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Individual and ecological determinants of social information transmission in the wild

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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. Furthermore, few previous studies of social information use have considered the potential effects of traits such as dominance and personality, which have been found to influence group social structure. We used network-based diffusion analysis, which incorporates information on individual social associations, to examine whether wild flocks of black-capped chickadees, *Poecile atricapillus*, utilize 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 and habitat level characteristics on the rate of information transmission. Social information transmission was found to occur in all flocks, as individual time of discovery of the novel foraging patches was explained by network connections 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 also found that the rate of social information transmission was higher in rural than urban environments. 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.

For animals, collecting and maintaining accurate information about foraging opportunities is a vital task. Individuals are required to frequently resample their environment, to acquire updated information and reduce uncertainty, particularly when food resources are patchy and/or ephemeral in nature (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005). While there are a variety of ways animals may attempt to optimize searching, maintaining accurate information through personal exploration requires expending significant time and energy (Chittka, Skorupski, & Raine, 2009; Dall & Johnstone, 2002). 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; Hoppitt & Laland, 2013).

Social information has been defined as information acquired through the observation of other individuals (reviewed by Aoki & Feldman, 2014; Dall et al., 2005). It can be acquired in a variety of ways, including local enhancement, eavesdropping and observational learning (Bonnie & Earley, 2007). Current theory suggests that while social information may be less costly than individual exploration, it may also be less reliable (Galef, 2009; Kendal, Coolen, van Bergen, & Laland, 2005). Therefore it has been suggested that social information should only be used under specific circumstances, such as when individual tactics are unproductive or when personal exploration is risky (reviewed by Galef, 2009; Laland, 2004). The usefulness of social information is also expected to vary with its reliability (Hall & Kramer, 2008). Additionally, the relevance of social information can depend on an individual's spatial, social and temporal distance from the

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information source as distance can erode the value of the information, for instance if information acquired about a temporal resource is employed at a later date once the resource has already been depleted (Seppänen, Forsman, Mönkkönen, & Thomson, 2007).

Social information implicitly relies on the connections between individuals, which can include physical interactions (i.e. grooming, aggression), co-occurring in the same group (i.e. group foraging), or observing one another. Thus, it is likely that not all individuals in a group will have equal access to social information, as not all individuals will interact equally or at all (Krause, James, Franks, & Croft, 2015). However, only recently have studies begun to account for such variation in social connections when attempting to assess social information use. While accurately mapping social connections within groups presents some challenges, social network analysis provides a well-defined framework for examining both direct and indirect social connections (Croft, James, & Krause, 2008; Sih, Hanser, & McHugh, 2009; Wey, Blumstein, Shen, & Jordán, 2008). Social networks can describe a snapshot of social interactions, and within a group multiple different networks can exist reflecting different social connections, such as co-foraging, aggression, mating and many others. As individuals vary in their social connections within their social group (Krause et al., 2015) information should be transmitted more readily between connected individuals. 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, Boogert, & Laland, 2010). Specifically, NBDA infers social transmission when the pattern of information acquisition follows network associations, assuming the rate of transmission in a naïve-informed dyad is linearly proportional to their social association. NBDA has been used to assess social information transmission in a variety of taxa in both laboratory-based (fish; Atton, Hoppitt, Webster, Galef, & Laland, 2012; Webster, Atton, Hoppitt, & Laland, 2013; birds; Boogert, Nightingale, Hoppitt, & Laland, 2014) and wild studies (primates; Hobaiter, Poisot, Zuberbühler, Hoppitt, & Gruber, 2014; Kendal et al., 2010; birds; Aplin, Farine, Morand-Ferron, & Sheldon, 2012; Aplin et al., 2015; Farine, Aplin, Sheldon, & Hoppitt, 2015; whales: Allen, Weinrich, Hoppitt, & Rendell, 2013).

An individual's position in its social group depends on the strength and frequency of its interactions with other group members. Individual characteristics such as age, sex and even personality type can influence social network position (Aplin et al., 2013; Croft et al., 2008; Lusseau & Newman, 2004; Pike, Samanta, Lindström, & Royle, 2008). Additionally, such traits have been shown to affect an individual's likelihood of favouring the use of social information. For instance, shy barnacle geese, *Branta leucopsis*, have been shown to utilize 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 an individual's age (Allen et al., 2013; Aplin et al., 2015), as well as sex (Aplin et al., 2015). However, no studies have explicitly tested for an effect of exploratory 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 (Edenbrow et al., 2011; Mokross, Ryder, Côrtes, Wolfe, & Stouffer, 2014; Sundaresan, Fischhoff, Dushoff, & Rubenstein, 2006). For instance, Sundaresan et al. (2006) found that network metrics, including number of associations and clustering coefficient 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 social information followed network connections in a complex but not simple environment (Webster et al., 2013).

In this study, we applied NBDA to wild flocks of black-capped chickadees, *Poecile atricapillus*, to determine how information about novel foraging opportunities is acquired. Chickadees are well suited to social foraging studies, as they form social flocks during the nonbreeding season and utilize 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, Mennill, Ratcliffe, & Smith, 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 asked how foraging information is acquired in wild chickadees. If foraging information is acquired socially, we predicted that the timing of arrival by naïve individuals at a novel foraging patch will be positively correlated with their social foraging connections from the association network (Aplin et al., 2012; Hoppitt et al., 2010). We then aimed to determine whether, given an individual's social network position, its use of social information varies with 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 predicted that higher exploration, measured as faster exploration of a novel environment, 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 network structure, a study of the transmission of parasites through a network of macaques, *Macaca fuscata*, showed the dominants had higher network centrality and higher parasite transmission rates (MacIntosh et al., 2012). Therefore, we predicted that dominant individuals may also have higher access to social information due to their network position.

Finally, as there is evidence that characteristics of the environment may influence social transmission (Webster et al., 2013) and that social information may be relied on more in variable environments (Rafacz & Templeton, 2003), we assessed flocks from urban and rural sites. Although urban and rural environments vary in a number of characteristics, for wintering birds it has been suggested that a key difference between them is increased stability and predictability in food availability in urban areas due to food provided in birdfeeders (Atchison & Rodewald, 2006; Chamberlain et al., 2009). Thus, we predicted that the rate of social information use would be higher in more rural environments.

METHODS

Study Species, Study Sites and Individual Traits

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 autumn, chickadees form stable social flocks that consist of unrelated individuals, and retain these associations throughout the winter (Smith, 1991). Flocks consist of approximately 3–12 individuals, with a linear dominance