SOCIAL LEARNING IN RELATION TO THE PHYSICAL AND SOCIAL ENVIRONMENT: INSIGHTS FROM CASE STUDIES IN *PARIDAE*

EMIL ISAKSSON

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Department of Biology
Faculty of Science
University of Ottawa

Abstract

Information about the environment is essential for making appropriate behavioural decisions, especially for animals that are exposed to periods of greater environmental challenges. For group-living animals, this information may be easily accessible via social connections which allows individuals to circumvent potentially hazardous and costly interactions with the environment to acquire first-hand knowledge. Despite this advantage of acquiring and using socially available information – social learning – in challenging environments, little is known about how the use of social learning is influenced by harsh environments. In *Chapter 2* and *3* of this thesis, I investigate how social learning and information use are influenced by the environment on a spatial and temporal scale, respectively. *Chapter 2* investigates the hypothesis that environments that challenge food acquisition will favor the use of social learning to overcome these challenges. I tested the social learning performance of great tits from high (harsh) versus low (mild) elevation and found no support for the hypothesis, which suggests that social learning is of equal value across environments. There were, however, substantial individual differences in social learning performance. In *Chapter 3*, I investigated how variation in winter temperatures affected the social information use in groups of black-capped chickadees and found a negative correlation between temperature and social information use. This suggests that the use of social information works as a risk-sensitive strategy to avoid energetic shortfalls during winter in these chickadees. In addition to the interaction between social learning and the physical environment, I also investigated its interaction with the social environment in *Chapter 4*. Being more connected within one's social group can have a positive impact on an individual's survival. Moreover, providing new information to the group can increase an individual's value as a social partner in the eyes of their peers and lead to an increase in social connectedness.

However, tests of this hypothesis are lacking. In *Chapter 4*, I test this hypothesis in the black-capped chickadee. Acquiring information was positively correlated with social connectedness. The effect was stable over time for individuals that were consistent in investing time and energy on updating their information, whereas it weakened over time for individuals that were more variable in their information acquisition. Thus, providing information can act to temporarily improve an individual's social connectedness which may improve short-term survival. Overall, this thesis links social learning with variation in the physical and social environment and emphasizes their intricate relationship. To improve our understanding of the factors that have shaped social learning, future studies should take a multilevel approach that includes consideration of this relationship.

Résumé

Les informations sur l'environnement sont essentielles pour prendre des décisions comportementales appropriées, en particulier pour les animaux qui sont exposés à des environnements plus difficiles. Pour les animaux vivant en groupe, ces informations peuvent être facilement accessibles par le biais de relations sociales ce qui permet d'éviter des interactions directes potentiellement dangereuses avec l'environnement afin d'acquérir des connaissances. Malgré ce clair avantage d'acquérir et d'utiliser des informations sociales - l'apprentissage social - dans des environnements difficiles, nous savons peu de choses sur la façon dont l'utilisation de l'apprentissage social est influencée par les environnements difficiles. Dans les chapitres 2 et 3 de cette thèse, j'étudie comment l'apprentissage social et l'utilisation de l'information sociale sont influencés par l'environnement à une échelle spatiale et temporelle, respectivement. Le chapitre 2 étudie l'hypothèse selon laquelle les environnements qui posent des problèmes d'acquisition de nourriture favorisent l'utilisation de l'apprentissage social pour surmonter ces problèmes. J'ai testé les performances d'apprentissage social des mésanges charbonnières provenant d'une altitude élevée (environnement difficile) par rapport à une altitude faible (environnement doux) et je n'ai trouvé aucun soutien pour l'hypothèse. Cela suggère que l'apprentissage social est d'une valeur égale dans tous les environnements. Il y avait cependant des différences individuelles substantielles dans les performances d'apprentissage social. Dans le chapitre 3, j'ai étudié comment la variation des températures hivernales affectait l'utilisation de l'information sociale dans les groupes de mésanges à tête noire et j'ai trouvé une corrélation négative entre la température et l'utilisation de l'information sociale. Cela suggère que l'utilisation d'information sociale fonctionne comme une stratégie sensible au risque pour éviter les déficits énergétiques pendant l'hiver chez ces mésanges. Outre l'interaction entre l'apprentissage social et

l'environnement physique, j'ai également étudié son interaction avec l'environnement social dans le chapitre 4. Le fait d'être mieux connecté au sein de son groupe social peut avoir un impact positif sur la survie. En outre, le fait de fournir de nouvelles informations au groupe peut accroître la valeur d'un individu en tant que partenaire social aux yeux de ses pairs et conduire à une augmentation de la connectivité sociale. Toutefois, les tests de cette hypothèse sont rare et insuffisant. Dans le chapitre 4, je teste cette hypothèse dans les groupes de mésanges à tête noire. L'acquisition d'informations est positivement corrélée à la connectivité sociale. L'effet est stable dans le temps pour les individus qui investissent régulièrement du temps et de l'énergie dans pour maintenir leur niveau de connaissance de l'environnement, alors qu'il s'affaiblit dans le temps pour les individus qui sont plus variables dans leur acquisition d'informations sur l'environnement. Ainsi, fournir de nouvelles informations au groupe peut agir pour améliorer temporairement la connectivité sociale d'un individu, ce qui peut améliorer la survie à court terme. Dans l'ensemble, cette thèse établit un lien entre l'apprentissage social et la variation de l'environnement physique et social et met l'accent sur leur relation complexe. Pour améliorer notre compréhension des facteurs qui ont façonné l'apprentissage social, les études futures devraient adopter une approche à plusieurs niveaux qui tienne compte de cette relation.

Co-Authorship

Chapter 2. Environmental harshness does not affect the propensity for social learning in Great tits, *Parus major.*

Authors: Emil Isaksson (E.I.), Julie Morand-Ferron (J.M.-F.), & Alexis Chaine (A.C.).

Author contributions: E.I. and J.M.-F. conceived the study. E.I. designed the study, collected data, performed statistical analyses, and wrote the manuscript. J.M.-F. helped with statistical analysis and early drafts of the manuscript. A.C. helped with study design, animal housing and care, and helped write the manuscript.

Chapter 3. Social information use increases with decreasing winter temperature in a passerine bird

Authors: Emil Isaksson (E.I.), Jan J. Wijmenga (J.J.W.), Alexis Chaine (A.C.), Roslyn Dakin (R.D.), Julien G. A. Martin (J.M.), & Kimberley J. Mathot (K.J.M).

E.I. and K.J.M. conceived the study. K.J.M. and J.J.W. collected the data. E.I., J.M., and R.D. analyzed the data. E.I. wrote the manuscript. E.I., K.J.M., A.C., R.D., J.M. and J.J.W. revised and finalized the manuscript.

Chapter 4. Information gain predicts network centrality, but the effect varies with acquisition method

Authors: Emil Isaksson (E.I.), Jan J. Wijmenga (J.J.W.), Roslyn Dakin (R.D.), Kimberley J. Mathot (K.J.M) & Julien G. A. Martin (J.M.).

E.I., K.J.M., R.D., and J.M. conceived the study. K.J.M. and J.J.W. collected the data. E.I., J.M., and R.D. analyzed the data. E.I. wrote the manuscript. E.I., K.J.M., R.D., J.M. and J.J.W. revised and finalized the manuscript.

Data availability

Chapter 2. Envirronmental harshness does not affect the propensity for social learning in Great tits, *Parus major.*

Data and code used in the project are available in the Figshare Digital Repository: https://figshare.com/s/b280a6d32110e63c9087 (Isaksson et al. 2022).

Chapter 3. Social information use increases with decreasing winter temperature in a passerine bird

Data and code related to the project can be accessed on the Open Science Framework digital repository at: https://osf.io/h4693/?view_only=fc7ac1dffc4341919988dd45b21860bd (Isaksson et al. 2023).

Chapter 4. Information gain predicts network centrality, but the effect varies with acquisition method

Data and code related to the project can be accessed on the Open Science Framework digital repository at: https://osf.io/k7zqs/?view_only=4d4171d48355441cae6b4f9b579dd6c6

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This thesis is about social learning, harsh environments, and social connections, all of which are phrases that could be used to describe core components of a PhD thesis. I have throughout my program experienced periods of increased harshness in my immediate environments, when things seemed stacked against me. A feeling I believe most graduate students feel at one point or another. However, with the help and support (perhaps in the form of learning something socially) of our peers (or social connections), we can overcome these harsh periods and eventually reach our goals. Here, I would like to acknowledge everyone that has helped me get this far.

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Chapter 1

Thesis introduction

1.1 Background

Most animals are social to some degree during their lifetime. For example, at the very least sexually reproducing animals need to find a mate to produce offspring. Consequently, interaction with other individuals plays an important role in shaping the life of animals. While group-living animals may enjoy additional benefits such as safety in numbers, they may also incur costs such as resource competition. Regardless of whether an animal is group living or solitary, all social encounters for any animal may involve a transfer of information that will change how the animal will interact with its surroundings in the future. The ability to extract and use information from such interactions can help animals make adaptive decisions across both social and non-social environmental conditions. However, there are still gaps in our knowledge about the interaction between these components; social learning, sociality, and the physical environment, which I explore in this thesis.

Transmission of information among, and the subsequent acquisition of behaviors by, individuals has been of central interest in the study of behavioural ontogeny (Galef 1976, 1988; Whiten et al. 2017). Any learning stemming from social sources can be classified as *Social Learning* (Galef 1988; Heyes 1994; Shettleworth 2010). In contrast to learning from first-hand interactions with the environment – *Asocial Learning* (Heyes 1994) – social learning circumvents many costs and risks associated with asocial learning (Galef 1976). For example, baby meerkats, *Suricata suricatta,* learn socially from adults how to handle and consume scorpions safely (Thornton and McAuliffe 2006), which could be dangerous to learn asocially. Social learning is now well known to be widespread in the animal kingdom, with evidence from arthropods (reviewed in Leadbeater and Chittka 2007), molluscs (Fiorito and

Scotto 1992), fish (Laland and Williams 1997; Vila Pouca et al. 2020), lizards (Noble et al. 2014; Whiting et al. 2018), birds (Fisher and Hinde 1949; Aplin 2019), and mammals (Kawamura 1959; Terkel 1995; McComb et al. 2001; Rendell and Whitehead 2001).

The study of social learning is of particular value as social learning can act as a non-genetic mode of inheritance to propagate adaptive behaviors between generations (Cavalli-Sforza and Feldman 1973; Dawkins 1976; Whiten 2005; Whiten et al. 2017). It also allows for the transfer of these behaviors among peers within the same or overlapping generations (Rogers 1988; van Schaik and Burkart 2011), and even between species (reviewed in Seppänen et al. 2007; an example from Parids in Hämäläinen et al. 2020). Learning from peers lies at the core of cultural evolution (Richerson and Boyd 1984; Birch and Heyes 2021). Culture is sometimes defined as any propagation of behaviour via social means but is more generally thought of as socially learned and persistent behavioural differences between populations (Laland and Hoppitt 2003). Much of the ecological success of humanity has been accredited to our culture of building on and adding to the knowledge of our predecessors, improving our skills and tools over time, in a way that other animals do not (Tennie et al. 2009; Boyd et al. 2011; Richerson and Boyd 2020; Birch and Heyes 2021). Social learning therefore has the potential to influence the evolutionary trajectory of a species.

Theory predicts that animals should be selective in their use of social learning in order to avoid adopting potentially maladaptive behaviours (Laland and Williams 1998; Giraldeau et al. 2002). Indeed, social and asocial learning each come with their own set of costs and benefits. A major benefit of learning from first-hand interaction with the environment is that the information gained is a 100% accurate representation of how the individual experienced the environment at that place, in that moment of time. This gives the individual the most complete knowledge base upon which to make behavioural decisions. Asocial learning, however, may often involve substantial costs or risks. Some of the costs and risks include

possible consumption of dangerous food, like in the meerkat (Thornton and McAuliffe 2006), elevated predation risk while gathering information, cost of missed opportunities elsewhere, and the energetic cost of exploring (discussed in Laland 2004; as well as in Rieucau and Giraldeau 2011). While social learning can mitigate a large proportion of these costs, learning socially will never be able to yield the same level of accurate information as asocial information. This is due to the fact that, by definition, the information has been filtered through a social intermediary. Conversely, it has been suggested that socially mediated information filtering is more accurate than what the traditional view of social information transfer assumed. This increased accuracy of socially available information was suggested to be because individuals likely exhibit behaviours that have been successful to them in the past rather than exhibiting a suboptimal behaviour (Galef 1995). These costs and benefits outlined above are central for animals to determine whether they should favour social learning or asocial learning in any given situation. However, there is still much that we do not understand about how they shape social learning use. One major aspect that complicates our understanding of their interaction, and a central theme to this thesis, is that environments vary and change constantly which may affect those costs and benefits.

