variation in information holding among members of a population and simple mechanisms of coordination (e.g., Couzin et al., 2005).

However, these kinds of simple decision rules are more likely to be present in societies where individuals do not form differentiated relationships with each other. When group members have the opportunities to recognize each other and memorize past interactions that influence future ones, they do form differentiated relationships that can condition and influence their decision-making processes (Sueur, 2011; Lee and Harris, 2013; Pasquaretta et al., 2014). The heterogeneous distribution of social connections within a group also creates heterogeneous opportunities to observe and learn from certain individuals (as in directed social learning, Coussi-Korbel and Fragaszy, 1995). As such, the structure of the social network of a group can have important consequences for the social transmission of information (Coussi-Korbel and Fragaszy, 1995; Croft et al., 2008; Aplin et al., 2013; Cantor and Whitehead, 2013). For example, observer deer mice (*Peromyscus maniculatus*) have stronger reactions of preparatory analgesia and self-burying in reaction to biting flies when the observer is genetically related to or is more familiar with the demonstrator, although the demonstrator's behavior does not vary with social conditions (Kavaliers et al., 2005). High-ranking rhesus macaques solve a color-discrimination problem equally well when in a whole group or only amongst high-ranking individuals, whereas low-ranking individuals perform better when with other low-ranking individuals only than when with the whole group (Drea and Wallen, 1999). In a cooperation task, spotted hyenas adjust their behavior to the skills and capabilities of their partners (for example, when an adult is paired with a youngster) and their level of cooperation is modulated by the composition of their social group inasmuch as an individual's performance is better predicted by the presence of high-ranking individuals – which can be quite aggressive – than by the subject's prior experience in the task to solve (Drea and Carter, 2009). An entire field of research in animal communication is dedicated to these moderating effects of social context, so-called "audience effects," i.e., individuals adjust their decisions or behaviors depending on who is with or around them (Zuberbühler, 2008). Conformity, i.e., doing what the majority does, is a very influential mechanism by which culture emerges, evolves and persists (Laland, 2004; Morgan and Laland, 2012). Reaching a consensus decision, on where to go for example, is also a well-studied example of social modulation of behavior (Conradt and Roper, 2009).

Social network analysis (SNA) has proven a useful and powerful tool in understanding social influences on the patterns of acquisition and use of social information (Croft et al., 2008; Voelkl and Noë, 2010; Kurvers et al., 2014; Brent, 2015). A simulation study based on a substantial dataset of primate interaction matrices tested the hypothesis that the social structure of a group has a strong influence on patterns of social learning (Coussi-Korbel and Fragaszy, 1995) by comparing information flow within networks in empirical (structured) social groups and theoretical well-mixed groups in terms of propagation speed, path length of transmission and resilience against information loss (Voelkl and Noë, 2010). This study showed that information spreads faster in well-mixed groups compared to structured groups. In structured social networks, information also spreads faster when the frequency of interactions was either disregarded (unweighted or topological networks) or distributed randomly amongst interacting individuals. Similarly, the number of transmission events (path length) from an innovator individual to a target individual was greater in structured groups compared to well-mixed groups and was related to reduced connectivity and variation in interaction frequencies. Furthermore, variance in average path length was related to variation in group size, the larger the group the longer the path length, but also to community modularity, a measure that quantifies the structuring of a group into subgroups (Voelkl and Noë, 2010). Actually, there is more and more evidence that the structure of a social group, rather than its absolute size, influences network flow (e.g., pathogens or diseases: Griffin and Nunn, 2012; Nunn et al., 2015; emotions, tastes, or health outcomes: Fowler and Christakis, 2008; Bakshy et al., 2012; Christakis and Fowler, 2014). At a more global level, this is illustrated by the differences found in cooperative performance, enhanced in socially tolerant bonobos compared to more aggressive chimpanzees (Hare et al., 2007), or in socially tolerant Tonkean macaques compared to non-tolerant rhesus macaques (Petit et al., 1992). Those differences have been attributed to the fact that social networks of tolerant species are more diverse and open because individuals tolerate each other's proximity better and this potentially offers a greater opportunity for information diffusion.

In humans, mathematical modeling has shown that social influences can lead to disproportionate diffusion of a trend or a fashion, an effect called the majority illusion (Lerman et al., 2015). In a network setting, behaviors can be contagious and spread to an entire population from a small subset of initial individuals. The speed and spread of this contagion has been shown to be heavily dependent on the network structure: a trend or a disease is transmitted faster if the initial adopters are very well connected and/or belong to very well connected clusters, e.g., superspreaders (Fujie and Odagaki, 2007; Garcia-Herranz et al., 2014). Because individuals take their social cues from their local neighbors, the characteristics and positions in the network of these initial adopters can greatly influence the contagion of a behavior, making it appear far more common locally than it is globally (Christakis and Fowler, 2014; Garcia-Herranz et al., 2014; Lerman et al., 2015). This has been termed the majority illusion and stems from the friendship paradox in which one's friends appear to have more friends than one has (it also concerns tweets and academic citations for instance). The mathematical model developed by Lerman et al. (2015) quantifies the strength of this phenomenon and shows that it is stronger in networks with active high-degree nodes (active knowledgeable individuals) and heterogeneous degree distribution (because active knowledgeable individuals are more attractive and others in the population, non-active non-knowledgeable, pay more attention to them). Similarly, in health programs dedicated to educate people about hygiene and safer practices, targeting friends of individuals – themselves chosen randomly – in the population can have greater effects on the spread of behavioral changes than targeting individuals with the most social ties (Kim et al., 2015). This effect is attributed to the specific structuring of human social networks, which show subgroups of interconnected individuals each with their own locally influential nodes (Newman and Park, 2003; Fowler and Christakis, 2008; Kim et al., 2015). It also suggests that the assumption of greater centrality linked to greater influence on social processes is not always straightforward as this relationship can be mediated by sub-structuring, individual role or position, and synergies between indirect and direct connections. In fruit flies, social network structure [for example, homogeneous (individuals behave similarly) vs. heterogeneous] also affects information use, specifically in oviposition site choice: uninformed flies would either follow or avoid choices of informed flies depending on the amount of variance in individual network centrality among informed group mates, the greater the variance the more uninformed individuals avoided the same site as informed individuals (Pasquaretta et al., 2016). Social network modeling can thus improve the underpinning social variance and the understanding of why some behaviors spread – or on the contrary do not spread.

A factor that is often overlooked is that, although social life is extremely beneficial, it can also be stressful because individuals not only have to satisfy their own needs but also must do so while coordinating with the needs of others (Krause and Ruxton, 2002). Whether test subjects are in their social group settings or tested singly can have tremendous effects on their stress level and cause concomitant effects on decision-making in the laboratory or under natural conditions (van den Bos et al., 2013). As such, on the one hand experimental studies done in isolation of the social context may have little predictive value in terms of social information use in general, although they allow for the dissection of mechanisms and functions quite difficult to achieve in natural settings. On the other hand, the social group context can be very inhibiting for some individuals and thus can impede social information diffusion, such as potential or actual conflicts with conspecifics, or the fact that performing a task in front of conspecifics can be overwhelming (van den Bos et al., 2013). Stress affects memory and learning (Schwabe et al., 2012) and biases decisions (Aureli and Schino, 2004; Naqvi et al., 2006; Starcke and Brand, 2012). For example, individual ravens (*Corvus corax*) approach a novel object faster but spend less time interacting with it when alone than when in pairs or groups, seemingly trading off vigilance against innovation depending on risk and opportunity assessment (Stöwe et al., 2006). Brown rats (*Rattus norvegicus*) experiencing stress significantly and progressively lose the ability to adjust their responses toward a larger reward when transitioning from equal to unequal reward quantities (Graham et al., 2009). The effect of stressors on decision-making may not be of great consequence in animal social diffusion studies apart from failed experiments, but in humans, having to make a decision under high stress is linked to variation and volatility which likely reflects uncontrollability and unpredictability and can lead people or groups to make irrational choices (Starcke and Brand, 2012).

A final aspect of the influence of sociality on social information use is the social competence of animals. Social competence refers to the ability of individuals to regulate the expression of their social behavior in order to optimize their social relationships

(Taborsky and Oliveira, 2012; Bshary and Oliveira, 2015). For instance, it allows individuals to avoid engaging in overly costly fights ("winner-loser" effect; Hsu et al., 2006; Taborsky and Oliveira, 2012) and to increase or decrease their degree of aggressiveness according to the familiarity of their opponents (familiar = "dear enemy" effect, stranger = "nasty neighbor" effect; Temeles, 1994; Taborsky and Oliveira, 2012). Social competence can also explain why individuals tend to cooperate more readily with social partners if they themselves have received help from others previously ("generalized reciprocity"; Pfeiffer et al., 2005; Taborsky and Oliveira, 2012). Although established from an evolutionary ecology point of view, with reference to phenotypic behavioral flexibility and plasticity, the vantage point of social competence provides an overview of the general ability and performance of individuals in a social environment (Taborsky and Oliveira, 2012). Recently, the social competence perspective has been paired with a game theoretic approach in animal cooperation with exactly this goal in mind. This more integrative framework also highlights the importance of studying the behavior and underlying decision rules/strategies of individuals across different social contexts, in the same way that behavioral syndromes encompass links and feedbacks of individual reaction norms across a variety of contexts (Bshary and Oliveira, 2015). Social diffusion studies would benefit enormously from taking such an integrative approach and accounting simultaneously for variation in the individual, social, and physical worlds.

SMART ANIMALS

Animals produce and receive, acquire and use social information from different individuals in different contexts and circumstances. The circumstances under which an animal uses social information rather than selects an option based on its own environmental sampling or the different rules animals adopt when making such decisions have been investigated in great details. Social diffusion experiments of all kinds are great tools to investigate the social insights of animals. Nevertheless, many important questions remain: how do animals distinguish informed and uninformed individuals? How do they judge the quality of a piece of information? What if several individuals are deemed knowledgeable but the information they provide conflict? What if the context in which social information is produced changes its value compared to another context? What if certain pieces of information are easier/less risky to get, but are also less accurate? To what extent the spread, reach and speed of transmission of a social information are affected by these parameters? Answering these questions, from our point of view, will require a more integrative approach, marrying different fields to reflect more realistically the probable holistic understanding animals have of their environments (Laland, 2004; Taborsky and Oliveira, 2012; Bshary and Oliveira, 2015).

On a practical side, with the accumulation of studies of diffusion, building a database of successful and failed experiments could better inform the scientific community. This could take the form of depositing protocols into an open-access database, such as the Dryad Digital Repository[1], with the advantage of having corresponding digital object identifiers (doi), or creating a dedicated website on which to aggregate studies, pre-prints, and protocols in the same fashion as the Global Mammal Parasite Database[2], with the advantage that it is searchable and collaborative. With the technology available today providing small cost-effective electronic devices [touch-screens, eye-trackers, automated feeders, accelerometers, radio-frequency identification (RFID) technology, GPS, etc.], broad-scale experiments and modeling could be possible as is now done regularly in cognitive science (Fagot and Bonté, 2010), ecology and social network studies (Rutz et al., 2012; Krause et al., 2013; Farine and Whitehead, 2015). One could setup providing automated food boxes with automatic food delivery devices and remote-controlled openings triggered by the approach of an animal equipped with RFID tags. Providing dozens of such boxes in a group setting would allow varying the quality, quantity, and reliability of the information available to group members both as producers and receivers. Tracking natural demographic changes or experimentally inducing changes by removing/adding individuals or manipulating the quality of a social bond could also give insights into the causes and consequences of social network structure on social information transmission.

This kind of diffusion experiments, with broad yet individualized parameters, could help tackle integrated questions related to variation and complexity of the environment, be it social or ecological. As has already been proposed for studies in cognitive science (see e.g., Barrett, 2011 and Wilson and Golonka, 2013 for an overview), social diffusion studies would also benefit from being more "embodied," i.e., investigating social information use within individual, social and environmental contexts. Furthermore, studies on social information transmission could get inspiration from other domains such as epidemiology, informatics security, or social media, especially in humans, where studies also account for and integrate social network processes in empirical and mathematical studies, thereby providing tremendously important insights into biological and social processes. Finally, most of the experimental examples are situated in foraging, mating and anti-predator contexts, but far less has been done in social contexts such as aggression or affiliation. We know that animals are socially aware in the sense that they recognize their group mates or conspecifics, that they can keep track of their relationships and that they can use social concepts such as dominance and triadic relations (Whiten and Byrne, 1997; Dunbar, 1998; Emery, 2004; Holekamp et al., 2007; Silk, 2007). We have evidence that animals can recognize facial expression in conspecifics (Micheletta et al., 2015), that emotional arousal can spread through a group (collective arousal or emotion contagion, e.g., De Marco et al., 2011) and that animals can also judge and use the social reputation of others in their decisions (Alexander, 1987; Bshary and Bronstein, 2010). How animals make use of these kinds of social information to guide their decisions in their social relationships is an open field of investigation where

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[1] http://datadryad.org/pages/organization

[2] http://gmpd.nunn-lab.org/

social diffusion experiments can find their place. Better or further accounting for characteristics of information, of individuals, of cognitive and social competences is essential in making progress in the social information field and in the understanding of how animals make use – or not - of social information.

AUTHOR CONTRIBUTIONS

All authors made substantial contributions to the conception and design of the work; participated in the acquisition, analysis, or interpretation of data for the work; participated in drafting the work or revising it critically for important intellectual content; gave their final approval of the version to be published; and agree to be accountable for all aspects of the work.

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A New Semi-automated Method for Assessing Avian Acoustic Networks Reveals that Juvenile and Adult Zebra Finches Have Separate Calling Networks

Marie S. A. Fernandez[1, 2]*, **Hedi A. Soula**[2, 3], **Mylene M. Mariette**[1, 4] **and Clémentine Vignal**[1]

[1] Univ Lyon, UJM-Saint-Etienne, Centre Nationnal de la Recherche Scientifique, Neuro-PSI/ENES UMR9197, Saint-Etienne, France, [2] EPI BEAGLE INRIA, Villeurbanne, France, [3] Institut National de la Santé et de la Recherche Médicale U1060 INSA, Villeurbanne, France, [4] Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Geelong, VIC, Australia

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University of Alberta, Canada

***Correspondence:**
Marie S. A. Fernandez
marieferndez@gmail.com

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Social networks are often inferred from spatial associations, but other parameters like acoustic communication are likely to play a central role in within group interactions. However, it is currently difficult to determine which individual initiates vocalizations, or who responds to whom. To this aim, we designed a method that allows analyzing group vocal network while controlling for spatial networks, by positioning each group member in equidistant individual cages and analyzing continuous vocal interactions semi-automatically. We applied this method to two types of zebra finch groups, composed of either two adult females and two juveniles, or four young adults (juveniles from the first groups). Young often co-occur in the same social group as adults but are likely to have a different social role, which may be reflected in their vocal interactions. Therefore, we tested the hypothesis that the social structure of the group influences the parameters of the group vocal network. We found that groups including juveniles presented periods with higher level of activity than groups composed of young adults. Using two types of analyses (Markov analysis and cross-correlation), we showed that juveniles as well as adults were more likely to respond to individuals of their own age-class (i.e. to call one after another, in terms of turn-taking, and within a short time-window, in terms of time delay). When juveniles turned into adulthood, they showed adult characteristics of vocal patterns. Together our results suggest that vocal behavior changes during ontogeny, and individuals are more strongly connected with individuals of the same age-class within acoustic networks.

Keywords: development, ontogeny, songbird, acoustic communication, vocal interactions, turn-taking, conversation rules

INTRODUCTION

Social interactions with adults during ontogeny are likely to shape the social developmental trajectories of juvenile individuals. Indeed, some behaviors like courtship, mate choice preferences or foraging skills are partly shaped by social conditions during ontogeny (Freeberg, 1996; Farine et al., 2015) or at adulthood (Freeberg, 2000; Verzijden et al., 2012; Westerman et al., 2012). It has been shown that complex social environments, providing more opportunities for learning, allow individuals to improve their courtship performance or mate choice (during ontogeny, Miller et al., 2008; at adulthood, Oh and Badyaev, 2010; Jordan and Brooks, 2012). For example in brown-headed cowbirds (*Molothrus ater*), young males housed with adult females improvise more song elements than males housed with juvenile females (Miller et al., 2008). Adult females seem to be more selective in their interactions with males than juvenile females, and this study suggests the role of social interactions with adults in young male vocal development (Miller et al., 2008).

Social interactions between peers also take place during ontogeny and may shape the social behavior at adulthood (Bertin et al., 2007; Mariette et al., 2013). For example in zebra finches, the presence of male siblings interferes with the learning of the father's song (Tchernichovski and Nottebohm, 1998). The presence of a female sibling seems to have a positive effect (Adret, 2004). Moreover, it has also been shown that a horizontal transmission of the father's song can occur between two young zebra finch males (Derégnaucourt and Gahr, 2013).

Therefore, studying how juveniles fit into social networks may be central to our understanding of individual developmental trajectories.

Most of the time, social interactions and networks are inferred from proximal measures such as spatial co-occurence or close-contact interaction (Aplin et al., 2013; Farine, 2015; Strandburg-Peshkin et al., 2015). However, it is likely that in groups where members are in close proximity, not all members interact equally with each other, making the social network analysis ineffective in that case. Moreover, in many species, acoustic communication is likely to play a central role in social interactions. However, since acoustic signals can be directed both to individuals at short or long distances, spatial proximity may not necessarily correlate with vocal interactions. Therefore, directly characterizing networks of acoustic communication may be extremely useful for understanding social interactions.

Vocal communication has long been studied in the context of pairwise exchange between one sender and one receiver, but communication networks have progressively received more attention (McGregor, 2005). For example, audience effects are defined as the influence of the presence of other conspecifics on a sender's vocal behavior (Evans and Marler, 1994; Vignal et al., 2004). Eavesdropping is defined as extracting information from signaling interactions while not being the main recipient and seems to occur in many species (McGregor and Dabelsteen, 1996). In birds for example, "eavesdroppers" can respond to vocal exchanges even if they were not part of it initially (Mennill et al., 2002). Multiple individuals may also be involved on both sides of the communication process, such as when a group acts collectively as senders, directing acoustic signals to a group of receivers (Harrington and Mech, 1979; Farabaugh, 1982; Mitani, 1984; McComb et al., 1994).

Vocal communication often relies on temporal and structural regularities in the emission of vocalizations, such as turn-taking (Takahashi et al., 2013; Henry et al., 2015). For example, in humans, turn-taking allows interlocutors to enhance mutual attention and responsiveness (France et al., 2001). Some studies showed that the ability to respect conversation rules, in particular turn-taking may be acquired during development (Hauser, 1992; Miura, 1993; Black and Logan, 1995; Lemasson et al., 2010, 2011; Chow et al., 2015; Takahashi et al., 2016).

The zebra finch (*Taeniopygia guttata*) is a perfectly suited model for studying social interactions during ontogeny using an acoustic communication network. The zebra finch is a socially monogamous and highly social passerine native to the semi-arid zone of Australia, that forages and moves in groups (Zann, 1996). After nutritional independence, juveniles mostly associate with individuals of the same age, with whom some may form affiliative bonds (Zann, 1996). Social experience with peers has developmental consequences, as it affects mating success at adulthood (Mariette et al., 2013). Zebra finches rely heavily on acoustic communication for social interaction (Vignal et al., 2004; Elie et al., 2010; Boucaud et al., 2015; Gill et al., 2015) and start to do so early in life. Indeed, nestlings beg for food and the structure of these begging calls is plastic in response to social interactions with parents (Villain et al., 2015). After fledging, juveniles discriminate the calls of their parents (Jacot et al., 2010; Mulard et al., 2010) and their nest-mates (Ligout et al., 2015) from the calls of other individuals. Young males learn their song by imitation of an adult tutor (Slater et al., 1988). When adult, both males and females utter a repertoire of single-syllable calls while only males sing very stereotyped songs of several syllables (Zann, 1996). Among the calls categories, distance calls are the loudest calls, and convey information on both the sex and the identity of the bird (Vignal et al., 2004, 2008; Forstmeier et al., 2009; Vignal and Mathevon, 2011; Elie and Theunissen, 2016).

The main objective of the present study was to describe zebra finch vocal interactions within an "acoustic network" during ontogeny by comparing the dynamics of vocal interactions of (1) individuals when they were juveniles among adults and (2) the same individuals once they become young adults.

To this aim, we designed a set-up that allows recording of vocal interactions but controls the spatial network. Birds were in individual cages so that they were not able to physically interact and inter-individual distances were fixed. We developed an in-house software that automatically detects vocalizations from hours of passive recording, tags individuals' vocalizations as well as automatically removes non-vocalizations (wings or cage noise) using classification. The resulting vocal signal was analyzed using metrics of vocal activity (number of vocalizations, vocalization rate), vocal timing (cross-correlation), and vocal sequence or turn-taking (Markov analysis).

MATERIALS AND METHODS

Subjects and Housing Conditions

Fifty-six juveniles (28 males and 28 females) aged from 36 to 84 days (mean ± sd: 50.2 ± 10.6, $N = 56$ birds), as well as eight adult females were recorded in the first phase. In the second phase, we recorded the juveniles from phase 1 when they were young adults (48 young adults, including 23 females and 25 males aged from 158 to 230 days). Both phases took place from May 2011 to February 2012. All birds came from our breeding colony (ENES laboratory, University of Saint-Etienne).

The juveniles were born in a large indoor aviary (6.5 × 5.5 × 3.5 m; temperature: 20–30°C, daylight: 07:30–20:30) where 28 adult domestic zebra finch pairs were allowed to breed freely and produced 45 broods in total (from April to August 2011). Genetic parents of the broods were not known (because of potential extra-pair copulation and egg dumping), but social parents were known because all juveniles were identified with an individually numbered band before fledging from the nest. After reaching nutritional independence (30–35 days), juveniles were caught in the aviary and transferred to individual cages (40 × 40 × 25) equipped with perches. The eight adult females were also housed in individual cages. In the first phase, adult females were familiar with each other and not with the juveniles, and juveniles were familiar with each other and not with the adult females (juveniles could come from the same nest or not). In the second phase, familiar and unfamiliar young adults (i.e., hold in the same or different rooms between the first and second phases) were present in each group. All birds were kept under the same environmental conditions: temperature between 24 and 26°C, daylight: 07:30–20:30, water, seeds and cuttlefish bones *ad libitum* and supplemented with salad once a week.

Protocol

Recordings took place in a sound-attenuating chamber (2.22 m height × 1.76 m width × 2.28 m length, Silence Box model B, Tip Top Wood, France) fitting four cages (40 × 40 × 25 cm) with one microphone per cage (**Figure 1**). Cages were separated by 1 m. Microphones (Sennheiser MD42) were connected to a recorder (zoom R16) and suspended from the ceiling 20 cm above the top of the cage. A group of four birds was recorded on two morning sessions, separated by 1 day. On the day between the two sessions, we moved the cages to a second sound-attenuating chamber mimicking the recording chamber. On days of recordings, we moved cages to the recording chamber 15 min before starting the recording. All groups were placed in a sound-attenuating chamber the day before each day of recording so that they could habituate to new surroundings. This protocol allowed studying two groups of four birds in parallel. Each time we moved the cages into a room, we randomly changed the relative positions of the cages so as to control for the potential effect of neighbors' identity and position in the chamber. On each recording day, we recorded vocal exchanges during 3 h starting at 10:30 ± 01:24 (mean ± sd, $N = 77$, recording start time was random according to groups and conditions).

Groups' Composition

We recorded birds during two phases. During the first phase, we recorded groups of four birds made with two adult females and two juveniles of either sex (**Figure 1A**). During the second phase we recorded groups of four young adults (2 females and 2 males), using the juvenile birds from the first stage (**Figure 1B**). The time between the two recording phases was on average 148 ± 28 days (mean ± sd, $N = 36$) for a given bird.

Vocalization Extractions

Vocalizations from 250 h of recording were automatically extracted using in-house software. These programs were written in python (http://www.python.org) by authors H.A.S. and M.S.A.F using open-source libraries. This software accuracy was validated and used in previous studies (Elie et al., 2011; Perez et al., 2015). Vocalization detection was a pipeline of three stages.

The first process was a simple threshold-based sound detection based on a high-pass filtered energy envelope (1024 samples FFT; 441 Hz sampling; cut-off frequency: 500 Hz). During the second stage, each sound whose peak was extracted was reconstructed by exploring the two sides of the sound and keeping area with energy higher than 10% of the peak. Thus, each event was either lengthened or shortened to obtain the same amplitude range during the event. This allowed a good estimate of the vocalization duration. The third stage simply merged overlapping waveform segments. Together, the three stages produced start, end, and duration values for each sound event detected in the recording.

Two additional stages enabled to assign each vocalization to its emitter and also remove cage or wing noises. The first additional stage attributed each vocalization to a bird by removing double vocalization, i.e., vocalization emitted by one bird and recorded by its microphone but also recorded by the microphones of all other birds of the group by using energy and delay differences. This allowed us to precisely determine who vocalized at any moment, even in the case of two birds producing two overlapping vocalizations. The second stage removed cage or wings noises using a machine learning process. We trained a supervised classifier using a data set composed of 4500 random extracted sounds from all of our data. Each sound was classified by one expert (MSAF) as "vocalization" or "non-vocalization." The classification was performed on the spectrogram of the sounds reduced to 50 ms. The idea is to reduce the quantity of information in term of time and frequency, and sample this information in such a way that we will get the same amount of information for each vocalization (short or long). The spectrogram matrix was first reduced to the frequencies of interest—between 500 Hz and 6 kHz. Then two cases appear: if the vocalization duration is longer than 50 ms, we extract 50 ms in the center of the spectrogram, and if the vocalization duration is lower than 50 ms, we keep all the spectrogram and we center it in a 50 ms spectrogram padding the remaining with zeros. The resulting matrix is seen as a vector which contains the flattened spectrogram.

We trained a Random Forest classifier (Breiman, 2001) with 1500 sounds. This classifier had an overall rate of error below 10% of the remaining 3000 sounds.

This procedure allowed us to extract two types of calls from the zebra finch repertoire: tet calls i.e., soft and short harmonic stacks with almost no frequency modulation (Zann, 1975, 1996; Elie and Theunissen, 2016), and distance calls i.e., complex sound consisting of a harmonic series modulated in frequency as well as amplitude (Zann, 1996; Elie and Theunissen, 2016). Males can also perform songs, which are stereotyped series of syllables in a short period of time.

Finally, because we were primarily interested in the temporal dynamic of the exchange, we did not distinguish between different types of vocalizations in the following analyses.

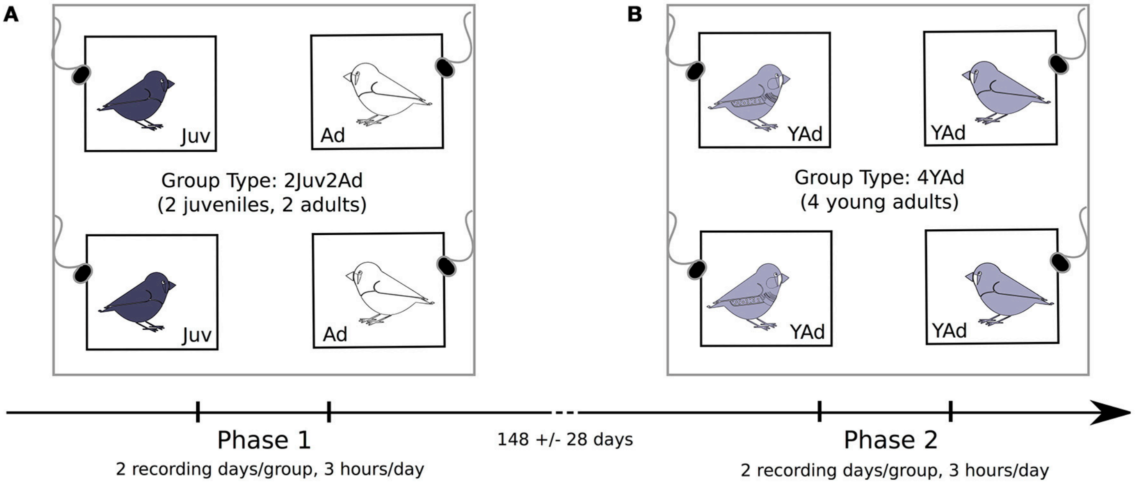


FIGURE 1 | Schematic of the recording room. Groups of 4 birds were used, with one bird per cage in each corner of the recording room and one microphone on top of each cage. Two types of groups were tested: **(A)** groups composed of two juveniles and two adult females (Phase 1), and **(B)** groups of four young adults (already tested as juveniles in the first type of group) (Phase 2). The recording duration as well as the average time between the two phases for a given bird is indicated (mean ± sd, $N = 36$).

Data Analysis

We separated the analysis in three parts described below: vocal activity, as well as cross-correlations and Markov analyses used to build acoustic networks.

Vocal Activity

We computed two types of vocal activity metrics. The first type described the group general vocal activity. First we measured the overall vocalization rate, i.e. the total number of vocalizations produced by all individuals in the group divided by the duration of the recording. Then, we measured some characteristics of the vocal bursts. In order to find vocal bursts in a recording, we computed the mean vocalization rate over the whole day, and we extracted the bursts as periods in which the vocalization rate was 10% higher than the mean vocalization rate (with a time step of 1 min with an overlap of 30 s). We then measured the number of bursts, the average vocalization rate in bursts, the burst mean duration, the total duration of bursts in a recording, the inter-burst interval, and the latency to burst (i.e., the time between the recording' start and the beginning of the first burst).

Secondly, we measured the number of vocalizations per individual. We did not need to normalize this number of vocalizations by the recording duration because all recordings lasted the same time (3 h).

Cross-Correlation

We first characterized the groups' acoustic networks, based on the temporal proximity of vocal activity (functionally equivalent to spatial proximity in co-occurrence networks). In the network, each node is a bird, and the (undirected) edge between two nodes is weighted by the temporal synchrony between the two corresponding birds.

We assessed the vocal temporal synchrony between two birds by computing the cross-correlation using 500 ms time bins. To do that we split the time into 500 ms bins, and each bird signal was one if the bird vocalized within this period, and zero if it did not vocalize. We computed the cross-correlation (cc) between two birds signals with the following formula:

$$\begin{aligned} \mathrm{cc} = \mathrm{mean}[(\mathrm{S}_{\mathrm{bird1}}(\mathrm{t}) - \mathrm{mean}(\mathrm{S}_{\mathrm{bird1}})) * (\mathrm{S}_{\mathrm{bird2}}(\mathrm{t}) \\ - \mathrm{mean}(\mathrm{S}_{\mathrm{bird2}}))]/(\mathrm{std}((\mathrm{S}_{\mathrm{bird1}})) * \mathrm{std}(\mathrm{S}_{\mathrm{bird2}})) \end{aligned}$$

Where Sbird1 and Sbird2 are the vocal signals of the two birds as a function of t (time).

The cross-correlation is computed with normalization, i.e., by centering and scaling by the standard deviation (zscoring) of both vocal signals. The result is therefore independent of the total number of vocalizations.

If the cross-correlation shows high positive values, it means that both birds vocalize and remain silent together more often. If the cross-correlation is negative, it means that whenever one bird is vocalizing or silent the other is more often silent or vocalizing respectively.

For each day of recording we computed cross-correlations for all possible dyads of birds.

Markov Analysis

We then studied the groups' acoustic networks by analyzing the turn-taking.

To establish turn-taking, we only considered the order in which vocalizations were emitted, without consideration of the time between these vocalizations. For that we used Markov chains.

Vocal sequences (taken over the 3 h of recording) were simply transformed into a sequence of caller's identity numbers (e.g. 1,123,113,134). Modeling this as a "four states" process (corresponding to four birds), this vocal sequence can be viewed as a stochastic process that "jumps" from state to state (from one bird to one other). In the Markov hypothesis the caller's identity depends only on the previous caller according to a transition probability (for example the probability of having bird 1 after bird 2). More precisely, a Markov matrix of size 4 × 4 depicts the probability of jumping from one identity to the other: in this matrix, an entry at line i and column j is the probability when the caller is i that the next caller will be j. By construction, this matrix reproduces both the average number of vocalizations for each individual and the first order transition.

We compared the maximum transition probabilities between dyads of birds (e.g., between bird i and bird j, the max transition probability is max(proba(i,j); proba(j,i)), with proba(i,j) the probability for j to vocalize just after i). As for the previous analysis, in the network each node is a bird, and the (undirected) edge between two nodes is weighted by the maximum transition probability between the two corresponding birds.

Stastistics

All statistical tests were performed using R software (R Core Team, 2014). Linear mixed models were built with the lmer function (lme4 R package), and generalized mixed models were built with the glmer function (lme4 R package) (Bates et al., 2014). Models outputs from "Anova" (car library) (Fox and Weisberg, 2011) and "summary" functions are presented.

Model Validation

Before being interpreted each model was checked, paying particular attention to its residuals. For generalized linear models with a Poisson family, overdispersion was tested with the "overdisp.glmer" function of the "RVAideMemoire" package (Hervé, 2014), and if the model presented overdispersion we used a negative binomial family. The model validity was also checked with the plotresid function from the "RVAideMemoire" package before interpreting the model results.

Model Selection

We chose to build biologically relevant models and we kept the full model as recommended by Forstmeier and Schielzeth (2011).

Model Estimates and Confidence Intervals

When possible we added information about the quantification of the biological effect given by the models. Confidence intervals were computed with the "confint.merMod" function of the lme4 package. We used the "profile" method for the linear mixed models and the "Wald" method for the negative binomial models.

Model Random Factors

We only kept random factors that had a non-null variance in the model. If we were interested in the significance of the random factors included in the model, we used the following method. We first looked at the values of their residuals in the model summary ("summary" function in lme4 package). We then built two different models: one model including the random factor, and one model without the random factor. We compared these models using the "Anova" function, and if these models were not significantly different we assumed that the random factor effect was not significant. All random factors with non-null variance were kept in the models even if they had no significant effect.

Vocal Activity

Group general vocal activity

First, for the group general vocal activity we built a Principal Component Analysis (PCA) over six parameters: the number of bursts, the average vocalization rate in bursts, the burst mean duration, the total duration of bursts, the inter-burst interval, and the latency to burst. We found two axes with eigenvalue above 1 that explained 88.5% of the data variability. The first axis describes the general pattern of how bursts were distributed in time (61.7%), and the second axis the density of vocalizations during the recording both within burst and overall (26.8%) (**Figure 2**).

