Social network dynamics and information transmission in wild black-capped chickadees *(Poecile atricapillus)*

Theresa Jones

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University of Ottawa

Abstract

Animals exhibit a wide variety of social behaviours that are shaped by the external group social structure. Thus, understanding social behaviours and processes requires examining the individual social associations that form the basis of a group's social network. The first objective of this thesis was to assess the consistency of social position within wild networks of black-capped chickadees (*Poecile atricapillus*) and to evaluate the effects of individual behavioural traits (exploratory personality and social dominance) on network position. Intra-annual social position was found to be repeatable and centrality increased with dominance rank, suggesting that dominant individuals occupy more central positions. The second objective of this thesis was to evaluate how network position and individual traits influence the transmission of social information through groups; the use of information acquired by other group members is expected to be an important benefit to group living. Social information regarding the location of novel foraging patches was observed to be transmitted through all eight chickadee groups. The rate of information transmission was found to be positively associated with dominance rank, but was not influenced by exploratory personality, indicating that dominant individuals may have greater access to social information than more subordinate individuals. The final aim of this thesis was to assess if social information transmission varied between urban and rural environments, as increased resource variability in more rural sites was expected to lead to higher reliance on social foraging cues. However, no effect of level of urbanisation was detected on the transmission of social information regarding novel food sources, which may indicate a habitat-independent strategy of social information use in chickadees. In general the results from this thesis indicate the importance of dominance status on individuals' position within a social group, which can lead to differential exposure to social processes, such as social information transmission.

Résumé

Les animaux présentent une grande variété de comportements sociaux qui sont façonnés par la structure sociale du groupe. Ainsi, la compréhension des comportements et des processus sociaux repose sur l'étude des associations des individus qui forment le réseau social d'un groupe. Le premier objectif de cette thèse était d'évaluer la répétabilité de la position sociale des individus au sein de réseaux sociaux de mésanges à tête noire (*Poecile atricapillus*) en nature et d'évaluer les effets des traits comportementaux individuels (personnalité exploratoire et dominance) sur la position dans le réseau. La position des individus dans leur réseau était hautement répétable au cours d'une saison non-reproductive et leur centralité augmentait avec leur rang de dominance, ce qui suggère que les individus dominants occupent des positions plus centrales. Le deuxième objectif de cette thèse était d'évaluer comment la position dans le réseau et les traits individuels influent sur la transmission d'information sociale; l'utilisation d'information acquise par les autres membres du groupe est perçue comme un avantage important de la socialité. La transmission d'information sociale concernant la localisation de nouvelles parcelles alimentaires a été observée dans nos huit groupes de mésanges. Le taux de transmission d'information était positivement associé au rang de dominance des individus, mais n'était pas influencé par leur vitesse d'exploration, ce qui suggère que les individus dominants ont un meilleur accès à l'information sociale que les subordonnés. Le but final de cette thèse était d'évaluer si la transmission d'information sociale diffère entre les milieux urbains et ruraux. La variabilité accrue dans la disponibilité des ressources aux sites plus ruraux devrait conduire à une plus grande dépendance sur l'information sociale. Cependant, aucun effet du niveau d'urbanisation n'a été détecté sur le taux de transmission de l'information sociale en lien avec de nouvelles sources de nourriture, ce qui pourrait indiquer une constance dans l'utilisation d'information sociale chez cette espèce. En général, les résultats de cette thèse soulignent l'importance du rang social sur la position des individus au sein de leur groupe, qui peut conduire à l'exposition différentielle aux processus sociaux, tels que le transfert d'information sociale.

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Statement of Contributions

Chapter 2 and 3 of this thesis have been prepared as manuscripts. As such, some content may overlap between chapters and the pronoun “we” is used as manuscripts will be submitted with additional authors. However this thesis was written by myself.

Chapter 2: The statistical analysis in this chapter were designed and executed in collaboration with postdoctoral fellow Julian Evans. Measurements of dominance for this chapter were collected by MSc student Isabelle Devost. Honours students Zac Wagman and Sébastien Dubus participated in field data collection for network data. Honours student Jessica Cloutier contributed to personality data collection in the field.

Chapter 3: The statistical network based diffusion analysis (NBDA) required for this chapter was performed in collaboration with postdoctoral fellow Lucy Aplin (University of Oxford). Measurements of dominance for this chapter were collected by MSc student Isabelle Devost. Honours students Zac Wagman and Sébastien Dubus participated in field data collection for networks and the discovery trials. Honours student Jessica Cloutier contributed to personality data collection in the field.

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CHAPTER 1

General introduction

Sociality exists in a wide range of taxa, from insects to mammals, which exhibit a variety of social structures ranging from small kin-groups to colonial living, and can vary in stability from cohesive units to highly fission-fusion societies (Kerth 2010). There are a number of costs and benefits to living in groups. For instance, social animals are expected to experience reduced costs of predator vigilance. They may also benefit from increased foraging efficiency through group searching or access to social information, while in return enduring higher competition costs, and increased susceptibility to communicable diseases (reviewed by Krause & Ruxton 2002).

Traditionally, the early study of animal social behaviour considered social structure to be a result of the sum of individual innate interactions between pairs of conspecifics (Tinbergen 1953). As the study of animal sociality expanded, a broad top-down classification of social structures was proposed (Wilson 1975). Wilson's (1975) classification method was designed to be generally applicable to any study system and included ten qualities to describe social organization: (1) group size, (2) demography, (3) cohesiveness, (4) patterns of connectedness, (5) permeability, (6) compartmentalisation of groups, (7) role differentiation, (8) coordination of behaviour, (9) information flow, and (10) fraction of time devoted to social behaviour. However descriptions of social structures, particularly for non-primates, were often limited to measures of group size and demography, as these taxa were not considered to have the capacity for more complex social structure (Whitehead 2008; Hasenjager & Dugatkin 2015).

Group and population level effects of social interactions, particularly in the context of the evolution of cooperative behaviour and social foraging strategies, have been assessed by ecologists through game theoretic models (Maynard Smith 1982; Dugatkin & Reeve 1998). The producer-scrounger model for instance, has been frequently employed to model evolutionary stable strategies of social foraging behaviour (Barnard & Sibly 1981; Giraldeau & Dubois 2008).

However, game theory models generally assume all individuals are able to mix freely within a population and thus interact randomly in their group. Such assumptions of homogeneity of interactions have been found to be over simplified, and therefore variation between individual associations is an important factor to consider when examining population level consequences (Ohtsuki *et al.* 2006).

Taking a different approach on the study of sociality, Hinde (1976) introduced a more bottom-up framework that focused on interactions and relationships between individuals as the base levels of study. This approach placed the emphasis on dyadic interactions, and allows for the consideration of how attributes of the specific individuals involved shape the social connection between them. While also initially restricted to primatology, Hinde's framework eventually began to be employed in a wide range of taxa (reviewed by Whitehead 2008). However, this focus on the dyadic level does not put individual behaviours back into the context of the entire social group or wider population, particularly as dyads are often considered in isolation from the broader social group (Hinde 1982; Hasenjager & Dugatkin 2015).

An individual's position within a social group is dependent on all other individuals in a given group, as well as the connections between group members. As such, the study of social behaviours, processes and sociality in general require studying individuals within the context of their natural social group. Historically, the use of such an interaction based framework in natural populations has been hampered by the challenge of recording associations between individuals, which requires individuals to be uniquely identifiable, as well as the ability to detect interactions that may occur briefly or be difficult to observe. However, recent advancements in animal borne recording technology (Ryder *et al.* 2012; Krause *et al.* 2013) have begun to allow for the collection of large interaction (observed social tie, such as grooming event) or association (cooccurrence in time or space) based data sets. Additionally, developments in statistical techniques, in particular randomisations methods and the computing power required for such analyses, have further aided the implementation of network approaches (Croft, James & Krause 2008; Brent, Lehmann & Ramos-Fernández 2011). This has allowed for the use of social network analysis as a general approach to the study of animal social dynamics.

Social network analysis

Social network analysis is a cohesive quantitative framework that has recently been applied by ecologists to study a wide range of questions relating to sociality (see reviews by Croft *et al.* 2008; Wey *et al.* 2008; Sih, Hanser & McHugh 2009; Krause *et al.* 2014; Hasenjager & Dugatkin 2015; Farine & Whitehead 2015). This type of analysis is not entirely new to the study of animal sociality, as various measures have been previously developed to quantify the associations between interacting individuals or classes of individuals (Cairns & Schwager 1987) and used in association based matrices, which form the basis of social networks (see Sade 1989; Whitehead 2008; Pepper, Mitani & Watts 1999). However, these methods have generally been used to provide a descriptive view and have lacked rigorous and standardised statistical methods. The key advantages offered through social network analysis are to provide a unified framework, that is scalable from individual to community level studies, and incorporate statistical methods necessary to perform hypothesis testing (Croft *et al.* 2008; Krause *et al.* 2014; Farine & Whitehead 2015). Importantly, social network analysis allows for the consideration of the effects of both direct and indirect connections between individuals (Brent 2015), and accounts for individual variation in social connections.

Social network metrics can be broadly divided into two categories: node-based or individual metrics that are calculated for each individual within a network, describing an individual's social ties (e.g. number of connections, position within network), and global measures that are measured at the level of the network to describe overall social structure (e.g. network density, degree of assortativity) (see reviews by Croft *et al.* 2008; Wey *et al.* 2008; Krause *et al.* 2014; Hasenjager & Dugatkin 2015; Farine & Whitehead 2015).

Social position

Recently there has been increased interest in the study of how individuals fit within their overall group social structure. Previous studies of social structure have demonstrated that an individual's specific position within its group can greatly influence a wide variety of factors, including risk of disease (Godfrey *et al.* 2009; MacIntosh *et al.* 2012), access to mates (Oh & Badyaev 2010), breeding territories (Ryder *et al.* 2008; Farine & Sheldon 2015), and information (Atton *et al.* 2012; Aplin *et al.* 2012; Farine *et al.* 2015), as well as long-term reproductive success (McDonald 2007). As such it is important to study the variables that allow or restrict individuals to specific social positions within their group.