Despite the broad scientific interest displayed in the literature, we have only recently begun to scratch the surface of how environmental variation influences social learning. A good starting point for investigating this is to consider *when* animals should learn from their peers. The so called "social learning strategies" (SLS) framework provides predictions regarding the conditions under which animals should favour reliance on social learning over asocial learning (Laland 2004; Kendal et al. 2005, 2018). One of the more explored social learning strategies is the "copy when asocial learning is costly" (Laland 2004), which is based on the "costly information hypothesis" suggested by Boyd and Richerson in the 1980s (1985). This hypothesis states that animals should use socially available information when

the costs of acquiring information asocially become too great (Boyd and Richerson 1985, 1988; Laland 2004). Food scarcity leading to longer foraging trips as well as cold temperatures are both examples of environmental conditions that increase the costs of an animal. The former increases the energy spent while foraging whereas the latter increases energy required for thermoregulation. Another social learning strategy that is important to consider in the context of environmental influence suggests that animals should copy when they are uncertain (Boyd and Richerson 1988; Laland 2004). This strategy states that individuals should rely more on social learning the less they know about the environment (Boyd and Richerson 1988; Laland 2004). For example, naive individuals who are experiencing a change in the environment for the first time should be more inclined to learn from their peers. Paradoxically to the "copy when uncertain" strategy, animals are predicted to rely less on social learning the more frequent and stochastic environmental change is, i.e. the less predictable the environment is (Boyd and Richerson 1988; Feldman et al. 1996; Aoki et al. 2005). This is because any information acquired in such an environment will become outdated/inaccurate more quickly (Boyd and Richerson 1988). However, recent modelling suggests that biased social learning, like the SLS's conditions for when and from whom to learn, can mitigate some of the influence of environmental predictability on social learning (Aoki and Feldman 2014). Multiple characteristics of the environment, such as costs, uncertainty, and unpredictability, are thus proposed to be involved in determining the usefulness of social learning and shaping its expression.

In particular, environmental harshness has been suggested to be an important driver of social learning occurrence. A proposed hypothesis for the evolutionary influence of the environment on cognitive abilities, such as social learning, is the 'harsh environment hypothesis' (Pravosudov and Clayton 2002; Roth et al. 2010; Tebbich and Teschke 2014; Hermer et al. 2018). The harsh environment hypothesis was derived from the 'adaptive

specialization hypothesis' which states that certain cognitive abilities have evolved to deal with particular environmental problems (Rozin and Kalat 1971). While the adaptive specialization hypothesis is broadly applicable to any problem, the harsh environment hypothesis specifically poses that challenging environmental states will promote cognitive abilities to mitigate these challenges. These environmental challenges may include altitudinal and latitudinal differences in habitat quality, where high altitudes and latitudes represent lower-quality environments or seasonal changes in food availability. Food scarcity in the winter is an example of a significant environmental challenge for many animals. Tests of the harsh environment hypothesis in relation to social learning are still lacking in the literature (but see Heinen et al. 2021, 2022; Isaksson et al. 2024). The harsh environment hypothesis has, however, been more widely tested for other cognitive abilities such as asocial learning and memory (Pravosudov and Clayton 2002; Roth and Pravosudov 2009; Freas et al. 2012; Tebbich and Teschke 2014; Hermer et al. 2018, 2021), and innovation (Sol et al. 2005). For example, in a comparative analysis of 134 species of passerines, it was found that winter resident species, i.e. species that are exposed to periods of increased environmental harshness, had a higher tendency to invent novel foraging techniques compared to migratory species (Sol et al. 2005). This supports the predictions of the harsh environment hypothesis.

It is important, however, to note that environmental harshness is a multi-facetted concept. A useful distinction was recently suggested by Schradin et al (2023) between a harsh environment and a stressful environment. According to Schradin and colleagues, a harsh environment imposes long-term challenges on homeostatic maintenance and survival that short-term increases in energy expenditure cannot mitigate (Schradin et al. 2023; Makuya et al. 2023). In contrast, additional energy output could help an individual overcome the short-term hardships of a stressful environment (Schradin et al. 2023). Furthermore, environmental harshness or stress are not intrinsic properties of the environment but rather depend on the

interplay between animals and the environment (Love and Wagner 2023). To better understand how harshness influences cognition, we thus need to conduct cognitive tests across multiple environmental conditions.

In my thesis, I aim to investigate key aspects of the complex interaction between social learning and information transfer, and the environment - both the physical and the social. First, I test the influence of harsh environments on the use of social learning, using two different approaches in *Chapters 2* and *3*, respectively. *Chapter 2* focuses on the use of social learning in relation to altitudinal differences in environmental harshness. In this chapter, I use an experimental approach in which we caught wild great tits (*Parus major*, Figure 1.1) from high (harsh) and low (mild) elevations. A few individuals were then trained as demonstrators on two tasks while most were acting as naive observers with several of the observers acting as control individuals. In contrast to *Chapter 2* which compares social learning between two separate environments, *Chapter 3* investigates how temporal shifts in winter temperatures, a great challenge for many winter residents, influenced social information transmission. In *Chapter 3*, I followed 8 groups of black-capped chickadees (*Parus atricapillus*, Figure 1.2) over three winter months with starkly fluctuating temperatures, going as low as -40°C, as they repeatedly rediscovered intermittently filled bird feeders. I used data on individual feeder visits within each group at each feeder to construct weekly social networks. Visitation data was recorded using radio-frequency identification technology (RFID) which recorded each visit by any individual equipped with a passive integrated transponder (PIT-tag, Figure 2). The networks were created assuming the gambit of the group using spatiotemporal proximity (see general methods). Each time the feeders were refilled, I estimated the use of social information transfer at the group level using NBDA and modelled it against the measured ambient temperature at the time. In *Chapter 4*, I switched focus from how the physical environment impacts social learning and investigated

how information acquisition feeds back to influence the social environment. First, I estimated two traits that should reflect different aspects of how reliable an individual is as a source of information, henceforth "informed traits". Second, using the same data as in *Chapter 3*, I created daily social networks during the periods when the feeders were full. Finally, I looked at how well the informed traits predicted individuals' positions in the networks. Because I used daily networks, I could also evaluate whether the impact of each informed trait varied over time. Overall, this thesis provides new insights and opens new questions about the relationship between social learning, environmental challenges, and sociality.

1.2 General methods

There are a few different ways to measure social learning. One widely used method is to take an experimental approach, as I do in *Chapter 2*, which includes training some individuals on a task and having them demonstrate the task to naïve observer individuals (Alcock 1969; Sasvári 1979; Fiorito and Scotto 1992). The trained individuals, or demonstrators, are placed together with the naive observer and the task. After the demonstrator has completed the task in front of the observer the individuals are separated, and the observer is presented with the task alone. Whether or not the observer solves the task in the absence of the demonstrator (e.g. Fawcett et al. 2002; Bouchard et al. 2007; Seok An et al. 2011), how fast or how many demonstration trials the observer needs to solve it (e.g. Bouchard et al. 2007; Brodin and Utku Urhan 2014), or how similar the method used by the observer to solve the task was to the demonstrated methods (e.g. Fawcett et al. 2002; Aplin et al. 2015a; Kis et al. 2015) are usually measured. These can then be compared against the performance of control individuals that did not receive a demonstration. If the observers are significantly more likely to solve the task, solve it faster, or use a technique more similar to the demonstrator as compared to the control group, this is taken as evidence for social

learning. In addition, even if the observers do not solve the task following a demonstration, it can still be possible to evaluate the social influence of the demonstrator on the behaviour of the observers. For example, naive common marmosets were not able to open an artificial fruit following a demonstration, but individuals who observed a demonstration interacted with the artificial fruit and directed their attention toward the opening mechanism significantly more than control individuals (Caldwell and Whiten 2004).

Another more recently developed method for animal behaviour research known as network-based diffusion analysis (henceforth NBDA) has allowed us to test for social learning in groups of freely interacting animals (Franz and Nunn 2009; Hoppitt et al. 2010; Hoppitt and Laland 2011). NBDA can measure the relative importance of social and asocial learning in the acquisition of a new behaviour. The analysis estimate whether the individuals in a group acquire a behaviour sequentially in a pattern that closely resembles how the individuals are connected or whether the individuals are more random in their acquisition, i.e. acquisition via asocial learning (Franz and Nunn 2009; Hoppitt et al. 2010). This method gives a group-level estimate of the likelihood that the behavioural spread was achieved via social or asocial means. NBDA works on the assumption that information is more likely to spread quickly between individuals who are more strongly connected (Coussi-Korbel and Fragaszy 1995; Franz and Nunn 2009). Estimating the social connection between individuals within a group can be done by direct observation of positive (e.g. allogrooming) and negative (e.g. displacement) interactions between group members. This approach usually requires that the population is rigorously monitored to capture all interactions but has the advantage that it can give insight into affiliative connections (overview in Kulahci and Quinn 2019). Alternatively, we can estimate associative social networks based on pairwise spatiotemporal co-occurrences of individuals in a group, which is the approach I use in *Chapter 3*. A common assumption used when creating associative networks is that individuals that co-

occur in time and space are interacting, an assumption known as the "gambit of the group" (Franks et al. 2010). This assumption has enabled estimations of networks in wild populations by only needing to monitor places where they aggregate. After the social networks have been estimated, we can observe how novel behaviours spread among the individuals and through that infer whether the spread likely stemmed from social transmission or not.

Social networks also allow us to investigate how certain factors influence social phenotypes, i.e. individuals' social position within the group. For example, early life connectivity predicts later life social status within the context of mating in the long-tailed manakin *Chiroxiphia linearis* (McDonald 2007). To look at the social costs and benefits of social learning, we can observe how the social position of an individual changes after it acquires information that is novel for the group (Kulahci et al. 2018; Kulahci and Quinn 2019). Being more connected within a network has often been linked to eco-evolutionary benefits such as reproductive success (Formica et al. 2012), survival (Stanton and Mann 2012), and access to information (Aplin et al. 2012). If acquiring novel information makes an individual a valuable social partner, we may expect a positive correlation between information acquisition and network position.

Throughout this thesis, I chose to investigate my questions about the cognitive ecology of social learning and information transmission in two species of passerine birds in the group *Paridae*. Birds have historically been associated with knowledge and intelligence across human cultures from the owl of Athena in Greek mythology symbolizing wisdom, the ibis-headed god of knowledge Toth in ancient Egypt and, for social learning and information transmission, the ravens Hugin and Munin that brought news of the world to Odin in the European north in the era of the Vikings. Scientific progress in the study of animal cognition and social learning (Emery 2006; Aplin 2019) has revealed that ancient humans were wise in

depicting knowledge (or cognitive function) with iconography of birds. In the following chapters, I explore the links between social learning, the environment, and sociality in the great tit and the black-capped chickadee.

Great tits (Figure 1.1) are a common bird in Europe that has been the center of attention for many studies of avian cognition. For example, they have been shown to possess inhibitory control, an executive cognitive function fundamental to other cognitive processes, almost on the same level as ravens *Corvus corax* and chimpanzees *Pan troglodytes* (Isaksson et al. 2018). The social learning abilities of the great tits are also well known and include one of the oldest scientifically recorded examples of cultural transmission among animals. Fisher and Hinde (1949), reported that great tits (and blue tits *Cyanistes caeruleus*) in the UK were opening the tin foil cap of milk bottles to get at the cream sitting on top of the milk within. Not only was this foraging innovation exceptional on its own, but the innovation also spread among close populations until it had spread across most of the UK (Fisher and Hinde 1949). In addition to being known social learners, great tits provide an ideal study system to test predictions related to the harsh environment hypothesis as they inhabit an extreme range of different habitats, from lush oak forests to near alpine altitudes across most of Europe and Asia.

Figure 1.1. Great tits in hand at one of the low-elevation capturing sites in the French Pyrenees (Photo: Emil Isaksson).

The back-capped chickadee (Figure 1.2) is a close North American relative of the great tit (Johansson et al. 2013) and the first species whose cognitive abilities were tested across environments, giving raise to the harsh environment hypothesis (Pravosudov and Clayton 2002). Black-capped chickadees are food hoarding specialists, meaning that they gather and store food when it is abundant to be used later during winter when food is more difficult to acquire. This characteristic has made them the subject of many investigations into spatial learning and memory (Smulders et al. 1995; Pravosudov and Clayton 2002; Brodin 2005; Roth et al. 2010, 2012). The fact that they are winter residents, form flocks during winter, and frequently use supplemental feeders has also facilitated the investigation of black-capped chickadee social networks and potential factors influencing them (Jones et al. 2017, 2019; Evans and Morand-Ferron 2019). These characteristics also make them ideal to ask questions about social learning and sociality across a temporally shift in environmental harshness such as winter.

Figure 1.2. Black-capped chickadees. The left image is an individual from Ottawa (Photo: William Matthias). The right image is from the University of Alberta beside one of the RFID-equipped feeders in the background (Photo: Emil Isaksson). The white band on the leg of the bird is the PIT-tag.

The altitudinal range of the great tits in the French Pyrenees provided an ideal system for me to investigate whether general differences in environmental harshness influenced social learning performance. Similarly, the assortative winter flocking of the resident black-capped chickadees in Alberta enabled me to investigate the influence of cold winter temperatures on social learning expression and how information acquisition affected sociality.