We built one linear mixed model per PCA axis (PCi) with the following structure:

$\mathrm{PCi}{\sim}\mathrm{GroupType}{+}(1|\mathrm{GroupID}){+}(1|\mathrm{Day}){+}(1|\mathrm{StartTime})$, GroupType having two levels: 2Juv2Ad and 4YAd. The random factors were the group identity (GroupID), the day of recording (Day), and the hour of the recording start (StartTime).

The group type 4YAd had always the same sex ratio (2 females and 2 males). As a second step we restricted the analysis to the first group type 2Juv2Ad alone to study the potential influence of group sex ratio [possible sex ratio for juveniles: 2 males (2M), 2 females (2F) or 1 male and 1 female (1F1M)].

$$\mathrm{PCi}{\sim}\mathrm{SexRatio} + (1|\mathrm{GroupID}) + (1|\mathrm{Day}) + (1|\mathrm{StartTime})$$

Number of vocalizations per individual

We built the following generalized mixed linear model (negative binomial family):

$$\begin{aligned}\mathrm{NVoc}{\sim}\mathrm{GroupType} * \mathrm{Sex} \ &+ \ (1|\mathrm{GroupID/BirdID}) \ + \ (1|\mathrm{Day}) \\ &+ \ (1|\mathrm{SexRatio}) \ + \ (1|\mathrm{StartTime})\end{aligned}$$

The response variable was the number of vocalizations. The factor Sex had two levels, M or F. We used a negative binomial model because the model using a Poisson distribution presented overdispersion. The model indicated an interaction between GroupType and Sex at the significance threshold so we studied it using the lsmeans R function.

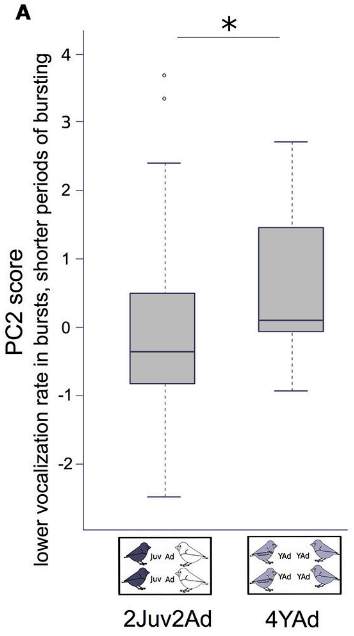
We built a second model to study the influence of being a juvenile or an adult for GroupType = 2Juv2Ad.

$$\begin{aligned}\mathrm{NVoc}{\sim}\mathrm{JuvAd} * \mathrm{SexRatio} \ &+ \ (1|\mathrm{GroupID/BirdID}) \\ &+ \ (1|\mathrm{Day}) \ + \ (1|\mathrm{StartTime})\end{aligned}$$

The factor JuvAd had two levels: Juv or Ad.

For groups including juveniles, as several factors were linked, we had to build additional models to deal with confounding effects. We built a model using juvenile data only to test the influence of the sex on the number of vocalizations. As the factor SexRatio was strongly linked to the factor Sex we did not include it in this model:

$$\begin{aligned}\mathrm{NVocJuveniles}{\sim}\mathrm{Sex} \ &+ \ (1|\mathrm{GroupID/BirdID}) \ + \ (1|\mathrm{Day}) \\ &+ \ (1|\mathrm{StartTime})\end{aligned}$$



B

	PC1	PC2
number of bursts	0.5858642	0.00614674
interburst interval	-0.5205126	0.26759565
vocalization rate in bursts	0.2772968	-0.49261805
mean length of bursts	-0.5370541	-0.30930811
total length of bursts	-0.1012809	-0.66638019
latency to burst	-0.1012492	-0.38203161

FIGURE 2 | General vocal activity between group types. (A) Boxplot of the PC2 values in each group type, from the PCA including six parameters describing the bursts of vocal activity. Linear mixed effect models were built. Detailed sample sizes and model results are given in **Table 1**. Boxes are median, first and third quartiles (Q1 and Q3 respectively). The upper whisker is located at the *smaller* of the maximum × value and Q3 + 1.5 Inter Quartile Range (IQR), whereas the lower whisker is located at the *larger* of the smallest × value and Q1 − 1.5 IQR. Individual points more extreme in value than Q3 + 1.5 IQR are plotted separately at the high end, and those below Q1 − 1.5 IQR are plotted separately on the low end. **(B)** Variable loadings of the PCA including six parameters on bursts. The first two axes (with eigen-value above 1) explained 88.5% of the data variability. $^*p < 0.05$.

We then built a model using the females' data only to test the difference between adult and juvenile females (as the males were juveniles only).

$$\text{NVocFemales} \sim \text{JuvAd} + (1|\text{Group/BirdID}) + (1|\text{Day}) + (1|\text{StartTime})$$

Cross Correlation

First we built a model in order to compare the cross-correlation between group types (2Juv2Ad and 4YAd):

$$\text{cc} \sim \text{GroupType} * \text{Sex1Sex2} + \text{Dist} + \text{Dist} : \text{GroupType} + \text{Dist} : \text{Sex1Sex2} + (1|\text{GroupID}) + (1|\text{Day}) + (1|\text{Bird1ID}) + (1|\text{Bird2ID}) + (1|\text{StartTime})$$

The distance between two birds could be 1 or 2 (1: birds were on the same edge of the square, 2: birds were placed on the diagonal). The factor Sex1Sex2 had three levels: FF, MM, or FM and represented the sexes of both birds from which we computed the cross-correlation.

As the interaction between the group type and the sex was significant we first separated the dataset by group type and analyzed them separately:

$$\text{GroupType} = \text{4YAd}:$$
$$\text{cc} \sim \text{Sex1Sex2} * \text{Dist} + (1|\text{GroupID}) + (1|\text{Day}) + (1|\text{Bird1ID}) + (1|\text{Bird2ID}) + (1|\text{StartTime})$$

GroupType=2Juv2Ad:
the factor Sex1Sex2 was strongly linked to the factors JuvAd (three levels: JuvJuv, AdAd, JuvAd) which indicated if the dyads of birds comprised only juveniles, only adults or one juvenile and one adult and SexRatio (as the SexRatio could differ between groups), therefore we first built the following model including factors SexRatio and JuvAd: cc∼JuvAd+Dist+SexRatio+ JuvAd:Dist+ JuvAd:SexRatio +(1|GroupID)+(1|Day)+(1|Bird1ID)+(1|Bird2ID)+(1|StartTime)

We then separated the dataset by sexes to assess the difference between the cross-correlations of two juveniles and two young adults. As we had only one data point per bird in this case, the only remaining random factor is Day. For each value of Sex1Sex2 (MM, MF, FF) we built the following model:

$$\text{cc} \sim \text{GroupType} + (1|\text{Day}) + (1|\text{StartTime})$$

Markov Analysis

We first built a model to compare the maximum transition probabilities between group types (2Juv2Ad and 4YAd):

$$\text{MaxProba} \sim \text{GroupType} * \text{Sex1Sex2} + \text{Dist} + \text{Dist} : \text{GroupType} + \text{Dist} : \text{Sex1Sex2} + (1|\text{GroupID}) + (1|\text{Day}) + (1|\text{Bird1ID}) + (1|\text{Bird2ID}) + (1|\text{StartTime})$$

As the interaction between GroupType and Sex1Sex2 was significant we analyzed the group types separately, as we did for

TABLE 1 | Impact of group type and sex ratio on general vocal activity.

PC2∼GroupType+(1|GroupID)+(1|Day)

Nobs = 70, N2Juv2Ad = 52, N4YAd = 18

Random Effects

Groups name	Variance	Std. Dev.
GroupID (intercept)	0.1074	0.3277
Day (intercept)	2.347e-16	1.532e-08
Residual	1.429	1.196

Fixed Effects

	Estimate	Std. Error	df	*t*-value	*p*-value
(Intercept)	−0.1823	0.1757	34.9	−1.037	0.3066
GroupType-4YAd	0.7394	0.3545	41.35	2.086	0.0432

PC2∼SexRatio+(1|StartTime)

Nobs = 52, N2F2M = 15, N3F1M = 23, N4F0M = 14

Random Effects

Groups name	Variance	Std. Dev.
StartTime(intercept)	0.119	0.245
Residual	1.478	1.216

Fixed Effects

	Estimate	Std. Error	df	*t*-value	*p*-value
(Intercept)	−0.5437	0.3859	6.010	−1.409	0.208
SexRatio-3F1M	0.3923	0.4067	47.93	2.086	0.340
SexRatio-4F0M	0.7170	0.4634	48.99	1.547	0.128

Model statistical results are shown. Linear mixed effect models ("lmer" function from "lme4" R package) were built. Number of observations in the dataset for each fixed effect is given. We present the results from the R "summary" function.

the cross-correlation.

$$\begin{aligned}\text{Juveniles only}:\ \text{MaxProba} \sim\ & \text{Sex1Sex2} * \text{Dist} + (1|\text{GroupID}) \\ & + (1|\text{Day}) + (1|\text{Bird1ID}) \\ & + (1|\text{Bird2ID}) + (1|\text{StartTime})\end{aligned}$$

RESULTS

Vocal Activity

Group General Vocal Activity

We found an effect of the group type on the second composite score of the PCA, which mainly depicted the vocalization rate in bursts and the total length of bursts. Groups including juveniles and adults presented lower scores in PC2 than groups including only young adults, which means that vocalization rate in bursts and total duration of bursting was higher in the former than in the latter (**Figure 2**, **Table 1**). We found no effect of the group type or sex ratio on the first composite score of the PCA (number of bursts, inter-burst interval, mean length of bursts) (**Table 1**).

Number of Vocalizations per Individual

We found differences between group types depending on the sex (**Figure 3**). The juvenile males emitted more vocalizations than all other birds (adults, young adults, and juvenile females). Adults emitted less vocalizations than juveniles. This difference was more pronounced for juvenile males than juvenile females (**Figure 3**, **Table 2**). Vocalization rate in juveniles was 1.34 times [1.03;1.71] higher than in adults (numbers in brackets are 95% confidence interval of the effect estimated by the model). Among juveniles, the vocalization rate was 1.39 times [1.18;1.63] higher in males than in females. Male songs may increase the number of vocalizations. To account for the song occurrence, we counted the total number of detected song syllables (from all males) over 10 min (randomly chosen from 1 day) for each group (i.e., we counted songs over 3.5 h of recording in total), which we compared to the total number of detected vocalizations of these males. For juveniles we found that song syllables represented only 2.3 ± 7% of the total detected vocalizations in males. Individual changes in vocalization rate along ontogeny are shown in **Supplementary Figure 1** (females) and **Supplementary Figure 2** (males).

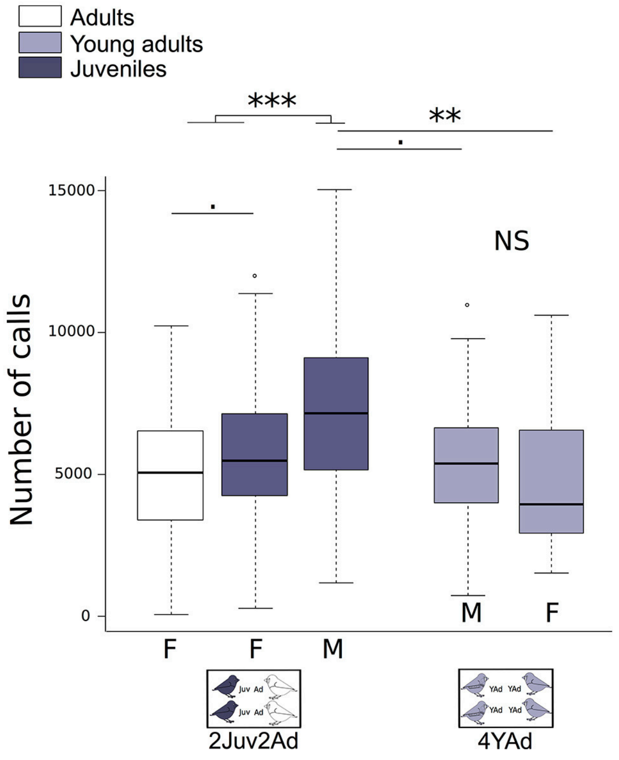


FIGURE 3 | Number of vocalizations per individual. Boxplot of individual vocalization rates in the different group types. Number of vocalizations per individual for each sex is detailed, as well as the age category (Juveniles, Young Adults, Adults). Generalized linear mixed effect models with negative binomial family were built. Detailed sample sizes and model results are given in **Table 2**. Boxes are median, first and third quartiles (Q1 and Q3 respectively). The upper whisker is located at the *smaller* of the maximum × value and Q3 + 1.5 Inter Quartile Range (IQR), whereas the lower whisker is located at the *larger* of the smallest × value and Q1 − 1.5 IQR. Individual points more extreme in value than Q3 + 1.5 IQR are plotted separately at the high end, and those below Q1 − 1.5 IQR are plotted separately on the low end. $^{***}p < 0.001$, $^{**}p < 0.1$, $p < 0.1$.

Cross Correlation

Young adult groups presented significantly higher cross-correlation values than groups of juveniles and adults. We found that cross-correlation values (i.e., temporal synchrony of vocalizations) between one juvenile and one adult (Juv-Ad) were lower than those between two adults (Ad-Ad). Cross-correlation values between two juveniles (Juv-Juv) were intermediate (**Figure 4A**, **Table 3**). **Supplementary Figure 3** illustrates these results with four examples of groups with juveniles.

We also found sex differences between groups: synchrony between 1 male and 1 female increased from juveniles to young adults, whereas it remained the same between 2 males or 2 females (**Figure 4B**, **Table 3**). Specifically, female-male dyads increased their cross-correlation value from 0.09 [0.07;0.12] (juveniles) to 0.13 [0.10;0.16] (young adults). There was no cross-correlation difference between the sexes within groups including juveniles and adults. Also, there was no difference in cross-correlation between the 2 days of recording.

Markov Analysis

The maximum transition probabilities (i.e., turn-taking) did not differ between group types (**Figure 5A**, **Table 4**).

The maximum transition probabilities were higher between two juveniles than between other dyads (AdAd, two adults or JuvAd, one adult and one juvenile). Thus, juveniles were more likely to vocalize after another juvenile's vocalization in the turn-taking sequence. The average of maximum transition probability was the same between two adults or two young adults (**Figure 5B**, **Table 4**). Also, there was no difference in transition probabilities between the 2 days of recording.

DISCUSSION

Using our in-house software we were able to automatically detect vocalizations from hours of passive recordings in groups of four zebra finches. This allowed us to assess information about the acoustic network of groups composed of adults and juveniles compared to groups of only young adults. We found that groups including juveniles presented periods with higher level of activity than groups composed of young adults only and within their groups, juveniles vocalized more than adults. Furthermore, we saw that two adults were more likely to vocalize together within a short time window (cross-correlation) than one adult and one juvenile, and that juveniles were more likely to vocalize after one another in turn-taking sequences (Markov analysis). Finally, when juveniles turned into adulthood, they showed adult characteristics of vocal patterns (number of vocalizations, cross-correlation, turn-taking).

Groups including juveniles had a higher vocalization rate during bursts, and these bursts lasted longer. At the individual level, juveniles had a higher vocalization rate than adults or young adults. First, juveniles could be more active in general in their behavior than adults. Indeed, in several species the locomotor activity is higher in young individuals than in older individuals (Van Waas and Soffié, 1996; Ingram, 2000). By vocalizing more, juveniles get opportunities to vocally interact in a greater diversity of contexts, which may be important to develop their social skills. In cowbirds, it has been shown that a complex social environment (in which birds changed regularly of social groups) can lead to a greater social competence and also a higher mating success (White et al., 2010). Vocalizing more might also allow juveniles to practice conversation rules, and more precisely to learn to respect turn-taking rules. Indeed, some studies show that the ability to respect turns may be acquired during development (Hauser, 1992; Miura, 1993; Black and Logan, 1995; Lemasson et al., 2010, 2011; Chow et al., 2015; Takahashi et al., 2016).

Juvenile males' vocalization rate was higher than juvenile females' vocalization rate. Two potential interpretations need to be addressed here. First, this result could be due to our method, which is not able to discriminate between calls and songs' syllables. However, as indicated in the results, we concluded that the contribution of songs represented an average of 2.3% of all male vocalizations. This could not account for the difference between juvenile males and females' number of vocalizations,

TABLE 2 | Impact of group composition on the number of vocalizations per individual.

NVoc∼GroupType*Sex+(1|GroupID/BirdID)+(1|Day) +(1|SexRatio)

Nobs = 319, N2Juv2Ad = 227, N4YAd = 92, Nmale = 103, Nfemale = 216

Random Effects

Groups name	**Variance**	**Std. Dev.**
GroupID/BirdID (intercept)	8.823e-15	9.393e-08
GroupID (intercept)	1.200e-02	1.095e-01
Day (intercept)	5.046e-04	2.246e-02
SexRatio (intercept)	3.110e-14	1.764e-07
Residual	7.534e-01	8.680e-01

Fixed Effects

	Estimate	**Std. Error**	***t*-value**	***p*-value**
(Intercept)	8.569	0.0504	169.9	<0.0001
GroupType-4YAd	−0.1549	0.0997	−1.55	0.1202
Sex-M	0.3012	0.0819	3.68	0.0002
GroupType-4YAd: Sex-M	−0.1441	0.1376	−1.05	0.2946

Pairwise Comparisons (Tukey Adjustment)

Contrast	**Estimate**	**SE**	**df**	***z*-ratio**	***p*-value**
F2Juv2Ad-M2Juv2Ad	−0.3230	0.0818	NA	−3.944	0.0005
F2Juv2Ad-F4YAd	0.0844	0.0973	NA	0.8671	0.8219
F2Juv2Ad-M4YAd	−0.0471	0.0936	NA	−0.5039	0.9582
M2Juv2Ad-F4YAd	0.4074	0.1143	NA	3.561	0.0021
M2Juv2Ad-M4YAd	0.2758	0.1112	NA	2.480	0.063
F4YAd-M4YAd	−0.1316	0.1193	NA	−1.102	0.688

NVoc∼JuvAd * SexRatio + (1| GroupID/BirdID) +(1|Day)+(1|StartTime)

Nobs = 227, NAd = 116, NJuv = 111, N2F2M = 64, N3F1M = 92, N4F0M = 56

Random Effects

Groups name	**Variance**	**Std. Dev.**
GroupID/BirdID (intercept)	2.567e-14	1.602e-07
GroupID (intercept)	2.159e-09	4.647e-05
Day (intercept)	7.536e-19	8.681e-10
StartTime (intercept)	2.186e-14	1.478e-07
Residual	6.524e-01	8.077e-01

Fixed Effects

	Estimate	**Std. Error**	***t*-value**	***p*-value**
(Intercept)	8.6395	0.0964	89.62	<0.0001
JuvAd-Juv	0.3087	0.1363	2.26	0.0236
SexRatio-3F1M	−0.1258	0.1239	−1.02	0.3100
SexRatio-4F0M	−0.1997	0.1387	−1.44	0.1501
JuvAd-Juv: SexRatio-3F1M	−0.0332	0.1752	−0.19	0.8496
JuvAd-Juv: SexRatio-4F0M	−0.2060	0.1962	−1.05	0.2938

(Continued)

TABLE 2 | Continued

NVocJuveniles∼Sex +(1|GroupID/BirdID)

Nmale = 55, Nfemale = 56

Random Effects

Groups name	**Variance**	**Std. Dev.**
GroupID/BirdID (intercept)	0.0	0.0
GroupID (intercept)	0.0113	0.1067
Residual	0.7419	0.8614

Fixed Effects

	Estimate	**Std. Error**	***t*-value**	***p*-value**
(Intercept)	8.65277	0.06956	125.39	<0.0001
Sex-M	0.21906	0.09865	2.22	0.0264

NVocFemales∼JuvAd +(1|GroupID)

NAd = 116, NJuv = 56

Random Effects

Groups name	**Variance**	**Std. Dev.**
GroupID (intercept)	0.0029	0.0542
Residual	0.6510	0.8068

Fixed Effects

	Estimate	**Std. Error**	***t*-value**	***p*-value**
(Intercept)	8.4999	0.05545	153.3	<0.0001
JuvAd-Juv	0.1452	0.0931	1.56	0.119

Model statistical results are shown. Generalized linear mixed effect models with negative binomial family ("lmer" function from "lme4" R package) were built. Number of observations in the dataset for each fixed effect is given. We present the results from the R "summary" function.

because males gave 24.8% more vocalizations than females. Second, the two adults with the juveniles were always two adult females. Juvenile males may vocalize more than juvenile females in the presence of adult females (and not adult males). A previous study analyzed the response of zebra finch juveniles (aged of 56.5 ± 2.4 days) to the playback of calls of familiar adult females (Mulard et al., 2010). However, the authors found no difference between the sexes in their response to adult female calls (number of calls and latency of response). Still, the vocal response to a playback and to real vocal interactions is probably different. Also, contrary to this previous study, our adult females were unfamiliar to the juveniles, and this could explain the differences between our results. It thus remains to be tested whether the difference of vocal activity between juvenile males and females in our results is triggered by the sex and/or the familiarity of the adults interacting with the juveniles.

Cross-correlation is a measure of vocal synchrony between individuals. A high cross-correlation between two individuals (two nodes in the acoustic network) means that these individuals usually vocalize together (or remain silent together) within 500 ms. Akin to spatial connectedness, we considered that birds that vocalize regularly together are connected. In our results, the cross-correlation was lower between one juvenile and one adult than between two juveniles, which was itself lower than between two adults. In our setup, all adults were females (no adult male), so interactions between juvenile males and adults could not be vocal imitation for song learning (like with a male song tutor) but could be social reinforcement of song production by adult females. However, more generally, interactions between juveniles (females or males) and adults could be social reinforcement of vocalization use. In our results, interactions between juveniles and adults showed less synchrony than vocal interactions between juveniles, so the latter probably function as stronger reinforcements of vocalization use. In our study adult females were familiar with each other and not with the juveniles, and juveniles were familiar with each other and not with the adult females. These differences in familiarity may therefore have contributed to the lower cross-correlation between adult females and juveniles, as individuals may respond more to familiar individuals. However, cross-correlation and maximum transition values were similar between young adults in the second phase and adult females in the first phase, even though not all young adults were familiar with each other. Furthermore, we did not observe an increase in average cross-correlation or maximum transition values between the first and second recording days per phase, although all four birds were presumably becoming more

TABLE 3 | Impact of group composition on the vocal cross-correlation.

CrossCorr∼GroupType*Sex1Sex2+Dist+Dist:GroupType+Dist:Sex1Sex2+(1|GroupID)+(1|Bird1ID)+(1|Bird2ID)+(1|Day)+(1|StartTime)

Nobs = 486, N2Juv2Ad = 348, N4YAd = 138, NFF = 205, NMF = 223, NMM = 43, NDist1 = 405, NDist2 = 81

Random Effects

Groups name	Variance	Std. Dev.
GroupID (intercept)	1.084e-03	0.0329
Bird1ID (intercept)	2.285e-04	0.0151
Bird2ID (intercept)	1.695e-04	0.0130
Day (intercept)	2.507e-05	0.0050
StartTime (intercept)	8.521e-05	0.0092
Residual	2.378e-03	0.0487

Fixed Effects

	Estimate	Std. Error	df	*t*-value	*p*-value
(Intercept)	0.0906	0.0107	12.9	8.440	<0.0001
GroupType-4YAd	0.0570	0.0180	93	3.156	0.0021
Sex-MF	−0.0152	0.0079	300.9	−1.902	0.0581
Sex-MM	0.0067	0.0177	282.6	0.382	0.7024
Dist-2	0.0252	0.0099	375.2	2.530	0.0118
GroupType-4YAd: Sex-MF	−0.0052	0.0148	417.8	−0.354	0.7233
GroupType-4YAd: Sex-MM	−0.0701	0.0228	394.6	−3.072	0.0022
GroupType-4YAd: Dist-2	−0.0260	0.0168	386.1	−1.549	0.1222
Sex-MF: Dist-2	0.0221	0.0159	388	1.391	0.1650
Sex-MM: Dist-2	0.0316	0.0271	363.9	1.164	0.2453

CrossCorr4YAd∼Sex1Sex2*Dist+(1|GroupID)+(1|Bird1ID)+(1|Bird2ID) +(1|Day)

Nobs = 138, NFF = 21, NMF = 90, NMM = 27, NDist1 = 115, NDist2 = 23

Random Effects

Groups name	Variance	Std. Dev.
GroupID (intercept)	0.0032	0.0572
Bird1ID (intercept)	0.0006	0.0258
Bird2ID (intercept)	0.0004	0.0208
Day (intercept)	0.0005	0.0240
StartTime (intercept)	0.0007	0.0267
Residual	0.0017	0.0416

Fixed Effects

	Estimate	Std. Error	df	*t*-value	*p*-value
(Intercept)	0.1422	0.0330	4.03	4.304	0.0124
Sex-MF	−0.0204	0.0124	103.83	−1.649	0.1021
Sex-MM	−0.0639	0.0177	60.19	−3.601	0.0006
Dist-2	0.0589	0.0425	29.4	1.384	0.1767
Sex-MF: Dist-2	−0.0422	0.0450	34.51	−0.937	0.3553

Pairwise Comparisons (Tukey Adjustment)

Contrast	Estimate	SE	*z*-value	*p*-value
Sex-MF-Sex-FF = = 0	−0.0204	0.0124	−1.649	0.2117
Sex-MM-Sex-FF = = 0	−0.0639	0.0177	−3.601	<0.0001
Sex-MM-Sex-MF = = 0	−0.0434	0.0122	−3.560	0.0011

(Continued)

TABLE 3 | Continued

CrossCorr2Juv2Ad∼JuvAd+Dist+SexRatio+JuvAd:Dist+JuvAd:SexRatio+(1|GroupID)+ (1|Bird1ID)+(1|Bird2ID)+(1|StartTime)

Nobs = 348, NAdAd = 58, NJuvAd = 232, NJuvJuv = 58, NDist1 = 290, NDist2 = 58, N2F2M = 96, N3F1M = 138, N4F0M = 84

Random Effects

Groups name	**Variance**	**Std. Dev.**
GroupID (intercept)	6.924e-04	0.0263
Bird1ID (intercept)	8.076e-05	0.0089
Bird2ID (intercept)	1.685e-04	0.0129
StartTime (intercept)	8.826e-05	0.0093
Residual	2.304e-03	0.0480

Fixed Effects

	Estimate	**Std. Error**	**df**	***t*-value**	***p*-value**
(Intercept)	1.193e-01	1.814e-02	52.77	6.577	<0.0001
JuvAd-JuvAd	−3.949e-02	1.507e-02	271.2	−2.620	0.0092
JuvAd-JuvJuv	−1.844e-02	2.004e-02	150.8	−0.920	0.3590
Dist-2	8.799e-03	2.123e-02	270.8	0.414	0.6788
SexRatio-3F1M	2.976e-02	2.035e-02	98.93	1.463	0.1467
SexRatio-4F0M	−2.933e-03	2.312e-02	91.45	−0.127	0.8993
JuvAd-JuvAd: Dist-2	3.538e-02	2.348e-02	273.4	1.507	0.1330
JuvAd-JuvJuv: Dist-2	3.147e-02	2.762e-02	278.4	1.139	0.2555
JuvAd-JuvAd: SexRatio-3F1M	−2.190e-02	1.844e-02	260.1	−1.188	0.2360
JuvAd-JuvJuv: SexRatio-3F1M	−4.473e-02	2.375e-02	247.4	−1.883	0.0608
JuvAd-JuvAd: SexRatio-4F0M	4.872e-04	2.052e-02	257.9	0.024	0.9810
JuvAd-JuvJuv: SexRatio-4F0M	−1.620e-02	2.651e-02	259.0	−0.611	0.5417

Pairwise Comparisons (Tukey Adjustment)

Contrast	**Estimate**	**SE**	***z*-value**	***p*-value**
JuvAd-AdAd = = 0	−0.0394	0.0150	−2.620	0.0229
JuvJuv-AdAd = = 0	−0.0184	0.0200	−0.920	0.6197
JuvJuv-JuvAd = = 0	0.0210	0.0152	1.385	0.3405

CrossCorrMM∼GroupType+(1|Day)

Nobs = 48, N2Juv2Ad = 16, N4YAd = 27

Random Effects

Groups name	**Variance**	**Std. Dev.**
Day (intercept)	0.00	0.00
Residual	0.0022	0.0470

Fixed Effects

	Estimate	**Std. Error**	**df**	***t*-value**	***p*-value**
(Intercept)	0.1009	0.0117	37	8.58	<0.0001
GroupType-4YAd	−0.0148	0.0153	37	−0.967	0.34

Fixed Effects

	Estimate	**Std. Error**	**df**	***t*-value**	***p*-value**
(Intercept)	0.0939	0.0130	95	7.196	<0.0001
GroupType-4YAd	0.0409	0.0149	95	2.740	0.0073

(Continued)

TABLE 3 | Continued

CrossCorrFF~GroupType+(1|Day)

Nobs = 40, N2Juv2Ad = 14, N4YAd = 21

Random Effects

Groups name	**Variance**	**Std. Dev.**
Day (intercept)	0.00	0.00
Residual	0.0073	0.0856

Fixed Effects

	Estimate	**Std. Error**	**df**	***t*-value**	***p*-value**
(Intercept)	0.0917	0.0229	29	4.005	3.95e-04
GroupType-4YAd	0.0586	0.0309	29	1.895	0.0680

Model statistical results are shown. Linear mixed effect models ("lmer" function from "lme4" R package) were built. Number of observations in the dataset for each fixed effect is given. We present the results from the R "summary" function.

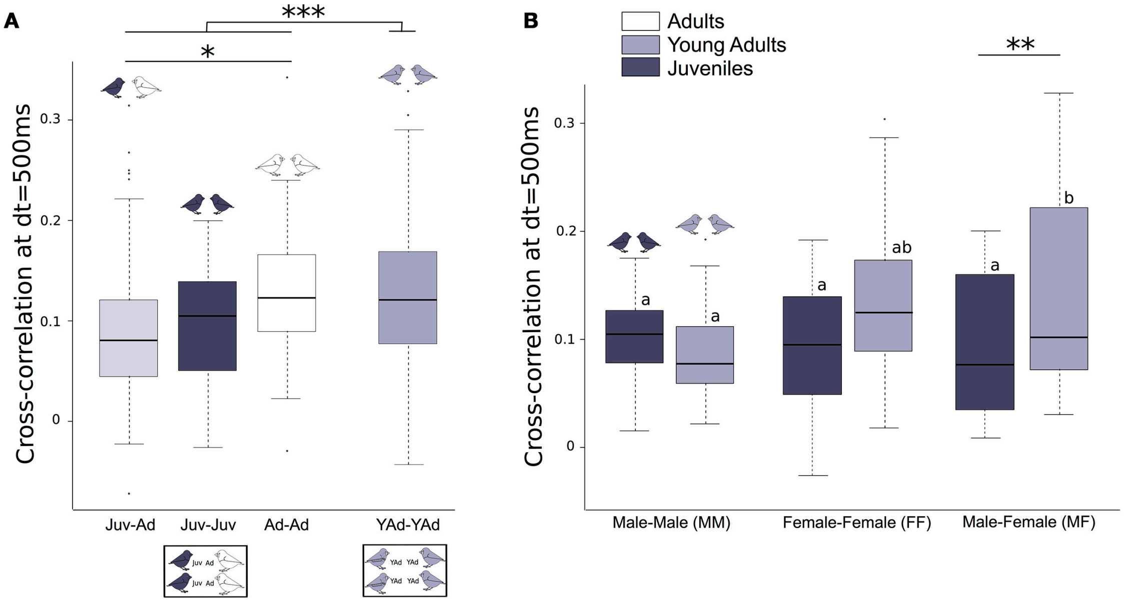


FIGURE 4 | Vocal cross-correlation between two birds. Boxplot of cross-correlation values at dt = 500 ms, between two birds **(A)** of different age categories (Juv-Juv, Juv-Ad, Ad-Ad, YAd-Yad), **(B)** of different sex (MM, MF, FF), within a given age category (Juv or YAd). Linear mixed effect models were built. Detailed sample sizes and model results are given in **Table 3**. Different letters indicate significant differences. Boxes are median, first and third quartiles (Q1 and Q3 respectively). The upper whisker is located at the *smaller* of the maximum × value and Q3 + 1.5 Inter Quartile Range (IQR), whereas the lower whisker is located at the *larger* of the smallest × value and Q1 − 1.5 IQR. Individual points more extreme in value than Q3 + 1.5 IQR are plotted separately at the high end, and those below Q1 − 1.5 IQR are plotted separately on the low end. ***$p < 0.001$, **$p < 0.1$, *$p < 0.05$, $p < 0.1$.

familiar with each other as they remain together in the same room. Overall, familiarity is therefore unlikely to fully explain our results.

Instead, our results suggest that (1) individuals interact preferentially within their age group (because the cross-correlation between one adult and one juvenile had the lowest value), and that (2) adults are more precise and regular in their vocalization timing (because they had the highest cross-correlation value). Adults may be less likely to interact with a juvenile when juveniles are less reliable in the timing or information content of their vocalizations or when the information juveniles provide is irrelevant for adults. For example, in juvenile Richardson's ground squirrels (*Spermophilus richardsonii*), if an individual frequently calls when no predators are nearby, its calls do not reliably predict the presence of a predator and the calls of this individual are ignored by others. Young individuals may call in response to more stimuli, many of which are not threatening to adults (Cheney and Seyfarth,

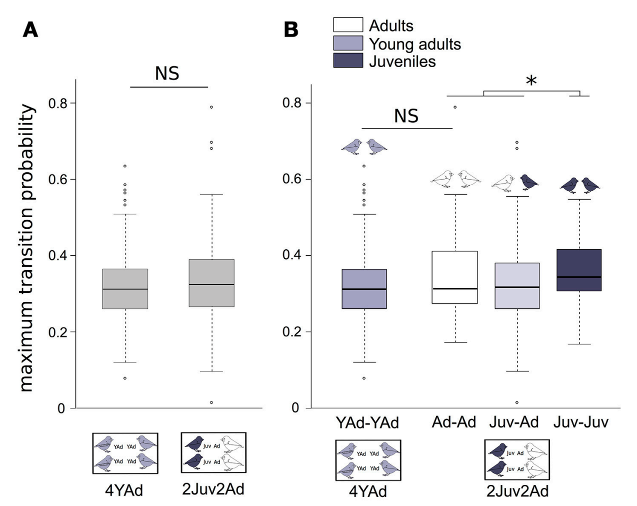


FIGURE 5 | Mean vocal transition probabilities between two birds. Boxplot of mean transition probabilities between two birds **(A)** in the different group types, **(B)** from different age categories (Juv-Juv, Juv-Ad, Ad-Ad, YAd-Yad). Linear mixed effect models were built. Detailed sample sizes and model results are given in **Table 4**. Boxes are median, first and third quartiles (Q1 and Q3 respectively). The upper whisker is located at the *smaller* of the maximum × value and Q3 + 1.5 Inter Quartile Range (IQR), whereas the lower whisker is located at the *larger* of the smallest × value and Q1 − 1.5 IQR. Individual points more extreme in value than Q3 + 1.5 IQR are plotted separately at the high end, and those below Q1 − 1.5 IQR are plotted separately on the low end. *$p < 0.05$.