Several network based studies have demonstrated that individual characteristics, such as age, sex, social status and personality (consistent individual differences in behaviour over time and/or across contexts (Réale *et al.* 2007)), can influence an individual's social network position. For example, exploratory personality type has been linked to network position, with fast explorers found to be more central in comparison to slower explorers (Schürch, Rothenberger & Heg 2010; Snijders *et al.* 2014). Snijders *et al.* (2014) proposed this may indicate that the costs and benefits related to maintaining certain social positions may vary between behavioural types. For instance if faster explorers are better able to benefit from social processes, such as access to information, this could balance the increased costs of frequent interactions (e.g. increased aggression) that may result from central positions (e.g. Schürch *et al.* 2010). Social dominance has also been suggested to influence social network position, with dominants having being found to maintain more central network positions than subordinates (Schürch *et al.* 2010; King, Clark & Cowlishaw 2011; MacIntosh *et al.* 2012). The higher centrality of dominant individuals has been proposed to result from dominants being more frequently involved in interactions within a group (e.g. involved in highest number of aggressive confrontations; Schürch *et al.* 2010 or grooming interactions; MacIntosh *et al.* 2012). Additionally, the high centrality of dominants has been suggested to be a product of dominant individuals' increased tolerance of others, for instance at a foraging patch, due to having access to highest quality patches and reduced competitive effects through their social status (King *et al.* 2011). However this relationship between dominance and centrality is not seen in all cases, such as was observed in multi-species passerine flocks, in which dominants were not found to be significantly more central than subordinates (Farine, Garroway & Sheldon 2012). It has also been cautioned that the individual attributes (such as dominance status or personality type) that have been found to influence social network position may in fact be the driving factors of any fitness related effects rather than network position itself (Formica *et al.* 2012). Thus understanding the relation between such individual traits and network metrics is important when making further inferences about the effects of network position.

In addition to individual characteristics, environmental factors have been shown to shape the social interactions of groups (e.g. Orpwood *et al.* 2008; Henzi *et al.* 2009). Due to the difficulties of directly comparing social networks (Croft *et al.* 2008), limited work has been done to assess the effects of environmental variables on network structure and metrics and the few studies that have considered networks in different environments have produced mixed results. For instance, several studies have suggested that variation in overall social structure, such as network connectivity and the stability of subunits, was related to differences in habitat complexity (a broad term generally encompassing the spatial distribution, size, diversity and density of physical elements; Kovalenko, Thomaz & Warfe 2011) (Sundaresan *et al.* 2006; Rubenstein *et al.* 2007; Leu *et al.* 2016). For instance, higher network density and stability was observed in a more structurally complex habitat in sleepy lizards (*Tiliqua rugosa)* (Leu *et al.* 2016). Similarly, while studying habitats with varying levels of anthropogenic disturbance Mokross *et al.* (2014) found that association rates in mixed-species bird flocks declined with increasing fragmentation. The availability and distribution of resources has also been found to influence social structure. For instance, resident killer whales (*Orcinus orca*) showed higher network connectivity when food availability was higher (Foster *et al.* 2012) and research on European shore crabs (*Carcinus maenas*) found that clumped food distribution drove the formation of social clusters (Tanner & Jackson 2012). However, several other network based studies have found that network structure and individual social position did not vary in response to habitat complexity (Edenbrow *et al.* 2011; Jacoby *et al.* 2014) or with variation in vegetation structure and climate (Stanley & Dunbar 2013). Thus, understanding the relationship between environmental characteristics, such as habitat type and resource distribution, and social structure requires further research. Importantly, anthropogenic alterations to habitat, such as through urbanisation, can have significant impacts on habitat structure which in turn can lead to previously understudied changes in social structure.

Social processes

Social processes, such as the transmission of communicable diseases or information through a group, depend on both the structure of the group and an individual's position within the group (e.g. Christley *et al.* 2005; Böhm, Hutchings & White 2009; Aplin *et al.* 2012; Farine *et al.* 2015). Thus certain individuals within a network may have significant impacts on the overall group; such as seen when highly connected individuals (termed 'super-spreaders') greatly increase the spread of a disease (Paull *et al.* 2012) or when removal of specific individuals (termed 'brokers') breaks a single connected network into separate networks (Lusseau & Newman 2004). More generally individuals that have a disproportionate effect on their social network have been termed 'keystone individuals' or may occupy a 'keystone role' (Modlmeier *et al.* 2014). Therefore, the study of social processes also requires an understanding of how individuals fit within their social group.

Social processes, such as social learning and social information use - defined as learning or information acquisition influenced by the observation of, or interaction with others (Dall *et al.* 2005; Hoppitt & Laland 2008) - can be beneficial to group living animals. In particular, social learning has been suggested to account for rapid diffusion of innovations through groups (Hoppitt & Laland 2008) which can lead to persistent group behaviours or traditions (Galef 2004; Laland & Galef 2009). Additionally, the use of social information has been found to reduce costs associated with information acquisition, although such information typically remains less reliable (Kendal *et al.* 2005; Galef 2009).

Accurately identifying information and learning processes as occurring socially rather than through asocial methods has remained difficult (Galef 2004; Kendal *et al.* 2009). Previously, diffusion curve analysis has been used to attempt to detect social transmission through groups (for example; Lefebvre 1995). However, this type of analysis has been shown to not accurately distinguish between social and asocial information use, and relies on the assumption that interactions occur homogenously within a group (Reader 2004). As recent social network studies have demonstrated, this assumption does not hold in natural social groups, in which individuals may vary greatly in the strength and number of their social connections. As such, social network methodology, which accounts for these individual variations in social connections provides a more realistic approach to studying social processes than previous diffusion curve analysis (Franz & Nunn 2009). In particular, network based diffusion analysis (NBDA) has been developed to detect if the diffusion of information or innovations through a group is occurring through social means, that is, whether the diffusion through the network corresponds with the connections between the individuals within the network (Franz & Nunn 2009, 2010; Hoppitt, Boogert & Laland 2010).

Individual characteristics have previously been shown to influence social behaviours and processes. For example juvenile female and subordinate male blue tits (*Cyanistes caeruleus*) were found to be more likely to acquire information socially compared to dominants and adults (Aplin, Sheldon & Morand-Ferron 2013b), supporting the hypothesis that individuals will prioritise social information when in a disadvantaged position ("copy when dissatisfied"; Galef 2009). Similarly great tits (*Parus major*) that expressed a fast exploring personality type were found to utilise social information more readily than slower explorers (Marchetti & Drent 2000). This difference in information use has been proposed to be part of a consistent alternate foraging technique between personality types, which has been shown to be heritable in this species (Dingemanse *et al.* 2002; Drent, Oers & Noordwijk 2003). In a similar fashion, social dominance has been shown to influence group foraging tactics, such as seen by the preferential use of scrounging tactics by more dominant individuals (Liker & Barta 2002).

It has also been proposed that environmental factors can influence social processes. This has been demonstrated by one previous network study of captive fish shoals in which information transmission occurred only in a more complex habitat type in comparison with a structurally simple habitat (Webster *et al.* 2013). Thus, it is also important to consider the influence that variation in environment has on social behaviours and processes, particularly as this has not previously been examined in natural environments.

Network consistency

Due to the nature of examining connections between individuals in a group, social network analysis violates the commonly held assumption of independence required by most parametric statistical methods. Thus, the use of network methodologies requires a number of specific statistical approaches. In particular, hypothesis testing utilising network data requires comparing an observed test statistic to a null distribution obtained through data randomisations (Croft *et al.* 2008; Croft 2011). There are a number of approaches to randomising network data, and a variety of factors to consider, such as retaining spatial restrictions or number of associations observed; yet as long as appropriate permutations are performed, social network analysis offers the best methodology to understanding behaviours and processes occurring in social groups (see Farine & Whitehead 2015).

Although recent studies have begun to use social network analysis methods to examine how intrinsic traits correlate with individual network metrics, there has been limited work assessing the consistency of these social network metrics (James, Croft & Krause 2009). To fully understand the fitness consequences that may arise from holding a specific position within a social group, it is important to also understand the temporal stability of social network metrics (Wilson *et al.* 2013). To date, most studies using a social network approach have looked at only a single network, taken from a particular moment in time (but see Boogert, Farine & Spencer 2014; Jacoby *et al.* 2014; Aplin *et al.* 2015), and as such, the consistency of network metrics has been generally assumed rather than examined empirically.

Research goals

The main goals of this thesis are to examine the effects of individual characteristics and external environment on social position and processes through network analysis. To address these research aims, I studied eight groups of black-capped chickadees (*Poecile atricapillus*) sampled from in and around Ottawa, ON. Black-capped chickadees are resident passerines found to winter in a variety of habitat types including forest edges, parks and urban environments, who form social flocks in the fall that are maintained throughout the non-breeding season (Foote *et al.* 2010). Generally these social flocks have been described as having stable membership and exhibiting strongly linear dominance hierarchies (Smith 1991), although there has not been any work to assess if individuals maintain the same positions within their group throughout the winter, or if membership is constant but specific associations are fluid. As opposed to a number of related Parids commonly studied, black-capped chickadee groups establish and maintain highly linearly-structured dominance hierarchies, allowing for the additional examination of the relationship between social status and social behaviour. Moreover, personality traits have been previously quantified both in captivity (Verbeek, Drent & Wiepkema 1994; Dingemanse *et al.* 2002) as well as in the field (Kluen *et al.* 2012) in other members of the family Paridae, and differences in these personality types have been linked to social structure (Aplin *et al.* 2013a). Due to these described qualities, their general abundance and small group sizes which allow for replicate sampling, chickadees are a particularly useful model to address the questions posed in this thesis. Specifically, chapter 2 addresses temporal consistency in chickadee social networks and the effects of personality and dominance status on social position, while chapter 3 examines the diffusion of social information through these networks, and how individual characteristics and the degree of urbanisation of the habitat influence this transmission.

CHAPTER 2

Temporal consistency in social position and the role of individual behavioural traits in foraging networks

Abstract

Sociality leads to a variety of costs and benefits for group living animals. As the trade-off between such costs and benefits has been found to vary between individuals, based on their position within the overall group structure, it is important to understand both the structure and stability of social groups when seeking to understand the implications of social behaviours. Here we utilise repeat social networks to assess the temporal stability of individual social position. We then evaluate the effects of individual behavioural traits (exploratory personality and social dominance) in wild networks. To assess network consistency, we sampled eight foraging networks of wild black-capped chickadees (*Poecile atricapillus*) weekly throughout the non-breeding season, and applied network-specific randomisations to test for repeatability of network centrality. We found that intra-annual social network position and group size were repeatable. Additionally, network centrality was found to increase with dominance rank, but was not observed to be significantly influenced by exploratory personality type. Our study is one of only a few to date to evaluate the common assumption that observed network metrics remain consistent over time. We provide evidence that social position may reflect a stable measure of sociability. We also observed that more dominant individuals maintained more central network positions which may lead to differential fitness consequences between social classes, particularly in hierarchically structured social groups.

Introduction

Animals experience a variety of costs and benefits associated with sociality (Krause & Ruxton 2002). Recently ecologists have begun to examine how these cost-benefit trade-offs may vary for individuals within groups, as it has been demonstrated that individuals can differ in their social connections and position within the social structure (Whitehead 1997; Croft *et al.* 2008; Krause *et al.* 2014). It has previously been shown that an individual's position within a social group can have important influences on fitness, such as by altering access to mates (Oh & Badyaev 2010) and overall reproductive success (McDonald 2007) or through increasing susceptibility to disease and parasites (Christley *et al.* 2005; MacIntosh *et al.* 2012). However, to date there is limited understanding as to what factors determines an individual's social position.