Chapter 2

Environmental harshness does not affect the propensity for social learning Great tits, *Parus major*

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2.1 Introduction

Survival is greatly impacted by the spatio-temporal variation in resource availability and some environments present greater challenges than others. Cognitive adaptations, which concern how animals collect, store, and use information (Shettleworth 2010), are one means of coping with food scarcity. For example, heightened spatial learning and memory evolved for storing food for later use (Sherry 1989). The 'harsh environment' hypothesis (henceforth HEH) for the evolution of cognition proposes that environments characterized by uncertain access to food due to climatic variables, like temperature and precipitation, should favour cognitive abilities that help mitigate this uncertainty (Pravosudov and Clayton 2002; Roth et al. 2010; Tebbich and Teschke 2014; Hermer et al. 2018). Altitudinal and latitudinal gradients have been frequently used to test the HEH, as increases in either correlates with colder, longer, and more intense (i.e. harsher) winters which restricts access to food and exerts higher metabolic demand on endothermic animals (Pravosudov and Clayton 2002; Freas et al. 2012; Roth et al. 2012; Heinen et al. 2021).

The HEH has been repeatedly tested in scatter hoarding species, such as black-capped- (*Poecile atricapillus*) and mountain-chickadees (*P. gambeli*), that rely on spatial memory and learning to retrieve food that they have hidden throughout their home range (Pravosudov and Clayton 2002; Freas et al. 2012; Tello-Ramos et al. 2018). Outside of such food hoarding systems, the wider applicability of the HEH is still largely unknown. Indeed, non-hoarding species likely experience selection pressures on different cognitive abilities than hoarding species that rely primarily on spatial memory. However, the limited number of studies on non-hoarding species show mixed results. For example, woodpecker finches (*Cactospiza pallida*), from an arid (harsh) area were faster at reversal learning than individuals from a cloud forest (mild), which is consistent with the HEH (Tebbich and Teschke 2014). In contrast, two studies of great tits showed no support for the HEH. Great

tits (*Parus major)* from mild, low elevation environments were more accurate than individuals from harsh, high elevation environments in a serial reversal learning test (i.e. learning flexibility Hermer et al. 2018). Furthermore, great tits from high and low elevations showed no difference in the accuracy of short term spatial memory (Hermer et al. 2021).

Studies of the HEH have largely focused on individual "trial-and-error" learning in the absence of social influences, known as *asocial learning* (Heyes 1994), despite the widespread use of social learning in animals (Galef 1976; Galef and Laland 2005; Hoppitt and Laland 2008; Aplin 2019). Compared to asocial learning, a social learner learns from the successes and failures of others (Galef 1988; Shettleworth 2010), which allows them to gain knowledge about the environment with lower risks and costs in terms of time and energy spent (Boyd and Richerson 1988; Galef and Giraldeau 2001; Griffin 2004). However, social learning can also provide less accurate information as it is not first-hand information, potentially leading to suboptimal behaviour (Giraldeau et al. 2002). The balance of these costs and benefits also likely depends on the environmental context. Furthermore, social interactions within groups create unequal access to social learning opportunities depending on each individuals' social phenotype (Coussi-Korbel and Fragaszy 1995; Lonsdorf and Bonnie 2010). This can lead to differences in the propensity to use social information among individuals within a population (Aplin and Morand-Ferron 2017). Social learning might thus be consistent within individuals but vary with shifts in environmental states.

Despite the benefits of social learning when an individual has limited or incomplete personal information, there is theoretical debate as to whether social learning provides an advantage in uncertain or harsh environments leading to two contrasting views. On the one hand, the suggestion that social learning can provide sub-optimal information about the environment (Giraldeau et al. 2002), combined with increased severity of consequences for erroneous decisions in harsher environments has led to the theory that asocial learning should

be favoured over social learning in variable environments (Boyd and Richerson 1988; Laland and Kendal 2003; Aoki and Feldman 2014). On the other hand, recent theoretical models show that social learning could be favoured in variable environments (Rendell et al. 2010; Arbilly et al. 2011) as it could reduce costs of foraging. Empirical tests of whether social learning is favoured with increased environmental uncertainty or not are rare. Mountain chickadees from harsh, high elevation use social learning, but less than conspecifics at low elevation, consistent with the first theory (Heinen et al. 2021, 2022). Mountain chickadees are food hoarding specialists that rely on asocial learning and memory to create and retrieve food caches for winter survival, so lower use of social learning and higher use of asocial learning at high elevation is consistent with predictions from the HEH. Whether the HEH holds for foraging generalists that could greatly benefit from social information about alternative food sources unlike specialist species, remains unknown.

In this study, we compared the use of social learning in wild great tits from populations located at high (800-900m asl) and low (400-500m asl) elevation to assess how the HEH applies to social learning in a generalist species. Great tits are a common European foraging generalist that are related to chickadees and known to use social learning to access a variety of food sources (Fisher and Hinde 1949; Aplin et al. 2013; Brodin and Utku Urhan 2014). Birds from these two elevations brought into captivity have been used to show that low elevation great tits have higher reversal learning performance than high elevation great tits (Hermer et al. 2018). The elevational contrast is marked by differences in temperature (~8°C; Bründl et al. 2020) and snowpack which should increase variability in food availability and impact the importance of food for survival. Furthermore, breeding behaviour is delayed and breeding success is lower at high elevation in the region for both the great tit (Sallé 2016), and the closely related blue tit, *Cyanistes caeruleus* (Lejeune et al. 2019; Bründl et al. 2020). Here we designed two foraging tasks and trained great tits to act as

demonstrators for naïve observers for each task. We were specifically interested in the onset of socially learnt behaviours in the observers and thus took steps to exclude influences of asocial learning. We first asked if individuals use social learning in colour-associative and spatial learning foraging tasks and if the propensity to use social information differed across environments (elevation) both in terms of: 1) approaching the task and 2) solving the task. If the theory that asocial learning is preferred over social learning in uncertain environments holds, we predict that behaviours associated with social learning should decrease as elevation increases. Conversely, if social learning is preferred over asocial learning in unpredictable environments, as suggested in recent models, then we predict that behaviours associated with social learning should increase as elevation increases. Second, we examined if there was evidence for a social learning phenotype in these populations by asking if individuals consistently differed in their use of social learning use across color associative and spatial tasks through repeatability analysis.

2.2 Material and Methods

2.2.1 *Capture and handling*

We captured great tits from Oct 2019 – Mar 2020 (3 batches), and Oct 2020 – Dec 2020 (2 batches) in the French Pyrenees using mist nets at high (800-900m asl; n=37) and low (400-500m asl; n=37) elevation sites. This elevation difference has been linked to environmental harshness having negative effects on life-history traits in great and blue tits (Sallé 2016; Lejeune et al. 2019; Bründl et al. 2020), as well as differences in asocial learning flexibility (Hermer et al. 2018). We used three high (Antras: 42.88111”N 0.94563”E , Cap de Sour: 42.93118”N 1.12235”E, Villargein: 42.90389”N 1.04648” E) and two low (Aubert: 42.96429”N 1.10310”E, Montjoie: 42.99886”N 1.16945”E) elevation sites. Following capture, birds were taken to the Station d’Ecologie Théorique et Expérimentale (SETE; 430m asl) field station in Moulis where birds were banded, aged, and sexed following standard procedures (Svensson 1992). Birds were designated either as *observers* (n=20 per elevation), *controls* (n=7 per elevation), or *demonstrators* (10 adult males per elevation) and released into individual aviaries at the field station (Fig 1A). We were unable to balance age and sex within and across elevations due to constraints imposed by capture methods, availability of birds, and aviary space. Likewise, we chose to increase the number of observers relative to controls given the limited number of birds and aviaries available. Each batch of birds was released back into the wild before the next batch was captured (sample composition details in Appendix A S1).

2.2.2 *Housing*

Observers were housed in individual aviaries that had both outdoor (W=1m, L=4m, H=3m) and indoor compartments (W=1m, L=1m, H=2.5m) for shelter and experiments (Fig 1). Birds were separated by one empty aviary such that they could see and hear each other

(i.e. social enrichment) while in the outdoor compartment, but would not be able to observe social learning trials of their neighbours, which were conducted in the indoor compartments (Fig 1). Outdoor compartments contained natural vegetation and several perches. Ad libitum food (mealworms, *Tenebrio molitor*, sunflower seeds, and suet cake) was provided in both compartments before and after experimental tests (Fig 1A). Indoor compartments had a roosting box as well as a heater and light that were on for the first two nights to ensure acclimation to the aviary. Birds were held for a total of 30 days for other experiments and social learning tests were conducted between days 16-25 of captivity.

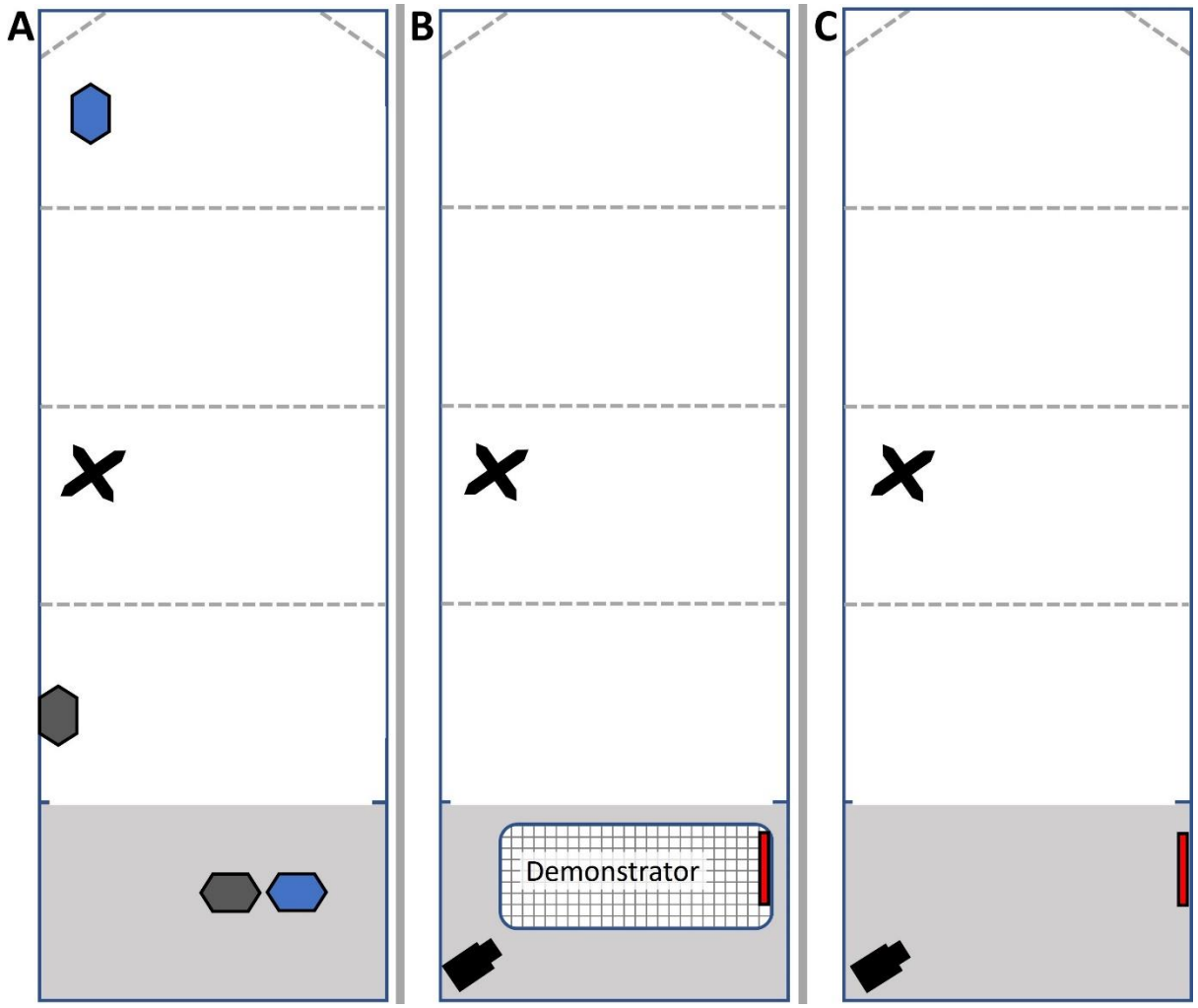

Figure 2.3. Top-down view of an observer aviary across the three experimental stages, A) Pre- and post social learning experiment, B) during demonstration, and C) during observer testing. The light-grey and white sections indicate the indoor and outdoor compartment, respectively. The dotted lines indicate perches and the black X-mark represents an artificial tree also used as a perch. Blue and grey hexagons in panel A represent locations for food and water. The black camera silhouette in the lower left corner of panels B and C indicates camera placements. The hatch-marked rectangle labeled "Demonstrator" in panel B indicates placement of the demonstrator cage with the smaller, red rectangle indicating the placement of the demonstrator board. The red rectangle in panel C indicates the placement of the test board.