1990; Hanson and Cross, 1997), and it might be advantageous for adults to ignore the calls from the juveniles. In a learning context, Chimpanzees (*Pan troglodytes*), are highly specific in their selection of conspecifics as models for observation: in response to a novel item, they watch and learn from the nut-cracking activity of individuals in the same age group or older, but not younger than themselves (Biro et al., 2003).

Our analysis of turn-taking involving Markov chains showed that the probability of having a juvenile vocalization following a juvenile vocalization was higher than any other possibility. Contrary to the cross-correlation, turn-taking does not take into account the delay between vocalizations. Therefore, a high Markov probability between juveniles means that juveniles vocalized preferentially after a juvenile vocalization (without having an adult's vocalization between them), but the delay can be of any value (so potentially above the 500 ms threshold used in the cross-correlation analysis). The respect of turn-taking requires attention and control and may be less easy to achieve for juveniles. Hauser (1992) showed that juvenile Vervets monkeys *(Chlorocebus pygerythrus)* overlap other individuals' calls more often than adults. This study estimated that 1/38 calls were interrupted when the exchange was between adults compared to 6/20 when the interacting individuals were young. This observation suggests that the ability to respect turns may be acquired during development. In Campbell's monkeys (*Cercopithecus campbelli*), the young are 12 times more likely than adults to interrupt turn-taking by vocalizing twice successively. Besides, only adult Campbell's monkeys displayed different levels of interest when hearing playbacks of vocal exchanges respecting or not the turn-taking rule (Lemasson et al., 2011). In nightingales (*Luscinia megarhynchos*), it has been suggested that overlapping (and therefore breaking the turn-taking rule) may be perceived as a directed aggressive signal (Naguib and Kipper, 2005). In this species, alternation in exchanges suggests that turn-taking rules allow turns to be taken between two or more interlocutors, and overlapping elicits "irritation" or a rupture of the exchange.

The cross-correlation between 1 male and 1 female increased from juveniles to young adults, whereas it remained the same between 2 males or 2 females. The young adults had reached the sexual maturity (between 2 and 3 months in zebra finches). In the wild, zebra finch juveniles are fully independent at 35 days and may start forming pairs at 3 months old (Zann, 1996). The tendency to interact with individuals from the opposite sex may increase after sexual maturity. In wild Chacma Baboons (*Papio Cynocephalus Ursinus*), females' reproductive state affects males' tendency to call to them (Palombit et al., 1999). Males grunted more often when approaching estrus females and lactating females, and rarely when approaching pregnant females. In addition, affinitive interactions between 1 male and 1 female occurred significantly more often when males grunted than when they silently approached females.

In this study we decided to keep all vocalizations types together, because we had too many factors interacting to be able to analyze rules of vocalization type use with a sufficient sample size. Besides, among all vocalizations types that zebra finches can produce, in the conditions of our experiment (cages at short distances) only three of them were produced: tets, distance calls, and songs. However, it would be interesting to study the vocal dynamics by separating the different vocalization types, because the dynamic of vocal exchange could change according to call type, as suggested by Gill et al. (2015).

Also, preventing physical contact and free movement of the birds is a limitation. However, our approach has the advantage to control the position of the birds. In a recent study, devices mounted on the birds were used to assign vocalizations in freely moving individuals (Gill et al., 2015) but it did not give the spatial position of each bird. New technologies are needed to be able to control for these different aspects at the same time.

Taken together, our results suggest that juveniles and adults have a separate vocal network (i.e., same age class individuals form distinct connected components within the network), and juveniles integrate the properties of the adult vocal network during ontogeny. Our findings highlight the benefits of considering acoustic networks, beside spatial associations, to infer social interactions within groups.

ETHIC STATEMENT

Experiments were performed under the authorization no. 42-218-0901-38 SV 09 (ENES Laboratory, Direction Departementale des Services Veterinaires de la Loire) and were in agreement with French and European legislation regarding experiments on animals.

TABLE 4 | Impact of group composition on the dyads average mean transition probabilities.

MaxProba∼GroupType * Sex1Sex2+Dist+ Dist:GroupType+ Dist:Sex1Sex2+ (1|GroupID)+ (1|Bird1ID)+ (1|Bird2ID)+ (1|Day)

Nobs = 457, N2Juv2Ad = 344, N4YAd = 134, NFF = 197, NMF = 206, NMM = 39, NDist1 = 380, NDist2 = 77

Random Effects

Groups name	**Variance**	**Std. Dev.**
GroupID (intercept)	0.0112	0.1059
Bird1ID (intercept)	0.0093	0.0968
Bird2ID (intercept)	6.197e-04	0.0248
Day (intercept)	1.068e-04	0.0103
Residual	0.0129	0.1139

Fixed Effects

	Estimate	**Std. Error**	**df**	***t*-value**	***p*-value**
(Intercept)	−0.8655	0.0324	53.4	−26.693	<0.0001
GroupType-4YAd	0.0453	0.0443	190.3	1.024	0.3073
Sex-MF	0.0471	0.0357	62.7	1.317	0.1925
Sex-MM	0.1208	0.0595	144	2.029	0.0443
Dist-2	0.0079	0.0234	294.1	0.338	0.7357
GroupType-4YAd: Sex-MF	−0.0690	0.0482	355.6	−1.433	0.1528
GroupType-4YAd: Sex-MM	−0.2073	0.0669	418.2	−3.095	0.0021
Sex-MF: Dist-2	0.0122	0.0380	294.1	0.323	0.7467
Sex-MM: Dist-2	−0.0398	0.0668	286.8	−0.597	0.551
GroupType-4YAd: Dist-2	−0.0222	0.0431	279	−0.516	0.6064

MaxProba4YAd∼ Sex1Sex2*Dist+ (1|GroupID)+ (1|Bird1ID)+ (1|Bird2ID)+ (1|Day)

Nobs = 114, NFF = 17, NMF = 74, NMM = 23, NDist1:95, NDist2 = 19

Random Effects

Groups name	**Variance**	**Std. Dev.**
GroupID (intercept)	6.032e-17	7.767e-09
Bird1ID (intercept)	9.097e-03	9.538e-02
Bird2ID (intercept)	1.371e-02	1.171e-01
Day (intercept)	2.129e-04	1.459e-02
StartTime (intercept)	4.058e-05	6.370e-03
Residual	1.528e-02	1.236e-01

Fixed Effects

	Estimate	**Std. Error**	**df**	***t*-value**	***p*-value**
(Intercept)	−0.8186	0.0537	29.28	−15.221	<0.0001
Sex-MF	−0.0447	0.0567	40.71	−0.789	0.4349
Sex-MM	−0.1229	0.0703	50.05	−1.749	0.0864
Dist-2	−0.0040	0.1522	66.17	−0.027	0.9788
Sex-MF: Dist-2	−0.0117	0.1581	65.38	−0.074	0.9410

Pairwise Comparisons (Tukey Adjustment)

Contrast	**Estimate**	**SE**	***z*-value**	***p*-value**
Sex-MF-Sex-FF = = 0	−0.0447	0.0567	−0.789	0.703
Sex-MM-Sex-FF = = 0	−0.1229	0.0703	−1.749	0.181
Sex-MM-Sex-MF = = 0	−0.0781	0.0488	−1.601	0.238

(Continued)

TABLE 4 | Continued

MaxProba2Juv2Ad~JuvAd+ Dist+ SexRatio+JuvAd:Dist+ JuvAd:SexRatio+ (1|GroupID)+ (1|Bird1ID)+(1|Bird2ID)

Nobs = 344, NAdAd = 57, NJuvAd = 229, NJuvJuv = 58, NDist1:286, NDist2 = 58, N2F2M = 96, N3F1M = 138, N4F0M = 80

Random Effects

Groups name	Variance	Std. Dev.
GroupID (intercept)	0.0023	0.0489
Bird1ID (intercept)	0.0068	0.0829
Bird2ID (intercept)	0.0102	0.1012
Residual	0.0085	0.0924

Fixed Effects

	Estimate	Std. Error	df	*t*-value	*p*-value
(Intercept)	−0.8494	0.0575	47.29	−14.754	<0.0001
JuvAd-JuvAd	0.0065	0.0462	131.61	0.141	0.8881
JuvAd-JuvJuv	0.1351	0.0711	57.81	1.900	0.0625
Dist-2	0.0075	0.0424	233.88	0.178	0.8589
SexRatio-3F1M	0.0569	0.0402	55.95	1.414	0.1628
SexRatio-4F0M	0.0963	0.0456	52.21	2.112	0.0395
JuvAd-JuvAd: Dist-2	0.0229	0.0476	234.04	0.481	0.6311
JuvAd-JuvJuv: Dist-2	−0.0215	0.0551	216.05	−0.392	0.6957
JuvAd-JuvAd: SexRatio-3F1M	−0.0282	0.0452	237.88	−0.624	0.5335
JuvAd-JuvJuv: SexRatio-3F1M	−0.1225	0.0671	122.41	−1.825	0.0704
JuvAd-JuvAd: SexRatio-4F0M	−0.0707	0.0512	259.63	−1.381	0.1683
JuvAd-JuvJuv: SexRatio-4F0M	−0.1498	0.0761	143.71	−1.969	0.0509

Pairwise Comparisons (Tukey Adjustment)

Contrast	Estimate	SE	*z*-value	*p*-value
JuvAd-AdAd = = 0	0.0065	0.0462	0.141	0.9879
JuvJuv-AdAd = = 0	0.1351	0.0711	1.900	0.1243
JuvJuv-JuvAd = = 0	0.1286	0.0460	2.792	0.0129

MaxProbaJuvJuv~Sex1Sex2*Dist+(1|Bird1ID)+(1|Day)

Nobs = 58, NFF = 14, NMF = 23, NMM = 16, NDist1 = 47, NDist2 = 11

Random Effects

Groups name	Variance	Std. Dev.
Bird1ID (intercept)	0.0053	0.0733
Day (intercept)	0.0023	0.0480
Residual	0.0133	0.1155

Fixed Effects

	Estimate	Std. Error	df	*t*-value	*p*-value
(Intercept)	−0.8258	0.0559	3.42	−14.754	0.0003
Sex-MF	0.0398	0.0568	25.26	0.701	0.4894
Sex-MM	0.1006	0.0618	28.05	1.628	0.1147
Dist-2	−0.0442	0.0825	33.85	−0.536	0.5955
Sex-MF: Dist-2	0.0349	0.1070	32.44	0.326	0.7461
Sex-MM: Dist-2	0.0091	0.1100	33.95	0.083	0.9341

Model statistical results are shown. Linear mixed effect models ("lmer" function from "lme4" R package) were built. Number of observations in the dataset for each fixed effect is given. We present the results from the R "summary" function.

AUTHOR CONTRIBUTIONS

MF carried out the data extraction and analysis, statistical analyses, drafted the manuscript. HS participated in the data analysis and drafted the manuscript. CV and MM designed the study, coordinated the study, performed the recordings and drafted the manuscript; All authors gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fpsyg.2016.01816/full#supplementary-material

Supplementary Figure 1 | Females' number of vocalizations from juvenile to young adult. Red points with red bars are mean ± *SE* values on all female individuals ($N = 33$). Black points with black bars are mean ± *SE* values on each female for all recordings, when the number of vocalizations decreased from juvenile to young adult. Gray points with gray bars are mean ± *SE* values on each female for all recordings, when the number of vocalizations increased. Lines connect paired values from same individuals.

Supplementary Figure 2 | Males' number of vocalizations from juvenile to young adult. Red points with red bars are mean ± *SE* values on all male individuals ($N = 33$). Black points with black bars are mean ± *SE* values on each male for all recordings, when the number of vocalizations decreased from juvenile to young adult. Gray points with gray bars are mean ± *SE* values on each male for all recordings, when the number of vocalizations increased. Lines connect paired values from same individuals.

Supplementary Figure 3 | Acoustic networks of four groups with juveniles. Nodes are individuals (J_i states for juvenile i and Ad_i states for adult i). Edges thickness is an affine function of the average vocal cross-correlation on all recording days for each dyad.

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Understanding Dynamics of Information Transmission in *Drosophila melanogaster* Using a Statistical Modeling Framework for Longitudinal Network Data (the RSiena Package)

Cristian Pasquaretta[1,2*†], Elizabeth Klenschi[1,2†], Jérôme Pansanel[1,2], Marine Battesti[3], Frederic Mery[3] and Cédric Sueur[1,2]

[1] Département Ecologie, Physiologie et Ethologie, Centre National de la Recherche Scientifique, Strasbourg, France, [2] Institut Pluridisciplinaire Hubert Curien, Université de Strasbourg, Strasbourg, France, [3] Evolution, Génomes, Comportement and Ecologie, Centre National de la Recherche Scientifique, Institut de Recherche pour le Développement, Université Paris-Sud, Université Paris-Saclay, Gif-sur-Yvette, France

Edited by:
Thomas Bugnyar,
Universität Wien, Austria

Reviewed by:
Mathieu Lihoreau,
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Ipek Gokce Kulahci,
University College Cork, Ireland

***Correspondence:**
Cristian Pasquaretta
cristian.pasquaretta@gmail.com

† These authors have contributed equally to this work.

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Social learning – the transmission of behaviors through observation or interaction with conspecifics – can be viewed as a decision-making process driven by interactions among individuals. Animal group structures change over time and interactions among individuals occur in particular orders that may be repeated following specific patterns, change in their nature, or disappear completely. Here we used a stochastic actor-oriented model built using the RSiena package in R to estimate individual behaviors and their changes through time, by analyzing the dynamic of the interaction network of the fruit fly *Drosophila melanogaster* during social learning experiments. In particular, we re-analyzed an experimental dataset where uninformed flies, left free to interact with informed ones, acquired and later used information about oviposition site choice obtained by social interactions. We estimated the degree to which the uninformed flies had successfully acquired the information carried by informed individuals using the proportion of eggs laid by uninformed flies on the medium their conspecifics had been trained to favor. Regardless of the degree of information acquisition measured in uninformed individuals, they always received and started interactions more frequently than informed ones did. However, information was efficiently transmitted (i.e., uninformed flies predominantly laid eggs on the same medium informed ones had learn to prefer) only when the difference in contacts sent between the two fly types was small. Interestingly, we found that the degree of reciprocation, the tendency of individuals to form mutual connections between each other, strongly affected oviposition site choice in uninformed flies. This work highlights the great potential of RSiena and its utility in the studies of interaction networks among non-human animals.

Keywords: social network analysis, social learning, information transmission, actor-oriented model, social interactions

INTRODUCTION

Social learning, defined as the transmission of behaviors through observation or interaction with conspecifics (Heyes, 1994), has been extensively studied in many different taxa (e.g., bumblebees, Leadbeater and Chittka, 2005; rodents, Galef and Clark, 1971; sperm whales, Weilgart and Whitehead, 1997; primates Whiten, 2000; van de Waal et al., 2013). Because of the advantages and drawbacks traditionally associated with social learning, it was first described as a fitted adaptation in environments where it is significantly less costly than individual, trial-and-error learning (Boyd and Richerson, 1988).

Individuals should not look for information indiscriminately within their group, as some individuals may hold a piece of information that is irrelevant, outdated, or misleading to the receiver (Kendal et al., 2005; Enquist et al., 2007; Rieucau and Giraldeau, 2011). Social learning strategies thus rely on the identification of the most successful individuals as best potential sources of information inside the group, taking into account the associated risk of inaccuracy (Kendal et al., 2005). In other words, some individuals may contact, or be contacted by, more members of the group or more often. In this regard, the social structure that emerges from inter-individual interactions is crucial in understanding how information is transmitted and if this transmission is efficient (Pasquaretta et al., 2014).

A social structure can be represented as a network where individuals are nodes connected by edges representing one or several types of interactions or relationships occurring among them (Wasserman and Faust, 1994). As summarized by Newman (2003), social network analysis can be used to draw and visualize networks, run statistical analysis of network properties, model networks, and predict the behavior of individuals or patterns in the networks. Connections among individuals (e.g., interactions) are channels for the transmission of information from one individual to another, and they are continually rearranged over time (Blonder et al., 2012). Each individual behaves differently during such a process, transmitting or receiving information from different conspecifics at different times.

Recently temporal dynamic approaches have been developed to study the structural changes occurring in a network along discrete and/or continuous time scales. Such methods are well suited to study social processes in animals such as communication, disease transmission, social learning, and many others (Pinter-Wollman et al., 2014). In particular, a temporal network approach may help to clarify how the dynamics of animal interactions modify network topology and relates to information flow (Charbonneau et al., 2013) and learning (Skyrms, 2009). Some of these methods come from human social science and have principally been developed to predict behaviors based on social structure (Steglich et al., 2006; Mercken et al., 2010; Snijders et al., 2010b; Schaefer et al., 2011). In this context, the use of the dynamic actor-oriented model developed in the R package RSiena (Ripley et al., 2013a) provides powerful estimations of individual behaviors and their changes through time. These methods, developed in the RSiena package (Ripley et al., 2013a), allow users to perform a wide range of data analysis on the same platform used for dynamic modeling operations. Despite having been developed for human social sciences, such techniques can prove very useful in studying the dynamics of interactions in animal societies as they integrate temporal analysis into an actor-oriented modeling approach (described in Snijders et al., 2010b). These methods assume that the dynamics of network structure are the product of a multitude of small changes happening continuously, of which the results are observed over a discrete time line. Moreover, the evaluation of the dynamic processes occurring inside a social structure is strongly dependent on the timescale used. Blonder and Dornhaus (2011) recently underlined the importance of using an appropriate timescale to observe information flow, and a study on the ant *Temnothorax rugatulus* had also shown a discrepancy in the results obtained depending on the time-scale used (Charbonneau et al., 2013). Indeed at large timescales, it was observed that information flow within the colony was slower than expected, whereas at smaller timescales it was faster, suggesting that the network facilitated local rather than global information transmission.

In this work, we performed a social network analysis using the RSiena package to evaluate the dynamic of social interactions during social learning experiments, using the gregarious species *Drosophila melanogaster,* which has already been demonstrated to rely on social learning regarding oviposition site preferences (Sarin and Dukas, 2009; Battesti et al., 2012). Schneider et al. (2012) have demonstrated the existence of non-random interaction networks in wild-type individuals in this species, and more recently, experiments performed by Battesti et al. (2012) provided evidence for social learning through the observation of oviposition site preference. In their protocol, they used uninformed flies that were left free to interact with individuals that had been trained to favor one of two oviposition media. Their results showed that, after that interaction phase, uninformed flies significantly favored the oviposition site the other individuals had been trained to prefer. In another recently published work we have also showed that uninformed flies, in addition to favoring the oviposition site the other individuals had been trained to, can also clearly avoid the information received by laying their eggs on the opposite site informed flies were trained to choose (Pasquaretta et al., 2016). The "avoid" or "follow" decision appeared to be driven by the homogeneity of contact behaviors among informed flies; that homogeneity was a *condition sine qua non* for the information to be successfully followed.

The current study aims at evaluating individual behaviors that could explain the varying outcome of social transmission by studying the dynamics of interactions among flies. RSiena was used to highlight the impact of social network dynamics on the diffusion of information. While fruit flies use olfactory and gustatory sensory organs to identify the sex of encountered individuals (Fernández and Kravitz, 2013), they seem to strongly rely on direct mechanosensory interactions as well in order to elicit responses from flies (Ramdya et al., 2015). Since the success of social transmission strongly relies on interactions between informed and uninformed flies (Battesti et al., 2012) and is affected by direct contacts among individuals (Battesti et al., 2015; Pasquaretta et al., 2016), we expect to find a discrepancy in the way these two fly types (i.e., informed and uninformed) interacted in accordance with the transmission

TABLE 1 | Sum of interactions experienced by 12 female flies (eight informed and four uninformed) during 48 video recorded transmission phases.

	Video ID	Total interaction	Total binarized interaction
Follow			
1	Video 7	6897	2478
2	Video 9	3434	1629
3	Video 10	3952	1703
4	Video 11	3524	1485
5	Video 13	2931	1368
6	Video 14	3564	1626
7	Video 23	3877	1622
8	Video 24	3609	1559
9	Video 28	4036	1767
10	Video 30	4287	1803
11	Video 31	5130	2017
12	Video 59	4255	1744
13	Video 65	6098	2207
14	Video 66	6411	2307
15	Video 67	5329	1862
16	Video 68	4314	1897
17	Video 69	3512	1573
18	Video 71	2721	1332
19	Video 73	4689	1813
20	Video 76	4393	1715
21	Video 77	5655	2215
22	Video 78	5468	2151
23	Video 79	6592	2371
24	Video 84	6753	2284
25	Video 89	4600	1903
26	Video 90	6626	2345
27	Video 92	2636	1260
28	Video 97	2072	1121
29	Video 103	5018	1885
Avoid			
1	Video 6	5109	1912
2	Video 15	3492	1604
3	Video 21	3345	1545
4	Video 22	4480	1695
5	Video 25	4079	1593
6	Video 26	3952	1749
7	Video 64	6049	2255
8	Video 70	3267	1497
9	Video 72	3041	1463
10	Video 74	4126	1620
11	Video 80	4171	1726
12	Video 83	6146	2252
13	Video 87	4899	1971
14	Video 91	1757	976
15	Video 95	3042	1432
16	Video 96	4107	1694
17	Video 99	5222	1991
18	Video 100	4264	1774
19	Video 103	6026	2114

Both weighted and binarized matrices for follow (n = 29) and avoid (n = 19) conditions are presented here. Video ID column, indicating the time order at which experiment were run, is also presented.

outcome. Uninformed flies show an increase in their activity level when facing informed individuals in the arena (Battesti et al., 2015), which may directly affect the rate of contacts experienced. Here, we focus on the analysis of the numbers of contacts sent and received (also known as *outdegree* and *indegree* in social network analysis) by both informed and uninformed flies, and we expect to find higher *outdegree* and *indegree* measures in uninformed flies compared to informed ones. We evaluated the presence of homophily – the tendency of individuals to associate with similar conspecifics – in the networks to assess the presence of a possible bias in interaction exchanges within classes. Indeed, significantly high levels of homophily for both classes suggest the existence of closed subgroups where information may get fixed (in the case of homophily in informed flies) or never transmitted (in the case of homophily in uninformed flies). Finally, in order to evaluate the impact of both individual and neighboring degrees on the probability of receiving and starting future interactions, we estimated the effect of being linked to individuals that have received many contacts and the effect of being linked to individuals that have sent many contacts in the transmission arena.

MATERIALS AND METHODS

Behavioral Experiments

Using already published data on information transmission in flies (Battesti et al., 2015), we processed recordings of the social transmission phases of the experiments to identify interactions between individuals and analyze the resulting social networks. In those experiments eight female drosophilae were conditioned by introducing them into a 120 mm × 50 mm × 90 mm plastic cage and leaving them for 8 h with the choice between two oviposition media (3 ml contained in 30 mm diameter Petri dishes with 20 g/l of sucrose, 10 g/l of agar and 6 ml/l of artificial banana or strawberry flavors, la Gazignaire SA). Females were trained to prefer one oviposition site over the other with the help of quinine, an alkaloid known to induce gustatory repulsion in fruit flies (Quinn et al., 1974); 50% of the replicates had quinine in the banana-flavored medium and 50% had quinine in the strawberry-flavored medium. Following this conditioning phase, the eight informed females were introduced together with four uninformed individuals in a semi-opaque white polyoxymethylene (Delrin) arena (diameter 100 mm; height 3 mm) covered with transparent Plexiglas (design based on previous work by Simon and Dickinson, 2010). After a social transmission phase lasting 4 h, flies were gently removed from the arena and immediately introduced into a plastic cage containing two oviposition sites again, this time using quinine-free banana- and strawberry-flavored media. We subsequently calculated the proportion of eggs laid by uninformed individuals on each medium at the end of each experiment. Two conditions were then defined: (1) "Followed" (flies followed the information gathered by informed individuals) when uninformed flies mostly laid their eggs on the medium informed flies had learn to prefer in the conditioning phase (proportion of eggs laid on the informed medium by uninformed flies greater than 0.8, $N = 29$, of which

16 on strawberry-flavored medium), and (2) "Avoided" (flies avoided the information gathered by informed individuals) when they laid their eggs in majority on the other medium (proportion on informed medium lower than 0.2, $N = 19$, of which 8 on strawberry-flavored medium).

Video Analysis

The social transmission phases were recorded using a camera placed vertically above the arena. Using the Ctrax software (Branson et al., 2009), the movements of each individual were automatically followed and its coordinates in the arena recorded for each frame of the video, at a rate of 10 frames per second. Using these coordinates as our raw data, we constructed interaction matrices for each experiment using an automated code we specifically developed in R (code available under request). To this end, we defined an interaction between two individuals based on spatial and temporal constraints: proximity between two flies had to (1) be smaller than 1.1 average body lengths and (2) last for more than five frames of the video (i.e., 0.5 s). These thresholds were derived from several preliminary assumptions and observations. We calculated the average body length of the individuals for each video based on the body length measured by Ctrax for each individual in each frame. Flies can interact using different angles of approach, but the largest distance between two flies would only occur in the case of an approach from the front or rear (for a better graphical explanation of the interaction see Figure 2 in Pasquaretta et al., 2016). In these types of interactions, the distance between the centers of the two individuals will thus be equal to one body length in the case of direct head-to-head contact. We added a 10 percent margin to account for possible contacts between antennae or front legs (structures which are too small for Ctrax to be detected) even when bodies were not in direct contact. Secondly, our temporal criteria to define interactions were based on our observations that proximity lasting under 0.5 s usually corresponded to individuals crossing paths without stopping to interact. Moreover, to discriminate between the initiator and the receiver, we estimated the mean speed of the individuals during an interval lasting four time-frames and preceding each contact by calculating their traveled distance during this interval; the initiator was defined as the fastest individual between the two involved in the contact. Each transmission phase was divided into intervals of 5, 10, and 15 min and each set of intervals was tested.

Dynamic Analysis

A stochastic agent-based model was run using R (version 3.1.3) (R Core Team, 2015) and the RSiena package (version 1.1-232) (Ripley et al., 2013a) after testing for the different time-scales we had previously defined (i.e., 5, 10, and 15 min). Indeed, changes between two consecutive networks can be too small to rise above the significance threshold, or too large for the model to consider the networks as consecutive stages of the same process. In our case, this lead to an impossibility for the models to converge on our data based on the 5 (few individuals are connected in the matrix) and 15-min (all individuals are connected) intervals. All modeling was thus performed on the 10-min intervals, for which convergence was always successful and satisfying; all t-statistics for convergence were inferior to 0.1, suggesting a satisfying estimation of the model (Ripley et al., 2013b).

We checked for the amount of changes between consecutive networks using the Jaccard index, which expresses the similarity between two sets of matrices ranging from 0 (completely different) to 1 (exactly the same). A Jaccard index higher than 0.2 indicates that consecutive networks are similar enough to be considered as successive states of the same network, thus allowing for an RSiena modeling approach (Ripley et al., 2013b). Before running the analysis, we also removed the first time interval from the data; live observations of the flies after they were introduced into the arena showed enhanced activity in all individuals during the first interval of the transmission phase.

The dynamic analysis for weighted networks is not yet implemented in RSiena; we thus performed all the following analysis using binary matrices (Ripley et al., 2013b). The network measures discussed in this study are thus referring to unweighted degrees. We consider these measures just as relevant as their weighted equivalents in our case (see **Table 1**). Indeed, a binary matrix based on degree instead of strength, actually informs on the total number of different individuals that contacted or have been contacted by each focal fly.

Actor-Oriented Model

The actor-oriented dimension of the model allows us to test hypotheses regarding how individuals affect the network structure by changing their outgoing ties, i.e., who they interact with. However, our study focuses more specifically on two classes of individuals, informed and uninformed flies, and how these classes interact by comparing behaviors at the class level. Moreover, one of the assumptions of the model is that network ties can be regarded as states, rather than events. Conceptually, it is more intuitive to consider a network of flies interacting as a succession of events, one event being described as one interaction between two flies. Another major assumption of RSiena is that the network's probabilities of change follow a Markov process, i.e., that the current state of a network is the only probabilistic determinant of its dynamic. However, this does not necessarily imply that past states are irrelevant; they can intervene through the influence they have on the current state itself. In our case, this will be reflected by the fact that past interactions will affect an individual's current behavior, as it is likely to have changed its state along the way (i.e., acquired information) or have a different knowledge of its social environment as it contacts other informed and uninformed flies.

Several methods of estimation have been implemented into Siena since its development: the Method of Moments (Snijders, 2001), the Maximum Likelihood method (Snijders et al., 2010a) and the Bayesian method (Koskinen and Snijders, 2007). While the two latter sets of methods usually yield smaller standard errors for estimates, their use is strongly encouraged in situations with small network datasets and/or very complex models. Considering the size of our data as well as the relative simplicity of our models, the Method of Moments was deemed sufficient and allowed for faster computing calculations (Ripley et al., 2013b). The principle of this procedure is to condition on the first observation; the first observed network (i.e., the network built from observations in the first time interval) is used as the starting point of the simulation, rather than estimated, and thus used to estimate changes between the first interval and successive ones. At each time step, the same procedure is applied until the final interval is reached. We applied the *evaluation function* to determine the probability of change for actors in the network based on the state of the network and on actor behavioral covariates. This function is described as the primary determinant of the probabilities of change of a network, and it can be expressed using the wide range of covariate effects defined in RSiena (Ripley et al., 2013b).

RSiena allows for the combined analysis of several independent networks and estimation based on repeated measures. Networks are considered independent when they are composed of different sets of actors and when it can be considered that these networks do not influence each other. Such was the case in our study, where new individuals were used for each experiment. Several methods are proposed to achieve this type of analysis. We selected the multi-group analysis for its fast computing time and its estimation of rate parameters for each independent network, as opposed to other methods which yield a single rate parameter for all networks for each interval (Ripley et al., 2013b). These rate parameters express the rate of change between two successive networks, i.e., – the speed at which new interactions between individuals who were not previously interacting occur and existing interactions disappear. In such an actor-based model, several effects can be analyzed: (1) structural effects, describing the variation of the whole structure of the network over time and only depending on the network itself, (2) monadic covariate effects, which use individual characteristics as statuses of individuals in the network, and (3) dyadic covariate effects, typically used to analyzed the effect of more than one actor on the individual network measures (see Ripley et al., 2013b for a detailed description of all the available effects in RSiena). However, because the model implemented by RSiena was constructed with studies of human networks in mind, not all effects are relevant for our purpose. We consequently identified and tested the effects most relevant to our question (**Figure 1**). Each effect was tested using a Wald t-test. We followed a two-step procedure; we first tested some pertinent effects in a preliminary global model including both structural (i.e., density, reciprocity, square of contacts sent, and sum of contacts received by neighbors) and monadic (actors hereafter called *ego*, receivers hereafter called *alter*, and homophily) effects (**Figure 1** provides a detailed description of the tested effects). Secondly, in order to better characterize the impact of individual status on information transmission processes, we implemented monadic effects alone (i.e., *ego*, *alter*, and homophily) on time-based subsets of our data. *Density* cannot really be interpreted by itself, as all other statistics are correlated with it; it is included to control for the density of the network, as advised by the RSiena developers (Ripley et al., 2013b). We modeled subsets of increasing size, starting with the first two interaction matrices (i.e., the second and the third time intervals from our original data). Following subsets were generated by incrementing their length by 10 min, or one time interval, each time. Thus, the dynamics of the t-statistics for the *ego* and *alter* effects were estimated using two linear models, with time intervals and experimental condition as predictors in each model. We also tested for the presence of a quadratic relationship of the *ego* and *alter* effects with time, comparing linear and quadratic regressions using the F-test. A quadratic relationship can suggest the existence of a possible plateau in the relationship between time and the number of contacts sent or received, above which the transmission process stabilizes. We applied a forward stepwise procedure to select our models. To implement the selection we first created a model for each effect previously described and we then aggregated the estimates and we excluded all the non-significant effects. All the models were tested for their goodness of fit to ensure their likelihood in explaining original data by using the "sienaGOF" function from the RSiena package[1].

RESULTS

Jaccard indexes were superior to 0.2 in 675 out of 696 and 437 out of 456 10-min matrices used from our "Followed" and "Avoided" conditions respectively, ensuring a sufficient change among consecutive networks to apply our subsequent RSiena analysis. Indeed, mean rate parameters evolve over time as a sinusoidal distribution for both the "Followed" and "Avoided" conditions, meaning that the dynamics of the networks reveal similar, comparable patterns between conditions (**Figure 2**). Applications of the multi-group stochastic estimation procedure performed by RSiena on our experimental data (conditions "Followed" and "Avoided") yielded models illustrating the dynamics of network measures and the influence of oviposition experience on behavior and network structure. The stepwise model selection procedure yielded a parsimonious model defined by the *density*, *reciprocity*, *alter*, and *ego* effects. For the "Followed" condition model, the square of the number of contacts sent was also retained. Whether information was followed or not, uninformed individuals received interactions from the opposite fly type (*alter* effect) more frequently than informed ones (Followed: $t = -3.973$, $P < 0.001$; Avoided: $t = -4.103$, $P < 0.001$) and they initiated interactions toward the opposite fly type (*ego* effect) significantly more than informed individuals (Followed: $t = -10.036$, $P < 0.001$; Avoided: $t = -13.449$, $P < 0.001$).

Reciprocity, the tendency of individuals to form mutual connections between each other, was always significant both in the "Followed" and "Avoided" conditions, but showed opposite trends: uninformed flies followed the information carried by informed individuals when reciprocity was significantly lower than random ($t = -12.166$, $P < 0.001$), while they avoided it when it was higher ($t = 10.396$, $P < 0.001$). The number of contacts received by neighbors did not influence the transmission process, neither in the "Followed" nor in the "Avoided" conditions (Followed: $t = -0.493$, $P = 0.622$; Avoided: $t = -0.551$, $P = 0.582$).