There has been interest in examining how the intrinsic attributes of individuals may influence their ability to obtain and maintain specific social positions within a group. In the past decade ecologists have adopted social network analysis, a formal quantitative framework, to address questions related to social interactions and to assess the importance of such variation in social position (Croft *et al.* 2008; Krause *et al.* 2014). Importantly, social network analysis considers both direct and indirect interactions between individuals (Brent 2015) and implements standardized metrics to evaluate social position and social structure at both the individual and group levels (Croft *et al.* 2008; Krause *et al.* 2014; Farine & Whitehead 2015). Social network-based studies have demonstrated that individual attributes, such as age, sex (Lusseau & Newman 2004; Aplin *et al.* 2013a) and developmental stress (Boogert *et al.* 2014a) can influence an individual's social associations and network position.

In particular, there has been interest in the influence of animal personalities, or consistent individual differences in behavioural responses (Réale *et al.* 2007), on social interactions and group social structure. For instance, it has been shown that personality traits can affect social associations (reviewed by Krause et al. 2010), and this can in turn influence social processes such as collective decisions (e.g. Brown and Irving 2014) and information access (e.g. Nomakuchi et al. 2009). Animal personalities have frequently been examined in terms of the proactive-reactive axis, with proactive individuals being defined as more aggressive, bold and exploratory, while reactive individuals are less aggressive, shy and have reduced exploration (Sih, Bell & Johnson 2004). Previous work has demonstrated that shyer and slow exploring individuals tend to have fewer, but stronger associations than bolder and fast exploring personality types in several taxa (fish; Pike *et al.* 2008; Croft *et al.* 2009; birds; Aplin *et al.* 2013a). These differences in association patterns have in turn been found to influence social position, with bolder and more exploratory individuals tending to have more central network positions (Schürch *et al.* 2010; Aplin *et al.* 2013a; Snijders *et al.* 2014).

Social status is another important trait that is expected to influence individuals' social associations and position within social groups. Dominance hierarchies are a feature observed in many social species, and are expected to reduce competitive costs associated with social living (Piper 1997; Preuschoft & van Schaik 2000). Particularly, in species with strongly linear dominance hierarchies, social status may influence which individuals directly interact; for instance, individuals may avoid interacting when interaction costs are high, or when a contest outcome has been pre-determined based on observations of third-party associations (Shizuka & McDonald 2012). As such, social status may be expected to influence an individual's ability to hold a specific position within its social group. Indeed, previous work has found that dominant individuals may occupy more central roles within their network (Schürch *et al.* 2010; King *et al.* 2011; MacIntosh *et al.* 2012; Hughes & Driscoll 2014).

Although it has been suggested that individual traits may influence social position, and there is some evidence that network metrics may be heritable (Fowler, Dawes & Christakis 2009; Lea *et al.* 2010; Brent *et al.* 2013), an important consideration to take into account when assessing the biological importance of network position is the temporal stability of network metrics (Wilson *et al.* 2013). If social networks are highly unstable over time, then measures of network metrics are unlikely to reflect long term fitness consequences. However to date, most social network studies have only considered one network over a single time period (but see Blumstein, Petelle & Wey 2013; Jacoby *et al.* 2014; Aplin *et al.* 2015b). Thus, many studies have described networks in a static state that may fail to accurately describe the dynamics of the social interactions of interest (Hock & Fefferman 2011). When determining the importance of individual variation in social network position and the individual factors that may determine social position, it is necessary to assess consistency in network position (Wilson *et al.* 2013), something that has been generally been assumed, but rarely tested.

In this study we first aim to describe the social networks of multiple groups of black-capped chickadees. Chickadees form social foraging flocks during the non-breeding season (October-April) that generally range in size from 3-12 unrelated individuals (Smith 1991). Throughout the winter, flocks remain within a local home range which has been found to vary in size from approximately 8.8 to 22.6 ha (reviewed in Smith 1991). Chickadees are thus particularly well suited to the investigation of social associations and the stability of these associations through time via repeated sampling.

As the majority of previous network studies have only assessed networks during a single time point, we aim to determine the consistency of network positions over time, by measuring repeated weekly networks across the non-breeding season. We then ask if individual behavioural characteristics, namely exploratory personality and dominance, influence the network position, in particular the centrality, of an individual. Centrality is an important metric of social position, especially in terms of measuring 'flow' through groups, for instance in the case of information or disease transmission (Borgatti 2005). Highly central individuals will be to able reach or influence other individuals in the network faster than individuals occupying more peripheral network positions. As previous studies have suggested more proactive personality types may maintain a higher number of associations and more central network positions (Schürch *et al.* 2010; Aplin *et al.* 2013a; Snijders *et al.* 2014) we expect that faster exploring birds will have higher centrality than slower explorers. Previous work has also indicated that dominant individuals may have more central network positions (Schürch *et al.* 2010; King *et al.* 2011; MacIntosh *et al.* 2012; Hughes & Driscoll 2014) and in black-capped chickadees, dominant individuals have been found to have increased access to social information (Jones et al. in rev; see Ch. 3), which is expected to be related to higher network centrality. As such, we expect that more dominant individuals will be better connected within their network and thus have higher centrality scores.

Methods

Study system

Black-capped chickadees were captured at eight study sites located in and around Ottawa, ON, Canada (45^{o} 25' N, 75^{o}, 40'W) between September 26 and December 9 2014, using mist nets and potter's traps baited with sunflower seeds. Sites were located in urban (N = 4) or rural

(N = 4) environments that were semi-forested regions containing a mix of both coniferous and deciduous forest. Urban sites were located in city parks, within 30-90 m of residential development, while rural sites were > 15 km from Ottawa's city centre and > 250 m from residential buildings, located in larger forested patches. Birds were tagged with a passive integrated transponder (PIT) tag (IB Technology, UK) to allow for automated recording of social associations, as well as a Canadian Wildlife Service-issued aluminium band and an additional plastic colour band to allow for visual identification. Measurements of tarsus, tail and wing length (mm) and mass (g) were recorded to determine sex based on a discriminant function (Mennill, unpublished data) that has been shown to accurately sex birds in our population (97% of determined individuals; Devost 2016). Age class was determined as either hatch year (HY) or after hatch year (AHY) from the shape, wear, and colouration of the outermost rectrices (Pyle 1997).

Personality assay

Following banding and measurements, birds were assessed for exploratory personality using an open field cage test (adapted from Kluen et al. 2012). Birds were released into a novel environment (commercially available bird cage; 40x60x40 cm) and their movements in the cage were recorded by video, for a ten minute period. During video analysis, four regions were delimitated in the cage, spanning separately from each of the four front corners to the back corners. Exploration score was recorded as latency (in seconds) for an individual to visit all four corner regions of the cage. Birds that did not explore all regions were given a maximum latency of 600 (10 minutes). In this population, exploration scores obtained from this open field test have been found to be repeatable (intra-annual R = 0.53; Devost 2016, N = 20 individual's sampled twice with 3-10 weeks between tests), thus falling in the range of repeatability estimates for similar behaviours (Réale et al. 2007).

Dominance rank

During the non-breeding season, black-capped chickadees form strongly linear dominance hierarchies within flocks (see Smith 1991, Devost 2016). Males are typically dominant over females, and older individuals generally will dominate younger birds (Smith 1991; Ratcliffe, Mennill & Schubert 2007). To determine within group dominance rank, agonistic interactions were video recorded on a baited feeding platform from February 9 to March 24 2015. Individuals were scored as winning a dominance interaction when i) supplanting an opponent, ii) resisting an attack, iii) eliciting submissive posture in opponent or iv) feeding while opponent waits (see Ratcliffe et al. 2007, Devost 2016). Within group dominance rank was then weighted between 0 and 1 (1 being the most dominant individual) to control for different flock sizes between sites.

Social networks

Although black-capped chickadee are typically found to maintain flocks throughout the winter (Smith 1991), it has not been previously assessed if specific associations and network positions are maintained within a flock or if these associations fluctuate while overall group membership is retained. To examine the stability and properties of social network positions, association data were collected weekly during the non-breeding season: from October 29, 2014 to January 5, 2015 and January 29 to April 16, 2015. Due to ongoing capture efforts (October-December), as well as occasional technical failures, data were not obtained for every week during the sampling period at all eight sites (see Table 2.1 for details). At each site, a seed feeder fitted with a single radio-frequency identification (RFID) antenna (Priority 1 Design, Australia) was filled once per week. This restricted access at the feeder to one bird at a time, thus social associations were determined as birds using the feeder within the same 60 second time window (for a similar procedure see Aplin et al. 2012), following a gambit of the group approach, which assumes all individuals appearing within the same time-window are associated (Franks, Ruxton & James 2010). For each week, at each site, a separate undirected weighed social network was constructed using the simple ratio index (SRI) (Cairns & Schwager 1987), a measure of association between individuals which ranges from 0 (pair never seen associating) to 1 (never detected apart), using the R package asnipe (v0.81) (Farine 2013). Birds that were recorded in fewer than 5 separate sampling weeks were excluded from analysis.

For each individual, two social network metrics were calculated in each recording period: strength (weighted degree) and eigenvector centrality. Strength is the sum of an individual's associations, representing a measure of gregariousness (Whitehead 2008). Eigenvector centrality is an indication of an individual's connectedness in the network, and is proportional to the sum of the centralities of an individual's neighbours (Farine & Whitehead 2015). However, as strength and eigenvector centrality were highly correlated in our networks (Pearson's $r = 0.50$, $p < 0.001$), analysis was limited to centrality. Metrics were calculated in the R package sna (v 2.3-2) (Butts 2014).

Statistical analysis

Network consistency

We assessed repeatability, defined as the proportion of total variation accounted for by repeated measurements of the same individual (Nakagawa & Schielzeth 2010), of individual centrality across the non-breeding season as well as for group size of each network. We first used a linear mixed model (LMM) to determine repeatability of group size and network centrality. As network metrics like centrality depend on the number of individuals in a network, centrality score was ranked within weekly networks and scaled between 0 and 1, to control for any variation in group size while still allowing assessment of the consistency of relative network position (see Wilson et al. 2013). Additionally, due to the lack of data independence in network metrics, we tested for statistical significance of network stability in two ways. First we assessed significance of the traditional repeatability estimate by comparing the observed repeatability to a distribution of repeatabilities obtained from randomised networks. To do this we performed 1000 node-based permutations per network by randomising all association values within each association matrix, while maintaining the number of associations. We then calculated significance (p-values) as the proportion of times the observed repeatability was found to be more extreme than the randomised repeatabilites. Confidence intervals were calculated for each repeatability estimate using a parametric bootstrap with 1000 permutations.