2.2.3 *Demonstrators and demonstrator housing*

Only adult male great tits were chosen as demonstrators to reduce variance among demonstrators (e.g. Aplin et al. 2015a; Hämäläinen et al. 2020). Demonstrator individuals were housed and trained in separate mobile cages (internal dimensions: W=0.58m, L=0.355m, H=1.13m), which were all contained within one large indoor aviary for a given batch (4 cages for each session) to provide social enrichment, except for batch 1 in which the demonstrators were kept in separate, smaller indoor aviaries. Demonstrator cages contained several perches, natural vegetation, ad libitum food (sunflower seeds, mealworms and suet cake) and water. Demonstrators were habituated to task components prior to training by mounting an empty task board (see below) on a wall in the cage and hanging a bowl with five differently colored cotton balls and two artificial leaves used in the learning tasks next to the board. Demonstrator birds were trained in either the *Colour* or the *Spatial* task (see below).

2.2.4 *Learning Tasks*

Each observer bird (n=40) was tested for social learning on both learning tasks, performed by demonstrator birds, on separate days. The colour discrimination learning task (*Colour*) and the spatial learning task (*Spatial*) aimed to engage different contexts of the cognitive process for the birds (what vs. where). Both tasks used wooden testing boards (32W x 32Hx 2D cm) with 15 evenly spaced wells (Fig 2), and a perch in front of each well that the birds could use to easily inspect the well. During demonstrator training, a mealworm was placed in specific wells as a reward for correct choices. In the *Colour* task, observers were tested on their ability to learn to sample blue cotton balls, called “pompoms” (Hobbyworld Arts and Crafts Inc.), from an array including four other coloured pompoms (green, yellow, pink, red) used to cover the feeding wells (Fig 2A). *Colour* task boards had an equal number of each pompom colour (3 each). In the *Spatial* task, observers were tested on their ability to

learn three locations on a testing board that included spatial landmarks (patterns made with grey and black tape), and on which all wells were covered by grey, artificial “leaves” (washers covered in tape, Fig 2C). Pompoms and “leaves” were attached to the boards with fishing line so that they returned to their original position covering the well again following

sampling. Pompoms and “leaves” have been successfully used previously in avian cognition research (Roth et al. 2010; Rojas-Ferrer et al. 2020).

2.2.5 *Demonstrator training*

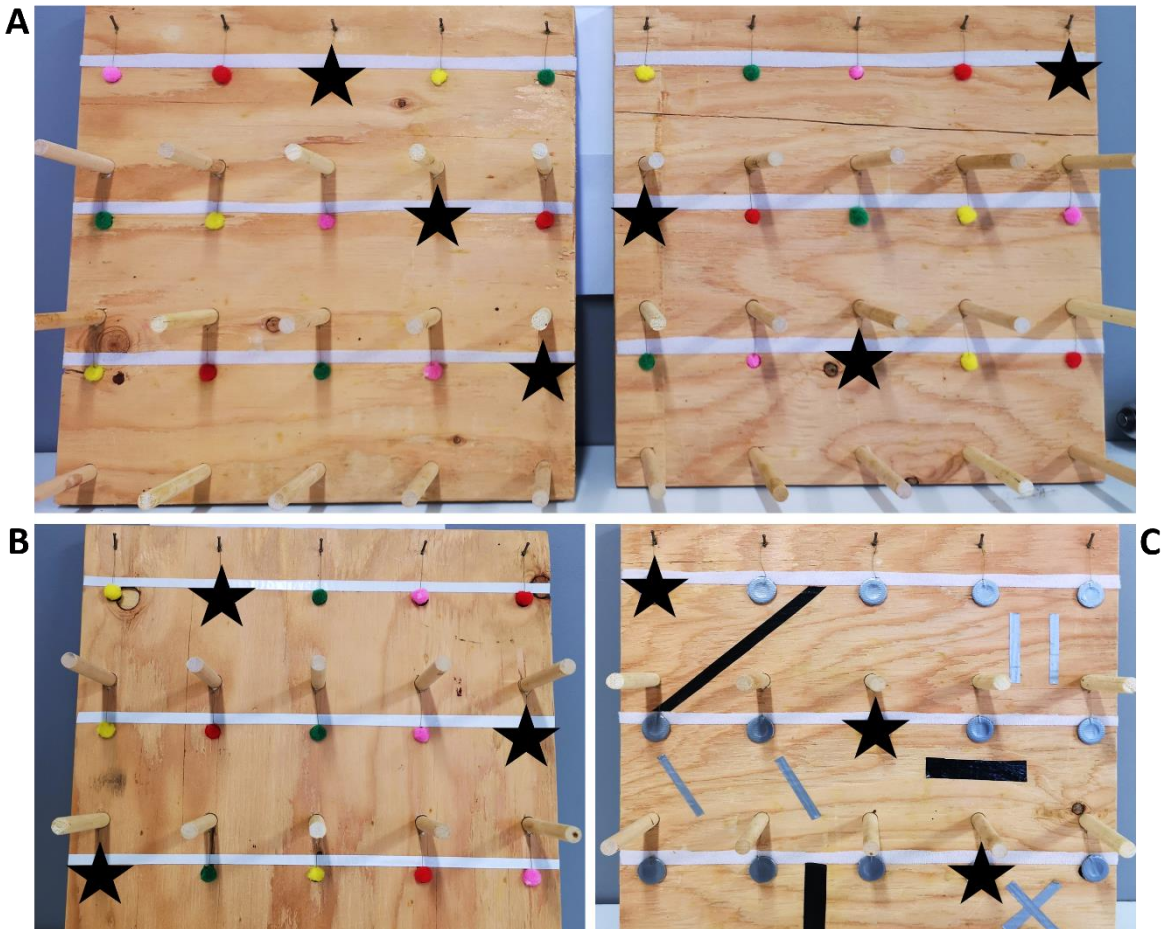

Figure 2.4. Training and testing board schematics. A) The two configurations of coloured pompoms used to train the demonstrators and used during demonstrations in the *Colour* task. B) The testing board used when testing observers in the *Colour* task. C) Design and configuration of the *Spatial* task, both during training and observer testing, including the landmark patterns in grey and black tape. Black stars indicate the correct choices (blue pompom in the *Colour* task, and artificial leaves in the *Spatial* task), both on the training boards (panels A and C) and the testing boards (panels B and C).

All habituation items and food other than rewards on the learning board were removed during training and demonstration sessions. Two demonstrator individuals in each batch were trained in the *Colour* task and the other two were trained in the *Spatial* task (one high and one low elevation bird for each task). Training followed a successive approximation methodology in which the birds were presented with wells fully uncovered first and for each training step that the bird passed, the wells were covered more until wells were completely covered. Rewarded wells (Fig 2) contained immobilized (decapitated) mealworms. This type of training method has been used successfully in previous experiments with related species (Thompson and Morand-Ferron 2019; Rojas-Ferrer et al. 2020). All demonstrator birds in our experiment successfully learned their task prior to social learning experiments.

Demonstrators trained in the *Colour* task were trained over four steps. Each *Colour* task demonstrator was trained with two different colour configurations on the board (Fig 2A), to ensure that demonstrators learned the color association rather than the spatial location of rewarded wells. Each training step was repeated at least twice per training board, except step 1 (fully uncovered wells) for board 2, and the demonstrator had to choose the three rewarding items first in consecutive repeats to move to the next step. In the last step of training (fully covered wells), a demonstrator had to choose the three blue pompoms first across twelve consecutive presentations, alternating training board 1 and 2 every two presentations, with a maximum of three errors across all twelve presentations to be considered trained.

Demonstrators for the *Spatial* task were trained over five steps starting with no leaf in front of the wells and ending with the leaf fully covering the wells. Demonstrators were trained on identical boards to those used to test observers in the spatial task (Fig 2C). Each training step was repeated at least three times and a demonstrator was considered fully trained in the task when they successfully pulled the correct leaves first when presented with a board with all wells covered and did so over five consecutive repetitions. Although we did not

allow any sampling errors for reaching this criterion, we did not consider quick pecks on the outer face of a leaf by the demonstrator as a sampling error since these differed considerably from attempts to get behind the leaf. A sampling attempt was defined as an interaction with a leaf that lasted at least 1 second involving manipulation of the leaf to get behind it (pulling, lifting, or pecking from the side so that the leaf lifted from the board).

2.2.6 *Individual activity level*

Consistently more active individuals could have a higher chance of approaching and interacting with the test boards by chance alone, so we estimated the mean activity level of each observer and control bird before social learning tests. Over three days preceding the social learning test, we recorded the number of continuous movements longer than one body length made by birds during a three-minute period in the afternoon. Individuals in batch 1 and 4 were only scored on two rather than three days due to time constraints, resulting in a total of 148 scoring sessions across all 40 individuals.

2.2.7 *Social learning procedure and variables*

All observer birds were assayed first on the *Colour* task over 2-3 days, with a maximum of 3 observers assayed per day, and then assayed in the same order in the *Spatial* task over 2-3 days to keep the time between tasks consistent among birds. The order of task presentation was kept the same throughout the study to avoid introducing variance in observer performance that might exist if the chance of success in one task impacts the chance of success in the second task differently depending on which task was presented first. Two days before the first social learning presentation, habituation items were placed inside the observer's aviary to minimize item neophobia during social learning tests. These included an empty testing board without pompoms, leaves, or markings, mounted 1.5m off the ground on

one side of the indoor chamber (same location as during observer testing, Fig 1C), and a bowl containing one pompom of each colour and two artificial leaves. Habituation items and food, including food dropped on the floor by the bird, were removed from the focal observer's aviary one hour before social learning tests began. During this food deprivation period, two stacked video cameras (Sony HD handicam) were placed in the aviary so that the observer could acclimatize to them. After experimental testing, food and habituation items were placed back in the aviary until the second social learning test.

Tests were conducted between 09.00-18.00, with no individual starting their test after ~16:30 to minimize effects of inactivity after sunset (except for one individual). Demonstrators were food deprived for 30-45 minutes prior to tests to ensure they would demonstrate the learning task during the trial. During social learning experiments, a total of four demonstrators did not perform their trained task within the first 15 minutes of demonstration and were not used for subsequent tests (see below). Observer and control bird motivation was verified before the first trial of each task by providing a single mealworm in the regular feeding place at the entrance to the indoor aviary section and the observer had to consume it before tests began. If they did not eat the mealworm, we tried again after a five-minute break and continued this pattern until the meal worm was consumed. Therefore, all observer and control individuals were food-motivated at the start of social learning trials.

Once motivation was verified, the door separating the indoor and outdoor compartment of the aviary was closed and the demonstrator cage was placed in the observer's aviary (Fig 1B). A task appropriate demonstration board with mealworms behind the trained colours or locations was then placed in the demonstrator cage (Fig 1B). Finally, the door between compartments was then opened and the experiment began. The demonstration was ended when either all three worms were taken or when the 15-minute time limit was reached. An observer's social learning assay consisted of a maximum of five consecutive trials where

each trial included a demonstration followed by an observer test. Each demonstration provided the observer with up to three opportunities to learn to approach and sample the correct items (the three rewarded wells). Demonstrators extracted worms from behind all three correct items in most (94%) trials, and from behind two or one item in 5% and 1% of trials, respectively. If a demonstrator failed to reveal any worms, it was given a five-minute break before a new attempt. During this break period, the demonstrator was left in the observer aviary but the door between the indoor and outdoor compartments was closed. In one case, the demonstrator failed a second time and it was replaced by a new demonstrator. If a demonstrator extracted fewer than three worms across five trials for a given observer, we deemed it a poor demonstrator and it was replaced by another demonstrator for the remaining observer tests that day. By testing observers in their long (4m) home aviary, it is possible that some observers might not closely watch the demonstrator. Individuals who are not interested in social learning are not expected to pay attention to demonstrations and allowing birds the opportunity to pay attention to demonstrations or not closely resembles the natural context of social learning responses from observers. However, there are three reasons to believe that most birds noticed demonstrators in our trials. First, food and tasks for other experiments were provided in the indoor space where the observer was placed, so birds generally were attentive to that space (Fig 1A). Second, cages were small enough that it would be impossible for the bird to not notice the presence of a demonstrator. Finally, birds with a demonstrator showed differences in behaviour from those who did not get a demonstrator (see results below) suggesting that in most cases observers paid attention to the presence of the demonstrator.