The more the square of the number of contacts sent (*outdegree activity*) increased, the less likely information was to be followed

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[1] http://www.inside-r.org/packages/cran/RSiena/docs/plot.sienaGOF

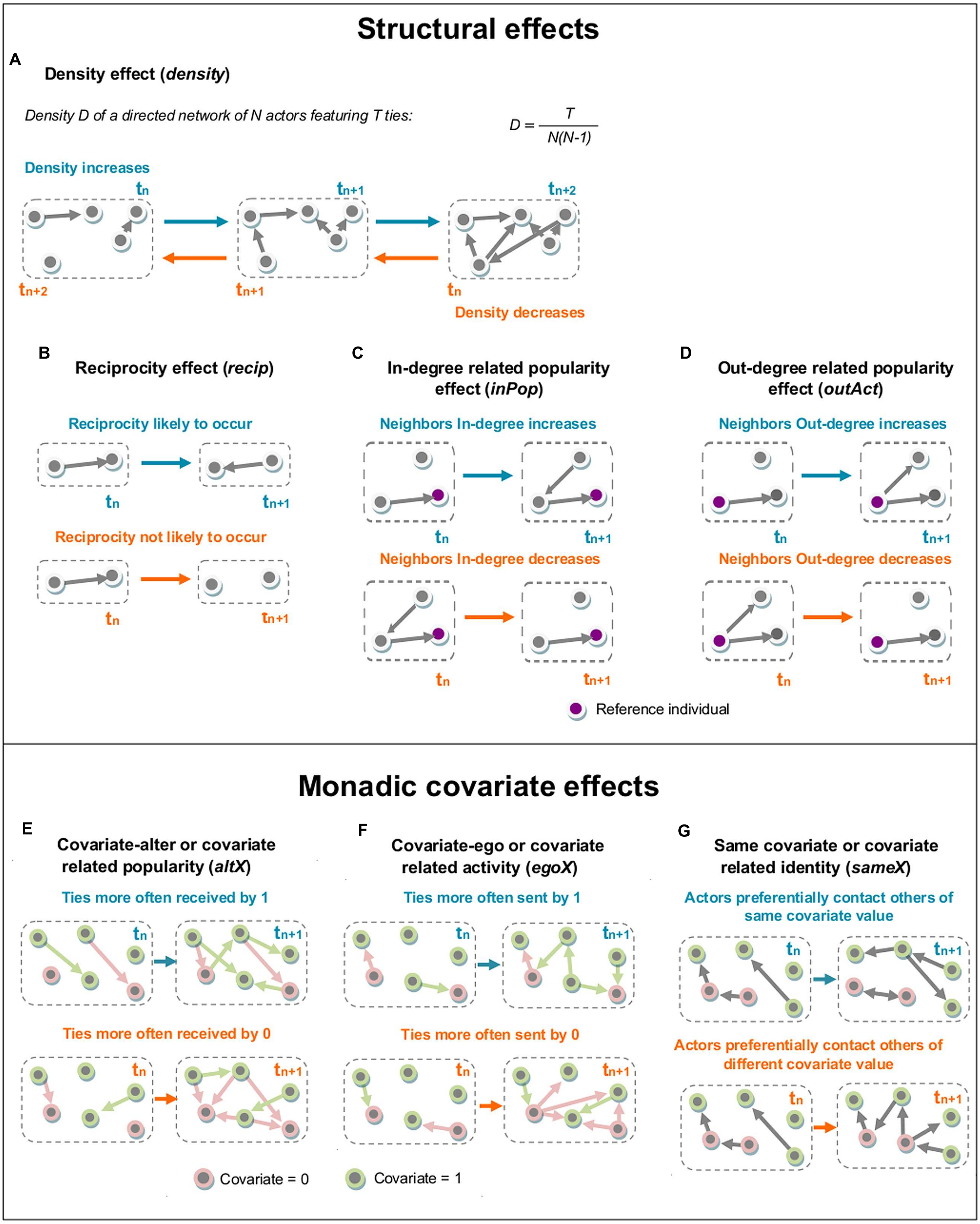

FIGURE 1 | Interpretation of the RSiena structural effects tested on the "Followed" and "Avoided" data. Each graph delimited within a single dashed gray box represents an observation of a directed network during a given time interval (denoted by t_n). Successive states of the network and the dynamics of each effect through time are shown by successive dashed gray boxes (denoted by t_{n+1} and t_{n+2}). (1) Structural effects are effects related to network measures only, while monadic covariate effects are related to individual characteristics defined by a binary covariate (here, informed vs. uninformed). Color keys are the same over all figures, with blue elements describing cases where the effect in question has positive and significant dynamics, and orange elements where these are negative and significant. Pink nodes represent uninformed flies (covariate = 0), and green nodes informed ones (covariate = 1). Structural effects are only related to the network:

(*Continued*)

FIGURE 1 | Continued

(A) The <u>density effect</u> *(density)*, defined by the outdegree of the actors. When significant, it expresses whether density in the network is increasing or decreasing over time, i.e., whether relations are more often created or dissolved. A positive significant statistic (blue) indicates that density overall increases, and a negative significant statistic (orange) that density overall decreases. **(B)** The <u>reciprocity effect</u> *(recip)*, defined by the number of reciprocated interactions, i.e., the number of instances in which the actor of interest also received an interaction from the actor it contacted. When positive (blue), it expresses that an actor is more likely to send an interaction to actors that have previously sent it one and when negative (orange) it represents avoidance. Non-significant values for this effect represent cases in which the reciprocal behavior is random. **(C)** The <u>indegree related popularity effect</u> (*inPop*) reflects the tendency of the neighbors of each actor to receive interactions by others in the network. When significant it underlines the role of neighbors as bridges of information. **(D)** The <u>outdegree related activity effect</u> (*outAct*) reflects the probability of the actor to be contacted by neighbors with a large number of contacts sent. Significant statistics for this measure mean that an individual is largely contacted by highly active individuals. (2) Monadic covariate effects are related to an individual covariate, in our case the class of the actor of interest (informed or uninformed): **(E)** The <u>covariate-alter or covariate related popularity</u> (*altX*), defined by the sum of the covariates over all actors with whom the actor of interest has an interaction. When significant, it expresses which class of actors receives interactions from others more rapidly. For a significant statistic, the interpretation will be that informed flies are contacted by others more rapidly than uninformed flies if it is positive (blue), and *vice versa* if the statistic is negative (orange). **(F)** The <u>covariate-ego or covariate related activity</u> (*egoX*), defined by the actor's outdegree weighted by its covariate value. When significant, it expresses which class of actors starts interactions more rapidly. For a significant statistic, the interpretation will be that informed flies contact others more rapidly than uninformed ones if it is positive (blue), and *vice versa* if the statistic is negative (orange). **(G)** The <u>same covariate or covariate related identity</u> (*sameX*), defined by the number of interactions of the actor of interest to all other actors who have exactly the same value of covariate (i.e., informed-informed or uninformed-uninformed). When significant, it expresses how likely the actor of interest is to interact with others who share the same covariate value. A positive statistic (blue) will thus express homophily (i.e., actors interact more often with others who have the same covariate value) and a negative one (orange) heterophily (i.e., actors interact more often with others who have a covariate value different from their own).

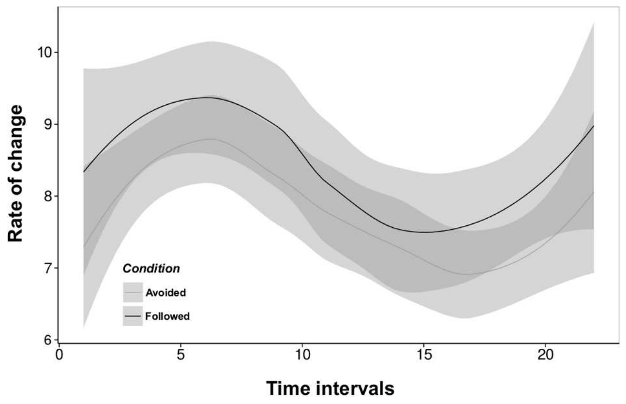

FIGURE 2 | Rate parameters of the networks estimated from the multi-group analysis in RSiena for each of our two experimental conditions ("Followed" and "Avoided"). Rate parameters express the number of opportunities for change between successive networks for one given actor. A change is understood as the creation or the deletion of relations among actors during two successive networks. The number of observed changes is, however, always lower than what rate parameters imply; an opportunity for change can be resolved by a 'no change' decision, and successive changes can cancel each other out (e.g., create then dissolve a given relation during the same interval). They do not differ between conditions; in both cases actors always have opportunities for change from one network to the next, and although the number of opportunities varies over time, it evolves similarly whether information was followed or not. The success of information transmission is thus not primarily dependent on the opportunities actors get to change their connections to other actors. Best fitted lines for a non-linear model are represented for "Followed" (black) and "Avoided" (grey) conditions. Shaded areas represent the standard errors of the models.

($t = -2.185$, $P = 0.029$), meaning that an elevated mobility of flies inside the arena was somehow impeding the acceptance of the information by uninformed individuals. Finally, homophily within classes of flies had no effect on the transmission process, neither in the "Followed" nor in the "Avoided" conditions (Followed: $t = -0.313$, $P = 0.751$; Avoided: $t = -0.413$, $P = 0.682$).

To better evaluate the influence of the *ego* and *alter* effects over time we repeated the RSiena procedure over intervals of increasing lengths, starting from the first 10-min interval and adding successive intervals one by one. An analysis of variance showed that both *ego* and *alter t*-statistics were better explained as a quadratic function of time ($\text{ego}_{\text{quadratic\_linear}}$: $F = 63.732$, $P < 0.001$; $\text{alter}_{\text{quadratic\_linear}}$: $F = 17.016$, $P < 0.001$), meaning that informed and uninformed flies first increase their differences in terms of numbers of contacts started and received, then reduce these behavioral differences over time (**Figure 3**). The difference in the number of contacts received by informed and uninformed flies was larger when information was followed than when it was not ($\text{Condition}_{\text{Followed\_Avoided}}$: $t = 3.084$, $P < 0.001$). There is also a large discrepancy in the magnitude of the t-statistics associated with the *ego* effect: the difference in the number of individuals contacted by informed and uninformed flies is constantly smaller in the "Followed" condition ($\text{Condition}_{\text{Followed\_Avoided}}$: $t = -19.231$, $P < 0.001$). These results suggest that a large heterogeneity in the number of contacts sent and received by both fly types drove uninformed flies to choose the opposite oviposition site informed flies were previously trained to choose.

DISCUSSION

Using data collected on fruit flies in the context of social learning, we have investigated how the behaviors of informed and uninformed individuals could explain the varying success of information transmission, as reflected in the different strategies adopted by uninformed flies after they had interacted with informed individuals.

The RSiena multi-group analysis shows that uninformed flies always contacted and were contacted by more individuals than informed ones. This result is in accordance with a previous work we have done on the same set of flies where we showed an increase in the mean activity level for uninformed flies during transmission phase, probably due to an increased interest in interacting brought upon by flies bringing some novel odors

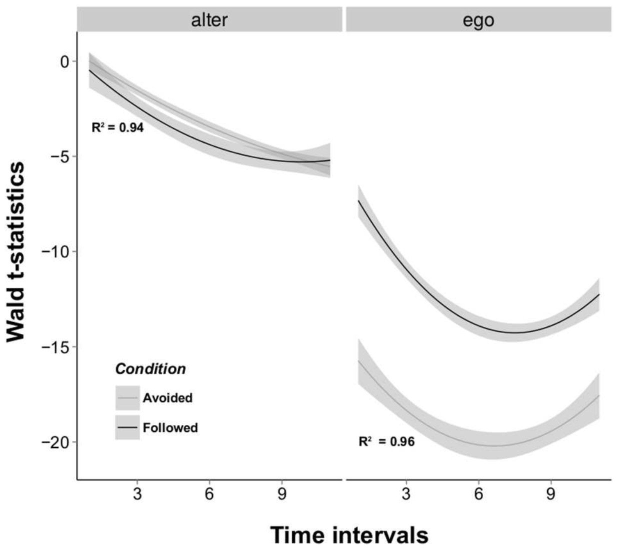

FIGURE 3 | Wald *t*-test values for the *alter* and *ego* effects obtained by the RSiena model estimation. The *alter* effect represents which class of actors increases its indegree more rapidly, while the *ego* effect expresses which class increases its outdegree more rapidly. These *t*-statistics were estimated over time intervals of increasing length for the two transmission conditions. Results show that uninformed individuals display both a higher outdegree and indegree than informed individuals (negative *t*-statistics) and that the difference in outdegree between the two classes is more important than in indegree. Best fitted lines for the quadratic models are represented for "Followed" (black) and "Avoided" (grey) conditions. Shaded areas represent the standard errors of the models.

into the uninformed flies' environment (Battesti et al., 2015). Indeed, uninformed flies were always more active both as sender and receiver. Interestingly, uninformed flies tended to follow the information provided by informed ones when the difference in contacts sent between the two fly types was moderate. This phenomenon occurs either because uninformed flies have contacted fewer individuals, or because informed flies have contacted more. This result suggests that information transmission may occur following an active rather than a passive process, which can be explained both by a search of the information performed by uninformed individuals and/or by an active exchange performed by informed individuals. The active participation of informed flies is not obviously expected following Battesti et al.'s (2015) results. In Battesti et al. (2015), we have shown that the performance of informed flies after the transmission phase was negatively affected by the rate of previous interactions with uninformed individuals, revealing a possible associated cost to information transfer for informed flies. In that study we suggested that the observed transmission process from informed to uninformed flies, and the resulting change in the behavior of informed flies, could be adaptive as the survival rate of larvae might depend on a balance between optimal resource exploitation rate and larval competition. Indeed, an increased number of larvae will exploit the resource more efficiently than a small aggregate, and will be more likely to prevent the development of bacterial and fungal competitors (Rohlfs and Hoffmeister, 2003; Rohlfs, 2005). However, an extremely large number of larvae foraging on the same medium will also impact the per-capita resources available for individual use, thus increasing competition among individuals (Pulliam and Caraco, 1984).

Interesting results were found in relation to the reciprocal behavior of flies: uninformed flies tended to avoid the information brought by informed ones when a large number of reciprocated interactions occur. For information to be transmitted, non-reciprocal contacts are crucial. Network reciprocity has been suggested to negatively affect the formation of smoothed boundaries in clustered population. In particular, in a recent prisoner's dilemma game developed to study the impact of network reciprocity and individual conformism on cooperation, Szolnoki and Perc (2015) have demonstrated that, starting from a clustered population made of two type of individuals (cooperators and defectors) experiencing a relatively high value of network reciprocity, an increase in the fraction of conformist individuals in the population led to an increase in cooperative behaviors among individuals by smoothing the interaction boundaries among clusters. In accordance to this theoretical work our results suggest that network reciprocity may direct uninformed flies toward an "anti-conformist" site choice underlining the regulatory role, especially as social obstacle, played by high level of reciprocal interactions. It is interesting to note that in a previous work describing the genetic determinants of social structure in different *Drosophila* strains, Schneider et al. (2012) found that olfactory mutant flies (individuals with a severe loss of smell) showed a higher percentage of reciprocated interactions and a disrupted social interaction network compared to wild-type flies. These results may bring additional improvements to the understanding of both the ultimate and proximate factors influencing the efficiency of information transmission processes in this species.

The dynamic network analysis performed over intervals of increasing lengths shows that differences in the estimation of the number of contacts sent and received by informed and uninformed flies best fit a quadratic distribution, with a positive concave curve (**Figure 3**). This suggests that the interaction network stabilized with time through a reduction of the differences between the behaviors of informed and uninformed flies. A large variability in the number of contacts can be caused by the abnormal activity of a few individuals in a network (also known as the friendship paradox; Feld, 1991) which may experience higher rate of interactions in their social milieu. This time-leveling phenomenon is in accordance with the synchronization of activities in fruit flies which has been shown to be affected by social interaction between individuals (Lone and Sharma, 2011).

To the best of our knowledge, this is the first time that an actor-oriented model approach was used to evaluate the correlation between network dynamics and information transmission in animals, suggesting that RSiena might provide useful analytical tools to answer other ecological and evolutionary questions. RSiena allowed us to analyze the dynamics of interaction networks during social transmission experiments and to identify the flies' involvement in the process of information transfer.

The implementation of additional effects taking into account social processes observable in more complex animal societies would make this tool even more useful to biologists studying other species by allowing them to construct complex models to explain the dynamics of their observed interaction networks. For instance, RSiena's actor-oriented models might be used to estimate the dynamic formation of triadic subgroups (i.e., *transTrip* effect in the RSiena manual) in species experiencing triadic coalitions among group members (e.g., primates Kappeler, 2012; *Corvus corax* Loretto et al., 2012). Moreover, estimation in RSiena is based on the analysis of unweighted networks, meaning that the data used as input for this program reflects the interactions between individuals in the group, but not their frequency. Being able to work directly on weighted networks would allow for the integration of the number of interactions occurring between a given pair of individuals. Because biological processes involving information transmission are likely to rely heavily on repeated interactions between animals (Wei et al., 2015), this improvement would certainly provide even more insight into the mechanisms regulating such processes.

Results obtained in this work show a strong effect of network properties on the future oviposition site choice of uninformed flies. In this context, our results may grant more interest as well because they were obtained from an oversimplification of the repeated interactions occurring between flies in the arena. However, it is possible that in our experiments, uninformed flies may have switched from an uninformed state to an informed state before the transmission was over. Flies may need to pass a threshold of a minimum number of interactions before they can make this switch. Understanding the timing of this switch, and its integration with social interactions, is critical for information transmission studies where a threshold process may occur (Watts, 2002).

The information transmission process is likely to be affected by the proportion of informed and uninformed flies interacting. Previously unpublished experiments run by Mery' lab (personal communication) have revealed that twice as many informed as uninformed individuals are needed in the arena for the information to be transmitted. It would be interesting in the future to analyze variable proportions of informed and uninformed flies to better evaluate the existence of such a threshold mechanism, which has already been well described theoretically in social learning literature (i.e., see social learning benefit when copying is rare: Boyd and Richerson, 1985; Giraldeau et al., 2002).

Finally, a well-determined subset of videos (i.e., 77% of the total videos run) was used to understand the dynamic effect of network measures on oviposition site choice in this work (i.e., where the proportions of eggs laid by uninformed flies was outside of the [0.2; 0.8] interval). RSiena's multi-group analysis allows for a parallel comparison of multiple binary networks that can be merged based on clear definitions (follow and avoid information in our case). More studies are needed to understand which network properties affect the remaining random choice we obtained in 23% of the data. In particular, the random outcome obtained in such videos might be caused by different spreading dynamics that could have been actually produced by repeated interactions among individuals. In this context, Relational Event Models (REMs: Tranmer et al., 2015) might be an interesting tool to estimate the impact of multiple repeated interactions on the transmission process. REMs indeed evaluate the sequence of events occurring in each network, allowing also for weighted network analysis and thus possibly explaining the effect of multiple interactions among individuals on future oviposition site choice.

Using *Drosophila* as a model allowed us to make use of the powerful multi-group analysis developed in RSiena while using a substantial data set, obtained from independent repeated experiments. Likewise, studies using different experimental conditions, different mutant strains, or groups with different ecological or physiological characteristics could benefit from a similar approach. However, many studies of animal networks focus on species and social processes for which fewer observations are available, meaning that a multilevel network analysis (such as the multi-group analysis we used here) may not always be possible. However, past uses of RSiena have yielded interesting and valid results, even when repeated experiment cannot be performed (Ullrich et al., 2010; van Zalk et al., 2011). It thus seems that this tool could be used to study a wide range of animal species, varying in group size, social complexity, and access by observers, as recently shown in Ilany et al. (2015). We confirm here that a network dynamic approach is a strong tool for understanding information transmission in a mixed group of flies. This transmission process notably involves specific social behaviors from both informed and uninformed individuals, such as reciprocity between individuals and number of contacts sent or received upon which the success of information diffusion is conditioned.

AUTHOR CONTRIBUTIONS

CP and EK carried out the data analysis and paper writing; MB and FM supplied fly videos; JP performed the calculation on the Cloud Computing platform at the IPHC-CNRS in Strasbourg. CS and FM supervised the study. CP, EK, JP, MB, FM, and CS wrote the manuscript. All authors gave final approval for publication.

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Bayesian Model Selection with Network Based Diffusion Analysis

Andrew Whalen[1]* *and William J. E. Hoppitt*[2]

[1] School of Biology, University of St. Andrews, St. Andrews, UK, [2] School of Biology, University of Leeds, Leeds, UK

A number of recent studies have used Network Based Diffusion Analysis (NBDA) to detect the role of social transmission in the spread of a novel behavior through a population. In this paper we present a unified framework for performing NBDA in a Bayesian setting, and demonstrate how the Watanabe Akaike Information Criteria (WAIC) can be used for model selection. We present a specific example of applying this method to Time to Acquisition Diffusion Analysis (TADA). To examine the robustness of this technique, we performed a large scale simulation study and found that NBDA using WAIC could recover the correct model of social transmission under a wide range of cases, including under the presence of random effects, individual level variables, and alternative models of social transmission. This work suggests that NBDA is an effective and widely applicable tool for uncovering whether social transmission underpins the spread of a novel behavior, and may still provide accurate results even when key model assumptions are relaxed.

Keywords: Network Based Diffusion Analysis, Bayesian model selection, WAIC, social learning, statistical methods

Edited by:
Cédric Sueur,
Institut Pluridisciplinaire Hubert Curien,
France

Reviewed by:
Mathieu Lihoreau,
CNRS - Centre for Integratve Biology
of Toulouse, France
Frédéric Amblard,
Université Toulouse 1 Capitole, France

Correspondence:
Andrew Whalen
awhalen@gmail.com

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1. INTRODUCTION

There has been a substantial interest in better understanding how and why animals use social information (Heyes, 1994; Laland, 2004; Galef and Laland, 2005), and particularly understanding if certain behaviors diffuse through populations as a result of social transmission (learning from others) (Reader, 2004). A capacity for social transmission has been demonstrated in many species using a traditional demonstrator-observer paradigm (Hoppitt and Laland, 2013). In contrast, recent studies have focused on studying the diffusion of behavior in freely interacting groups of animals in the field (e.g., Allen et al., 2013; Hobaiter et al., 2014) or in the laboratory (e.g., Boogert et al., 2008; Atton et al., 2012), aiming to asses the importance of social transmission in the spread of behavior, and elucidate typical pathways of transmission. However, in many cases it can be challenging to determine whether the spread of behaviors is facilitated by social transmission, or purely the product of independent asocial learning. This challenge increases the difficulty in inferring the presence of, and understanding the mechanisms that underlie social learning in animals.

An early approach in detecting social transmission and asocial learning was to analyze the shape of the "diffusion curve," the number of animals in the population who had performed the novel behavior over time (Lefebvre, 2000). The theory was that if the diffusion followed an accelerating pattern, or an "s-shaped curve," this was likely a product of social transmission (Reader, 2004). However "s-shaped curves" can also be produced by other mechanisms, like individual differences in the rates of learning, which has lead to the technique to be considered unreliable (Reader, 2004; Franz and Nunn, 2009; Hoppitt et al., 2010).

More recent research has responded to concerns over the validity of diffusion curve analysis to develop novel statistical tools to analyze the rates of diffusion of novel behaviors. Network Based Diffusion Analysis (NBDA), is one such approach that infers social transmission if the spread of the novel behavior follows a social network (Franz and Nunn, 2009; Hoppitt et al., 2010). In most cases the social network is a pre-established association network (e.g., Aplin et al., 2012; Allen et al., 2013) that is assumed to reflect opportunities for learning between each pair of individuals (Hoppitt et al., 2010). However, the networks used can instead directly reflect the pattern of recorded (probable) observations among individuals if such information is available (Hobaiter et al., 2014), or different networks can be used to represent different hypotheses about the pathways of transmission (e.g., Farine et al., 2015). In addition to analyzing the diffusion of behavior in natural populations, NBDA has also been used in laboratory studies (e.g., Atton et al., 2012). Here, fewer individuals are used, but with the advantage that replicate groups can be easily created, and researchers can track the diffusion of multiple behavioral traits through the same groups (e.g., Boogert et al., 2008). NBDA then potentially allows researchers to make inferences about individual differences in innovation and social learning ability. As such NBDA has potential to provide a unifying analytical framework for studying social transmission in the laboratory and the field.

Although initially a frequentist method, NBDA has been recast into a Bayesian framework to allow better specification of different models of social learning, and the inclusion of random effects allowing for correlations in learning rate within individuals when they are subjected to multiple diffusions (e.g., Boogert et al., 2014; Nightingale et al., 2014). Although the move to a Bayesian model of NBDA has advantages, one of the disadvantages has been the ability for researchers unfamiliar with the method to use it, a problem exacerbated by the existence of a number of alternatives for model selection, several of which have been used in the context of NBDA.

In this paper, we address these issues by presenting and evaluating a framework for performing NBDA where model selection is done using the Watanabe Akaike Information Criteria (WAIC; Watanabe, 2013). Use of WAIC has the advantage that it is computationally relatively more straightforward to implement than alternatives like reversible jump Markov chain Monte Carlo (RJMCMC). One of the goals of this paper is to evaluate the performance of WAIC in performing model selection in the context of NBDA, and use a large simulation study to examine how the performance changes if key model assumptions are not met.

2. NETWORK BASED DIFFUSION ANALYSIS

NBDA is a general framework for evaluating different hypotheses for the spread of a novel behavior. At its core, NBDA relies on a two-step process to evaluate, and select a most likely model that describes observed data. First, we construct a likelihood function to represent the likelihood that each model generated the observed data. Many of these likelihood functions require the values for large number of parameters to be estimated. To estimate these parameters, Bayes' rule is used to fit the parameters to the data. The resulting model and parameters are then assessed using WAIC, which evaluates the predictive fit of each model. In the simplest case the model with the best (lowest) WAIC is chosen as our model.

NBDA falls under a wide class of hierarchical Bayesian models (Gelman et al., 2014), and many of the steps below are applicable to a broad range of settings. NBDA is distinguished from other hierarchical models by explicitly modeling social influences on learning. There are two variants of NBDA. Time of Acquisition Diffusion Analysis (TADA) analyzes the time at which an animal first performs a novel behavior, and can be analyzed in continuous (Hoppitt et al., 2010) or discrete (Franz and Nunn, 2009) time. In contrast, Order of Acquisition Diffusion Analysis (OADA) analyzes only the order in which animals first perform the behavior. Here we focus on continuous TADA and evaluate the effectiveness of NBDA with WAIC in this context, although the same approach is applicable to other variants of NBDA like OADA.

3. TIME OF ACQUISITION DIFFUSION ANALYSIS

Time of Acquisition Diffusion Analysis is a modeling technique which evaluates whether the rate at which an individual first perform a novel behavior is dependent on the behaviors of other individuals in that population. Because the method focuses primarily on acquisition of a novel behavior, it typically only analyzes the initial performance of the behavior and ignores subsequent performance.

As an example, imagine a population of birds learning to flip open the lid of container to receive a food reward. When the task is initially presented, none of the birds are able to solve it. Over a long period of time, all or most of the birds are eventually able to solve the task and receive the food reward. The question we wish to ask is, was the spread of the novel behavior (flipping the lid) acquired through asocial learning alone, or asocial learning aided by social transmission. If learning was done through pure asocial learning (including the effects of individual-level covariates), then the rate at which each bird solves the task should be constant (though this assumption can be relaxed Hoppitt et al., 2010), and independent of other birds having solved the task. If the learning was aided by social transmission, that rate of solving should increase as more other birds solve the task.

We can formalize this logic using an instantaneous rate model. This model assumes that at each instant, a given bird has some chance of learning the novel behavior. In the case of asocial learning, this rate does not depend on the number of other birds that had previously solved the task. In the case of social transmission, this rate will be sensitive to other birds solving the task.

To generate a likelihood function, we assume that at each instant the rate that bird *i*, solves the task (i.e., acquires the novel behavior) is $\lambda_i(t)$, where

$$\lambda_i(t) = a_i(t) + s_i(t), \tag{1}$$

the sum of an asocial learning rate *a* and social learning rate *s*. These rates are allowed to change over time, allowing the model to capture changes in the birds' environment, and the birds' social environment.

There may be individual-level differences in the rate at which the birds learn novel behaviors, to capture these differences we parameterize asocial learning as

$$a_i(t) = exp(\lambda_0 + A_i + \phi_i), \tag{2}$$

where λ_0 stands for a base rate of learning, modified by some set of individual-level covariates, A_i and individual-level random effects ϕ_i.

To incorporate social information we must provide a model of how an individual's learning rate is influenced by other animal's actions. In TADA we assume that animals are only influenced by the number of other individuals who have solved the task. We assume that the social learning rate is

$$s_i(t) = \sigma_i S_i(t), \tag{3}$$

where σ_i is an individual-level rate which determines the influence of social information and S_i captures how much social information is in the environment. Like asocial learning, we allow for individual-level differences in social learning ability,

$$\sigma_i(t) = exp(s_0 + B_i + \psi_i), \tag{4}$$

where s_0 is a base rate of social learning, B_i the influence of individual-level covariates on social learning, and ψ_i the influence of individual-level random effects on social learning. S_i is given by

$$S_i(t) = \sum a_{ij} I_i(t), \tag{5}$$

where $a_{ij}(t)$ is the influence individual i has on individual j, and $I_j(t)$ is an indicator variable that is 1 if animal j has solved the task prior to time t, and 0 otherwise. The amount of influence each individual exerts on each other can be captured by a social network which can be empirically estimated (Boogert et al., 2008). If there are no network differences, then $S_i(t) = \sum I_j(t)$ or the number of animals who have solved the task at each point in time. This model assumes that the rate of learning due to social transmission depends linearly on the number of other animals who have solved the task. In reality, other learning rules are possible, and we discuss some of these below.

In TADA, the rates of solving are estimates from the observed data using a hazard model, where if an individual has not solved the task at time t_0 then the likelihood that they solve the task at t_1 is,

$$p(s_i = t) = \lambda_i(t_1) \int_{t_0}^{t_1} exp(\lambda_i(t))dt, \tag{6}$$

and the likelihood that they fail to solve the task by time t_1 is

$$p(s_i > t_1) = \int_{t_0}^{t_1} exp(\lambda_i(t))dt. \tag{7}$$

Note that the parametrization of the model presented here differs from the original presentation of the continuous TADA (Hoppitt et al., 2010), although it follows that used for previous versions of Bayesian NBDA (Nightingale et al., 2014). In the original formulation, a parameter $\lambda_0 = exp(\lambda_0)$ gives the baseline rate of asocial learning, and a parameter $s = exp(s_o)/exp(\lambda_0)$ gives the rate of social transmission per unit connection, relative to the baseline rate of asocial learning. The parametrization presented is better suited for Monte Carlo sampling (Nightingale et al., 2014) but estimates for the parameter for the original specification can still be obtained from the posterior distribution.

Using the hazard model and our parametrization of the learning rate, we can estimate the rates of different model parameters based on a given data set by using Bayes' rule. Bayesian inference can be accomplished by a multi-functional statistical software packages like JAGS or Stan. In this study, we use a hand-coded Monte Carlo sampler implemented in R (R Core Team, 2013). Once posterior distributions are obtained, we can then use a model selection technique to compare between different models of learning. We outline one model selection approach below.

4. MODEL SELECTION USING WAIC

The goal of model selection is to compare multiple competing models, given a data set, and determine a single, or set of likely candidate model(s) that are thought to be "best." In the context of NBDA, a primary goal of the model selection is often to tell if a social model describes the data better than a purely asocial model. Although there are many ways of defining a best model, in this context, we evaluate models based on their predictive validity. Other approaches are discussed in the discussion.

Predictive validity is an assessment of the ability of each model to predict the results of future experiments, or unanalyzed tasks. However, true measures of predictive validity can be hard to obtain since it is often not feasible, or expensive to collect further data. A traditional alternative is to examine the performance of the model on predicting already obtained data. In the best case, "leave one out" cross validation trains the model on all but one piece of data, and then examines how well the model predicts the left out piece of data. This process is repeated for every data point. This technique is computationally expensive with a large number of data points, and may be inappropriate with few data points, since leaving a single data point out may be a large fraction of the total data.

There exists alternatives to leave one out cross validation like information criteria, a set of techniques (including WAIC) for balancing goodness of fit to collected data, against the number of parameters in the model. In some cases these techniques are asymptotically equivalent to leave one out cross validation as the number of data points grows large, while being much more computationally tractable to compute.

In our case, we use the WAIC to score each model. WAIC is a new alternative to older information criteria like Akaike's Information Criterion (AIC; Akaike, 1973) or Deviance Information Criterion (DIC; Spiegelhalter et al., 2002). It has a number of advantages over AIC and DIC. Unlike AIC or DIC, which assess a model's fit based on a single point estimate, WAIC uses the entire Bayesian posterior distribution, making it more accurate when the posterior distribution is not normally distributed. The results of WAIC also asymptotically approach Bayesian cross validation in the large sample limit (Watanabe, 2013).

WAIC assesses model fit by computing the ability of each model to predict the entire data set that it is fit on, penalizing models that have an un-even fit across individual pieces of data. WAIC can be calculated by Gelman et al. (2014):

$$WAIC = -2(lppd - p_{WAIC}), \tag{8}$$

where *lppd* is the logpoint-wise predictive density, and pWAIC is a term that penalizes models with large numbers of parameters. The factor of -2 brings WAIC to be on the same scale as other information criteria. lppd is approximated using the posterior output of an MCMC chain by:

$$lppd = \sum log(E_{post} p(y_i|\theta)), \tag{9}$$

where the outer sum is over individual data points, and the inner term is the expectation of the likelihood over the entire posterior sample. This value is then corrected for the estimated number of parameters of the model by

$$p_{WAIC} = \sum var_{post} log(p(y_i|\theta)), \tag{10}$$

where the inner term is the variance of the likelihood over the entire posterior sample for each data point. This remaining term penalizes models that have uneven (i.e., high variance) fit across different data points, which may be an indication of over fitting.

To perform model selection, we can fit multiple potential models to the data and use WAIC to evaluate their predictive value, selecting the model with the smallest WAIC value as our chosen model.