In addition, we further tested for consistency in network centrality using a recently described network based method (Wilson et al. 2013). This method was specifically designed to account for the non-independent nature of social network data. To determine if individuals maintained consistent relative centrality within their social networks, we calculated the sum of variances for the ranked network centrality across the observed networks (SV_O) as described by Wilson et al. (2013). As SV_O is a measure of variance, low values indicate a similar relative ranking across networks. We again obtained 1000 node-based permutations of each network, re-calculating the sum of variance of each set of randomisation (SV_R). We then compared the observed SV_O values to the randomised SV_R values, and significance was obtained by computing the number of times the SV_O value was found to be more extreme than the distribution of SV_R values.

Behavioural traits

To determine how individual behavioural traits influence centrality we constructed a LMM with weighted dominance rank, exploratory personality score (mean centered and re-scaled to between 0 and 1 to ensure commonality of scale with ranked variables), month and all two-way interactions as fixed effects, with individual nested in site as random intercepts. We also initially assessed the effects of age and sex on centrality but these predictors were found to be non-significant and were excluded from final analysis due to correlation with dominance rank and a decreased sample size available with complete data. All possible models were fitted and a model selection procedure was performed using Akaike's information criterion (AICc; AIC corrected for small sample size) to evaluate predictor effect size. We then ranked models using Akaike weight (AIC_w) as a measure of relative importance of each model parameter (Burnham & Anderson 2004). To test for significance of variables highlighted by model selection, the observed parameter estimates were compared to a randomised null model (Farine and Whitehead 2015), in which the model of interest was re-run using 1000 randomisations of each network to create a null distribution of the parameter coefficient. All statistical analyses were performed in R v3.2.3 (R core team 2015).

Results

Over the recording periods a total of 172 532 visits were made to 8 network feeders by 91 birds (9 individuals were detected in fewer than five weeks, and thus excluded from analysis). Weekly networks ranged from 4-15 birds, and all sites had a minimum of 13 weeks of collection (range 13-20).

Network consistency

Within sites, group size was found to be repeatable ($R = 0.64$, 95% CI: 0.32-0.79). Eigenvector centrality of individual birds was also found to be repeatable across the non-breeding season in all sites ($R = 0.47$, 95% CI: 0.39-0.49), and this repeatability estimate was found to be significantly higher than repeatability estimates obtained from network randomisations ($p < 0.001$). Network consistency analysis returned similar results, in which the observed sum of variance (SV_O) was found to be significantly lower than the variance in centrality from randomised networks (SV_R) at all eight sites (Table 2.2, Fig. 2.1).

Behavioural Traits

Initial model selection indicated that three top models had an AICc of < 6. The top model was one including only dominance as a fixed effect with individual nested within site as random intercepts and had a high model weighting (AICw = 0.78). The second ranked model was a null model with no fixed effects and the final top-ranked model contained both dominance and exploratory personality as fixed effects, but had low weighting (AICw = 0.056) and was ranked below the null model (Table 2.3). Thus our model selection procedure indicated that of our examined parameters, only dominance rank had a large effect on an individual's centrality. Additional permutation analysis performed on the top model to test for statistical significance confirmed that dominance rank explained a significant amount of variation in an individual's centrality rank (dominance; $\beta = 0.24 \pm 0.09$ SE, $p < 0.001$), where an individual's relative centrality increased as dominance rank increased (Fig. 2.2). We also considered that individual variation in feeder use could influence network metrics as a consequence of the nature of recording interactions at a food source, although the proportional nature of the association index (SRI) does in part account for this variation. We thus repeated the analysis using residual centrality rank, controlling for individual feeder use as the response variable, and found qualitatively similar results (not shown).

Discussion

Although social network analysis is becoming a wide-spread tool for the study of social behaviours and processes (Krause *et al.* 2014; Farine & Whitehead 2015), there are currently only a limited number of studies which examine the same social networks over time (but see (Blumstein *et al.* 2013; Jacoby *et al.* 2014; Aplin *et al.* 2015b). In this study, we demonstrate that both group size and individual network position, measured as eigenvector centrality, are consistent across the social flocking period in eight networks of wild black-capped chickadees. Assessing the consistency of social networks over time is critical for understanding the evolutionary implications of network metrics (Wilson *et al.* 2013). Previous work has indicated that individual variation in social position may have fitness consequences (e.g. Christley *et al.* 2005; McDonald 2007; Oh & Badyaev 2010; MacIntosh *et al.* 2012), however without determining the temporal stability of such network measures the outcome of such network-fitness links remains unclear. For instance, in the case of network position influencing level of competition experienced or infection risk, the stability of the network will determine how important these factors are in terms of long-term or even lifetime fitness effects.

Centrality may be considered a personality trait in terms of the sociability axes (one of five main personality classes defined in animals) of animal temperament (Réale et al. 2007), as individuals were observed to maintain consistent social connectivity over time. Our measure of repeatability was 0.47, which is relatively high compared to average repeatability found across a variety of behavioural traits in multiple taxa (overall average R = 0.37, Bell, Hankison & Laskowski 2009). Despite current interest in animal personalities, there has been limited research attempting to quantify social personality types, particularly in the context of wild groups, rather than in dyadic or individual scenarios (e.g. Cote & Clobert 2007; Cote *et al.* 2010) which may fail to reflect a meaningful measure of sociality. The use of social network analysis provides a framework to quantify sociality in natural groups, and with appropriate randomisations can be used to assess behavioural consistency (Wilson *et al.* 2013; Farine & Whitehead 2015). To further investigate social personality through network metrics, future studies should assess the consistency of such metrics both through time and in varying contexts, such as measuring either various types of association networks (i.e. dominance and affiliation networks), or through removal/addition experiments.

Although a number of previous studies have suggested that proactive-reactive personality type may influence the strength of network associations and/or an individual's social position (Pike *et al.* 2008; Croft *et al.* 2009; Schürch *et al.* 2010; Aplin *et al.* 2013a; Snijders *et al.* 2014), we found no such link between network centrality and exploratory score in black-capped chickadees. The higher centrality of fast explorers that has previously been observed has been proposed to indicate an increased tendency to switch between subgroups (Aplin *et al.* 2013a). Maintaining low centrality has been suggested to be a method by which slower explorers avoid aggression and social stress (Schürch *et al.* 2010; Snijders *et al.* 2014). In our system, each network was a single cohesive unit, so movement between groups was not observed, and established dominance hierarchies are expected to reduce the escalation of aggression. Thus in our system, exploratory personality score may have less influence on social network position.

We observed that dominant individuals were more connected within their social network than subordinates. This finding of increased social centrality is interesting, as more spatially central positions within groups are expected to confer additional predator protection over peripheral positions (reviewed by Krause & Ruxton 2002). As such, social centrality may be partially a result of increased spatial centrality within a group, though physical group structure was not something we were able to measure in our current study. Our results add to previous studies of social networks which have found measures of centrality to increase with dominance rank (Schürch *et al.* 2010; King *et al.* 2011; MacIntosh *et al.* 2012; Hughes & Driscoll 2014). However, this relationship between dominance and centrality was not observed in a study in which mixed-species flocks were considered, suggesting that in such multi-species interactions it may also be important to consider social position within the broader global network as opposed to within a single species network (Farine *et al.* 2012).

High network connectivity and centrality have been shown to lead to an increased individual risk of disease and parasites (e.g. Godfrey *et al.* 2009; MacIntosh *et al.* 2012). Thus, occupying a central network position may be expected to be costly. However, as suggested in this and the afore mentioned studies, dominant individuals have been found to be more likely to occupy central network positions. Dominants may acquire central network positions passively, due to receiving the highest number of interactions within a group (e.g. involved in the most grooming interactions; MacIntosh *et al.* 2012). It is also possible that the potential advantages available to more central individuals, such as greater access to social information (Aplin *et al.* 2012, see Ch. 3), and increased access to breeding opportunities (McDonald 2007; Ryder *et al.* 2008; Hughes & Driscoll 2014), may offset the costs of higher disease risk. Additionally, dominants may be more able to cope with any costs of network centrality due to generally superior body condition, as a result of increased foraging ability from priority access to available food resources (reviewed by Piper 1997). It has also been suggested that position within a group could have differential costs and benefits for different classes of individuals (Krause & Ruxton 2002). For instance, as dominants can displace other individuals from a foraging patch (e.g. Liker & Barta 2002; Bugnyar & Kotrschal 2002), they may benefit more from acquiring social foraging information, while a subordinate could be unable to take full advantage of such information. Thus subordinates could prioritise independently locating food sources (i.e. producing; Giraldeau & Dubois 2008), which may be aided through maintaining a more peripheral network position (Barta, Flynn & Giraldeau 1997).

In conclusion, our study is one of only a few studies to date to examine frequently made assumptions about the consistency of network metrics over time, and the first to our knowledge to employ network-specific consistency analysis to replicated wild networks. As we found that individual network position was repeatable across the non-breeding season, we considered the importance of individual behavioural traits on network centrality. Notably, we found that dominance rank, but not exploratory personality type was related to network centrality. Although we were not able to quantify the potential fitness costs and benefits associated with network positon in the study, there is increasing evidence from numerous network studies that occupying specific social positions can have both short and long-term fitness consequences. Thus our study contributes to the understanding of the temporal consistency of networks, as well as the individual attributes that allow individuals to occupy certain network roles.

Table 2.1 Summary of feeder use including total number of birds detected per site and mean number of visits per bird, as well as the number and date of data collection weeks used to construct weekly social network associations, by site.

Site	Total Birds	Mean Visits/Bird (Range)	Start Date	End Date	Weeks
AP	10	2960 (487-4930)	29-Oct-14	16-Apr-15	20
BB	11	2026 (151-8805)	20-Nov-14	16-Apr-15	17
CW	11	1388 (3-4003)	07-Nov-14	16-Apr-15	17
HP	10	3557 (716-5581)	05-Nov-14	16-Apr-15	19
PP	9	407 (26-828)	29-Oct-14	14-Apr-15	15
SM	11	1708 (218-3006)	12-Dec-14	13-Apr-15	13
SS	19	1373 (17-5627)	13-Nov-14	16-Apr-15	18
WG	10	2124 (502-3488)	14-Nov-14	15-Apr-15	17

Table 2.2 Observed sum of variances (SV_O) of ranked centrality across all weekly networks, compared with the range of variances calculated from 1000 network randomisation (SV_R).

Site	SV_O	Range of SV_R	p-value
AP	0.307	0.679-0.862	<0.001
BB	0.346	0.638-0.877	<0.001
CW	0.669	0.662-0.922	0.002
HP	0.322	0.625-0.792	<0.001
PP	0.451	0.432-0.758	0.006
SM	0.505	0.581-0.888	<0.001
SS	0.504	0.901-1.125	<0.001
WG	0.482	0.590-0.973	<0.001

Table 2.3 Summary of models of ranked network centrality from model selection procedure; all top models (ΔAICc < 6) are shown. Models contain listed fixed effects, with individual nested within site included as random intercepts in all models. Models including dominance were restricted to the 66 individuals with dominance scores (N = 82 individuals for null model). All two-way interactions were included in model selection, but were not observed in any of the top models. Maximised Log-Likelihood (LogL), ΔAICc and AIC weight (AIC_W) values are presented for each model.