Following a demonstration, the demonstrator cage was removed from the observer's aviary. The observer's testing board without mealworms, was then mounted on the wall of the indoor compartment in the same location that the demonstrator's board had been, and the

five-minute trial began. The board was empty of mealworms as we specifically wanted to separate the effects of social information generated by the demonstrator from other cues such as the smell or sound of a mealworm on the board. During this period, we watched the observer through a viewing window and recorded: 1) whether the bird perched on/near (within one body length) of the test board, 2) whether a bird sampled an item on the board and how many items it sampled, 3) latency until first perch on/near the test board, and 4) latency until sampling both the first well overall and first correct well (the first correct well could also be the first overall). EI scored behaviors for all trials. EI conducted direct observations of all Observer trials and most Control trials and scored videos of all Control trials conducted by assistants. Video recordings were used to verify accuracy of events in trails that were scored live for a subset of tests. Behaviors scored were clearly defined (perching, pushing/pulling pompoms or leaves) and behaviors scored from video universally matched live scored measures. Latencies were calculated as the cumulative number of seconds across trials until the observer interacted (perched/sampled) with the board. If the observer did not sample any items during the 5-minute trial, it was given a new trial (demonstration and test). Each trial was a maximum of 301 seconds (five minutes + 1 second), with a maximum total of 1505 seconds across five trials. One second was arbitrarily added to each trial without the bird interacting with the board to avoid potential instances when an observer would perch/sample at exactly 1500 seconds. If the observer sampled any items in a trial, it was not tested again to avoid the influence of direct asocial learning on performance in subsequent trials. This point is important as it excludes the negative feedback of sampling a correct answer that did not contain a worm from the response we scored.

2.2.8 *Control*

To verify that the actions by the observer were influenced by the actions of the demonstrator rather than asocial learning, we conducted control tests on seven individuals from each elevation (composition in Appendix A S1). These control tests used the same methods as the social learning tests but without demonstration sessions. We chose to not present a bird, rather than an untrained bird, for these control tests since the presence of another bird in their cage could contribute to social information leading to local enhancement (approaching a foraging board). Local enhancement refers to when the likelihood of an observer visiting a location increases following demonstration (Thorpe 1963; Shettleworth 2010). By excluding any social information available in the control tests, we were able to quantify the social influence on observer behaviour. Birds were tested for five minutes with a five-minute break between trials during which the test board was removed from the aviary. As for the observer birds, trials continued until a bird sampled a well in a trial or failed in all five trials. The behavior of the birds experiencing the control trials was scored the same way as observer birds.

2.2.9 *Statistical analysis*

Data handling and statistics were conducted in R [version 4.2.1] (R Core Team 2020). To consider the inclusion of individual activity levels as a covariate in social learning analyses, we first evaluated the reliability of our measure of individual activity level. We evaluated individual repeatability in activity level using the *rptR*-package [0.9.22] (Stoffel et al. 2017). We estimated repeatability of activity level for individuals measured more than once (Bird ID) while controlling for time of day as a fixed effect, and the time of year (Batch) and the experimenter who recorded the measure (Person) as random effects. We ran 1000 bootstrap resampling (n=53, missing activity score for one individual) to estimate the significance of each random effect using a likelihood ratio test. Based on the results from the

repeatability test (see Results), mean individual activity level (2-3 days; see above) was added as a continuous variable, mean centered and scaled, for all relevant analyses.

We tested all controls and observers on two aspects of social learning in each task. First, local enhancement defined as whether the birds perched on/near the test board (Yes/No). Second, action copying was scored for whether a bird sampled the test board by interacting with an item (Yes/No, henceforth "action copying (Y/N)") as well as the number of items sampled per individual (henceforth "action copying (#)"). Action copying in this study was used to indicate that observers interacted with any item on the board following a demonstration. We were unable to evaluate individual accuracy of action copying due to too few correct responses by observers across tasks (Table 2.2), so we chose to focus on general action copying with any item in the analysis. Finally, we were unable to acquire standardized measures of local enhancement for one individual and action copying for three individuals (including the one missing the local enhancement score) due to time constraints (Table 2.2). These missing values are indicated as "NA" in descriptions below.

2.2.10 *Degree of local enhancement and environmental harshness*

We first assessed the impact of elevation on social learning by comparing the degree of local enhancement between individuals from high vs. low elevation. We used a binomial generalized linear mixed effects model (GLMM) with local enhancement as the response and elevation (high/low), test (observer/control), task (colour/spatial), individual activity, number of days since the start of the season (Oct 1st each year), sex (male/female), and age (juvenile/adult) as fixed effects and bird ID as a random effect to account for individual differences in responses across tasks (n=54 birds; observations=105, 3 NA). To evaluate the influence of receiving a demonstration on observer response between elevations, we allowed for an interaction between elevation and test in the model. The number of days since the start

of the season was mean centered and scaled prior to analysis. Mixed effects regression models were constructed using the *lme4*-package [1.1-30] (Bates et al. 2015), with significance tests from the *lmerTest*-package [3.1-3] (Kuznetsova et al. 2017), and model assumptions were validated using the *DHARMa*-package [0.4.5] (Hartig 2021). Graphics pertaining to this analysis were created using the *ggplot2*-package [3.3.6] (Wickham 2016).

2.2.11 *Latency of local enhancement and environmental harshness*

We also analysed how early in a trial individuals from either elevation used local enhancement as individuals might not differ in the ability to use local enhancement between elevations but rather how soon they use it. We used a mixed effects survival model, which allowed close examination of time steps until an event (perching = Yes), and accommodated observations with an unknown endpoint (perching = No after the maximum of five trials) (Therneau 2020). We tested latency until perching as a response against elevation, task, individual activity, days since the start of the season, sex, and age as fixed effects, while accounting for bird ID as a random effect (n=40 birds; observations=79, 1 NA). The control group was excluded from the survival analysis because we were interested in differences in the speed of social learning use across elevations given a demonstration. The proportional hazard assumptions were tested using the *cox.zph* function in the *survival*-package [3.3-1] (Therneau 2021). Multicollinearity in the survival models was tested using the variance inflation factor function (‘*vif*’) in the *rms*-package [6.3-0] (Harrell Jr 2021). The assumptions of: i) linearity between the predictors and log-hazard, ii) influential observations, and iii) outliers were tested on a non-mixed effects version of the model that accounted for the random effect of ID by including it as a ‘frailty’ argument in the model (see Therneau et al. 2003). The results of the mixed effect survival model and the frailty model were qualitatively the same, and thus validate the use of the frailty model to test assumptions. Linearity was

evaluated with a residual plot using the martingale residuals of the frailty model plotted against the continuous predictor variable (activity level). Survival curves were illustrated using the *survminer*-package [0.4.9] (Kassambara et al. 2021).

2.2.12 *Degree of action copying and environmental harshness*

We investigated whether observer propensity for action copying depended on elevation using the same approach as for local enhancement. Given the count structure of our action copying (#) response, we used a negative binomial GLMM to test action copying (#) against elevation, test, task, individual activity, days since the start of the season, sex, and age as fixed effects, allowing for an interaction between elevation and test. We also accounted for bird ID as a random effect (n=54 birds; observations=103, 5 NA).

2.2.13 *Latency of action copying and environmental harshness*

Finally, we also tested for differences in latency of action copying (Y/N) as individuals might differ in how fast they implement acquired information rather than in their ability to do so. As for local enhancement, we used a mixed effects survival model including the same model parameters and tests of assumptions as used to test local enhancement (n=40 birds; observations=77, 3 NA).

2.2.14 *Individual consistency in social learning*

The benefit of social information to an individual in the wild may depend on both their internal and external environments (Webster and Laland 2011; Jones et al. 2017). Individuals are thus expected to be consistent in their willingness to use social learning across similar contexts. We therefore tested contextual repeatability (Cauchoix et al. 2018) of social

learning at the individual level across the *Colour* and *Spatial* tasks. We used a binomial repeatability test for local enhancement with task (*Colour*/*Spatial*), individual activity, elevation, and days since the start of the season as fixed effects with bird ID as a random effect (n=40 birds; observations=79, 1 NA). We tested for repeatability of action copying (#) using a Poisson adjusted repeatability test with the same model structure as for the local enhancement repeatability test (n=40 birds; observations=77, 3 NA). Both repeatability tests were evaluated using 1000 bootstraps resampling. The control group was excluded from the repeatability tests as we were interested in the consistency of social learning use per se following a demonstration. Finally, we estimated the influence of elevation on the repeatability of social learning by running repeatability tests with only elevation as the fixed effect.

2.3 Results

2.3.1 *Repeatability of activity*

Consistent individual differences in activity could influence the behaviours we scored for social learning. We found significant repeatability of activity at the individual level (ID; Table 2.1) while controlling for time of day, potential effects of the person who recorded the measurement (Person; Table 2.1), and seasonal differences (Batch; Table 2.1).

Table 2.1. Repeatability test for individual activity level. *Random effect* indicates the level tested for repeatability, *R* indicates the repeatability coefficient, *SE* is the standard error, *95% CI* is the 95% confidence interval, and *P* is the p-value.

Random Effect	R	SE	95% CI	P
ID	0.14	0.09	[0,0.323]	**0.04***
Person	0.074	0.092	[0,0.298]	0.1
Batch	0.094	0.082	[0,0.291]	0.06

*= significant at the 0.05 level.

2.3.2 *Task engagement summary*

Two and three individuals, out of fourteen, in the control group perched in the *Colour* and *Spatial* tasks, respectively. In the social observer group 21/40 perched in the *Colour* task and 28/40 perched in the *Spatial* task (Table 2.2). No control individuals sampled any items on the test board, whereas 13/40 observers sampled in the *Colour* task, and 9/40 observers sampled in the *Spatial* task (Table 2.2).

Table 2.2. Engagement rates, as the number of individuals that exhibited each measured response.

Group	Elevation	Total N	Task	Perched	Sampled any item	Sampled at least 1 correct item	Perching NA's[a]	Sampling NA's[a]
Observers	High	20	*Spatial*	15	9	1	-	-
			Colour	12	8[b]	1	-	1
	Low	20	*Spatial*	13	9	4	-	-
			Colour	9[c]	5[d]	2	1	2
Control	High	7	*Spatial*	1	0	0	-	-
			Colour	0	0	0	-	-
	Low	7	*Spatial*	2	0	0	-	-
			Colour	2	0	0	-	-

a) NA = individuals that were removed from the sampling behaviour analysis due to missing observations caused by time-constraint in batch 1. b) Data for one female was missing due to incomplete trials (i.e. final N for "High" = 19). c) One male was removed due to an incomplete trial. d) Data from two males were missing due to incomplete trials (i.e. final N for "Low" = 18).

2.3.3 *Local enhancement and environmental harshness*

Birds from high and low elevation showed no significant difference in their propensity to use local enhancement (12/20 high elevation birds and 9/20 low elevation birds, Table 2.2; GLMM: Table 2.3). There was a significant difference between test groups such that observers were more likely to approach the test board than control individuals (Table 2.3). No effect of the interaction between elevation and test group was detected in the model (Table 2.3). Finally, we did not detect any effect of task type (*Colour* vs *Spatial*), individual activity level, days into season, sex, or age on the propensity to use local enhancement (Table 2.3).

Table 2.3. Parameter estimates for the models of local enhancement (binomial GLMM, N=79) and action copying (negative binomial GLMM, N = 77).

	Local Enhancement: Binomial GLMM				**Action Copying: Negative Binomial GLMM**			
Predictors	*Estimate*	*SE*	*z-value*	*p*	*Estimate*	*SE*	*z-value*	*p*
Intercept	-4.66	1.90	-2.45	**0.01**	-21.06	8735.73	-0.00	1.00
Elevation (Low)	2.76	1.96	1.41	0.16	-0.05	12339.76	-0.00	1.00
Test (Observer)	5.06	1.86	2.72	**0.01**	20.86	8735.73	0.00	1.00
Task (Spatial)	0.89	0.56	1.58	0.11	0.11	0.39	0.29	0.77
Activity	0.61	0.56	1.10	0.27	-0.14	0.30	-0.45	0.66
Days into season	-0.20	0.40	-0.49	0.62	-0.32	0.21	-1.49	0.14
Sex (Male)	-0.36	0.78	-0.47	0.64	0.15	0.42	0.36	0.72
Age (Juvenile)	-0.40	0.95	-0.42	0.67	-0.12	0.46	-0.25	0.80
Elevation (Low) * Test (Observer)	-3.68	2.11	-1.75	0.08	-0.10	12339.76	-0.00	1.00
Random Effects								
Residual	1				1.67			
Observer ID	2.54				0.00			

Although individuals from different elevations did not differ in their propensity to use social information for local enhancement, they might differ in how quickly such information is used for local enhancement. In the mixed effects survival model for latency to use local enhancement, 50 out of 79 possible perching events occurred, leaving 29 events right-censored (i.e. endpoint unknown). We found no significant difference in the latency of local enhancement between high and low elevation individuals (mixed-effects survival model: Elevation (low)=-0.05, z=-0.11, p>0.05, Table 2.4; Fig 2.3A-B). Individual activity level had

a significant effect on perching behaviour, with more active individuals being more likely to exhibit local enhancement (Activity =0.80, $z=2.17$, $p<0.05$, Table 2.4).