For example, if the question of interest is whether or not animals use social transmission to acquire behaviors, we could fit two models, one where animals are assumed to use social information, and a second where they are assumed to only use asocial information. After fitting both models and calculating the WAIC for them we can assess which model has a better fit, and whether the animals are more likely to have used social information, or to have relied only on asocial learning.

One open question is how big does the WAIC difference between models need to be, in order to be considered indicative of a true preference for one model. There is no hard and fast rule, although the difference should be greater than the variation due to Monte-Carlo sampling often greater than 1, or in the case study presented below, greater than 5.

5. SIMULATED PERFORMANCE OF NBDA

To evaluate the expected reliability of NBDA, we performed a large-scale simulation study to understand under what conditions NBDA will accurately determine whether social or asocial information was being used to solve the task. In this study, we used a single model to generate the results of 1000 diffusion experiments, and used NBDA to infer the model used to generate each simulation. The accuracy of NBDA is then the likelihood that the model inferred by NBDA was the model used to generate the data.

Unless otherwise noted, each simulation followed the same design. We considered a population of ten animals who were given a novel foraging task (similar to Boogert et al., 2008, 2014). In the task each animal was required to learn how to get a piece of food out of a container (e.g., by removing a lid). As each animal solved the task (got the food out of the container) the container was replenished giving the other animals a chance to solve the task. Each experiment was run until each animal in the group had "solved" the novel task at least once. This process was repeated ten times with new foraging tasks with the same group of animals. Although we consider primarily novel foraging behaviors here, the framework presented above, and the results presented below, likely will also hold for animals learning a range of new behaviors.

The data for each experiment was generated by turning the hazard model above, into a generative model. For each simulations a model of learning was chosen (e.g., asocial learning without random effects, social learning with random effects), and parameter values for the model were drawn from our prior distribution (see **Table 2**). The models, including parameters and the distributions for each parameter are given in **Tables 1**, **2**. The distributions given in **Table 2** were also used as the prior distribution for performing Bayesian inference (see below). Individual-level effects were treated as a product of an underlying measurable property, η, and a rate term a or b. We assumed that η was normally distributed with mean 0.

We allowed individuals to use the social information provided on either a homogeneous network, or on a lesioned network. As in Equation (5), we defined a social network to be an association matrix A, whose elements a_{ij} represent the amount of influence (between 0 and 1) that individual i has over individual j. In the homogeneous network, all individuals had the same

TABLE 1 | Model parameters and the rate equation for each model used in the simulation study.

Model name	Parameters	Rate equation
Asocial	λ_0	$\lambda = exp(\lambda_0)$
Social	λ_0, s_0	$\lambda = exp(\lambda_0) + exp(s_0)S$
Asocial with random effects	λ_0, ϕ	$\lambda = exp(\lambda_0 + \phi_i) + exp(s_0)S$
Social with random effects	λ_0, s_0, ψ	$\lambda = exp(\lambda_0) + exp(s_0 + \psi_i)S$
Asocial with individual-level effects	λ, A	$\lambda = exp(\lambda_0 + A_i)$
Social with individual-level effects	λ_0, s_0, B	$\lambda = exp(\lambda_0) + exp(s_0 + B_i)S$
Linear social model	$\lambda_0, s_0, \phi, \psi$	$\lambda = exp(\lambda_0 + \phi_i) + exp(s_0 + \psi_i)S$
Diminishing returns social model	$\lambda_0, s_0, \phi, \psi$	$\lambda = exp(\lambda_0 + \phi_i) + exp(s_0 + \psi_i)\sqrt{S}$
Threshold social model	$\lambda_0, s_0, \phi, \psi$	$\lambda = exp(\lambda_0 + \phi_i) + exp(s_0 + \psi_i)sign(S)$

The parameters refer to the inclusion of the terms in the model described in Equations (1)–(5). λ_0 and s_0 are the baseline asocial and social learning rates, A and B represent inclusion of a individual level effect on asocial or social learning, and ϕ and ψ are random effects for asocial and social learning.

TABLE 2 | Distribution of model parameters for the simulation study.

Parameter	Distribution
λ_0	Uniform(−7, −5)
s_0	Uniform(−7, −5)
ϕ_i	Normal(0, 1)
ψ_i	Normal(0, 1)
a	Uniform(−1, 1)
b	Uniform(−1, 1)

These parameter distributions were also used as prior distributions for performing inference on each simulation.

influence over each other; $a_{ij} = 1$ for all i and j. In the lesioned network, the network was initialized the same way as the homogeneous network and then half of the network connections were removed, ($a_{ij} = 0$. Because there may be cases where researchers are not able to measure the network accurately, we examined three alternative, inaccurate social networks, which incorrectly assessed the value of 25, 50, or 75% of the network connections—setting a connection to 1 if it was 0, or to 0 if it was previously 1.

We considered three models of social learning. In all cases, we assumed that the social information was transmitted on a homogeneous network. In the *Linear* model, social information term was set to $s = ck$, where k is the number of animals who have already solved the task (c is a constant). In the *Diminishing Returns* model, social information was set to $s = c\sqrt{k}$, to model the fact that subsequent solvers may have a diminishing influence. The choice of the square-root function to model this process was arbitrary; preliminary simulations suggest that similarly shaped functions produce analogous results. In the *Threshold model*, social information was set to $s = cI$ where I is 1 if at least one other individual has solved the task, and 0 otherwise.

After each simulated experiment, NBDA was performed using TADA, with the assumption that there was no social network between individuals. We used WAIC to evaluate a number of alternative models and select the best model. Unless otherwise stated, we ran 1000 simulated experiments for each set of models, with different parameter values for each experiment.

In the first set of simulations we look at recovering the correct underlying model and parameter values for when learners use only asocial learning (with random effects), or asocial learning and social transmission (with random effects). In the next set of simulations we examined whether we could correctly infer the influence of individual-level variables on learning. In the last set of simulations, we also examined whether we could correctly infer the underlying model of social learning for each experiment.

5.1. Model and Parameter Recovery

To estimate our ability to recover the correct underlying model used to generate the data set, we simulated diffusion based on four models: the asocial, social, asocial with random effects, and social with random effects models. The performance of model recovery is given in **Figure 1**. Overall the statistical technique was able to determine whether or not a model uses asocial information or social information, but there was a high false positive rate for detecting the presence of random effects, shown by the large number of asocial models without random effects being inferred to be asocial models with random effects (**Figure 1A**), with the same holding true for social models (**Figure 1B**). However, even though this method occasionally infers the presence of random effects it is still able to distinguish between social and asocial models, e.g., data generated from a social model may be inferred to have been generated from a social model with random effects, but is unlikely to be inferred to have been generated from either an asocial model, or an asocial model with random effects. This suggests that it may appear that there is underlying variation in social and asocial learning ability, where no such variation exists.

We are also interested in whether or not we can correctly infer the underlying learning rates. We assess this question by looking at the social learning model without random effects. The inferred (median) asocial learning and social transmission rates compared to the true rates are given in **Figure 2**.

The performance of inferring the correct value of the random effects was substantially lower, although in most cases this method correctly inferred the relative ordering of the random effect values (i.e., which bird learned faster) but mis-estimated the absolute value of the random effect values. The technique's ability to recover the ordering (expressed by the within-experiment correlation between the inferred values and the true values) is fairly good, with over 85% of the time the Spearman correlation coefficient was higher than 0.9.

These findings suggest that researchers are safe in using NBDA to infer population average rates of asocial learning, and social transmission, and thus draw conclusions about the overall importance of each (the primary goal of NBDA), if the model is correctly specified (see below). However, we suggest that researchers should not take estimates of individual variability in asocial learning and social transmission too seriously, but are safe to use the technique to obtain rankings of individual abilities in these domains.

5.2. Individual-Level Effects

There has been recent interest in understanding which other traits that an individual possesses might correlate with asocial or social learning abilities (e.g., Boogert et al., 2006, 2008). Individual-level effects allow us to include the influence of these covariates in our model. We found that NBDA could correctly interpret the presence of correlates for social, or asocial information some of the time. We also found that the technique could reliably estimate the true value of the covariate; and find that for the individual-level asocial effects 94.7% of the time the true value is within our 95% likely interval, and for the social effects 95.3% of the time the true value is within our 95% likely interval. We do find a high false negative rate in inferring the presence of a covariate (see **Figure 3**; although this technique was able to distinguish between models that included social learning and those that did not).

These results may in part be due to the presence of covariates that have only a weak impact on learning. In the simulations the

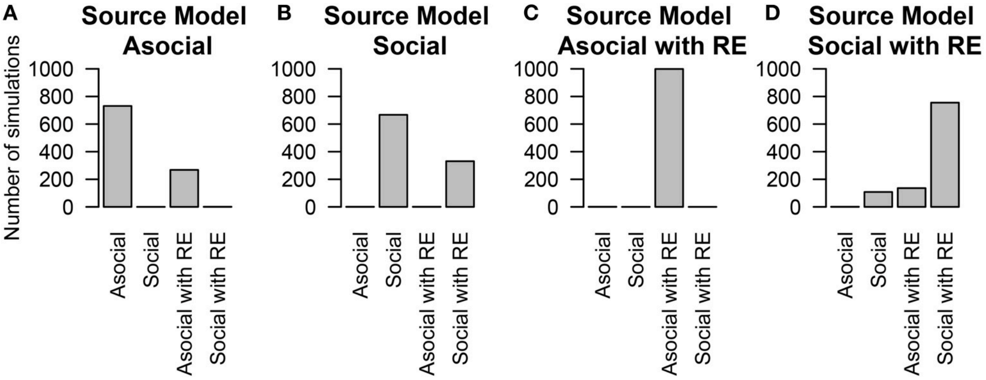

FIGURE 1 | The number of simulations each model was inferred to have been the source of the given data out of 1000 total simulations. The data was either generated from an **(A)** asocial model, **(B)** social model, **(C)** asocial model with random effects (RE), or **(D)** a social model with individual random effects (RE).

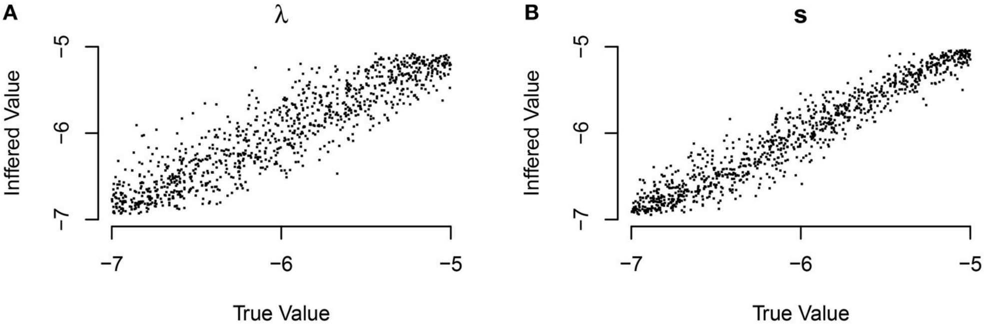

FIGURE 2 | Inferred model parameters compared to the true values of those parameters for the (A) asocial (λ) and (B) social (S) models. Perfect parameter recovery would be indicated by a straight line.

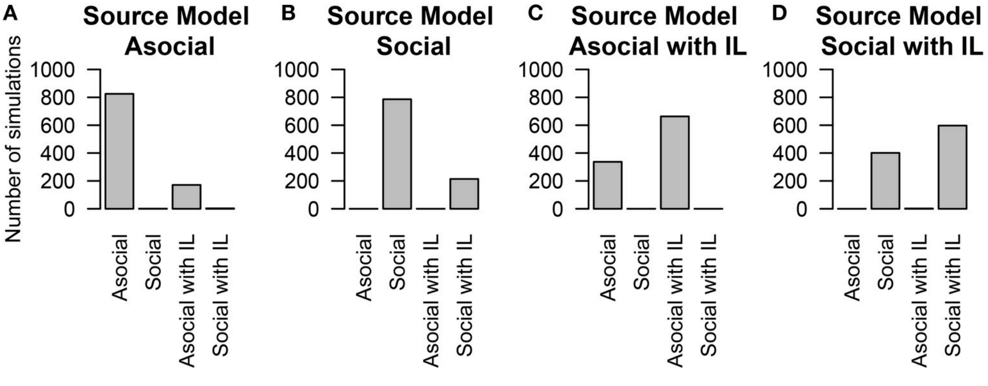

FIGURE 3 | The number of simulations each model was inferred to have been the source of the given data out of 1000 total simulations. The data was either generated from an **(A)** asocial model, **(B)** social model, **(C)** asocial model with individual level effects (IL), or **(D)** a social model with individual level effects (IL).

influence of the covariates varied between −1 and 1, meaning that some of the time, they could have a very small influence on social learning ability i.e., the parameter can be close to 0. We explored how the impact size of the covariate determined the likelihood of determining the correct model. We found that if the parameter had a large impact, most of the time the technique could recover its presence. However, if the parameter had a small impact, the technique had a high false negative rate.

Therefore, we advise that instead of just attempting to infer whether an individual-level effect is present or absent, researchers use the posterior distribution for a parameter to give credible intervals for how big or small the effect might be. Where these intervals are sufficiently small, conclusions can be drawn about the importance or lack of importance of that effect (Nakagawa and Cuthill, 2007).

5.3. Inaccurate Social Networks

We examined how NBDA would perform when diffusions followed a social network, and when researchers had incorrect knowledge of the social network. In these simulations, individuals had a baseline asocial and social learning rates, and their learning followed a lesioned social network.

We found that even when social learning followed an association network, the technique was able to determine the influence of social learning (**Figures 4B,C**) and of asocial learning (**Figure 4A**). The ability to distinguish between social and asocial learning was not substantially reduced when no knowledge of the network was known and it was assumed that transmission followed a homogeneous network.

To examine how performance may change as a function of network inaccuracy, we considered three alternative social networks, which had inaccurate values for either 25, 50, or 75% of the network connections. In all of these cases, even though the actual social network was not known, the technique was overwhelmingly able to interpret correctly that social transmission was at work (see **Figure 5**). When the network was accurate (25% inaccurate), the technique generally inferred that the social transmission followed the measured network. However, when the network was inaccurate (50 or 75% inaccurate), the technique inferred that social transmission followed a homogeneous network.

These results suggest that in many cases, analysis of a homogeneous network is warranted, but that if a homogeneous network is preferred over a non-homogeneous network it does not imply that social transmission was equal, but may simply imply that the measured non-homogeneous network was substantially different from the true network of associations.

5.4. Distinguishing Alternative Models of Social Learning

The last thing we tested was whether or not we could distinguish between alternative models of social learning. In these simulations, individuals had both individual and social-level random effects and social information was transmitted across a homogeneous network. We found that in general the technique could correctly recover the true underlying model at above-chance levels (except in the case of the Diminishing Returns model, **Figure 6C**), and had very good performance in determining whether or not a model was asocial, or social (**Figure 6**).

The above findings make it clear that when the true social transmission model is included in model selection, NBDA is successful in ruling out a model of purely asocial learning. However, it is more realistic that the model of social transmission will be mis-specified in some way, i.e., at best our model with be a good approximation of the social transmission process. In most cases the linear model is assumed.

These results show that even if the underlying model was not linear, the technique could still detect the influence of social information, at least some of the time. The success rate was much

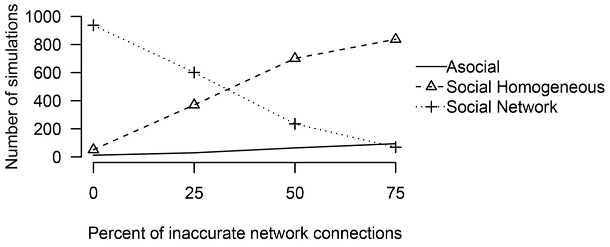

FIGURE 5 | The number of simulations either an asocial, social, or a social model with a non-trivial social network, was inferred to have been the source of the given data out of 1000 total simulations, varying the percent of inaccurate network connections.

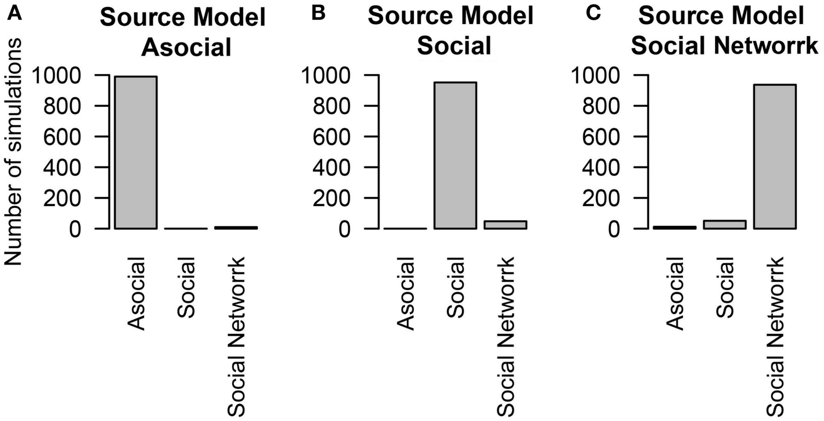

FIGURE 4 | The number of simulations each model was inferred to have been the source of the given data out of 1000 total simulations. The data was either generated from different models of diffusion across a social network, either through an **(A)** asocial model, **(B)** social model (i.e., homogeneous network), **(C)** social model with a non-trivial social network. Details of the social network structure can be found in Section 5.

higher when the true model was closer to linear, than when it was not. Furthermore, in such cases, the estimated learning parameter was generally lower than the true value of the parameter. These results suggest that if we suspect a linear model to be a poor approximation, then we should still trust the inference that social transmission is occurring. However, we should take estimates of the strength of social transmission to be conservative and understand that a negative result for social transmission may indicate that our social transmission model does not approximate the underlying process very well.

To estimate whether considering a linear model alone is sufficient for inferring the presence or absence of social information, we re-analyzed these simulations considering only the Asocial and Linear social learning models. Even if the underlying model was not linear, the technique could still detect the influence of social information, however the social learning parameter was generally lower than the true value of the parameter. **Figure 6** gives the results when all four models are considered. In contrast, **Figure 7** gives the results when our choice of models were restricted to an asocial and a linear social model.

Performance was worse when the influence of social information was smallest; particularly in the case of the threshold model, which will be behaviorally similar to the asocial learning model. In contrast, performance was best in the linear social learning model, where the vast majority of the time, we was able to correctly infer the correct underlying model.

6. GENERAL DISCUSSION

In this paper we have built on a growing literature using NBDA to infer under what conditions social information underlies the spread of novel behaviors. We present a unified framework for NBDA in the context of Time to Acquisition Diffusion Analysis (TADA). We analyzed the performance of NBDA in

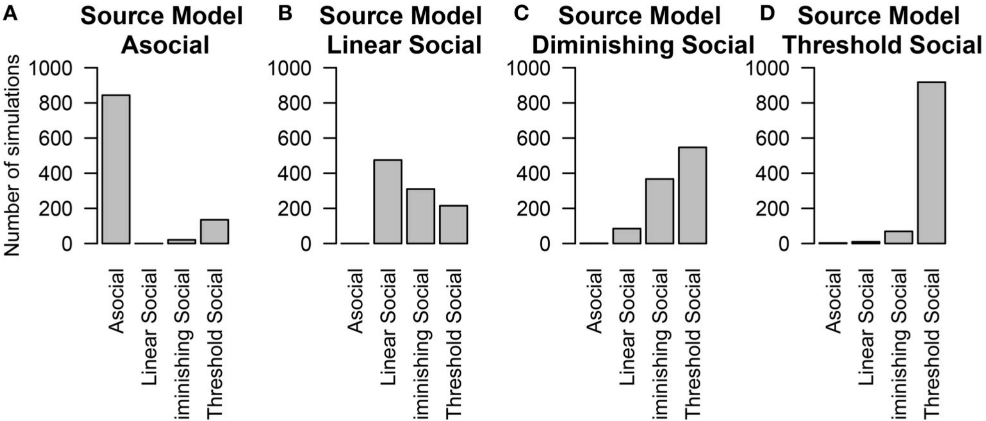

FIGURE 6 | The number of simulations each model was inferred to have been the source of the given data out of 1000 total simulations. The data was either generated from different models of social learning, either through an **(A)** asocial model, **(B)** linear social learning model, **(C)** diminishing returns social learning model, or **(D)** a threshold social learning model. Details of each model are provided in **Table 1**.

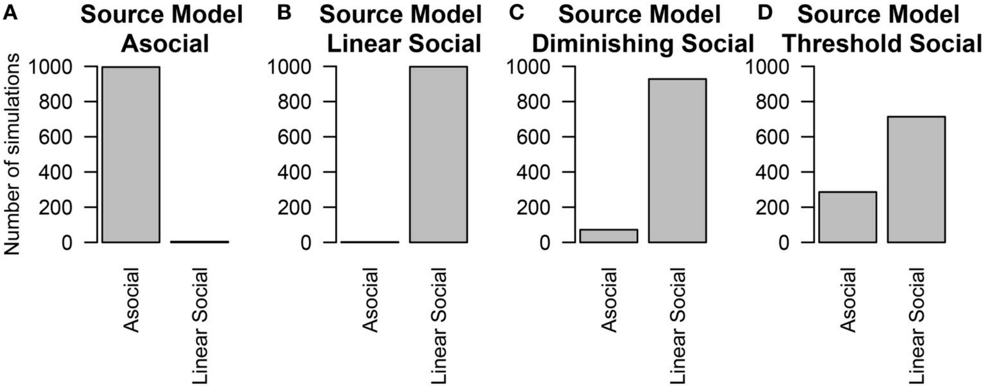

FIGURE 7 | The number of simulations each model was inferred to have been the source of the given data out of 1000 total simulations. Only the asocial model or the linear social learning model were considered. The data was either generated from either an **(A)** asocial model, **(B)** linear social learning model, **(C)** diminishing returns social learning model, or **(D)** a threshold social learning model.

this context on a series of simulated experiments and found that NBDA was robust to inferring the presence of social information in most contexts, could infer the influence of random effects, and in at least some cases, can distinguish between different patterns of social learning. We also find that NBDA is robust to errors in measuring the social network behaviors diffuse across, although in some cases if a network is poorly estimated the technique will infer that behaviors diffused across a homogeneous network. In this paper we solely analyzed simulated data, for a case study for applying this methodology to experimental data see Whalen et al., (under review), or Whalen (2016).

These findings offer new insights into our ability to infer when social transmission, as opposed to asocial learning, can account for the spread of a novel behavior. However, these findings are not without their own caveats. As part of our simulation study, we found that although we could recover the correct parameter values for population-wide effects, we often underestimated the influence of random effects. Our performance in determining the presence of external correlates for learning was better, but only when the influence of these correlates was strong. We also found that we had a high error rate in determining which model of social learning was used to generate the data. Our overall accuracy of determining if social learning was used was high, but our accuracy in estimating how it was used was much lower.

These findings lead us to suggest three new recommendations for the use of NBDA. (1) When fitting models to data where multiple diffusions are run on the same individuals, researchers should fit models with random effects to account for repeated observations on individuals, but expect the estimated magnitudes of the random effects to differ from the true underlying values. (2) Individual-level effects on learning are able to be inferred, but researchers should rely on credible intervals as providing the plausible magnitude of the effect, rather than using model selection to infer its presence/absence. (3) Researchers should focus on a single, likely model of social learning to detect the presence of social information. Our results suggest the standard NBDA model used thus far is robust to fairly major departures from the assumptions of linearity, so we suggest this is used in the absence of any reason to prefer a different model. If the use of social information is well established for the task, more detailed models of learning can be used, although a large amount of data may be required to determine the underlying shape of the model.

Unlike early versions of NBDA (Franz and Nunn, 2009; Hoppitt et al., 2010), in this paper we present NBDA in the context of a Bayesian methodology, which allows us easily to include the influence of random effects. However, while most previous studies using Bayesian NBDA have used Reversible Jump Markov Chain Monte Carlo methods to perform model selection (Boogert et al., 2014; Nightingale et al., 2014), we suggest using an information criteria approach. While RJMCMC, and other methods of approximating a posterior over models are an alternative way of performing model selection, these methods are computationally difficult to perform especially when models have a large number of parameters, as occurs when including individual-level random effects. The influence of random effects is a driving factor for the development and use of a Bayesian version of NBDA, since including random effects allows us to model cases where the same individuals take part in multiple diffusion, and reduces the impact of random effects (particularly in asocial learning) as a confound in inferring the presence of social information. Consequently, we believe that using a WAIC-based approach provides an ideal tradeoff between tractability in performing the analysis, and the advantages conferred by inclusion of random effects. We recommend using Bayesian NBDA with WAIC use for examining future diffusion experiments, and believe it can give us insights into how other animals learn, and how that might influence the development of animal and human culture.

AUTHOR CONTRIBUTIONS

AW, WH designed, carried out, and drafted this contribution together. The simulations were coded and executed by AW.

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Social Network Analysis and Nutritional Behavior: An Integrated Modeling Approach

Alistair M. Senior [1, 2*†], ***Mathieu Lihoreau*** [3, 4†], ***Camille Buhl*** [5], ***David Raubenheimer*** [1, 6, 7] ***and Stephen J. Simpson*** [1, 7]

[1] Charles Perkins Centre, The University of Sydney, Sydney, NSW, Australia, [2] School of Mathematics and Statistics, The University of Sydney, Sydney, NSW, Australia, [3] Centre National de la Recherche Scientifique, Centre de Recherches sur la Cognition Animale, Toulouse, France, [4] Centre de Recherches sur la Cognition Animale, Université Paul Sabatier, Toulouse, France, [5] School of Agriculture, Food and Wine, The University of Adelaide, Adelaide, SA, Australia, [6] Faculty of Veterinary Science, The University of Sydney, Sydney, NSW, Australia, [7] School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW, Australia

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France
Christophe Bousquet,
University of Zurich, Switzerland

****Correspondence:***
Alistair M. Senior
alistair.senior@sydney.edu.au

† These authors have contributed equally to this work.

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Animals have evolved complex foraging strategies to obtain a nutritionally balanced diet and associated fitness benefits. Recent research combining state-space models of nutritional geometry with agent-based models (ABMs), show how nutrient targeted foraging behavior can also influence animal social interactions, ultimately affecting collective dynamics and group structures. Here we demonstrate how social network analyses can be integrated into such a modeling framework and provide a practical analytical tool to compare experimental results with theory. We illustrate our approach by examining the case of nutritionally mediated dominance hierarchies. First we show how nutritionally explicit ABMs that simulate the emergence of dominance hierarchies can be used to generate social networks. Importantly the structural properties of our simulated networks bear similarities to dominance networks of real animals (where conflicts are not always directly related to nutrition). Finally, we demonstrate how metrics from social network analyses can be used to predict the fitness of agents in these simulated competitive environments. Our results highlight the potential importance of nutritional mechanisms in shaping dominance interactions in a wide range of social and ecological contexts. Nutrition likely influences social interactions in many species, and yet a theoretical framework for exploring these effects is currently lacking. Combining social network analyses with computational models from nutritional ecology may bridge this divide, representing a pragmatic approach for generating theoretical predictions for nutritional experiments.

Keywords: animal behavior, dominance hierarchy, geometric framework, nutrition, nutritional geometry, social networks

INTRODUCTION

Animals, from insects to human, have evolved sophisticated foraging strategies, which allow them to acquire nutrients in amounts and balances that maximize fitness (Simpson and Raubenheimer, 2012; Senior et al., 2015b). Over recent years, research in nutritional ecology has begun to reveal how these individual strategies can influence the ways animals interact within groups and populations, with far reaching consequences for collective dynamics and social structures (Simpson et al., 2006; Eggert et al., 2008; Salomon et al., 2008; Dussutour and Simpson, 2009; Bazazi et al., 2011; Lihoreau et al., 2015; Machovsky-Capuska et al., 2015). A striking example is the mass migrations of swarming crickets and locusts, where food depletion increases cannibalistic interactions and triggers the onset of the coordinated migration of tens of thousands of insects marching together in search of protein and mineral salts (Simpson et al., 2006; Bazazi et al., 2011).

Nutrient regulation strategies and their social consequences can be studied within a single modeling framework, which integrates state-space models used in nutritional geometry studies and agent-based models (ABMs) used in collective animal behavior studies (Lihoreau et al., 2014, 2015). In nutritional geometry, individuals, foods and their interactions are represented in a single nutritional space delimited by two or more nutrients (see examples in **Figures 1A,B**; Simpson and Raubenheimer, 1993, 2012; Simpson et al., 2015). The challenge for an individual is to eat the available foods so as to regulate its acquisition of nutrients and reach a nutritional state (NS) that maximizes fitness, known as the intake target (see examples in **Figures 1A,B**). Within a group or a population, these individual decisions may be complicated by social and competitive interactions, potentially creating conflicts over nutrient acquisition among the different foragers. Implementations of such nutritional geometry focused ABMs, in which multiple individuals simultaneously attempt to regulate their nutrient balance, illustrate how these simple nutritional behaviors can critically affect a range of social interactions and social structures across group types, species and ecological contexts (Lihoreau et al., 2014, 2015; Senior et al., 2015a).

Perhaps one of the best-documented examples of nutritionally mediated social structures are dominance hierarchies, where experimental studies point toward a direct role of diet in determining individual dominance and subordinate statuses (Baker et al., 1981; Whitten, 1983; McCarthy et al., 1992; Eggert et al., 2008; Salomon et al., 2008; Stears et al., 2014; Wright and Robbins, 2014). In social spiders (*Stegodyphus* sp.), for instance, the largest females of the colony tend to monopolize prey high in lipids through contest competition and thus become breeders, whereas smaller individuals that are deprived of lipids act as helpers (Rypstra, 1993; Whitehouse and Lubin, 1999; Salomon et al., 2008). In these cooperatively breeding groups, differential nutrition triggers significant skews in body size, with reproduction limited to just one or two larger females (Rypstra, 1993; Ulbrich and Henschel, 1999; Whitehouse and Lubin, 2005). Nutritional geometry focused ABMs, such as those outlined above, succinctly capture how contest competition over limited nutrients can lead to clear and stable dominance hierarchies where fitness is highly skewed toward a few individuals (Lihoreau et al., 2014; Senior et al., 2015a). In these models, access to foods is limited and individuals must engage in contests to gain a meal. The group is initially homogeneous, and early contests for access to foods have stochastic outcomes. However, after a few "contested meals," small differences in the NS of individuals can emerge purely by chance (Senior et al., 2015a). Given the assumption that better nourished individuals outperform more poorly nourished competitors in future contests, positive feedback amplifies initial small differences in NS into a hierarchy where a few individuals monopolize nutrients, thereby gaining considerable fitness benefits. Similar mechanisms have been observed in animal dominance hierarchies arising from various types of non-nutritionally related conflicts, and are called "winner effects" (Dugatkin, 1997; Franz et al., 2015; Kura et al., 2015).

So far these models have explored the effects of the nutritional environment on individual fitness (as measured by their NS) and its variance within groups or populations. Less studied however, but of fundamental importance, is the behavior of individuals, the dynamics of their interactions and the associated consequences for social structures. Social network analyses, which are increasingly used in behavioral studies to characterize pairwise interactions between all members of a group or population (Krause et al., 2007; Croft et al., 2008; Sih et al., 2009; Sueur et al., 2011; Pinter-Wollman et al., 2013), constitute a well-developed analytical framework with which to explore the role of nutrition in mediating social interactions and their evolution. This approach is particularly powerful when it comes to characterizing complex dominance relationships in animal groups (e.g., identifying dominant individuals and how they interact with other group members based on traits such as kinship, age, sex or previous experience), and understanding the processes that underlie the network structures and dynamics (Croft et al., 2008; Shizuka and McDonald, 2012; Nandi et al., 2014).

Here we argue that social network analyses can bring fundamental new insights into research on nutritional behavior, and the consequences of these behaviors for group dynamics. We demonstrate this concept using the well-known example of nutritionally mediated dominance hierarchies. We first show that the networks generated by simple nutritional models simulating the emergence of dominance bear striking structural similarities to those networks of dominance hierarchies observed in animal groups across contexts (i.e., conflicts not necessarily related to food access). We then go on to show that metrics from social network analyses predict the future fitness of agents in these simulated competitive environments. Our analyses demonstrate how network analysis of data from these nutritional models can be used to form new empirically testable predictions for studies on social groups, bridging the gap between theoretical and experimental data.

METHODS

Agent Based Model

An overview of our ABM's process is given in **Figure 1C**. The basal model has been previously defined in Lihoreau et al. (2014) and a detailed description (as recommended for ABMs; Grimm et al., 2006, 2010) is available in Senior et al. (2015a). The complete code, written in NetLogo version 5.1.0 (Wilensky, 1999), is available in the Supplementary File S2.

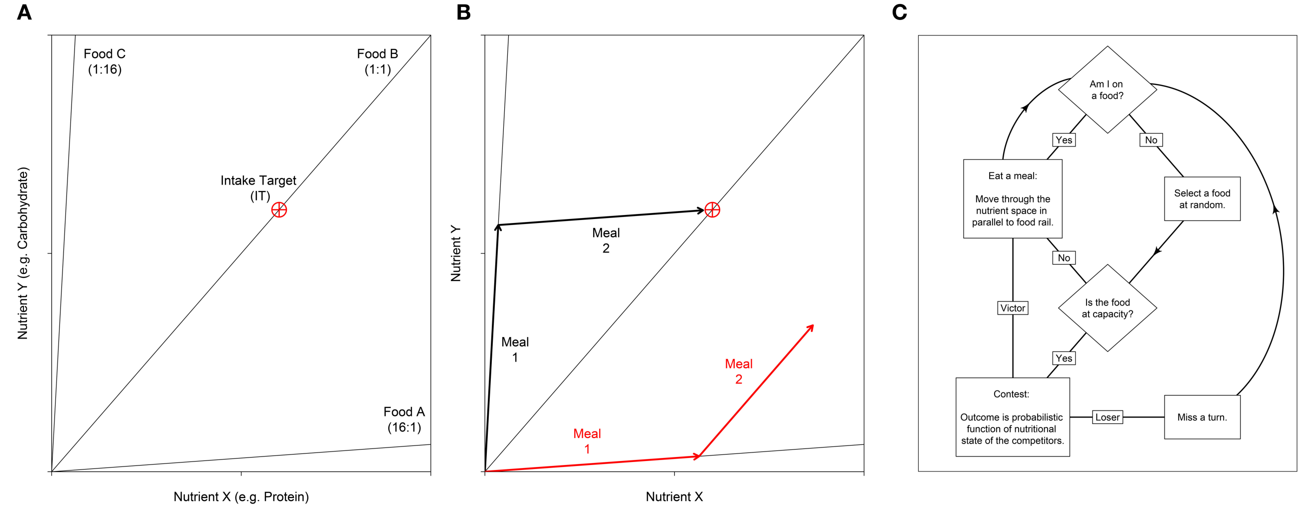

FIGURE 1 | (A) Nutritional geometry used to model the nutrient space available for two nutrients; e.g., the macronutrients protein and carbohydrate may be represented on the *x*- and *y*- axis respectively. Foods are represented by food rails, which project through the nutrient space with a slope denoting the nutrient content for the two foods modeled. In this example the environment contains three foods. Food A is high in nutrient X relative to nutrient Y (ratio = 16:1), food B is balanced for the two nutrients and food C is low in nutrient X relative to Y (ratio = 1:16). The optimal nutritional state for an individual is represented by the Intake Target (IT), which is shown as a red crosshair. **(B)** An individual's position in the nutrient space is its (*x*, *y*) coordinate, which moves as the individual eats. Here we show how two different individuals move as they eat two meals. Individual 1 (black) first eats food C then food A. With respect to the IT, these two foods are nutritionally complementary and as such the individual can get close to the IT. In contrast, individual 2 (red) has first eaten food A, then food B. These two foods are not complementary, and as such the individual cannot reach the IT. Given that the IT is the optimal nutritional state, individual 2 would have a lower fitness that individual 1. **(C)** An overview of the sequence of events in the agent-based model. Individuals are processed in a random sequence. Complete code is available in Supplementary File S2. A full model description is given by Senior et al. (2015a).