Model parameters	LogL	ΔAICc	AIC_W
dominance	81.36	0	0.778
null	78.80	3.1	0.165
dominance + exploratory personality	79.75	5.3	0.056

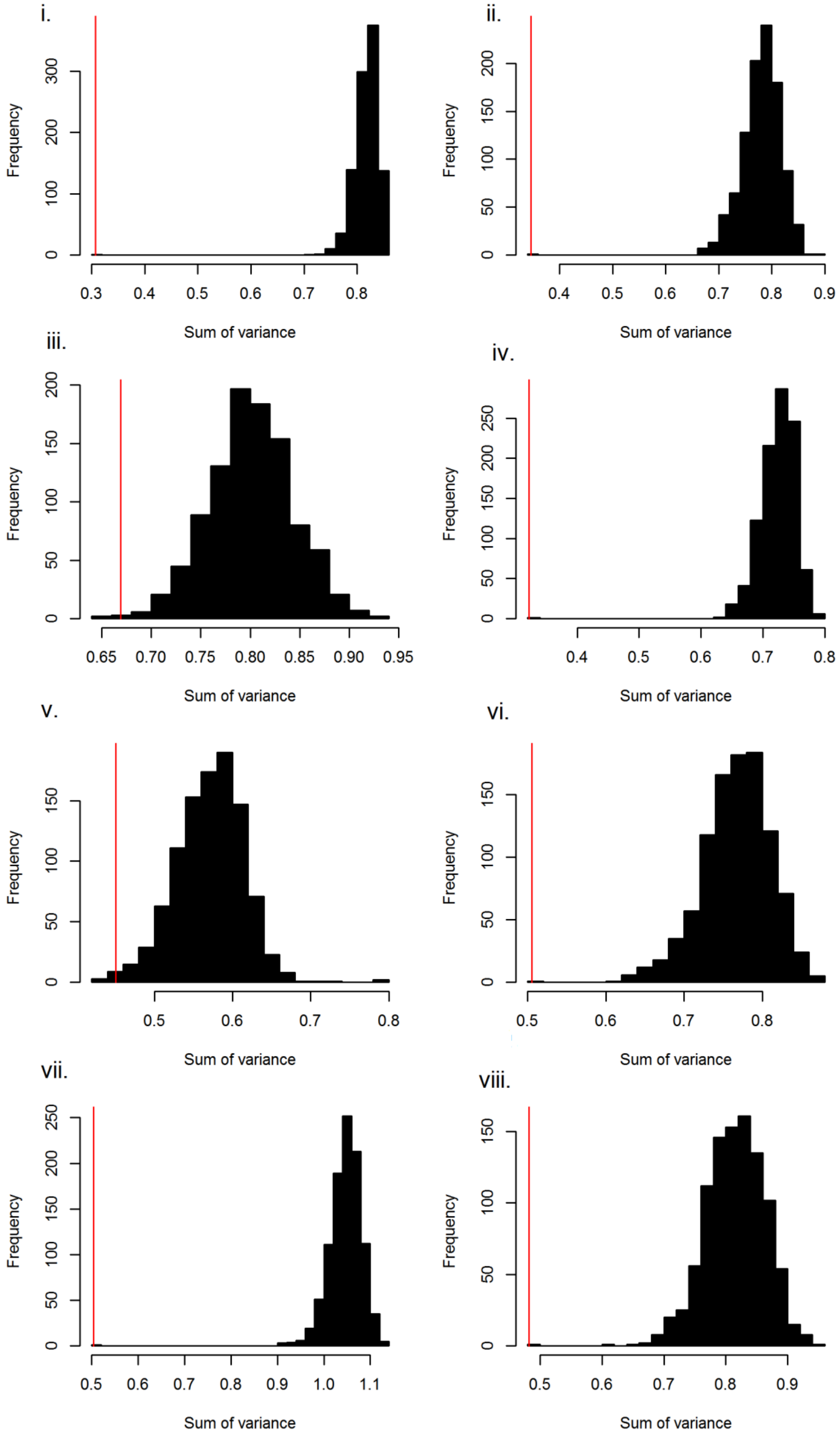

Figure 2.1: Distribution of sum of variances (SV_R) obtained from 1000 randomisations compared with SV_O (shown in red) obtained from each site (i-viii; sites AP, BB, CW, HP, PP, SM, SS, and WG in order)

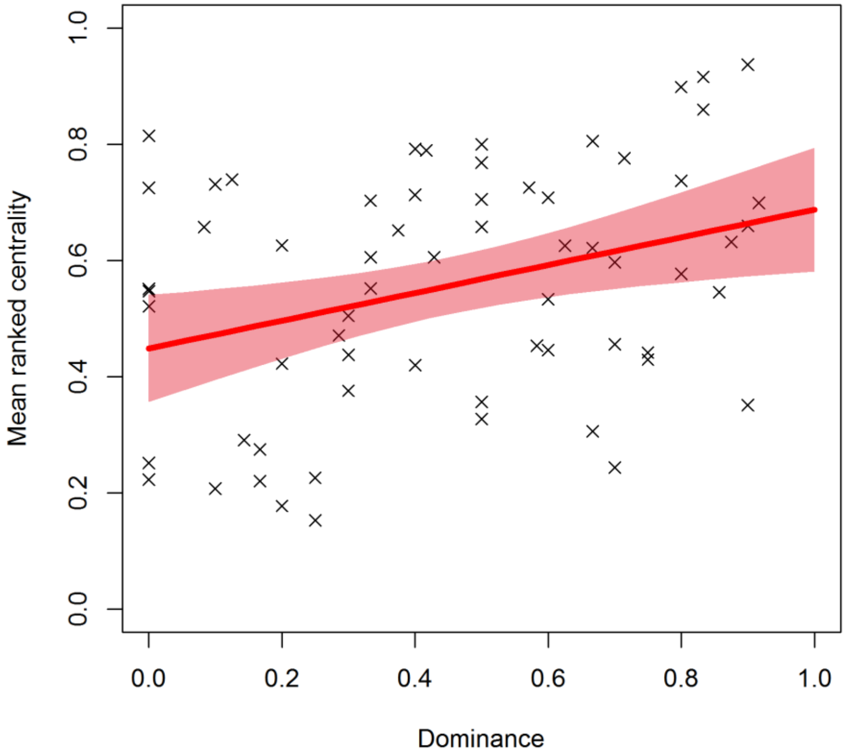

Figure 2.2: The relationship between weighted dominance rank and mean ranked centrality (averaged across all sampling weeks), while controlling for individual nested within site as random intercepts, N = 66 individuals. 95% confidence intervals around model estimate are shown.

CHAPTER 3

Individual and ecological determinants of social information transmission in the wild

Abstract

Social information, acquired through the observation of others, has been documented in a variety of adaptive contexts. The transmission of social information relies on social connections and therefore it is important to consider that individuals may vary in their access to, and use of, such information. Social network analysis allows for the consideration of individual variation in social connections, which until recently has been ignored in the study of social processes. Additionally, few previous studies of social information use have considered the potential effects of traits such as dominance and personality type, which have been found to influence group social structure. We used network-based diffusion analysis, which incorporates information on individual social associations, to examine if wild flocks of black-capped chickadees (*Poecile atricapillus)* utilise social information when locating novel foraging patches. Additionally, we incorporated individual traits (age, sex, dominance and exploratory personality) while examining flocks from rural and urban environments, to assess the influence of individual-level characteristics and urbanisation on the rate of information transmission. Social information transmission was found to occur in all flocks, with the timing of discovery at novel foraging patches following network associations, as predicted. However, the only individual-level variable found to influence social transmission was dominance rank; dominant individuals had higher rates of information transmission than subordinates. We observed no effect of urbanisation on the transmission of social information. Our results highlight the importance of considering social associations when examining social information use. Additionally, our results suggest that dominant individuals have greater access to social information than more subordinate individuals, which may demonstrate a previously undocumented additional benefit provided by social dominance.

Introduction

Collecting and maintaining accurate information about foraging opportunities is a vital task. Individuals are required to frequently re-sample their environment, to acquire updated information and reduce uncertainty, particularly when food resources are patchy and/or ephemeral in nature (Dall *et al.* 2005). While there are a variety of ways animals may attempt to optimise searching, maintaining accurate information through personal exploration requires expending significant time and energy (Dall & Johnstone 2002; Chittka, Skorupski & Raine 2009). Alternatively, in a variety of foraging contexts, animals may be able to acquire social information about their environment from other individuals, rather than relying solely on personal sampling (reviewed by Galef & Giraldeau 2001; Galef 2009).

Social information has been defined as information acquired through the observation of other individuals (reviewed by Dall *et al.* 2005; Aoki & Feldman 2014). Social information can be acquired in a variety of ways, including local enhancement, eavesdropping and social learning (Bonnie & Earley 2007). Current theory suggests that while social information may be less costly than individual exploration, it may also be less reliable (Kendal *et al.* 2005; Galef 2009). Therefore it has been suggested that the use of social information should only be expressed under specific circumstances, such as when individual tactics are unproductive, or when acquiring personal exploration is risky (reviewed by Laland 2004; Galef 2009). The usefulness of social information is also expected to vary depending on the reliability of the information (Hall & Kramer 2008), which can depend on an individual's spatial, social and temporal distance from the information source (Seppänen *et al.* 2007). Optimally, using a combination of both social information and personal information would be the most beneficial strategy; however, it has been suggested that attention to social information may impede other foraging tactics, such as personal sampling (Giraldeau, Valone & Templeton 2002; Rieucau & Giraldeau 2011).

As social information implicitly relies on an individual's social connections, it is likely that not all individuals will have equal access to social information, as not all individuals in a group will interact equally or at all (Krause *et al.* 2014). However, to date, most studies have not considered such variation in social ties when attempting to assess social information use. While accurately mapping social ties within groups presents some challenges, social network analysis provides a well-defined framework for examining both direct and indirect social connections (Croft *et al.* 2008; Wey *et al.* 2008; Sih *et al.* 2009). Network based diffusion analysis (NBDA) is a recently developed statistical method designed specifically for assessing the transmission of social information using social network associations (Franz & Nunn 2009, 2010; Hoppitt *et al.* 2010). NBDA has been used to assess social information transmission in a variety of taxa in both laboratory-based (fish; Atton *et al.* 2012; Webster *et al.* 2013; birds; Boogert *et al.* 2014) and wild studies (primates; Kendal *et al.* 2010; Hobaiter *et al.* 2014; birds; Aplin *et al.* 2012, 2015; Farine *et al.* 2015; whales; Allen *et al.* 2013).