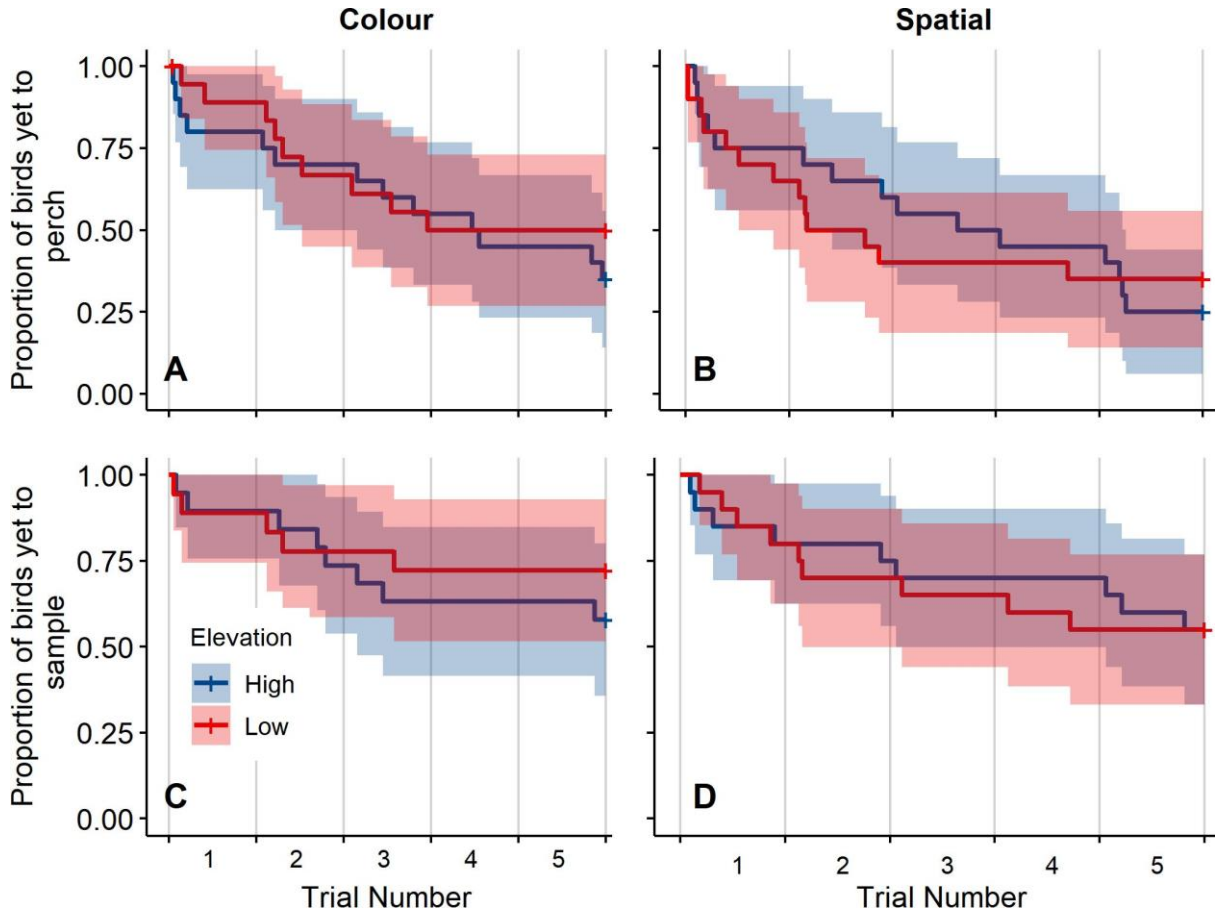

Figure 2.5. Survival plots of the proportion of individuals that engaged with the test boards over five trials for observer birds only (i.e. no control individuals). The graphs are based on the raw latency to engage with the boards plotted against elevation and not the full mixed effects survival models. The proportion of individuals that engaged increases as the line decreases. The x-axis shows time since start of the first trial in seconds and each tick represent the break between two trials. Blue and red lines represent high and low elevation, respectively, and the spread around the lines indicates 95% confidence intervals. Change in proportion of individuals that did not perch in the A) *Colour* task (n=80) and B) *Spatial* task (n=80) over time. Change in proportion of individuals that had not sampled any items from the test board in the C) *Colour* task (n=77) and D) *Spatial* task (n=77) over time.

Table 2.4. Summary of the mixed effects survival models. Log(hazard)= regression coefficient; a positive sign indicates higher probability of perching/sampling. Hazard ratio = Effect size. SE = standard error.

	Local Enhancement					**Action Copying**				
Predictors	*Log(hazard)*	*Hazard ratio*	*SE*	*z-value*	*p*	*Log(hazard)*	*Hazard ratio*	*SE*	*z-value*	*p*
Elevation (Low)	-0.05	0.95	0.49	-0.11	0.92	-0.15	0.86	0.53	-0.29	0.77
Task (Spatial)	0.42	1.53	0.31	1.37	0.17	0.24	1.27	0.38	0.64	0.52
Activity	0.80	2.22	0.37	2.17	**0.03**	0.30	1.35	0.36	0.83	0.40
Days into season	-0.24	0.78	0.24	-1.03	0.30	-0.25	0.78	0.25	-0.98	0.33
Sex (Male)	0.18	1.20	0.48	0.38	0.70	0.18	1.20	0.51	0.35	0.72
Age (Juvenile)	0.02	1.02	0.53	0.04	0.97	0.07	1.08	0.56	0.13	0.89

2.3.4 *Action copying and environmental harshness*

High and low elevation populations did not differ significantly in their propensity for action copying across tasks (GLMM: N=77 [3 observations missing], Elevation (Low)= -.05, z= -0.00, p>0.05, Table 2.3, Fig 2.4). Test, task, individual activity, days into season, sex, age, and the interaction between elevation and test group did not show a significant effect on action copying (Table 2.3). Finally, elevation did not significantly impact the speed of action copying, nor did any other variable included in the mixed effects survival model (Table 3.4, Fig 2.3C-D). The model detected 31 sampling events out of 77 possible events.

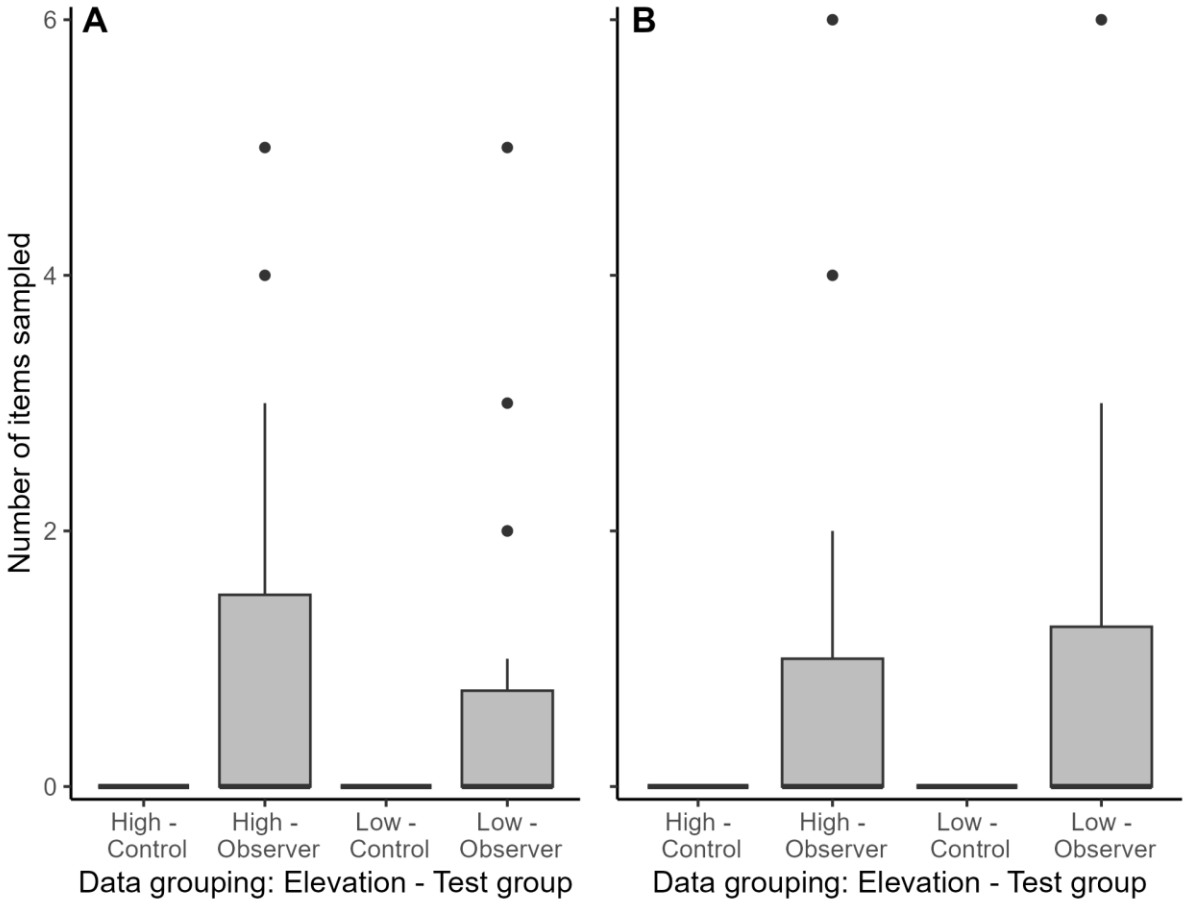

Figure 2.6. Number of items sampled (y-axis) in the *Colour* (A) and *Spatial* (B) tasks for each elevation and treatment group combination (x-axis). The thick black line represents the median, filled boxes indicate the 75th percentile, the lines indicate 1.5 IQR, and points show statistical outliers**.**

2.3.5 *Consistency in Social Learning*

Among individual consistency in the propensity to use social information across the color associative and spatial learning tasks could reveal the existence of a social learning phenotype. Individuals differed consistently from one another in their use of local enhancement across the two tasks (Link-scale approximation: R=0.40, SE=0.25, 95% CI = [0, 0.99], P<0.05). However, there was a negligible influence of elevation on consistency in local enhancement (partial R=0.027 SE=0.067). In contrast, the repeatability test showed that

individuals did not differ consistently in their action copying behavior across tasks (Link-scale approximation: R=0.04, SE=0.118, 95% CI = [0, 0.40], P>0.05). Elevation likewise did not influence the consistency of action copying (partial R=0.003 SE=0.038).

2.4 Discussion

Social learning can reduce costs of acquiring information about resources and should therefore be particularly important for survival in harsh environments where both the difficulty in finding resources and increased energetic needs are accentuated. Here we investigated the use of social learning in populations of great tits, a generalist forager, across an elevational gradient known to affect life-history traits in both great tits and the closely related blue tit in the study area (Sallé 2016; Lejeune et al. 2019; Bründl et al. 2020). We show that great tits that received demonstrations had higher success in our foraging related tasks than individuals that did not receive a demonstration. However, there was no difference in degree or speed of learning between elevations. This suggests a consistent benefit of social learning in great tits across environments rather than the increased benefit with elevation that we predicted. Our study showed that although many individuals exhibited use of local enhancement, only a few attempted to copy the demonstrator's action, which suggests that more advanced social learning (e.g. action copying) may require more demonstration, possibly combined with asocial trial and error learning. Finally, we found consistent individual differences in the use of local enhancement but not action copying suggesting some individuals are more prone to using social information for finding food patches than others irrespective of environmental conditions. These results improve our understanding of how the external environment impacts social learning and furthers the debate on the role that asocial trial and error learning plays in social learning (see below).

Social learning should be more advantageous in harsh environments where the consequences of missed foraging opportunities are more severe than in benign environments. Although evidence for social learning was clear, we found no difference in either degree or latency of local enhancement and action copying between elevations. One possible explanation for why great tits did not differ in social learning between elevations is that social learning might be equally advantageous at high and low elevation but compensate for different foraging challenges at either elevation. For example, if food patches at high elevation are small and ephemeral, using social information may only provide small benefits on the same order as at low elevation where patches might be more common but competition is higher. Alternatively, although learning is a form of plasticity as it allows for flexible responses to changes in the environment (Boyd and Richerson 1988; Dukas 2004), the use of social learning could also be plastic. If so, our approach of housing individuals from high and low elevation under standard conditions for several days before testing, might have led to convergence in social learning use among birds from different elevations. The contrast between patterns in a common garden and studies in the wild would help us understand plasticity in social learning. Indeed, despite initial discussion of plasticity in cognition two decades ago (Dukas 2004), it remains relatively unexplored to date (Cauchoix et al. 2020).