The ABM incorporates principles of nutritional geometry as described in **Figures 1A,B**. For simplicity we consider an environment containing just two nutrients (nutrients X and Y) in a Cartesian (*x*, *y*) coordinate system termed the "nutrient space." Foods are represented as radials at angles determined by the balance of the nutrients they contain. An individual's (*x*, *y*) position in the nutrient space is their NS, which moves as they eat the foods that are available. At any one time only a single food can be eaten, thus individuals move their NS in parallel to the food rail that constitutes the food consumed. A single (*x*, *y*) coordinate, the IT, represents the point in the nutrient space that is an individual's optimal state. As such, when an individual's NS reaches the IT, fitness is maximized. Here we assume that fitness declines as the Euclidean distance between the NS and the IT increases (see Equation 6 in Senior et al., 2015a).

All individuals are initiated with the same NS (0, 0), and are given a fixed number of iterations, or "meals," to reach the IT. Each food has a different nutritional composition, and these foods may be eaten in a number of combinations in order to reach the IT (**Figures 1A,B**). On each iteration, individuals attempt to eat one of the foods in the environment. However, each food has an upper limit and can thus only support a limited number of foragers. If individuals select a food that is already at this limit, they must first displace a randomly selected competitor via a dominance interaction. We began by exploring scenarios where the capacity of foods to support individuals, and thus the intensity of contest competition, was varied (manipulated via the "competition intensity" parameter *c*). Although we later focus solely on analyses of networks generated in scenarios where competition is intense (discussed further below). All data presented in the main text come from an environment containing three different foods (equivalent to that in **Figure 1A**). In a previous analysis of this model such a three-food environment, composed of one balanced food (i.e., individuals can reach their IT by eating only this food) and two imbalanced but complementary foods (i.e., individuals can reach their IT by mixing their intake of the two foods), produced results indicative of a wide range of environments (i.e., containing combinations of foods with different levels of nutritional complementarity; Senior et al., 2015a). Additional explorations of the model with only two imbalanced foods (equivalent to that in **Figure 1A** but without food B) yielded qualitatively identical results. These analyses are presented in the Supplementary Materials (Figures S1–S3).

In the model, the probability of an individual defeating another in a contest is a function of the NS of the two, as given by Equation (1):

$$Q_{ij} = \frac{1}{1 + e^{-\eta(F_i - F_j)}} = 1 - Q_{ji}, \tag{1}$$

where Q_{ij} is the probability of the *i*th individual defeating the *j*th, *e* is the natural exponent, F_i and F_j is the fitness of the two individuals, and η is a constant that scales how the difference in fitness between the two individuals governs the outcome of the contest (here fixed at 25; see Senior et al., 2015a). Accordingly, an individual with a NS closer to the IT is more likely to defeat a competitor with a NS further away. Contests between individuals with NSs close to one another have highly stochastic outcomes (this model of contest competition is based on that published by Bonabeau et al., 1996).

In previous studies involving nutritional geometry focused ABMs, the outcomes of individual interactions, have been largely overlooked. Rather, the analyses focused on the fitness and NSs of individuals after thousands of interactions, and in turn the effects that these interactions have on the evolution of nutritional strategies (e.g., Senior et al., 2015a). We here modified the model to record the outcomes of each specific individual contest at a number of different time steps with the aim of characterizing the dynamics of network growth and structure.

Network Analyses

For each simulation of the model, we constructed a time series of (after 1, 3, 5, 7, 10, 15, and 20 meals) "contest matrices." In these matrices each row and column represents an individual, and the cells in a specific row give the total number of contests that a specific individual (given by that row) won against each other group member (in each column). Contest matrices were used to build a time series of weighted and directional networks (one for each time point), where each node represents an individual and edges represent contests between two individuals. The size of the node represents the current fitness of the individual relative to the rest of the group. The directionality of the edge denotes the outcome of the contest (arrow points toward the loser), and the weight gives the total count of contests between those individuals at that time point (i.e., previous contests are not "forgotten"). We began by using simple network visualization techniques for small, easily visualizable, social groups of seven individuals. Network graphs were implemented with the "plot.igraph" function in the *igraph* package (Csardi and Nepusz, 2006) for *R* version 3.2.1 (R Development Core Team, 2015), to demonstrate how the network and individual fitness (a function of NS), co-vary over time in different nutritional environments.

In studies of animal dominance, deconstructive approaches where networks are separated into their constitutive triads, or "motifs," are increasingly popular tools for understanding social network structure (Shizuka and McDonald, 2012; Pinter-Wollman et al., 2013). We used this approach to compare the structures of dominance networks generated via nutritional mechanisms in our model with the typical structure of published animal dominance networks (based on the comparative results of McDonald and Shizuka, 2013). We ran replicates of the model assuming an environment where foods had a very low capacity to support individuals (i.e., where competition was intense and contests over foods frequent), and also using larger more complex social groups of 20 individuals (a group size more comparable to that of most published animal networks; McDonald and Shizuka, 2013). In these later analyses we focus solely on a food-limited environment, where competition intensity is high ($c = 0.8$). We restrict our analyses to these environments because, where foods are more abundant and competition intensity is weaker, between-agent variance in fitness is low, and strong dominance hierarchies/meaningful social structures do not arise (see Lihoreau et al., 2014).

The "contest matrices" produced by these models were converted to binary "outcome matrices," where for any given pair of individuals the dominant is that which won the majority of contests. We also allowed for draws, or "mutual" relationships (i.e., instances where individuals won equal number of contests against one another, which were also coded as 1). Triads can take one of 16 different configurations, ranging from null triads (no interactions) to completely reciprocal relations between all three nodes, and we refer to these triads according to the Mutual Asymmetric Null (MAN) system (Holland and Leinhardt, 1970, 1976). We used the "triad.census" function in the *R* package *statnet* (Handcock et al., 2008, 2015) to get counts of each type of triad in each network. We also simulated 1000 equivalent random matrices (using the "rguman" function in *statnet*), to estimate the difference in occurrence of each triad type between our ABM-derived networks and random networks with the same number of nodes, edges and null dyads (similar to the method of McDonald and Shizuka, 2013, although they did not include draws). Whilst it is clear that differences between our networks and random networks are to be expected (e.g., we know that nutritionally derived networks are based on winner effects), we were primarily interested to see whether our simulated networks differ from random expectations in similar ways to published animal dominance networks. We also calculated the triangle transitivity (t_{tri}) of networks, a statistic that denotes the "orderliness" of the group where 0 indicates a completely non-linear group (equivalent to a random network) and 1 a perfectly ordered linear hierarchy (McDonald and Shizuka, 2013). We calculated t_{tri} following the method described in Appendix 2 of Shizuka and McDonald (2012).

Finally, we assessed whether individual network statistics applied to dominance networks can be used to predict the final fitness of individuals in a social group (again using 20 individuals). To do this, we generated a weighted directional network at a number of time points as above (based on contest matrices and again where competition was intense). We calculated the (normalized) closeness of each individual (node) within the network at a given time with the "closeness_w" function in the *R* package *tnet* (Opsahl, 2009). In weighted directed networks such as which we generated, the closeness of a node is a function of: (1) the direction between two nodes (implying that the shortest path between nodes i and j is not necessarily equal to the shortest path between nodes j and i), (2) the number of edges a node has, and (3) the weight of those edges (Opsahl et al., 2010). The tradeoff between the influence that these last two characteristics have on closeness is governed by the tuning parameter α (Opsahl et al., 2010). Where α is zero, only the number of edges influence node closeness; where α is between 0 and 1 both the weight and the number of edges positively influence closeness; where $\alpha = 1$ closeness depends solely on the sum of the weight of edge weights; and where $\alpha > 1$ higher weights positively influence closeness and increasing numbers of edges reduce closeness (Opsahl et al., 2010). We explored closeness calculated via a number of different α-values (0, 0.5, 1, 1.5, and 2) and their biological interpretation is discussed further in the results. We then compared individual closeness to other predictors of final fitness, using linear regression implemented with the "lm" function in the *base* package in *R*. In these models the response was the fitness of the individual after 20 meals logit transformed for model fitting (fitness is bound at 0 and 1 in our models; Warton and Hui, 2010), and back-transformed for plotting.

RESULTS

Figure 2 shows examples of the development of three dominance networks over time in different three-food environments (i.e., identical to **Figure 1A**) where foods are either abundant, moderately available or scarce. The same analyses for two-food environments (i.e., foods A and C in **Figure 1A**) yielded qualitatively similar results (Figures S1–S3).

Where foods are more abundant, there are relatively few contests to gain access to foods. As a consequence the network is poorly connected even after 20 meals (**Figure 2A**). However, as food availability decreases, individuals must engage in contests to gain food access and networks become more connected (**Figures 2B,C**). A direct consequence of this is the increase of variance in the relative fitness of individuals within the group (variance in the size of the nodes in the network; **Figures 2B,C**). In the three environments all group members initially have the same fitness, but where food is less available variance in fitness gradually emerges and increases as contests and meals accumulate. For instance, in the low food environment, individual 4 has already lost multiple contests after only 10 meals (**Figure 2C**). After 20 simulated meals, this individual has lost a large number of contests, has the lowest fitness and a clear fitness skew has emerged. In this environment, individual 6 is the fittest, and the difference between individuals 4 and 6 is large (individual 4 is only 26.67% as fit as individual 6; **Figure 2C**). In contrast, where foods are relatively abundant, and networks are less connected (i.e., fewer contests), the difference between the fittest and least fit individuals in the group is less pronounced (the least fit individual is only 50.77% as fit as the fittest; **Figure 2A**).

There are 16 possible configurations of triads in networks that are both directional and contain mutual ties (**Figure 3**). In our simulated dominance networks in competition-intense environments ($c = 0.8$), the most frequent types of triads were 012, 030T, 021U, 021D, and 021C (**Table 1**, see also **Figure 3** for visualizations of these triad types). However, these results are most informative when compared to "null expectations" derived from random networks. **Figure 3** displays the difference between the triad census (% of each type of triad) of ABM derived networks and random networks. There were on average 4.52 more 021U (i.e., the difference in the % of 021U triads in ABM networks and random networks was 4.52), 3.34 more 021D, and 3.01 more 030T triads than would be expected purely by chance. In addition, there were on average 7.47 less

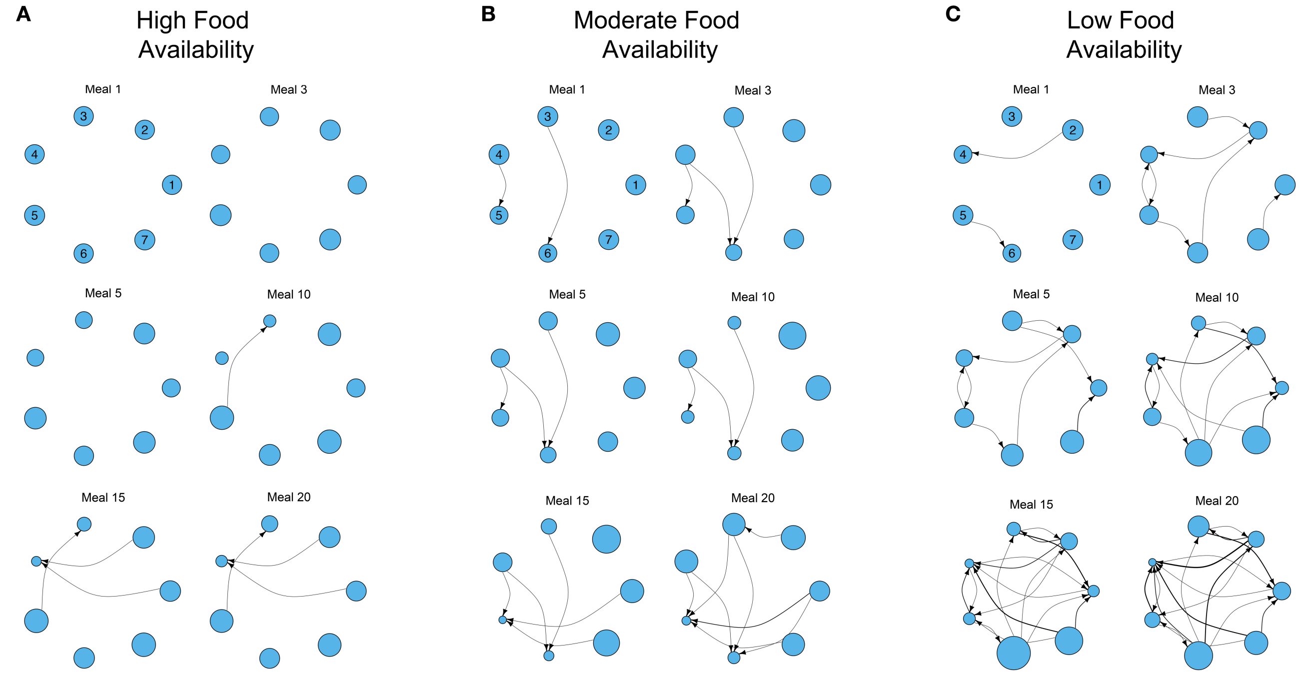

FIGURE 2 | Examples of the development of three different dominance networks in three different nutritional environments containing three foods (identical to Figure 1A) at (A) high, (B) moderate, and (C) low food availability after 1, 3, 5, 10, 15, and 20 meals, in groups of 7 individuals. Each network is directional and weighted. Each node represents 1 of 7 individuals, and the plotted position of each individual remains constant across meals in each environment (individual identities are given for meal 1). Edges represent contests, with the direction of the edge denoting the victor of the contest and the loser (recipient). Edges are weighted by the number of contests. The size of each node represents individual fitness relative to the rest of the group (larger nodes denote fitter individuals, that have nutritional state closer to the IT). The degree of food availability equates to a "competition intensity" (*c*) of 0.4, 0.6, and 0.8, as described in Senior et al. (2015a). The script is available in Supplementary File S2.

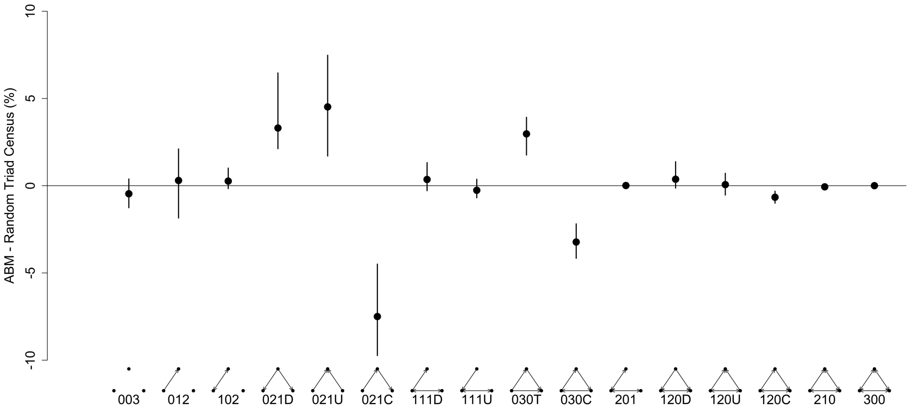

FIGURE 3 | Differences in the representation (%) of triad types between networks generated from the agent-based model and random networks with similar properties (same number of nodes, edges and null dyads) in a three-food environment (identical to Figure 1A). We created 10 different networks for groups of 20 individuals using our model, with a high level of "competition intensity" ($c = 0.8$) and after 20 meals. For each network we calculated the difference between itself and 1000 randomly generated networks, and took the mean of these 1000 differences. These results give the mean of the 10 sets of mean differences (black dots) and the 0.025–0.975 quantiles of these 10 (black bars). Triads are labeled according to the MAN labeling system (Holland and Leinhardt, 1970, 1976).

021C (even though among the most common type of triads in our simulated networks; **Table 1**) and 3.20 less 030C triads in the simulated dominance networks than would be expected in a random network (**Figure 3**; note that 0.95 quantiles for these differences exclude 0). The mean t_{tri} of these networks was 0.77.

To assess whether network metrics could be used to estimate an individual's performance and hierarchical rank, we examined how well closeness centrality after 5, 7, 10, and 15 meals predicted future fitness after 20 meals in environments where competition was intense, and between-individual variance in fitness high. We first explored how the tuning parameter α influenced the power of closeness to predict future fitness. At most time points (meals), linear models fitting closeness with $\alpha > 0$ had higher R^2 than those with $\alpha = 0$ (**Table 2**). In addition, at early time points α-values of 0.5, 1, and 1.5 tended to have better fit than $\alpha = 2$. These findings indicate that both the number of conspecifics an individual has defeated in contests (i.e., number of edges), and the number of times it does so (i.e., weight of edges) influence future fitness (as opposed to only one of these factors being of relevance). For instance a strategy whereby an individual dominates one or two conspecifics a large number of times (large α) early on in the simulation, may not be better than dominating all other conspecifics in a similar number of contests ($\alpha \sim 1$).

Within our ABM, mechanisms of winner effects based on current NS (fitness) operate. Thus, in theory the best predictor of final position in the dominance hierarchy at any given time point should be current fitness. Accordingly, closeness (calculated with any α-value) did not appear to be as good a predictor of future fitness as current fitness (i.e., R^2 for models fitting closeness were consistently lower than those fitting current fitness; **Table 2**). However, closeness values did correlate strongly with future fitness (**Table 2** and **Figure 4**). Importantly, at earlier time points, between-individual variance in closeness was much greater than between-individual variance in current fitness (**Figures 4A–C**). Thus, closeness is a valuable predictor of future fitness in experimental studies on nutritionally mediated dominance hierarchies, as it is easy to quantify from behavioral data and less sensitive to measurement inaccuracies that NS.

DISCUSSION

We combined social network analyses with ABMs of nutritional geometry to generate new insights into the role that nutrition can play in the formation of dominance hierarchies in animal groups. We found that network graphs based on contest matrices constitute succinct tools for characterizing the emergence of dominance hierarchies and for comparing those hierarchies across simulated nutritional environments and through time. As a well-established and widely implemented analytic framework (Krause et al., 2007; Croft et al., 2008; Sih et al., 2009; Sueur et al., 2011; Pinter-Wollman et al., 2013), social network analysis thus represents a promising tool for investigating the role of nutrition in mediating social interactions in animal groups.

One of the main advantages of nutritional geometry focused ABMs is that their predictions can also be tested using established experimental protocols from the same framework (Simpson and Raubenheimer, 1993, 2012; Simpson et al., 2015). For instance, our models predict a relationship between current and future NS of individual animals, and consequently their future position in a dominance hierarchy as well as their fitness relative to the rest of group (Lihoreau et al., 2014). A specific difficulty of evaluating such predictions is the logistical problem of quantifying NS/fitness in social groups that are relatively "young" (recently formed groups where few social interactions have occurred). Specifically, between-individual variance in fitness will likely be low at early stages (**Figures 2**, **4**), making accurate quantifications of the relative state of individuals difficult. In addition, without manipulative or lethal approaches, quantifying between-individual differences in NS is hard. Here, we have shown that simple measures of network centrality, such as closeness, can be used as good predictors of future

TABLE 1 | Mean (and standard deviation, SD) counts of each type of triad based on the triad censuses of 10 networks generated by our agent-based model with a high level of "competition intensity" ($c = 0.8$) and after 20 meals.

	Triad Type															
	003	**012**	**102**	**021D**	**021U**	**021C**	**111D**	**111U**	**030T**	**030C**	**201**	**120D**	**120U**	**120C**	**210**	**300**
Mean	78.70	331.4	22.90	145.6	159.0	129.8	29.50	22.40	176.5	10.80	1.800	12.40	8.900	8.800	1.400	0.100
SD	15.35	14.93	11.05	18.87	23.39	17.13	10.05	6.950	27.18	5.490	1.320	6.700	5.320	4.370	1.430	0.320

The 16 possible triad types are labeled according to the MAN system (Holland and Leinhardt, 1970, 1976), and visualizations of each type are given in ***Figure 3****.*

TABLE 2 | R^2 from linear models estimating fitness after 20 meals (logit transformed) as a function of closeness and fitness at 5, 7, 10, and 15 meals when there is a high level of "competition intensity" ($c = 0.8$).

Meals	**Closeness**					**Current fitness**
	$\alpha = 0$	$\alpha = 0.5$	$\alpha = 1$	$\alpha = 1.5$	$\alpha = 2$	
5	0.281	0.297	0.311	0.319	0.314	0.631
7	0.421	0.433	0.437	0.429	0.404	0.837
10	0.528	0.537	0.536	0.516	0.473	0.884
15	0.590	0.629	0.666	0.693	0.710	0.971

Closeness was calculated using α of 0, 0.5, 1, 1.5, and 2 (see main text), and we see how these values affect the power of closeness to predict final fitness. Higher R^2 is indicative of better model fit.

fitness. These global network metrics, among others, are easier to experimentally quantify than NS or fitness, and can be calculated based on behavioral data gleaned from simple group observations. A side note is that integrating weights in to analyses of the dominance networks that we generate here is of some importance, having consequences for the biological interpretation of the formation of a dominance hierarchy. However, accurately assessing the importance to ascribe to weights in calculations of closeness (i.e., which α-values is most appropriate) requires a detailed and systematic examination of the parameter space.

Local metrics are also very informative. Motif analyses revealed significant excesses of certain triads within the dominance networks generated by our model relative to random networks. Specifically, we found that triads with transitive properties (i.e., that indicate orderliness, or a linear hierarchy) were over-represented in our model. In contrast cyclical triads (A dominates B, who dominates C, who dominates A), which indicate the lack of a clear hierarchy were under-represented. Comparative analyses, which collate data from many different forms of social conflict (i.e., the proximate cause of conflicts was variable) and across taxa, have revealed similar excesses and deficits of these same transitive triads in real world animal dominance networks (McDonald and Shizuka, 2013; Shizuka and McDonald, 2015). In addition, previous analyses of dominance networks in animals have shown an excess of "double dominant" (021D) and a lack of "pass along" (021C) triads to be common in the early stages of hierarchy formation (Chase and Rohwer, 1987; Shizuka and McDonald, 2015). We repeated our analyses after only seven (out of a possible 20) simulated meals and found similar properties among these early networks (Figure S4).

The estimated transitivity of networks generated by our model was high ($t_{\text{tri}} = 0.77$), although lower than previous comparative studies of empirically determined animal hierarchies (0.88; McDonald and Shizuka, 2013). One possible explanation is the frequency of mutual ties in our networks (i.e., A and B dominate each other an equal number of times), which are known to be rare in animal networks, and have been excluded in calculations of transitivity in previous analyses (McDonald and Shizuka, 2013; Shizuka and McDonald, 2015). We can identify two non-mutually exclusive explanations for the abundance of mutual ties in our networks. Firstly, if previously published studies are based on hierarchies that were well established at the time of observation, they may overlook very early interactions between individuals, which can have stochastic outcomes as the hierarchy has a poor linear formation. Secondly, in our model individuals pick competitors at random, and individuals do not identify another's state, or their contest history with other conspecifics (i.e., bystander effects; Dugatkin, 2001). Future inclusions of mechanisms of social recognition in our models, such as status or individual recognition (Barnard and Burk, 1979), may lead to fewer mutual ties and an increased overall triangle transitivity.

Because our approach is grounded into nutritional ecology, it is perhaps one of a handful of methods with which it is possible to generate theoretical networks based on an explicit biological mechanism (i.e., interactions governed by NS). Previously, random networks with desired structural properties have been generated using tools based on graph theory, where the underlying algorithm for generating the network is entirely dependent on the final desired properties thereof. Perhaps the most popular mechanism of non-random network generation in biology remains the preferential attachments model, where nodes are more likely to generate edges with "more popular" nodes (i.e., those with the most edges; Barabási and Albert, 1999; Akbaş et al., 2015; Carletti et al., 2015; Zuev et al., 2015). Whilst preferential attachment models seem realistic for interactions involving communication and/or cooperative behavior, they seem less applicable to animal interactions related to nutrition (e.g., predation, food webs, or contests over food access). In contrast to the standing paradigm, using our models it is possible to generate networks from the bottom up, starting with an explicit (and fully testable) nutritional mechanism, which then gives rise to individual interactions and subsequent emergent network structures (apparently similar to those properties observed in animal groups). To our knowledge, this is the first time such an approach has been documented.

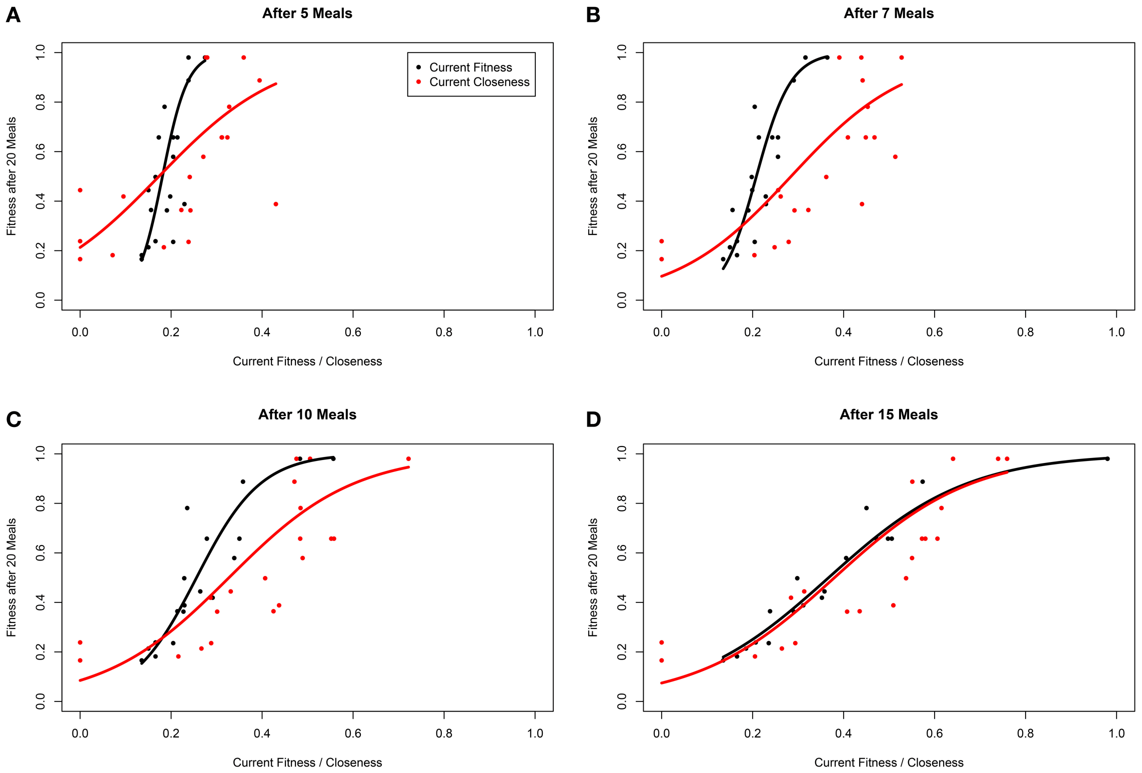

FIGURE 4 | Fitness of individuals within a simulation after 20 meals, as a function of current fitness (black) and network closeness (red), after (A) 5 meals, (B) 7 meals, (C) 10 meals, and (D) 15 meals for groups of 20 individuals in a three-food environment (identical to Figure 1A). The networks are based on an environment with a high level of "competition intensity" ($c = 0.8$). Curves are linear model estimates of fitness after 20 meals, as predicted by current closeness or fitness. Note that fitness after 20 meals was logit transformed for model fitting as fitness is bound at 0 and 1, before being back-transformed for plotting. Closeness values presented were calculated using $\alpha = 1$ (see Opsahl et al., 2010).

Social network approaches have become increasingly popular in behavioral and ecological research, enabling extensive analyses of simultaneous interactions among multiple individuals and across long periods of time (Krause et al., 2007; Croft et al., 2008; Sih et al., 2009; Sueur et al., 2011; Pinter-Wollman et al., 2013). Our study now illustrates how this approach can benefit research on nutritional behavior, ultimately helping to elucidate complex interactions between the environment, the nutritional strategies of individual animals and the consequences thereof for social interactions and collective phenomena. Beyond the example of nutritionally mediated dominance hierarchies, the broader integration of social network analyses into nutrition research has potential for investigating the nutritional ecology of species exhibiting a great diversity of social forms, from temporary aggregations of feeding animals to permanent and fully eusocial colonies of cooperatively foraging nestmates (Krause and Ruxton, 2002). These interactions may include several types of nutrient driven social networks, including social and competitive interactions among foragers (as in this study), transfer of social information about food resources, and exchange of foods (or specific nutrients) or microorganisms (symbionts or pathogens) between individuals. Predominantly, behavioral research utilizing network analyses has focused on descriptive approaches that identify the structure of animal interactions. However, recent developments show that network approaches can be exploited to study the temporal dynamics and the function of interaction patterns (Pinter-Wollman et al., 2013). Thus, network approaches may be used to study both the causes of complex nutritional strategies (i.e., modeling social interactions that influence the nutritional behavior of individuals; e.g., Senior et al., 2015a) and their associated consequences (as in this study). Here, we have dealt with networks and social structures that arise from entirely homogenous groups, but this need not be the case and the ABM may be initialized with a heterogeneous group. For example, each individual may express one of several different nutritional strategies (e.g., young and adults, males and females, producers and scroungers, healthy or diseased animals, or individuals with differing gut microbiota; Flint et al., 2015), allowing one to explore the role that such traits play in governing the emergence of complex social structures. Importantly, our geometric approach identifies explicit nutritional mechanisms, raising the possibility of generating system-specific, empirically testable, predictions about network formation in different nutritional environments and animal groups. Ultimately, a more detailed assessment of the nutritional basis of social behavior, as afforded by social network analyses, will inform our understanding of how nutrition can drive the diversity of social forms observed in nature, a major challenge for future research in nutritional and behavioral ecology (Lihoreau et al., 2015).

AUTHOR CONTRIBUTIONS

AS, ML, and SS conceived and designed the study. AS, CB, and ML collected and analyzed the data. All authors contributed to the writing of the manuscript. AS and ML contributed equally to this work.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fpsyg.2016.00018

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Connections Matter: Social Networks and Lifespan Health in Primate Translational Models

Brenda McCowan[1,2*], *Brianne Beisner*[1,2], *Eliza Bliss-Moreau*[1,2,3], *Jessica Vandeleest*[1,2], *Jian Jin*[2], *Darcy Hannibal*[1,2] *and Fushing Hsieh*[4]

[1] Department of Population Health and Reproduction, School of Veterinary Medicine, University of California, Davis, Davis, CA, USA, [2] California National Primate Research Center, University of California, Davis, Davis, CA, USA, [3] Department of Psychiatry and Behavioral Sciences, University of California, Davis, Davis, CA, USA, [4] Department of Statistics, University of California, Davis, Davis, CA, USA

Humans live in societies full of rich and complex relationships that influence health. The ability to improve human health requires a detailed understanding of the complex interplay of biological systems that contribute to disease processes, including the mechanisms underlying the influence of social contexts on these biological systems. A longitudinal computational systems science approach provides methods uniquely suited to elucidate the mechanisms by which social systems influence health and well-being by investigating how they modulate the interplay among biological systems across the lifespan. In the present report, we argue that nonhuman primate social systems are sufficiently complex to serve as model systems allowing for the development and refinement of both analytical and theoretical frameworks linking social life to health. Ultimately, developing systems science frameworks in nonhuman primate models will speed discovery of the mechanisms that subserve the relationship between social life and human health.

Keywords: translational, nonhuman primates, health status, well-being, social network analysis

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Cédric Sueur,
Institut Pluridisciplinaire Hubert Curien, France

Reviewed by:
Qawi K. Telesford,
University of Pennsylvania, USA
Julie Duboscq,
University of Kyoto Wildlife Research Center, Japan

****Correspondence:***
Brenda McCowan
bjmccowan@ucdavis.edu

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INTRODUCTION

No human exists in a social vacuum-rather, we live in societies full of rich, complex relationships that influence both our physical and mental health. The ability to treat and prevent illness and improve human health requires not only a detailed understanding of the complex interplay of biological systems contributing to disease processes but also how social contexts influence such biological systems. Approaches that empirically recognize the inherent complexity of the effects of social life on health are critical and must be applied across the lifespan. Health is an emergent phenomena which arises from the interplay between complex systems that are themselves influenced by a myriad of factors. These factors are specific to the individual (e.g., personality or temperament, genetic predispositions, ancestry) and/or specific to the environment (e.g., different types of environmental variables; social stressors). A longitudinal systems science approach provides methods uniquely suited to elucidate the mechanisms by which social systems influence health by investigating the effect of social systems on the interplay between biological systems (e.g., immune system, neuroendocrine system) across the life span. Here, we describe one possible systems science approach as applied to rhesus macaques (*Macaca mulatta*), a nonhuman primate species sharing close evolutionary history and behavioral biology with humans. We argue that despite the promise of new systems science approaches, many of those approaches have been developed without social and biological data in mind, necessitating their refinement in the context of complex biological and social systems—rather than, for example, a complex physical system or simulated system on which many new approaches are developed. Nonhuman primate model systems, such as those of rhesus macaques, are sufficiently complex to allow modeling of both biological and social systems while being tractable enough to collect nuanced and detailed data that is ultimately required for the refinement of systems science approaches.