Individual characteristics such as age, sex and even personality type, can influence social network position (Lusseau & Newman 2004; Croft *et al.* 2008; Pike *et al.* 2008; Aplin *et al.* 2013a). Additionally, such traits have been shown to affect an individual's likelihood to favour the use of social information. For instance, shy barnacle geese (*Branta leucopsis*) have been shown to utilise social information more than bolder individuals (Kurvers *et al.* 2010) and younger meerkats (*suricata suricatta)* were found to have a higher propensity to acquire information socially (Thornton & Malapert 2009). Several studies have further found a relationship between the flow of information through social networks and age (Allen et al. 2013;

Aplin et al. 2015), as well as sex (Aplin et al. 2015). However, as yet no studies have explicitly tested for an effect of personality on the transmission of social information through a network.

Few studies have looked at the effects of the external environment on social information transfer. However, several social network studies suggest that environmental factors can influence interactions and behaviours within groups (Sundaresan *et al.* 2006; Edenbrow *et al.* 2011; Mokross *et al.* 2014). For instance, Sundaresan *et al.* (2006) found that network metrics and association types varied between two similar groups of equids found in differing habitats and Edenbrow *et al.* (2011) found that in social networks of guppies (*poecilia reticulata*), environment structure and predation risk influenced the expression of social behaviours. To our knowledge, only one network-based study has previously considered any effects of environment type on social information transmission, finding that it occurred in a complex but not simple environment (Webster *et al.* 2013).

In this study, we apply NBDA to wild flocks of black-capped chickadees (*Poecile atricapillus*) to determine how information about novel foraging opportunities is received. Chickadees are well suited to social foraging studies, as they form social flocks during the non-breeding season and utilise a variety of patchy food sources, particularly in the winter (Smith 1991). Furthermore chickadees are found to occupy a range of habitat types, including mixed forests, forest edges and even suburban and urban areas, which may vary in winter food stability (Foote *et al.* 2010). Therefore, we conducted our study in two different habitat classes (urban and rural), to test for differences in social information use in differing environments.

We first ask how foraging information is acquired in wild chickadees. If foraging information is acquired socially, we predict that a naïve individual's arrival at a novel foraging patch will follow ties from the association network and will co-vary with network position (Hoppitt *et al.* 2010; Aplin *et al.* 2012). We then aim to determine whether, given an individuals' social network position, their use of social information varies depending on individual characteristics, including exploratory personality and dominance rank. As recent studies have suggested that more exploratory individuals may also more quickly exploit social information (Nomakuchi, Park & Bell 2009) and may be better connected within their network (e.g. Schürch, Rothenberger & Heg 2010), we expect that higher exploration score will be positively related to the social discovery of novel foraging patches. While little work has been done on the effect of dominance rank on social structure, a study of the transmission of parasites through a network of macaques showed the dominants had higher network centrality and higher parasite transmission rates (MacIntosh *et al.* 2012). As such, we expect that dominant individuals have higher access to social information due to their network position.

Finally, as there has been initial evidence indicating that characteristics of the environment may influence social transmission (Webster *et al.* 2013) and it has also been shown that the reliance on social information may be higher in variable environments (Rafacz & Templeton 2003), we assess flocks from urban and rural sites. Although urban and rural environments vary in number of characteristics, for wintering birds it has been suggested that a key difference between urban and rural environments is increased stability and predictably in terms of food availability in urban areas due to food supplementation through birdfeeders (Atchison & Rodewald 2006; Chamberlain *et al.* 2009). As such, we expect that the rate of social information use would be higher in more rural environments.

Methods

Study species and study sites

Black-capped chickadees are small (9-14 g) Parids that are year-round residents across their range encompassing most of North America (Foote *et al.* 2010). During the fall, chickadees form stable social flocks that consist of non-related individuals, and retain these associations throughout the winter (Smith 1991). Flocks are made up of approximately 3-12 individuals, with a linear dominance hierarchy, and defend a home range which range in size from 8.8 to 22.6 ha (reviewed in Smith 1991).

Chickadee flocks were sampled from 8 sites in and around Ottawa, ON, Canada (45° 25' N, 75°, 40'W). Sites were categorized as either urban (N = 4) or rural (N = 4). Urban sites were located in partially forested urban parks, at least 200x200 m in size, and were all located within 30-90 m of residential developments likely to contain supplemental feeders. Rural sites were located in large forested regions > 15 km from Ottawa's downtown core, and contained no buildings within a minimum of 300 m from the feeder sites, and thus contained only our study feeder within the estimated home range area (8.8-22.6 ha; Smith 1991) birds were expected to use. Both urban and rural sites contained mixed coniferous and deciduous forest.

Between September 26 and December 9 2014, birds were captured at each site through mist netting and potter's traps baited with sunflower seeds. Upon capture birds were fitted with a Canadian Wildlife Service-issued aluminium band, a single plastic colour band and a second modified colour band fitted with a passive integrated transponder (PIT) tag (IB Technology, UK), allowing birds to be uniquely identified both visually as well as electronically. Measurements were taken to determine sex (based on a discriminant function; Mennill, unpublished data), and tail wear and colouration was used to age birds as either juvenile (HY: hatch year) or adult (AHY: after hatch year) (Pyle 1997). Also at the time of capture, birds were assayed for exploratory behaviour using an open field cage test (adapted from Kluen *et al.* 2012). Birds were placed in a commercial bird cage (40 cm x 60 cm x 40 cm) and their movements in the cage were recorded by video for ten minutes. Exploration was measured as the latency in seconds to investigate the four corner regions in the cage, which is designed to emulate laboratory based novel room tests measuring latency to arrive at artificial trees (Verbeek *et al.* 1994; Drent *et al.* 2003). Individuals that did not explore all four regions within the novel exploration period were given a maximum score of 600 seconds. Exploration score in this population has been found to be a repeatable personality trait (R = 0.53; Devost 2016).

Birds were also assigned a within flock dominance rank determined by video-recording agonistic interactions between individuals on a baited feeding platform from February 9 to March 24 2015 (Devost 2016). Four interactions types were scored, with an individual exerting dominance when it: (i) supplanted or chased an opponent (ii) resisted an attack (iii) elicited a submissive posture in an opponent or (iv) fed while opponent waited (see Ratcliffe, Mennill & Schubert 2007). To control for difference in flock sizes dominance ranks, obtained via David’s score (described by Gammell *et al.* 2003; de Vries, Stevens & Vervaecke 2006), were subsequently weighed between 0 and 1 (1 being the least dominant), by dividing rank by group size. This rank corrected for flock size has previously been used to account for differences in flocks sizes in black-capped chickadees (Lewden, Petit & Vézina 2012)

Social networks

To determine the social foraging network at each site, a sunflower seed feeder was placed at the capture site and filled once per week between Oct 29 2014 and Jan 5 2015. The feeder was fitted with a single perch, which restricted access to one individual at any moment. The perch contained a radio-frequency identification (RFID) antenna (Priority 1 Design, Australia), which recorded the time and duration of visits by PIT tagged individuals. For each site, we used data collected after 89% or more of subsequently recorded birds were captured (range = 3-8 weeks of network data per site). Social associations were inferred using a gambit of the group approach (Franks *et al.* 2010), in which birds were deemed to be associating when arriving at the feeder within the same 60 second moving time window (for a similar procedure see Aplin *et al.* 2012). A weighted association matrix was created using the simple ratio index (SRI) (Cairns & Schwager 1987), which ranges from 0 (pair never seen associating) to 1 (never detected apart), using the package asnipe (v0.81) (Farine 2013) in R (v3.2.0) (R Core Team 2015). From the association matrices, a separate undirected weighted network was constructed for each site.

We calculated network centrality for each individual in a network. Here we utilise eigenvector centrality, which has been suggested to best predict the path of social information that is broadcasted publicly, such as would occur with local enhancement, as is expected in our system (Borgatti 2005). Eigenvector centrality is defined as the sum of the centralities of an individual's connections; with high eigenvector centrality indicating an individual's increased potential for the receipt and further transmission of information through the network (Farine & Whitehead 2015). Eigenvector centrality was calculated in the R package sna (v2.3-2) (Butts 2014).

Novel foraging patch discovery

To assess how chickadees discover and utilise novel foraging resources, network feeders were removed from their established location from Jan 5 – Jan 16 and Jan 21 – Jan 30 2015, and installed at a novel location 100 ± 5m distance in a randomly selected direction to create a novel foraging location. Network feeders were used during the novel patch discovery to eliminate any potential effects of neophobia related to a new feeder design. Feeders were installed at the discovery locations after dark to avoid unintentionally producing information about the novel location. Two discovery trials were performed at each site, with feeders left in place for 8 to 10 days, before being returned to their original location. Feeders were replenished every two nights as necessary to prevent being depleted during each experiment. The date and time of each individual's first visit to the discovery feeder was captured using the same RFID perch, allowing for the determination of the order and timing of each bird's discovery of the novel foraging location.

Statistical analysis

Network based diffusion analysis

To determine if information about the novel foraging patch was transmitted through the flock network, we utilised network based diffusion analysis (NBDA) (Franz & Nunn 2009), with the continuous time of acquisition diffusion analysis (NBDA code v. 1.2 in R, Hoppitt *et al.* 2010). NBDA assumes that the probability of information being socially transmitted from one individual to another is linearly proportional to the strength of association between them in the corresponding social network, with the diffusion of information thus broadly following the patterning of network ties. To account for individuals co-discovering the feeder, individuals that discovered the food patch within one minute of each other were considered joined by 'ties' and the transmission of information was prevented between tied individuals. The relative rates of social and asocial discovery were allowed to vary between sites and trials in the models, and we included the individual variables sex, age class, exploratory personality, weighted dominance rank and individual propensity to use feeders (number of visits by each individual to the network feeder; mean centered). All possible models were fitted, and model selection was performed using Akaike's information criterion (AICc; corrected for small sample size).

Eigenvector centrality

In addition to NBDA we also tested the prediction of social transmission of foraging information by examining the relationship between network centrality and the timing of arrival of individuals to the novel foraging patch. Using a binomial generalised linear mixed model (GLMM) we first compared the centrality of individuals who arrived at the patch within the first 24 hours after the initial discovery with those who did not arrive within this time period, including network feeder use, sex, age class, and individual exploratory personality as fixed factors, with individual nested within site included as random intercepts. We also looked at the effect of latency to arrive at the novel foraging patch (measured as log time to first record on discovery feeder), using a linear mixed model (LMM), including the same explanatory variables.

Urbanisation

To test for potential differences in social transmission between flocks in urban and rural environments, we included site type (urban or rural) as a variable in the NBDA model selection analysis. Additionally, we used a LMM to assess if the speed of social transmission, measured as the log of the time lag between the first and last bird to arrive at the novel foraging patch in each discovery trial, varied between the two habitat classes, with site identity as a random intercept. Finally, we used a LMM to determine if speed of initial discovery varied between urban and rural sites (measured as log latency to initial discovery) including the same explanatory variables. All analyses were carried out in R (v 3.2.0) (R Core Team 2015).