Differences across species with specialists versus generalists foraging strategies may also generate species differences in the use of social learning under different environmental contexts (Klopfer 1961; Sasvári 1979; Lefebvre and Giraldeau 1996; Galef and Giraldeau 2001). However, empirical results to date do not necessarily reveal a clear pattern. For example, great tits are extreme habitat and diet generalists (Fisher and Hinde 1949; Betts 1955; Estók et al. 2010) that learn socially (Sasvári 1979; Brodin and Utku Urhan 2014, 2015; Aplin et al. 2015a), and do so regardless of environmental harshness in our experiments. In contrast, mountain chickadees which are food caching specialists show

reduced use of social learning in harsh, high elevation populations compared to conspecifics at low elevation, possibly because asocial learning of cached food is more valuable at higher elevations (Heinen et al. 2021, 2022). However, this pattern does not hold for all food caching specialists. Black capped chickadees cache food in winter and rely on social learning more in harsh rural areas compared to urban areas where supplemental feeding generates stable food patches (Jones et al. 2017). Other Paridae species, including both specialist food caching marsh tits (*Poecile palustris*) and generalist blue tits show poor social learning compared to great tits (Sasvári 1979; Utku Urhan et al. 2017). Clearly the relationship between foraging strategy and social learning that has generally been assumed (Lefebvre and Giraldeau 1996; Galef and Giraldeau 2001) is not so straight forward when factoring in environmental harshness. Direct measures of the impact of "environmental harshness" on the organisms (Love and Wagner 2023; Makuya et al. 2023) as well as the size, stability and ease of finding new foraging patches which impact the value of socially vs asocially acquired information would greatly improve our understanding of how species ecology and the environment shape social learning use.

Most, if not all, studies of social learning inadvertently include asocial learning as it is very difficult to separate out the effects of copying a tutor from an individual's own experience during the learning process. In our study, we aimed to separate social from asocial learning by only testing observers up until the first trial in which they sampled an item to prevent asocial trial-and-error learning (Galef 1995). Furthermore, we did not provide mealworms behind correct answers during social learning testing of the observer to limit their use of alternative cues (e.g. sound or smell). Finally, we removed the demonstrator so it was not present during observer testing to separate social learning outcomes from a social facilitation of asocial learning (Klopfer 1961; Shettleworth 2010). This approach provided mixed results. Although we found evidence that presence of a demonstrator increased the

probability of approaching and interacting with the foraging task, individuals did not copy the correct choice more than expected by chance. This result suggests that individuals may require more demonstrations, that behaviour initially learnt by social learning requires fine-tuning via asocial learning or, most likely, both. Many studies that provide evidence of social learning have continuous contact with tutors and do not limit reinforcement by asocial trial and error (Terkel 1995; Marchetti and Drent 2000; Thornton and McAuliffe 2006; Mesoudi 2011; Guenther and Brust 2017). For example, Aplin et al. (2015a) followed the spread of seeded solutions to challenging foraging tasks in flocks of great tits to show the establishment of traditions via social conformity. These studies show that social learning occurs, but do not quantify the possible contribution of asocial learning to social learning. Indeed, in Aplin et al.'s study, social learning clearly instigates the behavioural tradition in each flock, but reinforcement by asocial learning is likely a key force after initial observation. More generally, learning socially might simply act as a dynamic source of information that introduces behavioural variation to be fine-tuned based on personal experience later (Galef 1995), yet separating out these effects remains a key challenge.

Social learning can occur to different degrees, from local enhancement to copying complex task solutions, reflecting an increase in required cognitive engagement (Hoppitt and Laland 2008). Indeed, we found that only a few individuals that used local enhancement, generally considered a simple form of social learning, also used action copying which involves a more complex cognitive process (Zentall 2006; Hoppitt and Laland 2008). A possible explanation of this may be that the time and energy investment required for copying the actions needed to accurately solve the task is unsustainably high compared to the combined use of local enhancement and asocial learning. Alternatively, it is possible that added costs associated with accurate action copying – either cognitive processing or additional observations – may mean that it is only profitable for very challenging tasks. Great

tits forage in flocks where local enhancement should be favoured (Krebs et al. 1972), but forage opportunistically on many different food sources such that copying specific actions to get food may rarely be useful. Conversely, accuracy of action copying might require multiple demonstrations as well as parallel task performance with a demonstrator which was not part of our experimental design. Additional social learning opportunities and feedback via asocial learning may explain why others have found accurate action copying in great tits previously (Brodin and Utku Urhan 2015; Hämäläinen et al. 2020), whereas we did not. If asocial learning is an integral component of action copying, providing such opportunities in future experiments could reveal differences in social learning among populations from different elevations.

If the propensity to learn socially is a personal information gathering tactic, we might expect to find consistent variation among individuals in how they responded to task demonstration. Furthermore, we might expect that the propensity to use social information might differ among individuals from populations that differ in the value of social information as a result of harsh environmental contexts. Few studies have attempted to estimate the repeatability of social learning but those who do, generally show moderate to high repeatability, r=0.30-0.52 (Guenther and Brust 2017; Watson et al. 2018). Although we did not find an effect of the environment on the propensity to use social learning (Table 3.3), we did find significant repeatable among-individual variation across tasks in local enhancement, but not for action copying. Furthermore, the degree of repeatability in social information use was not influenced by the elevation of origin of the bird (i.e. partial R of environment as a moderator was not significant). This suggests some individuals consistently use social information to cue into and approach feeding patches more than others as expected for species that forage in groups. The lack of repeatability in action copying could be because there is little variation among individuals or because individuals are not consistent in whether

they copy the actions of tutors. In the latter case, one possibility is that the two tasks we presented required different motor or cognitive skills such that one would not necessarily expect individuals to show similar behaviour across the two tasks. Alternatively, individuals may not show consistent action copying behaviour in general because it is not needed in great tits, as we argue above. Individual variation in local enhancement can be advantageous in group feeding contexts that include both producers (asocial learning users) and scroungers (social learning users) in a stable equilibrium or as mixed strategies (Barnard and Sibly 1981; Reichert et al. 2021). However, whether social learning of action copying follow producer-scrounger dynamics and to what degree they shift with population structure or ecology remains to be explored.

Studying cognition in an ecologically relevant context is a central tenant of cognitive ecology (Cauchoix and Chaine 2016; Morand-Ferron 2022), which allows comparisons among individuals, populations, and species to understand how cognition is shaped by the environment. Our findings that generalist great tits do not show an increase in degree of social learning with increased environmental harshness contrasts with results from mountain chickadees which showed decreased social learning use with increase environmental harshness as expected from a caching species. We suggest that a fruitful framework to understand such differences could be by examining costs and benefits of social learning given the species' behavioral strategies and population ecology (Morand-Ferron et al. 2016). The benefits of social learning are clear in a variety of taxa (Griffin 2004; Thornton and McAuliffe 2006; Manassa and McCormick 2013; White et al. 2017), but context dependent costs have largely been ignored. Costs have been observed in other forms of cognition (Mery and Kawecki 2003; Cole and Quinn 2012) and it seems likely that social learning carries costs under some contexts (Giraldeau et al. 2002). The cost-benefit relation of social learning can change over time, including short time scales, but examinations of plasticity in social

learning use are lacking. Regardless, if costs and benefits of social learning are context-dependent, then manipulations of contexts could be fruitfully used to measure these costs and benefits. Such an approach could provide important insights into the role that ecology and behavioral strategies play in the evolution of social learning.

2.5 Declarations

2.5.1 *Ethics approval*

Captures were conducted under permits to ASC from the French bird ringing office (CRBPO, project 576; permit 13619). Housing was approved by the Région Midi-Pyrénées veterinary services (DIREN, n°2012-07) in the SETE experimental aviaries (Préfecture de l'Ariège, institutional permit n°SA-12-MC-054; Préfecture de l'Ariège veterinary services, Certificat de Capacité n°09-321). The French Ministry of Education, Research and Innovation's Ethical committee approved the experimental protocol under the permit 30185-2021030410167866 v5.

2.5.2 *Funding*

Work was supported by an Early Career Research Award of Ontario, Canada [ER15-11-217] and Natural Science and Engineering Research Council of Canada Discovery grant and Accelerator supplement [RGPIN-2019-06558] to JMF, a Human Frontiers Science Program Collaborative Grant to ASC and JMF (RGP0006/2015), and the Agence National pour la Recherche (ANR-SoCo) to ASC. ASC was in part supported by the Laboratoire d'Excellence (LABEX) entitled TULIP (ANR-10-LABX-41) and IAST (ANR-17-EURE-0010).

Appendix A

Section S1. Sample information

We provide additional information about the birds participating in the study. Table 2.5. contain information regarding the individuals tested in the control group and Table 2.6 contain information about individuals in the social observer group.

Table 2.5. Information about the composition of individuals tested as controls in each batch (n=14).

Batch	*Elevation*	*Sex*	*Age*	*Nb. individuals*
1	High	Male	Adult	1
1	Low	Male	Juvenile	1
2	High	Female	Adult	1
2	Low	Female	Juvenile	1
2	Low	Male	Juvenile	1
3	High	Male	Juvenile	1
4	High	Female	Adult	1
4	High	Male	Adult	1
4	Low	Female	Juvenile	1
4	Low	Male	Juvenile	1
5	High	Male	Adult	1
5	High	Male	Juvenile	1
5	Low	Female	Juvenile	1
5	Low	Male	Juvenile	1

Table 2.6. Information about the composition of individuals tested as observers in each batch (n=40).

Batch	*Elevation*	*Sex*	*Age*	*Nb. individuals*
1	High	Female	Adult	1
1	High	Female	Juvenile	3
1	High	Male	Juvenile	1
1	Low	Female	Juvenile	2
1	Low	Male	Juvenile	2
2	High	Female	Adult	1
2	High	Female	Juvenile	1
2	High	Male	Juvenile	3
2	Low	Female	Juvenile	3
2	Low	Male	Juvenile	1
3	High	Female	Juvenile	1
3	High	Male	Adult	1
3	Low	Female	Juvenile	4
4	High	Female	Adult	1
4	High	Male	Adult	1
4	High	Male	Juvenile	2
4	Low	Female	Adult	2
4	Low	Male	Juvenile	2
5	High	Female	Adult	1
5	High	Male	Adult	3
5	Low	Female	Adult	1
5	Low	Female	Juvenile	2
5	Low	Male	Juvenile	1

Chapter 3

Social information use increases with decreasing winter temperature in a passerine bird

This chapter was adapted from a manuscript submitted to Royal Society Open Science on 2024-06-12.

3.1 Introduction

Learning is a cognitive trait that allows animals to gather and update information about their surroundings to match their behaviour to current conditions (Johnston 1982; Galef 1995; Morand-Ferron 2017) via behavioural plasticity (Mery and Burns 2010). Asocial trial-and-error learning about resource locations, whereby information is acquired directly from interaction with the environment (Heyes 1994), can be beneficial when resources are abundant, but costly when resources are limited. In contrast, using information about the environment gleaned from the behaviour of others, called social learning (Heyes 1994, 2012; Heyes and Pearce 2015), can alleviate costs related to asocial learning (Galef 1976, 1988; Boyd and Richerson 1988; Griffin 2004; Kendal et al. 2005).

Several evolutionary hypotheses exist to describe how social (Jolly 1966; Humphrey 1976; Dunbar 1998; Whiten and Van Schaik 2007), and ecological (Rozin and Kalat 1971; Allman et al. 1993; Pravosudov and Clayton 2002; Deaner et al. 2003; Roth et al. 2010) factors have shaped cognition, including relative reliance on social versus asocial learning (Boyd and Richerson 1988). Cognitive traits shaped by evolutionary processes may improve fitness in relation to average environmental conditions over generations. However, these processes are too slow to match within-generation fluctuations in environmental conditions, which instead require plasticity (West-Eberhard 1989, 2003). Early-life social (Riebel et al. 2012; Leris and Reader 2016; Ashton et al. 2018) and physical (Kotrschal and Taborsky 2010) environments can lead to lasting differences in cognitive performance later. However, the physical and social environment often change on shorter time scales, including from day to day. Animals should therefore also be rapidly and reversibly plastic in their use of different cognitive abilities to best match the current conditions. Indeed, theory predicts that animals should plastically adjust their reliance on social information in response to changes in the cost of asocial information acquisition (Boyd and Richerson 1988; Laland 2004; Galef 2009).

This prediction has been experimentally tested by altering costs of asocial information gathering, e.g. predation risk, task difficulty or quality/quantity of food (for overviews see Kendal et al. 2005, 2009; Galef 2009). These studies have yielded mixed results. For example, individuals experiencing higher perceived predation risk, in the form of predator scent cues or absence of hiding places within the enclosure, showed higher reliance on social information in several fish species (Laland and Williams 1998; Webster and Laland 2008; Lindeyer and Reader 2010; Zala et al. 2012). In contrast, Norway rats, *Rattus norvegicus*, generally use social information while foraging under no or low predation risk but showed no preference for either social or asocial information when predation risk was high (Galef and Whiskin 2006; Galef and Yarkovsky 2009). Thus, the relationship between asocial learning costs and social information use is seemingly context- and species-dependent. Moreover, while there seems to be some support for plasticity in social learning use when animals are exposed to certain cues in the lab, how rapid plasticity in social information use applies in the wild is largely unknown. Conditions can change quickly in the wild and we should therefore expect the value of social learning to change quickly as well. Measuring plasticity in cognitive expression in relation to a particular cue requires testing the same individuals or groups across multiple states of that cue (Cauchoix et al. 2020).