THE RELATIONSHIP BETWEEN SOCIAL ENVIRONMENT AND HEALTH

Social life and its interaction with factors related to the individual influence physical and mental well-being in both humans and nonhuman primates (Walker et al., 1999; Vandeleest et al., 2013). However, the multi-scale dynamic nature of the effect of social relationships on health remains poorly understood. One reason for this is that extant studies have computational obstacles that limit study designs to either specific individual attributes (e.g., gender, age) or specific physiological system dynamics [e.g., hypothalamic-pituitary-adrenal (HPA) axis or immune system] in isolation. That is, simply because of limitations in experimental design and data analysis, we have yet to be able to effectively model the extraordinarily complex dynamic nature of the social environment in concert with a full picture of what it means for an individual to "be healthy."

Decades of research have documented the effect of social context on physical and mental health in humans and nonhuman primates. In humans, characteristics of the social environment such as socioeconomic status influence diverse health outcomes ranging from cardiovascular disease (e.g., Winkleby et al., 1992) to mood disorders such as depression (e.g., Gilman et al., 2002) to mortality (e.g., Blaxter, 1987). For example, long-term studies of British civil service workers have provided decades of data demonstrating that social status has an important impact on a wide variety of outcomes such as cardiac (e.g., angina, ischaemia) and respiratory (e.g., bronchitis) health (Marmot et al., 1991; Singh-Manoux et al., 2003)—the lower a person's status the greater prevalence of disease. Low social status is associated with unpredictability of income, housing, healthcare access, as well as low control over working conditions, all features that contribute to chronic stress and illness (Weissman et al., 1991; Väänänen et al., 2008; Kim et al., 2012). Similarly, as discussed below, research from our group (and others) demonstrates that nonhuman primate's absolute social rank (akin to human class) and the certainty of that social rank (akin to predictably/unpredictably) are both key factors influencing individual-level health outcomes (Vandeleest et al., in revision).

The number and quality of specific social relationships are an additional aspect of social life which influence health has and these have been investigated both in humans and nonhuman primates. In humans, deleterious social relationships, such as those that occur in the context of abuse, have similar negative outcomes on physical health and mental health (for a review see: Springer et al., 2003)—the experience of abuse greatly increases the prevalence and progression of disease. The quality of social relationships also plays a role in shaping health outcomes across the lifespan. Patterns of these effects have largely been elucidated in nonhuman animals. At one extreme, nonhuman primates raised in social isolation develop behavioral pathologies characterized by an inability to regulate emotion-related behavior and experience (e.g., Harlow et al., 1965; Mitchell et al., 1966). The pathology resulting from limited social contact is so extreme that one interpretation is that it induces clinical depression (Harlow and Suomi, 1974). In addition, natural or experimentally induced variation in the quality of maternal care impacts neuroendocrine, immune, and neurotransmitter system activity, and these differences are detected into adulthood (Coplan et al., 1996; Levine and Mody, 2003; Vandeleest et al., 2013). Similarly, social stress as related to dominance rank in nonhuman primates is related to a variety of physiological outcomes including reduced synaptic plasticity and dendritic atrophy, immunosuppression, reduced gonadal hormones, and pathogenic cholesterol profiles and hypertension (for a review see: Sapolsky, 2005). Finally, social instability (i.e., new social group formation or frequently rotating small group membership alters neuroendocrine function and sympathetic innervation of lymphoid tissue, and reduces survival after infection with a HIV-like virus; Mendoza et al., 2001; Sloan et al., 2007; Cole et al., 2009). In contrast to these negative effects is the growing evidence that both humans and nonhuman primates that have many social connections are buffered against stressful experiences (Berkman, 1984), experience less loneliness (Cacioppo et al., 2002), recover more fully from acute episodes of depression (George et al., 1989; Corrigan and Phelan, 2004), experience less disease (Seeman, 1996) and live longer (Steptoe et al., 2013).

Studies of nonhuman primates demonstrate that individual-level factors (e.g., personality, genetic predispositions) moderate the effects of social factors on health. For example, although social instability has been associated with negative health outcomes, the magnitude of impact depends on the personality of the individual. Under experimentally-induced social instability (rotating membership of small groups), rhesus macaques rated to be less "sociable" in adjective-based personality assessments had elevated plasma cortisol concentrations and poorer immune responses to an HIV-like virus when compared to animals that were more sociable (Capitanio et al., 1999, 2008). Similarly, a polymorphism in serotonin transporter gene promoter region (5-HTTLPR) has been shown to moderate the effects of impactful momentary social experiences. Peer-reared infant rhesus macaques with a short allele of 5-HTTLPR showed higher adrenocorticotropic hormone level in response to separation compared to those who were mother-reared or those with long alleles of 5-HTTLPR (Barr et al., 2004). Individuals carrying the short alleles of 5-HTTLPR had greater depressive symptoms when experienced greater early or recent adversities, but fewer depressive symptoms when adversities were absent or experienced supportive environments (Taylor et al., 2006). Together these examples highlight the need for complex dynamic modeling techniques that allow for the simultaneous modeling of complex social systems and their interaction with individual characteristics (e.g., personality or genotype) to fully understand their impact on health outcomes.

The mechanisms by which the effects of social life manifest as predictors of individual health outcomes is not clear and have been, to date, largely speculative (House et al., 1988; Adler et al., 1994). One reason for this speculation, rather than the specification of causal models, is that both human and nonhuman primate research to-date has been largely limited to small assortments of specific features of social processes (e.g., number of social connections, the general social class to which an individual belongs, the ordinal or cardinal rank of the individual in the group, or the impact of specific social relationships; Christakis and Fowler, 2007; Fowler and Christakis, 2008; Lewis et al., 2012). Such approaches ignore the multiscale and temporally dynamic structure of social life—that is that individual relationships differ in number, quality and type that are embedded within multiple broader social contexts of family, social class, and community. Further, individuals can belong to multiple groups that differentially overlap and which may exert differential influence on the individual at different times or in different contexts. Factors like these shape an individual's "social role" and are known to relate to both physical and mental health (Phillips, 1981; Murrell et al., 1992; Brissette et al., 2002; Litwin and Shiovitz-Exra, 2010) and yet are incredibly challenging to model in humans. A solution to these issues is to use a nonhuman primate model of human social-life and health in concert with sophisticated novel statistical approaches.

We believe that the solution to modeling the complexity of social life as it impacts health is to adopt a quantitative method that use a *multi-scale, dynamic* approach. Multi-scale refers to integration of information about the individual, his or her primary social relationships, larger social group, and society in concert with the individual's biological systems (which are also multi-scale). *Dynamic* refers to the ability to quantify both slow and rapid frequency changes in the variables of interest. Such an approach to human health might seem only plausible through the study of humans. However, a large and growing body of evidence from nonhuman primates, and specifically the genus *Macaca*, suggests that our primate cousins exhibit sufficient complexity and variability in social dynamics and similar links between social dynamics and health to be good models for humans (Flack et al., 2005; Flack and de Waal, 2007; McCowan et al., 2008, 2011; Kutsukake, 2009; Lehmann and Ross, 2011; Beisner et al., 2011a,b, 2012; Daniels et al., 2012; Dobson, 2012; Micheletta et al., 2013; Evers et al., 2014). Modeling the effects of the social environment using a systems science approach on a nonhuman primate model is not only increasingly feasible but may be superior to less controlled human studies, with the potential to uncover significant biomedical breakthroughs that standard non-computational approaches lack in both scope and depth.

NONHUMAN PRIMATES AS AN IDEAL MODEL SYSTEM

New computational techniques (described below) represent incredibly powerful tools that can be used to understand the relationships between social and biological systems. These tools require appropriate and robust network data and health data from large samples. While human research provides one potential avenue for such research, nonhuman primate research provides a unique opportunity to obtain intensive social network and health data across time. Complex study designs involving multiple scales and dynamic relationships over the lifespan are difficult to conduct on human populations for multiple reasons. First, it is nearly impossible to collect multi-generational data over the time course of a single study. Monkeys, however, have substantially shorter lifespans and faster life histories—macaques reach sexual maturity at ∼4 years of age. Second, true population modeling of social network dynamics in humans is difficult because it is nearly impossible to define all participant nodes in the network. For every person in the network, there are thousands of others they do not know who may be able to influence their behavior or health via indirect connections. In contrast, every individual in the network is known and can be observed in groups of captive nonhuman primates. Further, the data used to generate networks are collected by direct observation rather than self-report, which is subject to recall bias and error.

In addition to being able to face the challenges posed by human research head on, nonhuman primate research offers some additional benefits. These benefits are particularly true of studies conducted with nonhuman primates living in large outdoor social groups. The genetic, biobehavioral, and social history of each macaque and social group can be fully characterized. Communities are sufficiently large (yet readily observable) to generate social heterogeneity at individual, family, and community levels. Nonhuman primate communities can be systematically perturbed (within ethical bounds) to elucidate causal links between social relationships and health. Finally, macaque communities are housed in controlled but complex environments but vary with respect to individual attributes and family and community structure across social groups.

Considering the environmental and social complexity is critical when selecting a model system and organism for human health. Most biomedical studies with nonhuman primates involve either indoor singly or pair-housed subjects or indoor/outdoor small-group housed subjects (Baker, 2007). Yet, research into the importance of the social environment on health requires greater environmental and social heterogeneity that mirrors human experience. Studies of nonhuman primates in large social groups offer just that possibility.

DEFINING THE NEW APPROACH AND ITS VALUE

Recent computational and statistical developments allow for the development of new tools to evaluate the multi-scale and dynamic aspects of social life. Contemporary network science is one field that has expanded its toolkit dramatically in the wake of these recent developments. Although network science is most commonly understood in the context of *social* networks, social network analysis is one component of a much broader set of network science approaches that are all designed to reveal emergent structure in any type of system. Network science therefore has significant potential to provide an important set of tools that allow us to move beyond simple associations toward more predictive and causal models. The power of these predictive models can then be harnessed to develop specific, even "individualized," interventions to promote human health, such as those sought after in the current goal to achieve "precision medicine."

Developing predictive, causal models requires basic information about how the spatial and mathematical relations of networks relate to the content and quality of relationships at the individual, family, and community levels. Further, it is critical to understand how variation in these relationships at different levels influences health and health-related outcomes both in the short- and long-term. Network structure must also be linked to the fundamental characteristics of the individuals in the network and to the environmental and social contexts in which individuals interact, and this is in both the past and present. Utilizing such an approach will provide greater insight into how and why basic behavioral and social processes influence specific health outcomes as well as overall health and well-being (see **Figure 1**).

INNOVATION IN METHODOLOGY: COMPUTATIONAL NETWORK ANALYSIS

Over the past few years our group and other research groups studying social networks have made significant strides toward developing innovative techniques for analyzing complex network structures that exhibit multiple spatial scales (e.g., individual, family, community levels), multidimensional topology (e.g., complexly correlated networks of different types of behaviors or relationships—such as friendship, Facebook and book club networks), and longitudinal temporal dynamics (e.g., changes to friendship networks over time; Berkman, 1984; George et al., 1989; Seeman, 1996; Cacioppo et al., 2002; Corrigan and Phelan, 2004; Capitanio et al., 2008; Steptoe et al., 2013). These are bottom-up (data-driven) model-generating approaches have been developed with biological and social data in mind and have been tested on these types of data. Importantly, these new techniques have few underlying assumptions and seek to understand the underlying mechanisms producing

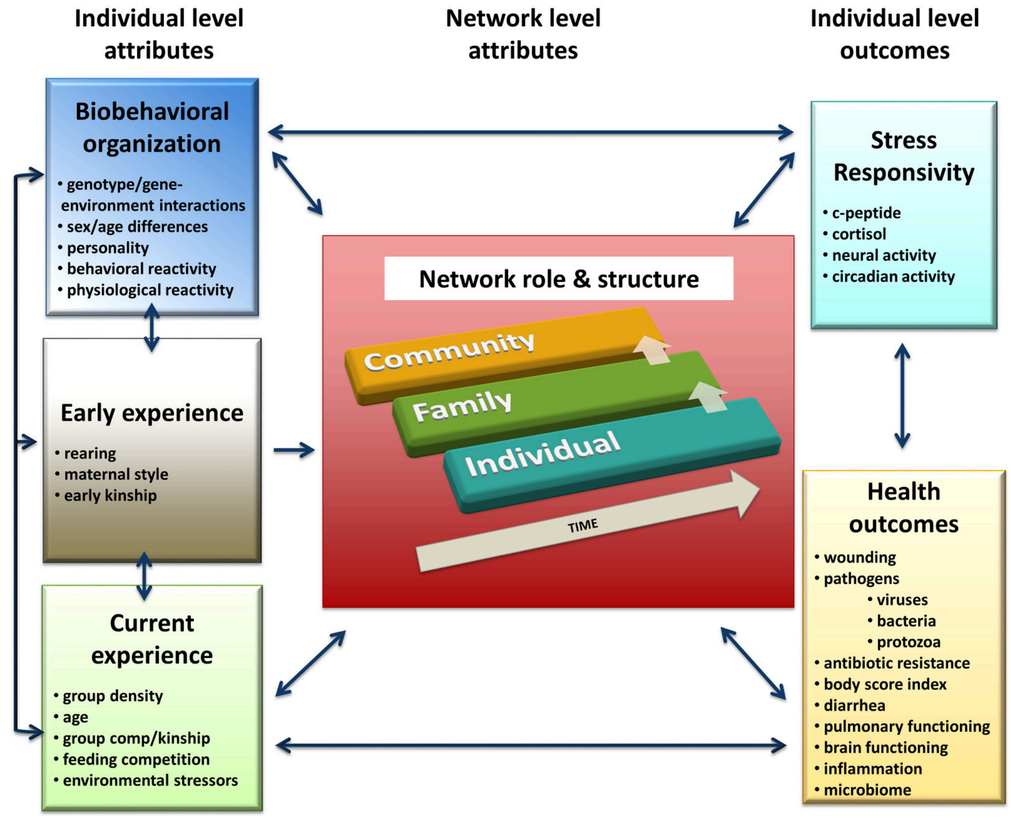

FIGURE 1 | Unifying conceptual framework for effects of individual characteristics and environmental/social stressors on network structure and dynamics leading to positive or negative health outcomes at each life stage and across the lifespan. Arrows indicate possible direction(s) of effects including reciprocal relationships.

patterns in relationships. They are designed to examine the hierarchical and dynamic architecture of networks, such as connectivity and community structure, information flow through networks, and joint relationships between networks. Two key aspects of network structure need to be modeled to address complexity in network structures: (1) multi-scale spatial structure (e.g., differences in network structure at different scales) and (2) multi-scale temporal dynamics (e.g., changes in network structure across time). Additionally, networks differ in the major characteristics and geometry that define them. Data represented by a single (one-mode) network (e.g., friendship network) and data represented by two or more networks (two-mode or bipartite networks) juxtaposed to one another (e.g., Facebook network and book club membership network considered together) have different geometric structures. In each geometric structure, networks can differ in the characteristics that define them. Networks can be comprised of either presence or absence of the relationship (e.g., Susan and Peter are Sam's Facebook friends, which is binary, or unweighted) or weighted by the number of interactions (e.g., Sally texts Sam five times per day). Each type of network also can consist of either undirected links or ties (Sally and Sam are friends on Facebook but no information is known about who "friended" whom or who initiates communication with whom) or directed links or ties (Sally walks toward Sam often but Sam walks away when she nears). As such, the appropriate techniques for modeling a binary, undirected network are very different from those necessary for a weighted, directed network. As an example of this growing area of computational development, below we describe some of our new models that address the analysis of these different network types as well their further development below. These methods work on social network data where individuals (nodes) are connected via behaviors that are either directed (i.e., each edge is drawn from a source individual to the receiving individual) or undirected (i.e., edges are shared without direction) and either weighted (i.e., edges are defined by the rate or frequency of interactions) or unweighted (i.e., edges are defined by presence or absence of an interaction). See **Table 1** for a summary.

Percolation and Conductance

Percolation and Conductance utilizes the information about both direct and indirect relationship pathways to characterize how information flows through directed networks (Fushing et al., 2011; Fujii et al., 2013; **Table 1**; **Figure 2**). This method uses a percolation algorithm to gather information from multi-step pathways network, which allows tracking and computation of the flow of information through indirect social interactions (e.g., Sally interacts with Sam who earlier interacted with John; Fujii et al., 2013). A conductance algorithm is applied to ensure that all potential flow pathways are explored. The contribution of each path to the imputed matrix is weighted by its likelihood of being successfully traversed during the random walk.

Joint Modeling

In a complex system, different social and biological networks rarely operate in isolation. Rather, dynamic relationships between different social behaviors often covary in highly complex, synergistic or even emergent ways. We would also argue that many negative and positive health outcomes likely have similar complexity in their etiology. Instead of analyzing these networks individually, we have developed methodology for analyzing networks at the same time (hence, "joint modeling") which produces metrics that characterize the multi-system dynamics as a whole.

Joint modeling uses a bottom-up iterative modeling approach (Chan et al., 2013) that begins with multiple component networks of the system (generated from empirical data) and links the networks via common nodes in each network (**Table 1**; **Figure 3**). The raw data are used to calculate expected probabilities of jointly observing a link in each network for every pair of individuals. For example, consider the e-mail and phone calling networks of a community of friends—joint network modeling begins by calculating what proportion of pairwise relationships are characterized by each possible combination of connections in the two networks, such as unidirectional e-mailing with bidirectional phone calling (e.g., Hank e-mails and calls Jane, but Jane only calls Hank and never e-mails him), or the absence of both e-mailing and calling interactions (e.g., John and Sally have never communicated with each other over e-mail or phone). In the

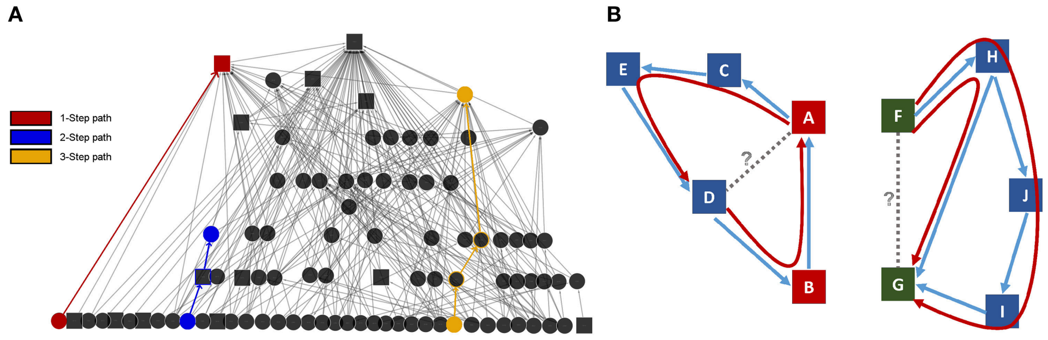

FIGURE 2 | Percolation and Conductance uses indirect pathways to determine consistency in a network. (A) Behavioral network illustrating direct (blue) and indirect pathways (yellow, red). **(B)** Low consistency from A to D represented by green and red arrow indicates an ambiguous dominance relationship. The high consistency from F to G represented by green arrows indicates high certainty that F outranks G.

TABLE 1 | Summary of computational network approaches.

New computation method	Purpose	Directed edges	Weighted edges	Description of output
Percolation and conductance	Method for quantifying how information flows through directed networks via direct and indirect pathways	Yes	Yes	Identifies all direct and indirect pathways in a network. Summarizes the overall consistency in the direction of these pathways for every pair of nodes (e.g., 100% of 1-step paths and 90% of 2-step paths flow from A to B), yielding a measure of the probability that any path flows from A to B vs. B to A.
Joint modeling	Method for modeling the inter-dependent relationship across multiple networks	Yes	No	Categorizes each pair of nodes according to their joint-network relationship (using a vector). Identifies a model whose predictors describe what drives the observed frequencies of each type of pair, such as abundance of pairs with opposite direction phone calling and e-mailing.
Data cloud geometry	Clustering methodology that identifies a community structure via a data-driven random walk	No	Yes	Identifies block structure in a matrix by clustering together nodes that are most similar. Creates a hierarchical tree that describes the multi-scale structure of the network.
Data mechanics	Method that allows the discovery of clusters of nodes from one network that are grouped based upon similarity across a series of metrics	Both directed and undirected	Both weighted and unweighted	Identifies block structure in a bipartite matrix by shuffling the ordering of rows and columns, yielding two hierarchical trees (one for rows, one for columns) that describe the inter-dependent relationship between them.

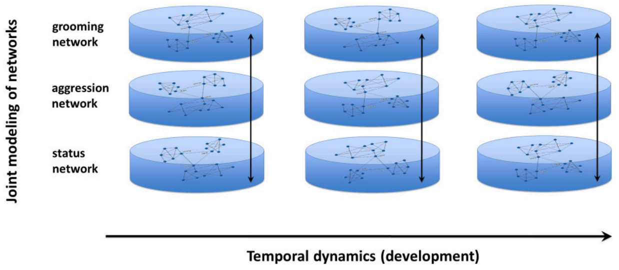

FIGURE 3 | Conceptual framework behind joint modeling of networks. Using this new technique, multiple networks can be evaluated for how they correspond to one another and how that correspondence changes over time, across development, during the aging process, or over the lifespan.

null model, the relationships across interactions are assumed to be independent, e.g., knowing that John never calls Sally is independent of whether Sally and John e-mail each other. Constraint functions are then iteratively applied to tune these probabilities to match the observed directed network data.

Once appropriate constraint functions (based upon existing theory or data) are applied to match the observed data, the relationships between these networks then can be assessed over time. This interactive process allows one to examine how multiple networks correspond to one another at a given point in time or how the relationship of these networks changes longitudinally (Chan et al., 2013). Monitoring the complex dynamics of a system provides a valuable way of quantitatively characterizing the potential impact of an individual's social environment.

Data Cloud Geometry

All social systems have inherent multi-scale structure (e.g., individual, family, community). This multi-scale geometry must be quantitatively defined and preserved during the modeling process in order to model how individuals relate to each other and to health outcomes. Data cloud geometry (DCG) is a new method that identifies community structure at multiple scales by performing a random walk through an empirical network. A random walk creates a path by moving through the data step by step. The direction of each step is determined randomly and the probability of each step is guided by the data. Cumulatively, these random walks produce a similarity matrix describing how similar two nodes (e.g., individuals) are in their social connections. This similarity matrix captures the geometric structure of the network by deriving a hierarchy of clustering. Individuals with greater similarity in social connections are considered to be "closer," and thus cluster together at a lower level of the hierarchical tree than individuals with few similarities in their connections (**Table 1; Figure 4**).

A key advantage of using DCG over other clustering algorithms is that DCG generates more accurate cluster membership than previous approaches because outliers do not, by default, cluster with each other (i.e., a cluster of outliers) simply because they significantly differ from other clusters (but may not be similar to one another). Instead outlier individuals must be similar to each other to be in the same cluster. Second, this approach has a built-in mechanism for self-correcting clustering membership across different levels, which is important for inferences of cluster membership across different levels of analysis (e.g., clusters individuals at family level in

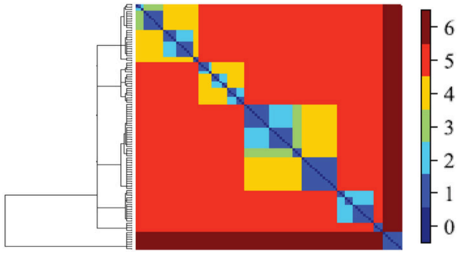

FIGURE 4 | Illustrative DCG-tree based on fMRI data (Fushing et al., 2013). Tree on left panel also corresponds to pattern on top panel. Note that different levels of the tree (known as "temperature") yield different blocking patterns corresponding to communities. At the highest temperature indicated in dark red, a single community is observed; at the lowest temperature, 19 communities are observed. DCG finds the best clustering solutions at multiple levels in the tree.

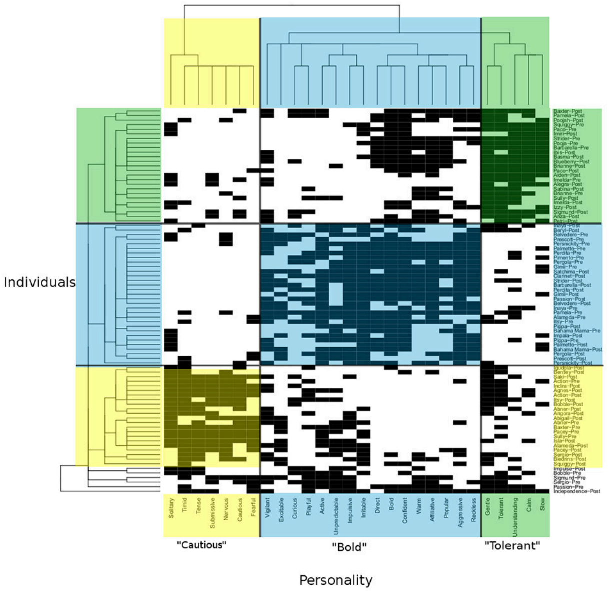

FIGURE 5 | Data Mechanics tree and heat map representing bipartite network analysis of clusters of individuals (macaques) set on the Y-axis with clusters of personality type on the X-axis. Note the blocks of individuals sharing personality profiles on the Y-axis as well as the blocks of personality traits on the X- axis. For illustration for the level in the tree where the red line is located, we can block personality according to individuals and individuals according to personality (highlighted yellow, blue, and green boxes). Note how individuals who are similar in personality profiles group together and personality traits corresponding to personality types group together.

comparison to clusters of families at community level). These two features allow robust classification of data into groups and thus identify community structure at multiple levels of analysis (e.g., how individuals group within families, and families into communities).

Data Mechanics

Data Mechanics begins with a bipartite matrix in which the rows represent a set of individuals from a network or system and the columns represent various metrics for which each individual has been assessed (**Table 1**; **Figure 5**). The rows and columns are then shuffled iteratively to reveal blocks of similar subjects. Shuffling occurs using principles from thermodynamics to assign "energy" to the organization of the network matrix. Network matrices with the lowest energy state are selected as the "best fit" for these blocks of subjects. Notably, this method generates a hierarchical tree of profiles that allows for the identification of higher order behavioral and social profiles that relate to negative (or positive) health outcomes in predictive or causal ways. Data mechanics (Fushing and Chen, 2014) can be used to identify clusters of individuals that share similar health profiles and social profiles as well as determine their inter-relationships over time. This new technique will allow us to quantify the collective influence of one's social environment on aspects of individuals' health status.

AN EXAMPLE: COMPUTATIONAL NETWORK APPLIED TO A NONHUMAN PRIMATE MODEL AS TRANSLATION FOR HUMANS

Below we discuss our group's work to provide brief, preliminary examples of the application of our computational network approach to a nonhuman primate social system as a translational model for enhancing human health. We focus on two examples. In the first example, we illustrate the effects of social network structure on individual health at a single time scale. In the second example, we illustrate the effects of social network on group health at multiple time scales (which in turn can positively or negatively influence individual health across these temporal scales) to illustrate the multi-scale (e.g., individual, group), multidimensional (e.g., joint modeling) and longitudinal aspects (before and after perturbation) of our holistic systems approach.

Example #1: Predictability of Status as Predictors of Individual Heath

Indicators of social rank in humans, such as socioeconomic status, are thought to be a source of stress. Yet studies on the presence and direction of this relationship between rank and stress in animal societies have been quite equivocal in terms of whether it impacts health. Preliminary results from our research group using computational network models, as outlined above, suggest that certainty or ambiguity of one's dominance relationships may have a greater impact on health than actual rank itself. Certain dominance relationships are those in which it is very clear who is dominant and who is submissive. In contrast, ambiguous dominance relationships are those in which the identity of the dominant and submissive individual is not clear. We can quantify the number of these relationships per individual into a metric that reflects an individual's general propensity to have dominance interactions that go with the global network "flow" of dominance (i.e., pathways in the network generally flow from dominance to subordinate individuals) or interactions that run counter to the global flow of dominance (what we term "dominance certainty").

We used "Percolation and Conductance" (Fushing et al., 2011; Fujii et al., 2013; see Section Innovation in Methodology: Computational Network Analysis above), to quantify dominance certainty. The dominance relationship of each dyad in the group is quantified using both direct and indirect agonistic interactions, which yields a holistic quantitative measure of the degree of certainty vs. ambiguity of dyadic relationships in the network.

Dominance certainty relates to health outcomes in situations where dominance rank does not. First, preliminary analyses of both physiological parameters as well as physical manifestations of stress (e.g., blood cytokine levels estimating inflammatory responses, frequency of diarrhea bouts, frequency of trauma, and severity of trauma) demonstrate that having ambiguous dominance relationships exhibits a dose dependent relationship with greater incidence of diarrhea and trauma, and higher cytokine levels (Vandeleest et al., 2014a,b; Beisner et al., 2015). Individuals with lower dominance certainty have higher incidences of poor health. Additionally, for the pro-inflammatory cytokines, dominance certainty modified the effect of dominance rank such that individuals with lower dominance certainty only experienced poorer health if they were also high-ranking. In other words, having ambiguous dominance relationships only negatively impacted cytokine levels for individuals that stood to lose their high status position (i.e., low-ranking individuals with ambiguous relationships stand to *gain* status). This suggests that uncertainty in relationships, such as dominance, may be more important for health outcomes than actual dominance status. Second, cohesion or interconnectedness in affiliative relationships, such as grooming, also may have an effect on health both directly and indirectly through dominance certainty. An analysis of community membership in a grooming network, using "Data Cloud Geometry" (Fushing and McAssey, 2010; Chen and Fushing, 2012; Chan et al., 2013; see Section Innovation in Methodology: Computational Network Analysis above), demonstrated that subjects who shared a grooming cluster with more family members evidenced less variance in their dominance certainty when compared to subjects who shared a grooming cluster with few family members. Thus, cohesion in affiliative relationships may influence certainty in relationships outside the affiliation context. Finally, personality is also associated with dominance certainty. Rhesus monkeys who score high in the trait "confidence" and who are also lower-ranking, have more ambiguous dominance relationships than lower-ranking individuals who are less "confident." It is possible, even probable, that confident individuals may challenge dominance relationships more frequently than animals who are not confident.

Taken together, these results demonstrate that family or community cohesion and certainty in relationships interact with properties of the individual, such as personality, to have a significant impact on aspects of health. Notably, these preliminary analyses indicate that certainty about one's position in social relationships may be more important than absolute rank in predicting health outcomes. We can determine thresholds for how much uncertainty or how many uncertain relationships, and with whom, are sufficient to impact health. However, distinguishing between actual class and predictability in relationships are likely confounded in many human societies. Therefore, these results from a nonhuman primate model can inform how measurement of actual direct and indirect social relationships, rather than simple socioeconomic class designations, can impact human health through a number of biological systems.

Indeed, the evidence from this work clearly indicates that knowledge beyond direct relationships, that is how individuals fit within the global social structure (i.e., fit with the global flow of dominance; fit with family-related clustering structure), is critical to understanding health. No longer is it enough to measure what an individual's direct social interactions are (e.g., number of friends, etc.); rather we need to know more precisely how those interactions are embedded within the structure/geometry of their social community.

Example #2: Stability of the Social Environment and Group Health

The stability of human and nonhuman social groups impacts health (e.g., German and Latkin, 2012). Animal societies are complex behavioral systems in which the dynamics of the system as a whole represent the synergistic interaction among multiple behavioral networks. Stability is an emergent property of the interactions between networks (e.g., Barrett et al., 2002). Ideally, then, the information from these separate behavioral networks should be combined in order to achieve a comprehensive understanding of a given system's stability (Barrett et al., 2012; Hsieh et al., 2014). This can now be accomplished with "Joint Modeling" (see Section Innovation in Methodology: Computational Network Analysis above).

Assessing the joint relationship between two behavior networks, such as aggression and status signaling in rhesus macaques, across multiple time points can reveal whether (a) the two networks interact in a predictable manner and (b) whether the pattern of interdependence between the two networks changes over time, particularly in response to perturbations to the system. In a recent study, we constructed two unweighted networks (aggression and status) for seven large outdoor captive groups of rhesus macaques. The groups varied in their stability—four groups were stable, three groups had to be disbanded completely after our data collection ended as the result of severe and widespread trauma. Macaque society is organized primarily by dominance relationships (e.g., Sade, 1967, 1969). In a society with a clear dominance hierarchy, most pairs of individuals are expected to have clearly communicated dominance relationships. We expected that the joint relationship between aggressive interactions (e.g., threatening, biting) and status interactions (e.g., facial expression to signal formal acceptance of subordinate status—the silent bared teeth display) should, in general, agree with the known pattern of dominance. Aggression and status are directed networks in which one monkey in a given dyad (the initiator) either aggresses or signals to the second monkey in a given dyad (the recipient; Chan et al., 2013; see Section

Innovation in Methodology: Computational Network Analysis above).

Joint Modeling revealed that stable groups all showed the same pattern of interdependence between aggression and status networks—in all groups, far more pairs than expected had relationships involving unidirectional aggression (from dominant to subordinate) along with unidirectional status signaling (from subordinate to dominant), yet other potentially problematic types of relationships (e.g., bidirectional aggression with no status signaling) occurred as frequently as expected by chance (Beisner et al., 2015). In stable groups, a highly complex dependent relationship between the aggression network and status network is present across time. That is there was a strong association between aggression is one direction and status signaling in the opposite direction. In contrast, the three unstable study groups exhibited a change in their pattern of network interdependence (Beisner et al., 2014) prior to the onset of extreme aggression. Two of the three unstable groups showed a dramatic reduction in the extent of interdependence between aggression and status networks. In other words, knowing that monkey A threatens monkey B does not necessarily mean that monkey B will signal its subordinance to A, as in stable groups. Thus, loss of interdependence between two behavioral networks is one feature of social instability. Network data can therefore be used to predict whether a group is at risk of social collapse (Hsieh et al., 2014). Critically, this same pattern of effects was observed in the banking industry prior to the 2008 financial crash—suggesting that patterns of change in joint models are translationally relevant.

All social systems are composed of multiple interconnected networks, but until now, it has been impossible to evaluate them simultaneously. Joint Modeling may be of greatest utility in quantifying the impact of environmental, ecological, or social changes over time on the underlying structure of a social group and their consequent health outcomes. Further analyses are underway to assess these effects on such health outcomes across the lifespan at the group, family and individual levels in our populations of rhesus macaques.