Results

A total of 80 563 visits from 80 birds were recorded on the 8 network feeders. Networks at individual sites ranged from 8 to 15 birds, with individual visits per site ranging from 3 to 3957 visits (see Table 3.1 for full by-site summary). While the social networks were generally highly connected (most birds associated with all other birds at each site), individuals varied in the strength of their associations (Fig. 3.1, Table 3.2). Seventy-four of the 80 network birds discovered at least one of the novel foraging patches in 1 to 10 days. There were seven birds recorded during the discovery trials that were not recorded during the network period, and as such were excluded from the analysis.

Network based diffusion analysis

The top three NBDA models had a ΔAICc of < 2 (ΔAICc = 0, 1.9, 2), and therefore we cannot differentiate between them. However all three indicated that information transmission occurred socially, with varying transmission parameters between sites and a non-constant declining rate of asocial discovery. There was no support for the highest ranked asocial model (ΔAICc = 121.1; Table 3.3). Model averaging, performed on the top ten models, provided complete support for social transmission (ωAIC = 1). In addition, model averaging supported an effect of dominance rank (ωAIC = 0.81), but no other individual-level variables. This effect was multiplicative, indicating that the effect of dominance rank influenced both social and asocial discovery parameter. In summary, the final top model containing all supported elements had a social transmission rate that varied significantly between sites (s = 12-383), with transmission rates on average 80x greater than the rates of asocial discovery (Table 3.4). Dominance score had a positive effect on social transmission, in which a decrease in weighted dominance score of one standard deviation (0.25) lead to a 45% decrease in social transmission rate.

Eigenvector centrality

Birds that had higher eigenvector centrality within their network were more likely to arrive at the novel foraging patch within the first 24 hours after its initial discovery, when controlling for difference in exploratory personality and feeder use (GLMM: N = 144, $\chi^2 = 6.02$, p = 0.01, Fig. 3.2). Exploration score was not found to significantly influence the speed of discovery (GLMM: N = 144, $\chi^2 = 0.24$, p = 0.62). The effects of age class, sex and dominance rank were also considered, but none of these factors were found to significantly explain the variation in first day patch arrival (all $p > 0.05$), and due to the smaller subset of data available with these variables, all were dropped from the final analysis. Additionally, there was a marginally non-significant trend for birds with higher centrality to have lower latency to arrival at the novel foraging patch ($F_{1,97} = 3.27$, p = 0.07), when controlling for individual explorative behaviour and feeder use.

Urbanisation

The NBDA analysis found that the rate of social transmission varied between sites (99% support from model averaging, Table 3.4). However this difference was not explained by differences between urban and rural habitats (0% support). The speed of information diffusion, measured as the log-transformed time lag between the first and last discoverer also showed no significant difference between rural and urban habitats ($F_{1,6} = 0.06$, p = 0.82). Additionally, the speed of initial discovery of novel patches (as measured by log latency to first discovery), did not vary between urban and rural habitat types ($F_{1,6} = 0.10$, $p = 0.76$).

Discussion

The use of social information in foraging contexts has been demonstrated in a wide variety of taxa, and has been argued to provide individuals with information about their environment without costs associated with personal exploration (Galef & Giraldeau 2001; Galef 2009). However, recently it has been noted that not all individuals in a group will have equal access to social information. The NBDA approach (Franz & Nunn 2009, 2010; Hoppitt *et al.* 2010) uses social network analysis to examine the spread of social information in a group while also accounting for variation in an individual's social connections. Using NBDA, we demonstrate that the transmission of social information follows network connections, and varies with both an individual's network centrality and dominance rank in wild flocks of black-capped chickadees.

We found that the transmission of social information explains the timing of arrival at novel foraging patches significantly more than models of asocial searching alone. Transmission rate varied between study sites, but at all sites social transmission was found to increase feeder discovery by a minimum of 12 times that of the asocial discovery rate. Previous NBDA studies have found similar findings both in large fission-fusion networks (e.g. Allen *et al.* 2013), and in smaller stable social groups (e.g. Boogert *et al.* 2014). However, many previous studies of small networks have been conducted in captivity (but see Kendal *et al.* 2010), thus our study demonstrates that these findings may be consistent between different social structures (i.e. loosely fission-fusion groups as well as stable small flocks) as well as between experimental and natural small networks.

Network centrality measures have previously been proposed as an important factor in an individual's susceptibility to disease and parasites (Christley *et al.* 2005; MacIntosh *et al.* 2012). However, central individuals should also be in a better position to receive socially transmitted information, and eigenvector centrality in particular has been suggested to be useful indicator of likelihood of social information acquisition (Borgatti 2005). As predicted, we found that individuals with higher eigenvector centrality also had a significantly increased speed of locating the novel foraging patch. This result is consistent with previous studies in which high eigenvector centrality has also been found to increase access to social information (Aplin *et al.* 2012; Claidière *et al.* 2013). These results highlight the potential benefits of highly connected network positions, which may present a trade-off with the increased disease risk associated with more central positions.

Although recent studies have indicated that individual-level behavioural traits can influence social network structure (e.g. Croft *et al.* 2009, Aplin *et al.* 2013), there have been few studies that have considered the effect of such individual variation in behaviour on social information transmission. Exploratory personality has been suggested to be a potentially important factor driving network structure (e.g. Schürch, Rothenberger & Heg 2010; Aplin *et al.* 2013). Here we examined for the first time the effect of exploratory personality of individuals on network processes, and found no effect of exploratory personality on the diffusion of social information. In three-spined sticklebacks (*Gasterosteus aculeatus*) faster exploration style was linked with increased use of social information (Nomakuchi *et al.* 2009), thus we would have expected to find individuals with faster exploratory personality types to have received social information at a higher rate. However, we did not observe an effect of exploration speed on social information transmission. It is possible that exploration speed could be more related to asocial discovery of foraging patches (Overveld & Matthysen 2010), something we were not able to look at fully in our experiment due to the low number of discovery events we can confidently determine were asocial.

Dominant individuals were found to receive social information at a higher rate than more subordinate individuals. It is possible that this result could be an artifact of interference, as more dominant individuals would be able to feed from the newly discovered feeder before subordinates in the case of simultaneous arrivals, thus altering apparent order. However, as individuals arriving within the same one minute were tied in the analysis and treated as joint-discoverers (making social transmission between them impossible), it seems unlikely that potential interference could account for our findings. Thus, our results suggest that dominant individuals have increased access to social information, which to our knowledge has not been demonstrated in any other study of social information. Whether this results from greater attention to social cues, or more weight given to social vs personal information by dominants remains to be determined. If considered in the context of a producer-scrounger game, in which asocial discoverers are producers while the use of social information to locate the novel patch is considered scrounging (Giraldeau & Dubois 2008), our results follow both the modelled prediction and experimental evidence that more dominant individuals would have a higher rate of scrounging (Barta & Giraldeau 1998; Liker & Barta 2002). By contrast, Boogert *et al.* (2014) found no effects of dominance on social information use in captive starling flocks. The difference between our findings and Boogert *et al.* (2014) could reflect species level variation in the importance of dominance ranks. For instance, dominance rank may have greater importance in small flocks exhibiting strongly linear dominance hierarchies, such as seen in black-capped chickadees and house sparrows (Liker & Barta 2002), compared with the more gregarious starlings (Boogert *et al*. 2014).

The relationship between habitat characteristics and social network structure remains unclear, due to the difficulties associated with comparing networks directly (see Croft *et al.* 2008). However, NBDA allows for the comparison of transmission rates through multiple networks without requiring direct comparisons of network metrics, which are highly dependent on network size. To date only one NBDA analysis had previously considered any effect of physical characteristics of the environment, finding that information was transmitted socially only through fish shoals in a more structurally complex environment (Webster *et al.* 2013). As fish require visual contact with others to acquire information, this likely explains why physical structure influenced information diffusion. How the environment may interact with the transmission of social information in natural systems has not been previously examined. Here we examined two site types (urban and rural) that varied in several dimensions including food reliability, as feeders provide stable food sources in urban areas (Atchison & Rodewald 2006; Chamberlain *et al.* 2009). Unpredictable food availability has been suggested to increase reliance on social information (Rafacz & Templeton 2003; Deygout *et al.* 2010), and thus we predicted stronger reliance in rural habitats. However, while we found that transmission rates vary between sites this variation was not explained by the site type. It is possible that in our system we did not consider habitats with strong enough differences to detect an effect, or that our introduction of supplemental food necessary to record interactions was enough to eliminate any effect that would have been observable in our rural sites. Alternatively, social information may simply be used in all types of habitats by chickadees when locating novel food location. Future research into this question should consider species-specific aspects of habitat composition that may alter the flow of social information. For instance, in Webster *et al.* (2013) the tested sticklebacks may have been relying most on visual cues, which would be affected by environment complexity, as was observed. Small passerines, such as chickadees, may use other senses, particularly auditory cues in conjunction with visual cues (Smith 1991), thus habitat variables are likely to impact individual species in different ways.

In summary, our study provides further evidence of the utility of NBDA to detect social information transmission through wild networks. We highlight the importance of considering network associations in the study of social processes, as both NBDA and network centrality analysis demonstrated that network connections are important for receiving valuable social information. To our knowledge, our study is the first to consider the potential effects of both individual characteristics and environment type on information diffusion simultaneously. Additionally, we identified a previously undocumented potential benefit to social dominance, as we observed an increased rate of social information transmission in more dominant individuals, and as such emphasise the importance of considering system-specific individual characteristics in the study of social information use.

Table 3.1 Summary of network feeder use and data collection periods, used to construct the social network associations, by site and habitat type.

Site	Total Birds	Total feeder visits	Range of visits by individuals	Mean number of visits	Start Date	End Date	Weeks
Urban							
AP	10	12735	227-2398	1273	29-Oct-14	05-Jan-15	9
CW	11	8744	3-1802	795	07-Nov-14	02-Jan-15	8
HP	10	19901	716-3597	1990	05-Nov-14	04-Jan-15	8
PP	9	2917	7-757	324	29-Oct-14	03-Jan-15	9
Rural							
BB	8	9764	31-4321	1220	05-Nov-14	05-Jan-15	8
SM	8	6646	12-1594	830	12-Dec-14	05-Jan-15	3
SS	15	9931	5-3145	662	13-Nov-14	03-Jan-15	7
WG	9	9925	193-1897	1102	14-Nov-14	05-Jan-15	7
Total	80	80563					

Table 3.2 Mean ± SE association strength and eigenvector centrality from association networks by site.