CONCLUSIONS AND FUTURE RESEARCH

The computational network approach used on data collected from large outdoor social groups of nonhuman primates promises a broad translational tool that can realistically model individual, family, and group health across the lifespan in human populations. The approach and examples we described here, however, are only the beginning. While nonhuman primates have served as a translational model for humans for decades, the importance of the complexity of the social and physical environment in biomedical applications is still essentially unrealized (e.g., Capitanio and Emborg, 2008; Shively and Clarkson, 2009). Future biomedical research should address this issue directly by using socially and environmentally relevant subjects whenever possible. Indeed, with newer more advanced and less invasive methods for collecting and analyzing biological samples in the field, wild populations of nonhuman primates may provide additional translational opportunities. Field-based biomedical research on genetically, socially, and behaviorally well-characterized nonhuman primate populations could transform our understanding of threshold, collective, and emergent effects of the social environment on health outcomes.

In contrast to the nonhuman primate as a biomedical model, computational approaches for modeling multidimensional and dynamic systems are only in their infancy, but the computational power and intellectual drive to model complexity in spatial and temporal dynamics is certainly now present. Further development of this approach could revolutionize medicine by allowing us to develop individualized medicine on an unprecedented scale. We believe that this innovative systems science approach for studying complex emergent health outcomes on socially and environmentally complex nonhuman primate models in either captivity or the field promises better and more timely solutions to the greatest physical and mental health challenges we currently and will continue to face as humans.

AUTHOR CONTRIBUTIONS

BM: Developed conceptual framework, funded research, wrote manuscript. BB: aided in writing of manuscript. JV: aided in writing of manuscript. EBM: aided in writing of manuscript. JJ: aided in writing of manuscript. DH: aided in writing of manuscript. FH: developed computational tools.

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Layered Social Network Analysis Reveals Complex Relationships in Kindergarteners

Mireille Golemiec [1†], ***Jonathan Schneider*** [1†], ***W. Thomas Boyce*** [2], ***Nicole R. Bush*** [2], ***Nancy Adler*** [2] ***and Joel D. Levine*** [1*]

[1] Department of Biology, University of Toronto Mississauga, Mississauga, ON, Canada, [2] Departments of Psychiatry and Pediatrics, University of California, San Francisco, San Francisco, CA, USA

The interplay between individuals forms building blocks for social structure. Here, we examine the structure of behavioral interactions among kindergarten classroom with a hierarchy-neutral approach to examine all possible underlying patterns in the formation of layered networks of "reciprocal" interactions. To understand how these layers are coordinated, we used a layered motif approach. Our dual layered motif analysis can therefore be thought of as the dynamics of smaller groups that tile to create the group structure, or alternatively they provide information on what the average child would do in a given local social environment. When we examine the regulated motifs in layered networks, we find that transitivity is at least partially involved in the formation of these layered network structures. We also found complex combinations of the expected reciprocal interactions. The mechanisms used to understand social networks of kindergarten children here are also applicable on a more general scale to any group of individuals where interactions and identities can be readily observed and scored.

Keywords: hierarchy, social, kindergarten children, social structure, layered networks, motifs

Edited by:
Cédric Sueur,
Institut Pluridisciplinaire Hubert Curien, France

Reviewed by:
Amael Arguel,
Macquarie University, Australia
Matjaž Perc,
University of Maribor, Slovenia

****Correspondence:***
Joel D. Levine
joel.levine@utoronto.ca

† These authors have contributed equally to this work.

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INTRODUCTION

The interplay between individuals forms building blocks for social structure. In some cases such as baboon troupes and human military units, rank is evident to outside observers and within the group (Hausfater, 1974; Dean et al., 1975). In other cases, such as schools of fish (Whiteman and Cote, 2004), flocks of birds (Noble, 1939) and groups of *Drosophila* (Yurkovic et al., 2006) the presence of hierarchical relations are less evident within the group, although they may emerge in the context of resource scarcity. One method assumed to reveal hierarchy is through the evaluation of aggressive conflicts. Winners and losers throughout the animal kingdom have to deal with the consequences of battling and even when there are wounds to lick on both sides, there often appears to be a strong correlation between winners and dominance on the one hand, losers and submission on the other. There is a noteworthy caveat to this view; although dominant males may be able to guarantee access to resources on demand, others may use alternative strategies to gain access. Consider the sneaky copulator (or other alternative mating tactics Gross, 1996), for example. This "gray" area extends through all interactions between organisms. Even when the fight may be consistently "won" by a specific individual the "dominant" label is often thought to transcend aggression and imply dominance and resource monopoly (Drews, 1993). But this supposition is almost never empirically tested.

The dominance/submissive relationship is an attractive framework within which to study social interactions as it allows quantification of often complex interactions, and is known to generate hierarchies which have been proven to affect many aspects of the social organization and subsequent interactions within the group (Barroso et al., 2000; Whiteman and Cote, 2004; Sapolsky, 2005). Charting interaction patterns within these groups reveals a stratification within a group, where individuals that are socially dominant hold positions that rank higher than those who are socially subordinate. Classically, hierarchies are described as a ladder-like relationship between an alpha individual and individuals of ever-decreasing ranks where the number of rungs, and the number of individuals occupying each rung, varies (Drews, 1993). There are specific measures used to describe and understand hierarchical arrangements—stability (how consistent the arrangement is over time), steepness (ease of movement between levels, de Vries et al., 2006) and linearity or transitivity (such that if A>B and B>C then A>C, de Vries, 1995).

These measures all quantify the level of hierarchy, but stability and steepness do not have clear null hypotheses—and hierarchical and non-hierarchical categories will rely on extensive study of interactions to determine what is a biologically relevant amount of stability and steepness (e.g., not a hierarchy that flips every 5 min in primates). Transitivity on the other hand makes definite predictions about the relationships between individuals, and provides an intuitive classifier for hierarchy. Herein we examine transitivity and not hierarchy, and we posit that highly structured groups do not necessarily mean highly hierarchical groups. While any dyadic interaction may be classified as having a quantifiable "top" and "bottom," these may simply be "roles" within a highly structured, but cooperative group, where dominant and subordinate labels are not static and dependent on the immediate social surrounding (i.e., A above B, but in the presence of C, B above A).

Many studies have shown that people innately behave in more dominant or subordinate ways when interacting, and that the roles a person takes affects education level, family background, income, and socioeconomic status (Boyce et al., 2012). In turn, these qualities also influence behaviors, leading to the seemingly-stratified system of organization we see in many human populations. Whether or not this social stratification is based on innate hierarchical relationships between interacting individuals, its effects on health and development are numerous and often begin early in childhood (Adler et al., 1994; Boyce et al., 2012). That these relationships exist and are relevant in young children opens up the possibility of studying human interactions in populations that may not be completely affected by cultural stratification but based largely on behavior. Kindergarten classrooms are therefore an excellent system within which to study the patterns of social interactions and the networks that they form.

In 2012 Boyce et al. examined the influence of socioeconomic status (SES) on the types of behavioral interactions and hierarchical positioning of kindergarten children within classrooms in Western California, suggesting that classrooms are stratified by behavioral rankings (Boyce et al., 2012). Here we use the same data set (described briefly in methods and in detail in Boyce et al., 2012) to examine all interactions within classrooms settings. We focus on six main interaction types, forming three reciprocal pairings (Resource Struggle and Prosocial, Aggression and Submission, and Leadership and Followship), removing hierarchy-specific quantitative classifications of individual children made by the observers. While the first four interaction types are easily understood, resource struggle and prosocial are less intuitive. We follow Boyce's definition of prosocial behavior as "a voluntary behavior to benefit another child" and resource struggle as the opposite, where a child struggles over access to either an object or the attention of another student or teacher (Boyce et al., 2012). These interactions are often considered reciprocal such that outputting one ensures input of the other (i.e., being led by someone equates to following them, struggling for a resource once may establish a dynamic of resource flow between individuals). Furthermore, our data set does not include emotional reactions to the physical/verbal interactions being observed and as such, bullying-type behaviors were not examined.

We first look at children's interactions through time from the vantage point of the average child. We use transition matrices to examine probabilities of moving from one interaction type to another. Using principal component analysis on these transition matrices allows us to look for group separation in the students based on their likelihood of interacting in a specific order. While this technique illustrates the effects of previous interactions (incoming or outgoing) on the average child's next interaction, a child's behavior is not only dependent on their past social experiences but also where they are situated in their social environment. To understand a kindergartener's interactions in the context of their broader social relationships, we use social network analysis.

While network analysis typically relies on a single network, our analysis applies an average across multiple samples to determine differences (Schneider et al., 2012; Kim et al., 2015). We use standardized Z-scores which allow us to ask about the regulation above or below what is expected of a null model (randomizing who is connected to who while maintaining the distribution of individual interactions). Up regulation (significantly positive Z-scores) implies active behavioral mechanisms are increasing the prevalence of a given motif. Conversely down regulation (significantly negative Z-scores) implies that behavioral mechanisms avoid the patterns of given motifs. Additionally we extended our network analysis to work with two behavioral interactions (one layered on top of the other). These multilayer networks often inform on the network dynamics (including robustness and transmission speed; see (Kivelä et al., 2014; Wang et al., 2015), and reviewed thoroughly in Boccaletti et al., 2014). We, however, are mainly interested in understanding how these layers are coordinated, and so we used a layered motif approach (Yeger-Lotem et al., 2004). Single layer motifs have been called the building blocks of networks (Milo et al., 2002), and represent distinct combinations of interactions between 2, 3 or more individuals. Our dual layered motif analysis can therefore be thought of as the dynamics of smaller groups that tile to create the group structure, or alternatively they provide information on what the average child would do in a given local social environment. It is worth noting that different combinations of motifs could give similar-looking networks, in which case the underlying mechanisms of networks formation in different classrooms may vary.

While the ordering of the layers (e.g., Aggression/Submission vs. Submission/Aggression) will determine the ID numbers of regulated motifs, the underlying data distribution is not affected, and the motif IDs can be interchanged with a look up table. Again we use Z-scores (with the null indicating a lack of coordination between layers) to understand the up and down regulation that characterizes relationships between two types of interactions, further elucidating the underlying interaction patterns and group dynamics in a broad manner.

We examine the 2 layer motifs of 3 types of reciprocal interactions to quantify the network structure and determine whether transitivity (not necessarily hierarchy), is the main mechanism behind their formation. With this approach we therefore test the overarching hypothesis of whether there is regulation of layered motifs. Specifically, if transitivity is the driving force in network formation, we expect up regulation of motifs that do not violate the transitive property, and down regulation of motifs that do.

MATERIALS AND METHODS

The dataset is described elsewhere in detail (Boyce et al., 2012). Briefly, 338 kindergarteners (representing ~60% of the enrolled students) within 29 classrooms were sampled from 6 public school classrooms across Berkeley, California. The children were aged 4.8–6.3 years old and included 163 girls and 175 boys. The dataset was acquired from 2003 to 2005. Interactions were observed by trained research assistants through focal sampling over several weeks. Interactions scored were grouped into six overarching categories:

- [*Aggressive*] Chase, Physical Aggression, Approach, Relationship Aggression, Tease, Threat, and Verbal Aggression.
- [*Submissive*] Apologize, Compliance, Seeks Help, Retreat, and Submission.
- [*Leadership*] Directs Behavior, Reprimands, And Leadership Other.
- [*Followship*] Follow/Copy, Solicit Instruction, Followship Other, and Watching.
- [*Resource Struggle*] Object Struggle, Position Struggle, Student Attention, Teacher Attention, and Resource Struggle.
- [*Prosocial*] Offers a Gift, Offers Help, Protects, Speaks Nicely, and Prosocial Other.

All analyses were coded in Matlab [MathWorks]. For transition matrices, interactions were imported and sorted temporally by child. Both subsequent-interaction transition probabilities and probabilities of outgoing-after-incoming were normalized by child, then averaged over all children and normalized again. For the analysis of child interactions, individual transition probabilities (subsequent behavioral outputs) were used to perform a principal component analysis. The first two components were kept, all others were not plotted as each explained less than 7.5% of the variance.

For network measurements (assortativity coefficient, betweenness centrality, clustering, and efficiency) the brain connectivity toolbox was used, and we extended it for the layered network motif analysis (Rubinov and Sporns, 2010). For betweenness centrality, clustering, and local efficiency, individual values were calculated for each child as well as for individual classrooms. For assortativity, only classroom level values were calculated. Raw scores (x) were normalized to Z-scores based on random expectation:

$$Z = \frac{x - \mu_{random}}{\sigma_{random}}$$

Where μ is the mean and σ is the standard deviation. For each Z-Score, 10,000 random networks were used, constrained to have the same in- and out- degree distribution.

Layered network motif analysis similarly used Z-Score normalization. Each network's motif count was normalized by permuting the order of children in one network while keeping the other constant. In this way, the number of motifs remained constant within each layer of the network, but any correlation between them was destroyed:

$$Z = \frac{x - \mu_{uncorrelated}}{\sigma_{uncorrelated}}$$

For each Z-Score, 10,000 uncorrelated networks were used. Z-Scores were tested with a modified sign test against the null (no regulation—0). Probabilities were calculated as follows; if the majority of Z-scores ($z+$) for a specific motif were positive the p-value was calculated as the chance of observing this result out of the total number of classrooms (classes); $p = \binom{classes}{z+} 0.5^{classes}$. Similarly if there was a majority of negative Z-scores ($z-$), $p = \binom{classes}{z-} 0.5^{classes}$ otherwise the probability was set at 1 if the majority of Z-scores were not regulated (i.e., 0). The p-value was evaluated at an alpha value of 0.05 divided by the number of possible layered-network motifs—for dyadic motifs (9 possible motifs) this value is 0.0056, for triadic motifs (710 possible motifs) this value is 7.04 23×10^{-5}.

RESULTS

To visualize the connectivity and temporal order of interactions across all classrooms, we used transition matrices indicating the percent likelihood that one behavioral output will follow another (e.g., there is a 22.23% probability of leading after following; **Figure 1A**), and the likelihood of a behavioral output given a specific behavioral input (e.g., leadership is the most likely response (28.48%) to a prosocial interaction; **Figure 1B**). Using principal component analyses on these transition matrices we can see slight group separations based on interaction patterns

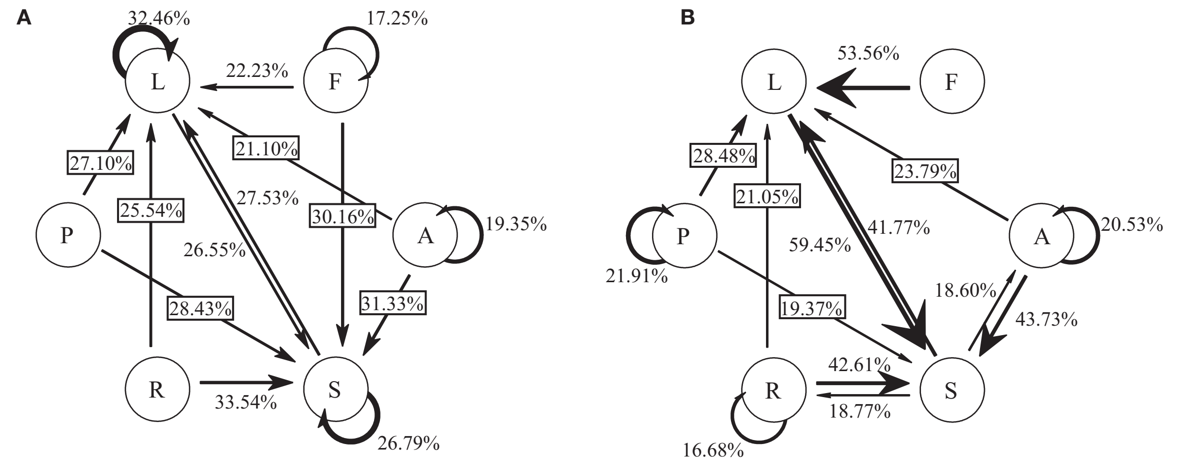

FIGURE 1 | Transition probabilities between interaction types. (A) The transition probabilities between subsequent outgoing interaction types. **(B)** The transition probabilities of a subsequent outgoing interaction given a specific incoming interaction type. Interaction types: (L)eadership, (F)ollowship, (A)ggression, (S)ubmissive, (R)esource struggle, and (P)rosoci.

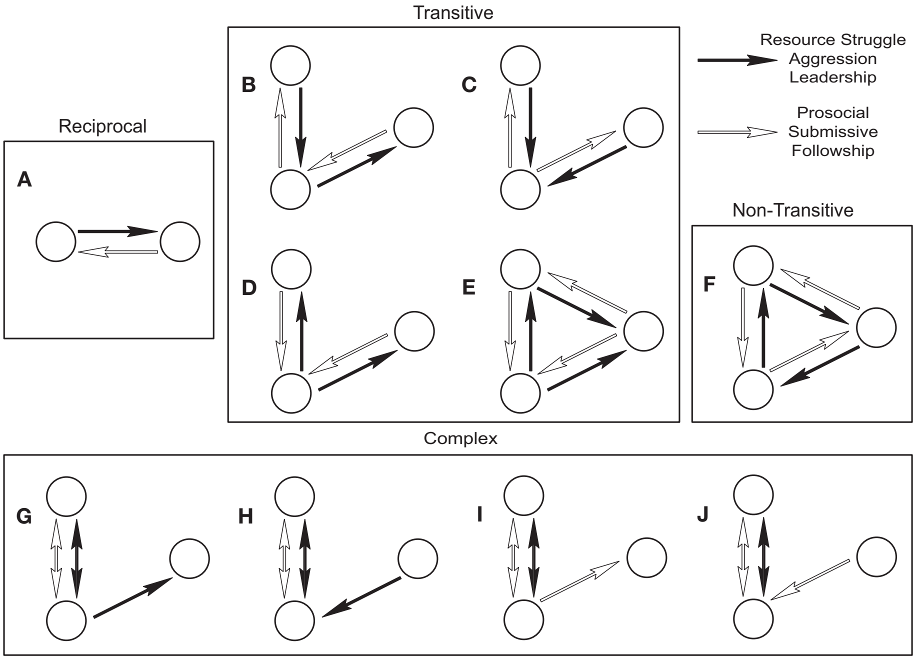

FIGURE 2 | Reciprocal, transitive, intransitive, and complex relations between interaction types. (A) Illustration of dyadic reciprocation **(B)** Pass along **(C)** Focused A **(D)** Focused B **(E)** Complete. **(F)** The non-transitive relationship **(G–J)** Complex relationships that are significantly over-represented in both Aggressive/Submissive and Leadership/Followship networks.

(**Figure S1**). We found a small group of kindergarteners that seemed separated from the rest of their classmates based on their likelihood to move from a prosocial interaction to a leadership interaction, lending support to the idea that while an average kindergartener may be a useful model, a child's behavioral repertoire can be a diagnostic tool to categorize children.

When moving from the individual child as a focus to a more group-level analysis, we aim to quantify the organization that classrooms exhibit. Social interaction networks can be described with four main parameters:

- *Betweenness centrality*: The number of shortest paths (between other nodes) that traverse a given node (e.g., the importance of an average node for information flow and network cohesion).
- *Clustering coefficient*: The likelihood that node neighbors interact amongst themselves (e.g., in a friendship network, are a node's friends are friends).

- *Assortativity*: The correlation between a node's degree (number of incoming and outgoing interactions) and the degree of his neighbors (e.g., do popular kids interact more with other popular kids).
- *Efficiency*: The inverse of the average shortest paths through a network (e.g., how quickly could information flow through the network).

The calculation of these measures are described in detail elsewhere (Newman, 2010). Once networks were extracted from each classroom for each interaction type, we compared the Z-scores for each network parameter among all students and classrooms to look at relationships between underlying mechanisms or characteristics in the formation of different interaction networks. Z-scores allow us to determine whether or not the classroom is up or down regulating aspects of organization above/below what is expected randomly. The highest correlation was found for the clustering coefficient of submissive and leadership interactions for all classrooms ($r^2 = 0.58242$; **Figure S2**). The assortativity ($r^2 = 0.21406$) and efficiency ($r^2 = 0.17387$) measures for these social interactions were also correlated, but the betweenness centrality measure was not ($r^2 = 3.519\text{e-}05$). This is a preliminary analysis; we look at correlations between all interaction types for both the same and different network measures at both the classroom and student levels. There is little to no statistical rigor associated with these comparisons, however, they provide preliminary data for future hypotheses.

To examine patterns in the reciprocal interaction pairings we looked at dyadic and triadic motifs (2 and 3 individuals respectively) of all types, rather than simply the transitive and non-transitive (cyclic) motifs. We found that the interaction pairings were not simply reciprocated in the dyadic motifs of Aggression/Submissive, Leadership/Followship and Resource Struggle/Prosocial networks (reciprocated interactions accounting for 46.78, 45.67, and 16.46% of all dyadic interactions respectively) (**Figure 2A**; see **Table S1**). To examine the level of similarity between motifs formed in the different layered networks we looked at the correlations between all up/down regulated motifs between each layered network. Down-regulated motifs were highly correlated among all three layered networks, however, the up-regulated ones were only correlated among Aggressive/Submissive and Leadership/Followship networks (**Figure S3**). These universally down-regulated motifs are often patterns where only one interaction type is present, indicating that the relationship between our interaction pairs is non-trivial and suggesting that their regulation is interdependent.

We found up regulation of one transitive triadic motif (termed "Focused A") in the Aggressive/Submissive and Leadership/Followship networks (**Figure 2C** and **Table 1**). Due to our relatively strict p-value correction, other transitive triadic motifs ("Pass Along," "Focused B," and "Transitive Triangle"; **Figures 2B,D,E**) for Aggressive/Submissive and Leadership/Followship networks had positive Z-scores and relatively small p-values but failed to achieve statistical significance. We found no evidence of down regulation of the non-transitive cyclic motif in the Aggressive/Submissive and Leadership/Followship networks (**Figure 2F**). In addition to these motifs commonly discussed in relation to hierarchy, we found up regulation of 4 complex triadic motifs (**Figures 2G–J**; **Table 1**). We note that the complex motifs of **Figures 2G,H** are the reciprocals of **Figures 2I,J**, and together with the high correlation in **Figure S3**, indicate that the relationship of Leading to Following is more similar to the relationship of Submissive to Aggressive than Aggressive to Submissive. We found an additional 27, 185, and 180 up/down regulated motifs (for Resource/Prosocial, Aggression/Submission and Leadership/Followship respectively; **Table S2**). Taken together, the results suggest transitivity is not the only social relationship organizing these interactions.

DISCUSSION

When examining dominant and subordinate behaviors within a population, the ways in which these behaviors or interactions are measured can influence the results identified. There are multiple methods of establishing winner/loser identity based on a particular signal, or behavior following a fight. Oftentimes pitting individuals against each other is done in round-robin or tournament set-ups to classify individuals as dominant or subordinate on the basis of their number of wins. Other times proxies of dominance, including body size (Archie et al., 2006, Fujimoto et al., 2011), age (Côté, 2000; Archie et al., 2006) or specific markings (Tibbetts and Lindsay, 2008), are used. The application of these calculated hierarchies to the group as a whole is limited, both in implied transitivity as well as in the sense that dyadic competition is likely not equivalent to combat within a group setting (Haemisch et al., 1994). This is in addition to the fact that designing tournaments that minimize previous-match effects are non-trivial (Russell, 1980). To generalize, the methods with which dominance and subordination are coded or classified dictates the scope of the results that can be appropriately interpreted. Furthermore, examining patterns of interactions with the intention of finding hierarchies limits and/or biases the extent to which the results characterize the social interaction patterns themselves. That is, searching for an answer to a specific question or phenomenon may lead to the acceptance of an incomplete explanation.

Here, we take a hierarchy-neutral approach to examine all possible underlying patterns in the formation of layered networks of "reciprocal" interactions. Like other studies specifically examining hierarchy, we examine interactions between individuals looking for transitive and non-transitive relationships that may indicate a hierarchical structure in the classrooms of kindergarten children (Shizuka and McDonald, 2015), with a couple of caveats. First, we do not focus on only a subset of the patterns, instead looking at all motifs to take a comprehensive approach to the mechanisms that could potentially be contributing to classroom structure. Second, we do not consider order in the hierarchical structure. That is, we avoid imposing the generally accepted order of aggressive or leading individuals being dominant to submissive or following individuals. We do this for two reasons. First, we did not have specific questions in mind where such an ordering was required

TABLE 1 | Observed, expected and *Z*-scores for motifs displayed in Figure 2.

	Motif # (*)	**Figure 2**	**Frequency**		**Expected Frequency**		***Z*-Score**		***P*-value**
			Mean	**Std**	**Mean**	**Std**	**Mean**	**Std**	
Resource struggle/Prosocial	3 (3)	A	2.93	2.62	1.78	1.16	0.94	1.60	1.87E−02
	470 (470)	B	0.45	0.91	0.10	0.09	1.13	2.96	7.99E−03
	424 (574)	C	0.17	0.60	0.07	0.07	0.44	2.10	8.85E−04
	574 (424)	D	0.41	1.15	0.07	0.08	1.11	2.92	1.87E−02
	622 (622)	E	0.00	0.00	0.00	0.00	−0.03	0.04	1.00E+00
	678 (678)	F	0.00	0.00	0.00	0.00	−0.01	0.02	1.00E+00
	44 (242)	G	0.45	0.99	0.29	0.49	0.22	0.99	1.00E+00
	45 (243)	H	0.41	0.82	0.25	0.42	0.28	1.12	1.00E+00
	242 (44)	I	1.66	3.56	0.69	1.17	0.65	1.99	1.00E+00
	243 (45)	J	1.55	3.70	0.64	1.10	0.35	1.08	1.00E+00
Aggressive/Submissive	3 (3)	A	13.21	5.45	5.47	2.12	3.73	1.75	**1.86E-09**
	470 (470)	B	3.24	3.39	0.44	0.23	3.69	4.14	7.99E−03
	424 (574)	C	4.00	3.55	0.47	0.30	3.99	3.22	**4.42E−05**
	574 (424)	D	2.62	2.91	0.27	0.19	4.23	4.70	8.85E−04
	622 (622)	E	0.66	1.20	0.05	0.05	2.57	4.21	9.67E−02
	678 (678)	F	0.10	0.41	0.01	0.01	0.81	3.28	1.00E+00
	44 (242)	G	8.52	8.14	2.24	2.03	2.67	1.84	**6.81E-06**
	45 (243)	H	9.10	7.38	2.63	2.02	2.48	1.75	**7.56E−07**
	242 (44)	I	1.86	1.94	1.29	1.17	0.46	1.15	9.67E−02
	243 (45)	J	1.79	1.72	1.02	0.91	0.69	1.14	6.44E−02
Leadership/Followship	3 (3)	A	16.66	10.25	5.93	2.92	4.62	2.31	**1.86E−09**
	470 (470)	B	6.21	8.79	0.47	0.37	5.90	6.63	8.85E−04
	424 (574)	C	6.14	8.09	0.63	0.58	4.79	4.88	**7.56E−07**
	574 (424)	D	2.72	3.30	0.30	0.18	3.65	3.91	7.99E−03
	622 (622)	E	1.45	2.40	0.08	0.11	3.67	5.00	1.44E−01
	678 (678)	F	0.10	0.41	0.00	0.01	0.82	3.27	1.00E+00
	44 (242)	G	0.90	1.35	0.69	0.65	0.14	0.98	1.87E−02
	45 (243)	H	1.55	1.92	0.85	0.74	0.52	1.18	1.00E+00
	242 (44)	I	8.14	7.80	1.65	1.37	3.03	2.46	**4.42E−05**
	243 (45)	J	5.00	4.52	1.12	0.97	2.37	1.75	**4.42E−05**

*Significant Z-Scores are indicated in bold. *Motifs IDs are indicated along with their reciprocal IDs if the layers were reversed.*

and second, the order applied to these interaction types depends on the frame of reference, or more specifically, what would be defined as a "win." Specifically, if we were to define winning as controlling information in a group, all six interactions we examine could be considered "dominant" to their partner interaction depending on the frame of reference. Leaders could be dominant because they choose which followers to share information with or followers could be dominant because they get information from all those they follow; aggressors fight and access information, submissives do not have to fight to get information; prosocial individuals control sharing of information or those involved in resource struggle retain information they hold. Because we do not impose order on the interactions we are investigating, we need not refer to one or the other as dominant or subordinate (those labels would depend on context), rather we simply refer to their networks as having a transitive structure or not.

We first showed that these interactions were not as reciprocal as they are often considered (**Figures 1B**, **2**). That is, a Leadership interaction does not ensure a Followship response, similarly for Aggression and Submission, and Prosocial and Resource Struggle. We note here that these dyadic motifs do not encompass order of interactions or timing as the individual analysis of transitions do. Both incoming Aggression then outputting Submission and incoming Submission then outgoing Aggression, over any time period, would be considered reciprocal. When we examine the regulated motifs in all three layered networks, we find that there are similarly high correlations in down-regulated motifs between the three layered networks (**Figure S3A**). However, only the Aggressive/Submissive and Leadership/Followship layered networks showed correlation for the positively regulated motifs (**Figure S3B**). This suggests that while there is a shared structure of highly unlikely motifs (mostly consisting of motifs of one layer only), the Resource Struggle/Prosocial has a different structure compared to the Leadership/Followship and Aggressive/Submissive networks.

Figure 2 shows the up regulated motifs common to Aggression/Submission and Leadership/Followship layered networks. The most intuitive are those in **Figures 2B–E**, and we can easily imagine kindergarten children behaving in such reciprocal ways (e.g., two kindergarteners being mean to one other; Focused A). The final 4 motifs shown in **Figure 2** are more difficult to understand in terms of children's interactions. They illustrate how non-intuitive, abstract, and non-hierarchical patterns of interactions can be found using unbiased network and motif approaches. Furthermore, by examining the order of layers in the networks, we can observe which behavioral relationships are similar. We see higher correlations between Leadership/Followship and Submissive/Aggressive than Leadership/Followship and Aggressive/Submissive (**Figures 2G–J** and **Figure S3**). This hints that the mechanisms and environmental pressures which shape the interactions of social "leaders" may be more similar to the interactions of social "submissives" and not social "aggressives."

The up regulation of the transitive motif Focused A indicates that transitivity is at least partially involved in the formation of these layered network structures. Transitivity is perhaps the most important property of structural hierarchy in a group (the other two being stability and linearity) as it, by definition (A>B and B>C then A>C), creates the characteristic orderly stratified layers. We also found complex combinations of the expected reciprocal interactions: two individuals in a fully connected dyad interacting with a third (**Figures 2G–J**). None of these can be created by overlapping the above transitive motifs, and their up regulation in both Aggressive/Submissive and Leadership/Followship networks is intriguing. While we cannot rule out "un-resolved" hierarchy (i.e., these are fingerprints of hierarchical establishment itself), another exciting possibility hints at more underlying mechanisms of network structure than simply hierarchy.

Boyce examined the influence of socioeconomic status on hierarchies in the same kindergarten classroom data we have presented here (Boyce et al., 2012). While we were aware that classrooms were not homogeneous for characteristics including SES, teacher profiles, instructional methods etc., we did not separate the dataset according to these external factors. That is, we did not perform separate analyses on low SES vs. high SES, similar for other potentially confounding factors which may be at play. We note, however, that our statistic (sign test) is non-parametric and does not require all classrooms to behave similarly to draw overall conclusions.

In children, the ability to examine behaviors in both one-on-one situations and within a larger social group could be used as a tool for finding behavioral abnormalities. Much of the diagnosis process for autism is based on behavioral observations of a child and understanding how such an individual would appear within, be affected by, and affect their social environment, could go a long way to clearer diagnoses (Stone et al., 1990). A potential avenue of diagnostic implication is the nurturing of extended social interactions within a group. By identifying normal rates of participation within a group via network motifs, one may be able to identify abnormal motif participation by students who may require more intervention to be able to properly flourish within a highly structured group (so called "orchid" as opposed to "dandelion" children Ellis and Boyce, 2008). The methodology outlined here could therefore provide a framework for identifying children to more readily ensure their support in an appropriately protective environment if they participate in abnormal network relationships (i.e., motifs).

The mechanisms used to understand social networks of kindergarten children here are also applicable on a more general scale to any group of individuals where interactions and identities can be readily observed and scored. We have shown that social interactions are not isolated behaviors and that the commonly paired types (Leadership/Followship, Aggression/Submission) interact with each other in a complex manner unpredictable given simple rules of reciprocation and transitivity. We further predict this method can be extended to more than two interaction types and to quadratic motifs and as computational resources improve, and will continue to improve our understanding of the multi-layered networks that more accurately represent the natural social environment in humans and other animals.

AUTHOR CONTRIBUTIONS

JL conceived of study together with JS and MG. Contributed to writing the paper with JS and MG and co-authors. JS wrote the code, conceived study and helped write paper. MG wrote first draft, conceived study. WB, NB, and NA provided data for analysis.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fpsyg.2016.00276

Figure S1 | Principal Component (PC) analysis of subsequent interaction transitions. The first and second principal components account for 22.11% of the total variance in a kindergartener's transition probabilities between interaction types. There appears to be a subset of kindergarteners that are defined by their shared propensity to transition from Prosocial to Submissive. Factors are plotted if their loading was greater than 0.25. Kindergarteners are colored by classroom.

Figure S2 | Correlation analysis between clustering of Submissive interactions and Leadership interactions. (A) The correlation when measuring local clustering. **(B)** The correlation when measuring the average clustering per classroom. Kindergarteners are colored by classroom.

Figure S3 | Correlation analysis using the *Z*-scores of the triadic motifs. (A) The Leadership/Followship network displays correlated significant motifs when compared to the Submissive/Aggressive network, even with very highly up-regulated motifs. **(B,C)** The Resource Struggle/Prosocial network correlates well with under-represented motifs, but poorly with over represented motifs with both the Submissive/Aggressive and Leadership/Followship networks. Motifs were excluded if they were never detected as significantly different (*Z*-scores) in any network. The ordering of the network layers was arranged to generate the higher correlation.

Table S1 | Observed, expected and *Z*-scores for dyadic motifs. Significant *Z*-Scores are indicated in bold. *Motifs IDs are indicated along with their reciprocal IDs if the layers were reversed.

Table S2 | Observed, expected and *Z*-scores for triadic motifs. Significant *Z*-Scores are indicated in bold. *Motifs IDs are indicated along with their reciprocal IDs if the layers were reversed.

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