Site	Strength			Eigenvector Centrality		
Urban						
AP	1.30	±	0.18	0.29	±	0.04
CW	0.52	±	0.07	0.28	±	0.04
HP	2.16	±	0.19	0.31	±	0.03
PP	0.96	±	0.13	0.33	±	0.05
Rural						
BB	0.48	±	0.11	0.27	±	0.08
SM	1.63	±	0.32	0.31	±	0.06
SS	1.07	±	0.20	0.21	±	0.04
WG	1.31	±	0.13	0.32	±	0.03

Table 3.3 Summary of top social and asocial NBDA models from model selection procedures. Parameters include a = age class, d = dominance rank, e = explorative personality, and s = sex, v = mean centered feeder visits and t = trial number. Effects of habitat was also included in model testing, but was not retained in any of the top models. Multiplicative models indicate that parameters influence both asocial discovery and social transmission rates. n-c, indicates non-constant rate of asocial discovery over time.

Model	Parameters	AICc	ΔAICc
Social			
multiplicative, n-c declining	P_d	3316.9	0
multiplicative, n-c declining	P_a,P_d,P_t	3318.8	1.9
multiplicative, n-c declining	P_d,P_t	3318.9	2.0
Non-Social			
multiplicative, n-c declining	P_s,P_e,P_d,P_v,P_t	3438	121.1

Table 3.4 Summary of the estimated effect of social transmission above the baseline rate of asocial discovery, from the final NBDA model containing all supported elements.

Transmission Rate	Estimate	Bounded
AP	34.44	0.972
BB	383.14	0.998
CW	22.21	0.956
HP	22.88	0.958
PP	25.21	0.962
SM	12.45	0.926
SS	103.72	0.990
WG	34.72	0.972

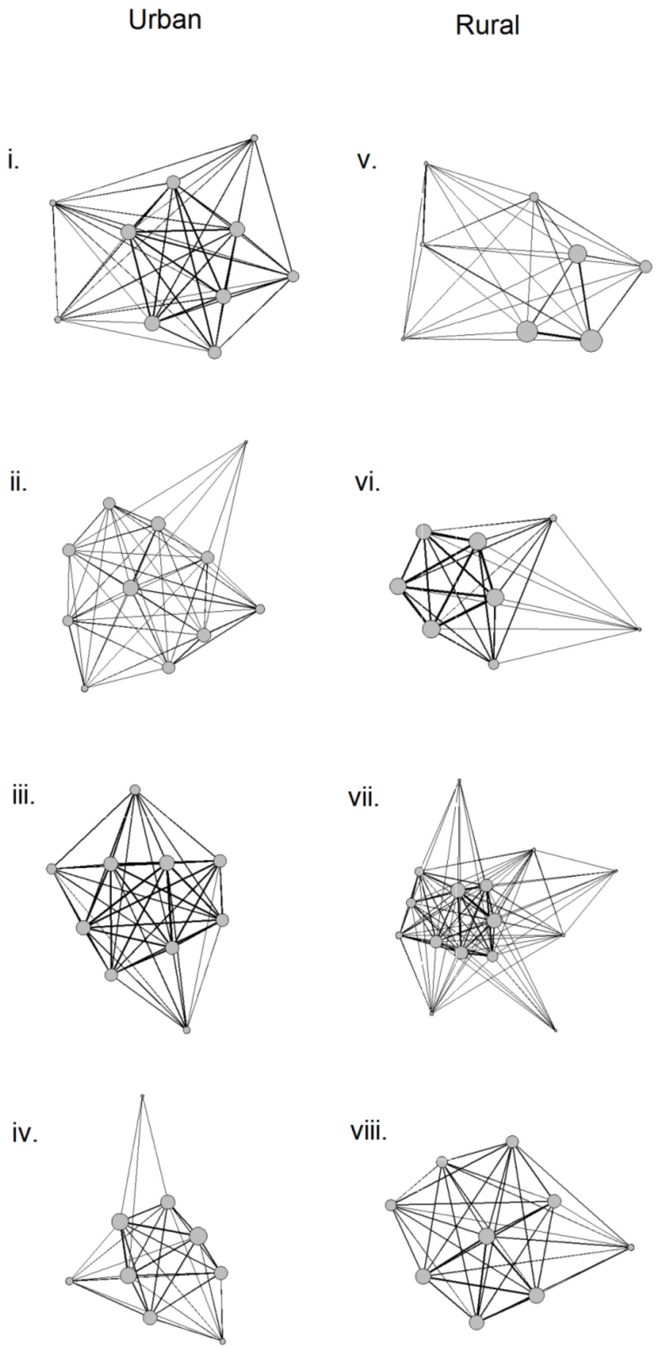

Figure 3.1 Social foraging networks for the eight study sites, determined using a simple ratio index (SRI) based on co-visitation at an RFID equipped feeder. Urban site (i-iv) in order are AP, CW, HP and PP, rural sites (v-viii) are BB, SM, SS, and WG. Increasing node size represents an increase in eigenvector centrality score and edge (line) thickness represents strength of association between individuals.

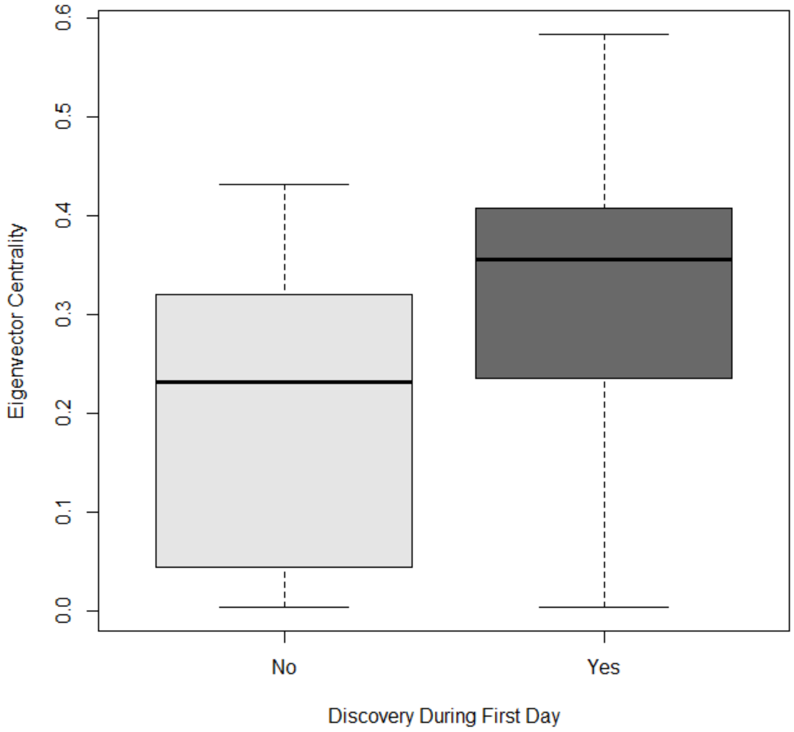

Figure 3.2 The relationship between eigenvector centrality and attendance at the novel foraging patch (yes (N = 112) or no (N = 32)) within 24 hours of initial patch discovery. Data were pooled across discovery trials and sites.

CHAPTER 4

General conclusion

The main objectives of this thesis were to examine the effects of individual characteristics and the external environment on social position and social process in wild networks. Specifically, chapter 2 evaluated the temporal consistency of network position and examined how social status and exploratory personality type influenced network centrality. The results of this chapter showed that over the non-breeding season black-capped chickadees maintain consistent positions within their social group. Additionally, network centrality was found to be positively associated with dominance rank but was not significantly influenced by personality type. While the exploration test in the thesis has been used in a number of studies (Kluen *et al.* 2012; Stuber *et al.* 2013; McCowan *et al.* 2015) and these measurements are based on commonly used captive assays (e.g. Verbeek *et al.* 1994; Dingemanse *et al.* 2002; Drent *et al.* 2003), there still is uncertainty around how accurately these tests reflect a measure of information gathering in a new environment, as opposed to a confounding responses (i.e. capture stress). There has been some evidence provided from similar assays that such tests are correlated with exploration in a natural environment (Herborn *et al.* 2010), but other studies of information gathering have not been able to (e.g. McCowan *et al.* 2015), or have not attempted to, demonstrate a link between movement through a novel room and information acquisition. Therefore it is important to interpret the relationship between exploration and network centrality, as well as between exploration and social information use, with the caveat that more validation is required to ensure this measure is an accurate quantification of information gathering in a novel environment. Chapter 3, in turn, used network based diffusion analysis to demonstrate that social foraging information was transmitted through network connections in all examined chickadee groups. Of the tested individual attributes, dominance rank was positively associated with access to social information. Taken together these findings indicate that dominants, rather than more subordinate individuals, may preferentially use a foraging strategy linked to social information use. This difference in strategy could potentially result from, or lead to, their more central network positions.

Finally, chapter 3 also examined the potential for the external environment to influence social information transmission. However, no difference in transmission rate was observed between urban and rural habitats, possibly indicating a habitat-independent social strategy of black-capped chickadees. Alternatively, the lack of difference observed between habitats may reflect a confounding effect of multiple aspects of urbanised habitats, a lack of statistical power due to sampling from only four sites of each habitat, or a lack of extreme habitats from the sampled sites. While this thesis is unable to address these possibilities, the work from this chapter does highlight the utility of studying network processes, through tools such as NBDA, as a method of network comparison as the results from such analysis are comparable and not impeded by the network-size relationship seen in many network metrics which make direct network comparisons problematic.

The results from this thesis highlighted both the utility and feasibility of studying social behaviours and processes within natural social groups. Importantly, chapter 2 empirically evaluated the common assumption that network metrics exhibit significant repeatability across time, while additionally being one of only a small number of network-based studies to assess replicate networks in the wild. Further research into inter-annual and inter-contextual network consistency (i.e. through removal or translocation of individuals between networks) would be an interesting continuation of this research. Chapter 3 is one of the only two network studies to assess any aspect of external environment on the social process of information transmission. This thesis furthers the field of social network analysis by using replicate wild social groups, and takes advantage of automated technology to collect association data from a multiple month time period.

Overall this thesis highlights how position within a social group can be impacted by individual-level traits. Particularly, for a species with strict linear dominance hierarchies, the findings from this thesis observed that social dominance can influence network connections. There is some evidence that such differences in network connections can be important for access to social information, although this has only been shown in a few studies of foraging information (Aplin *et al.* 2012; Ch. 3) or the learning of novel foraging tasks (Claidière *et al.* 2013), and has not to date been examined in terms of other types of information such as that relating to predation risk or mate quality, all of which are expected to be benefits of sociality (Krause & Ruxton 2002). Additionally, an important further step from this research would be validating the importance of dominance status in the access to, and use of, social information. For instance, an experiment which allowed individuals of known dominance status to choose between social information and asocial information, similar to those testing for social information use by personality type (Marchetti & Drent 2000; Kurvers *et al.* 2010), would help to tease apart the effects of dominance and network position in the use of social information.

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