The relative importance of social and asocial learning in a population can be evaluated using network-based diffusion analysis (NBDA) (Franz and Nunn 2009). NBDA allows us to estimate the strength of social information transmission in relation to asocial trial-and-error at the group level. The rate of social transmission, or s-value, is calculated based on how closely patterns of individual behavioural acquisition match the social connections in the group compared to a model with a baseline asocial learning rate (Franz and Nunn 2009; Hoppitt et al. 2010; Hasenjager et al. 2021). The NBDA is based on the assumption that the likelihood of information transmission between individuals is

proportional to their association frequency (Franz and Nunn 2009; Hoppitt et al. 2010), as individuals that interact more frequently should be more likely to learn from one another (Coussi-Korbel and Fragaszy 1995). NBDA has previously been successfully employed to study social learning effects on foraging behaviour in wild populations (Aplin et al. 2012, 2015a; Heinen et al. 2021, 2022; Klump et al. 2021). For example, a recent population comparison in mountain chickadees, *Poecile gambeli*, shows that high and low elevation populations that differ in several key ecological variables (e.g., frequency of winter storms, snow depth) differ in their use of social learning while foraging (Heinen et al. 2021, 2022).

Small birds overwintering at high latitudes face several challenges. The combination of little to no primary production and short day-lengths in which to forage (Grossman and West 1977; Clark and Dukas 2000; Brodin 2007) both restrict energy intake. At the same time, low temperatures significantly increase the costs of thermoregulation, leading to increased overall energy expenditure. Animals are expected to make various species-specific behavioural and physiological adjustments to conserve energy when costs of thermoregulation are high (Schradin et al. 2023; Love and Wagner 2023; Makuya et al. 2023), including how they invest in learning about foraging opportunities (Haave-Audet et al. 2024). Temperature varies markedly within seasons at high latitudes, and we should expect to see rapid and reversible plasticity in social information use in response to these fluctuations. Rapid and reversible plasticity in the use of asocial or social information about food patches could play an important role in reducing the risk of energy shortfalls by facilitating energy intake. During milder winter periods, asocial trial-and-error sampling of the environment to reduce competition for resources may be viable as starvation risk is relatively low (Caraco and Giraldeau 1991). In contrast, social information about potential food can become essential during colder periods as social information use can reduce the variance in food

discovery and minimize starvation risk when the baseline risk of starvation is relatively high (Caraco and Giraldeau 1991; Koops and Giraldeau 1996; Barta and Giraldeau 2000).

Here, we test whether winter foraging birds adjust their use of social information depending on daily changes in winter temperature. To do this, we recorded individual visits to feeders providing supplemental food intermittently in flocks of black-capped chickadees. From this we extracted the order and timing of first visit to a feeder for every individual in a group after the feeders were refilled. Using NBDA, we then estimated the impact of social transmission on the spread of the information that the feeders were full again within each group. Because temperature dictates energy requirements (Broggi et al. 2007; Petit and Vézina 2014), we predicted that social transmission should be negatively correlated with temperature such that at colder temperatures, chickadees would exhibit a higher relative use of social information. This is because social information use is expected to save valuable energy at low temperatures whereas asocial learning should be less costly (in terms of starvation risk) under warmer, milder conditions.

3.2 Materials and methods

3.2.1 *Data collection*

Birds were captured using mist nets between October and December 2020 at the University of Alberta Botanical Garden in Devon (Lat: 53.407, Long: -113.758). Each bird was fitted with a unique passive integrated transponder ring (PIT-tag) before being released (Arteaga-Torres et al. 2020). Following the capture period, supplemental feeding manipulations were conducted repeatedly from December to March (Figure 3.1). Within the study site, eight custom-made feeders were placed at least 270 meters apart (Arteaga-Torres et al. 2020). Each feeder had an RFID-reader (Priority 1 Design, Australia) which recorded

date, time (nearest second), and PIT-tag ID of each bird that accessed the feeder. Throughout the feeding manipulation period, the feeders alternated between being filled with black-oil sunflower seeds (1 week) and being empty (2 weeks). Each feeder received a similar number of visits across all periods when they were full (Appendix B, Figures 3.3-10). Each time a feeder was refilled, individuals needed to acquire the information that the feeder once again provided food (DP1-4, Figure 3.1).

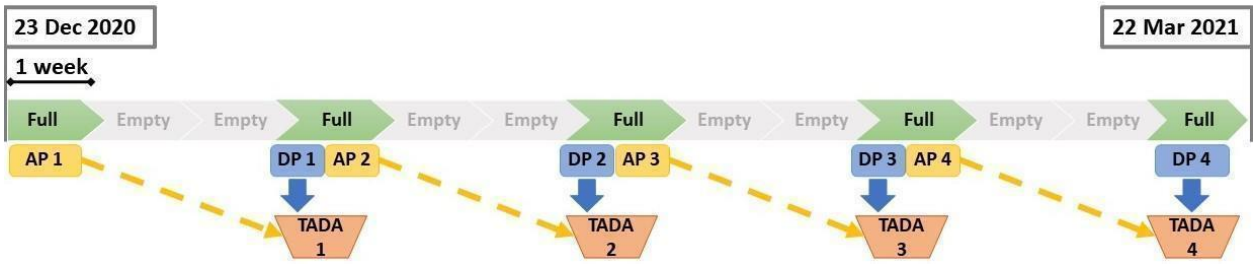

Figure 3.7. Feeder supplementation schedule illustrating the combinations of social network- and diffusion data used to estimate social transmission. Green sections and faded grey sections indicate when feeders were full and empty, respectively. Each section is one week. Yellow boxes indicate the association periods (AP1-4) used to construct social networks. Blue boxes indicate the diffusion periods (DP1-4) investigated for social transmission with time of acquisition diffusion analysis (TADA1-4, orange buckets). Dashed arrows indicate how each association period was used for the subsequent TADA.

3.2.2 *Weather data*

Hourly temperature data was acquired from the Edmonton International Airport (EIA) weather station, ~15km from the study site (climate.weather.gc.ca/historical_data, accessed: 2022-04-08). Although the temperatures recorded at EIA may have differed slightly from the temperatures in the garden due to differences in local scale weather conditions, that would

only reduce the precision of the temperature data we used relative to the actual conditions in our study site, reducing our statistical power. Thus, any estimated temperature effects would be conservative. For the analysis, we calculated the average daytime temperature across the hours when birds were active at feeders for the first day of each diffusion period (DP1-4, Figure 3.1). We also calculated daily average temperatures across the season to assess the temperature trend across the season (Appendix B, Section S2).

3.2.3 *Statistical analyses*

All data manipulations, calculations, and analyses were conducted using R (version 4.2.2, R Core Team 2020). We use a linear mixed effects model to assess individual feeder use across diffusion periods as differences in the propensity to use the feeders could affect the probability of asocial rediscovery of feeder profitability after refill. The propensity of individuals to visit a feeder is thus expected to influence the baseline asocial learning rate within a group in the NBDA. For each day during the diffusion periods, we counted the total number of visits to each feeder by each individual. We modeled individual feeder visits as a function of daily average temperature for the corresponding days. We accounted for repeated measures of feeders and individuals by including these as two random effects in all models. Mixed effects models were constructed using the "*lme4*" package (version 1.1-30, Bates et al. 2015), with additional significance tests from the "*lmerTest*" package (version 3.1-3, Kuznetsova et al. 2017). Model assumptions were evaluated using the "DHARMa" package (version 0.4.5, Hartig 2021).

As each of the variables included in our analyses (see below) were calculated at the level of feeders, we first evaluated the extent to which feeders could be considered independent sampling units. Based on earlier studies documenting winter flock territory sizes

for black-capped chickadees (Smith 1992), we expected that the spacing of feeders in our study site (i.e., minimum 270 m between adjacent feeders) was far enough that each feeder would be on a distinct winter flock territory, and thus represent relatively independent sampling units. Consistent with this, out of 153 individuals detected throughout the study period, over half (N = 80) visited a single feeder over the entire season. Of the birds that were detected at 2 or more different feeders over the course of the study (N =73, Appendix B Figure 3.12), they demonstrated clear preference for a single feeder (Appendix B, Figure 3.12).

3.2.4 *Association Index*

We used a modified version of the *Simple Ratio Index*, SRI (Cairns and Schwager 1987), to estimate connections between individuals at feeders for each association period (AP1-4, Figure 3.1). The SRI requires observations of discrete grouping events which are commonly identified using an algorithmic approach (Aplin et al. 2015a, b; Aplin and Morand-Ferron 2017; Evans et al. 2018) such as *Gaussian mixture models* (GMMs, Psorakis et al 2012). However, the stream of visits in our study was too dense for appropriate separation using GMMs (Appendix B, Figure 3.13). To accommodate our dense data structure, we used a modified version of the SRI calculation (modSRI). Our modSRI association index was calculated for every possible combination of two individuals (dyads) at each feeder, separately, within each association period. The modSRI was calculated as the number of times two individuals of a dyad were detected at least once within +/- 20 seconds of each other, divided by the total number of visits to the feeder made by both the individuals (Appendix B, Section S4 for derivation of the modSRI). We chose +/- 20 seconds as the threshold based on live observation of the birds' behaviour around the feeder. Birds often

perched in the trees around the feeder for several seconds before approaching and often consumed retrieved seeds over several seconds in nearby trees as well. Thus, we deemed +/- 20 seconds to be appropriate for capturing most opportunities for social interactions. We repeated all analyses using a +/- 30 second threshold for the modSRI calculation and confirmed that all of our conclusions were unchanged (Appendix B, Table 3.3).

The modSRI is thus based on repeated co-occurrences between two individuals at a feeder to estimate pairwise relation within an association period. This gives a single index measure, ranging from 0 to 1 for each dyad, per association period while accounting for among-individual differences in visitation rates. The pairwise association indices are then used to construct the social networks. Mean group size during the association periods ranged from 19.8 to 27.9 individuals (Appendix B Table 3.4, see Appendix B Table 3.5 for full AP and DP group sizes and matching individual IDs between them).

3.2.5 *NBDA*

Social transmission rate was estimated using functions in the "NBDA" package (version 0.9.6, Hoppitt et al. 2020). As the feeder visitation data was recorded continuously, we used continuous "time of acquisition diffusion analysis" (TADA, Hoppitt and Laland 2011) models to estimate the rate of social transmission for each feeder within each diffusion period (N=29 [3 NA, Appendix B Table 3.6, Appendix B Figure 3.14). The order and exact timing (to the second) of an individual's first visit to a feeder within a diffusion period was extracted from the visitation data and used in the TADA models as individual acquisition events. We used the modSRI networks from the association periods (AP1-4) as the sociality pattern against which to correlate the individual acquisition events in the corresponding diffusion period (DP1-4), Figure 3.1). Due to missing visitation data during AP2/DP1, we

were unable to run NBDA models for feeder 10A in DP1 as there was no information about individual times of acquisition, and DP2 as we could not calculate the social associations. Similarly, we were unable to extract times of acquisition data for DP4 at feeder 11A. Only individuals detected in a given association period were considered in the TADA for the corresponding diffusion period. Furthermore, the propensity of individuals to visit a feeder may influence the baseline asocial learning rate within a group in the TADA. To account for this, we included the number of visits an individual made to a feeder within an association period (mean centered and scaled) as an individual level variable affecting only the baseline asocial learning rate in the TADA models.

The social transmission rate, s-value, is estimated against a calculated baseline asocial learning rate in NBDA models, which can be set as constant, increasing, decreasing, or custom (Hasenjager et al. 2021). Since we had no a priori reason to assume a non-constant baseline and were primarily interested in relative comparisons of the strength of social transmission between diffusions, we assumed a constant baseline function for all models. The asocial baseline learning rate is estimated independently per NBDA (Hoppitt et al. 2010; Hasenjager et al. 2021). As we included the number of visits by an individual standardized by the mean number of visits across individuals as a moderator on the baseline asocial learning rate, the s-values represent the relative strength of social information use in relation to the asocial acquisition rate of an individual with average feeder visitation rate within each feeder and period.

A limitation of s-values is that they are also strongly dependent on the average of the social association indexes within a group and thus are not directly comparable across networks (Hasenjager et al. 2021). To address this issue, we instead estimated the proportion of acquisition events that can be accredited to social transmission (pST). pST is derived from

the s-values, provides a standardized estimate of social transmission varying between 0 and 1 and should be comparable across analyses and contexts (Hasenjager et al. 2021). We estimated 95% confidence intervals (CI) of the s-values using a profile likelihood approach from which we then extracted the 95% CI of pST, following the method outlined by Hasenjager et al. (2021).

3.2.6 *Proportion of social transmission model*

To estimate the relationship between pST and temperature we needed to consider the uncertainty in the estimate of pST and carry it forward in the analysis. To do so we used two approaches with different assumptions allowing us to evaluate the robustness of the relationship to different underlying model assumptions. In both approaches, we fitted pST as a function of average daytime temperature. We included diffusion period number as a covariate to account for a temporal effect that could be caused by phenological shifts in individual feeder use, sociality, and environmental variables other than temperature across the season. In addition, we accounted for the non-independence of pST within a feeder across diffusion periods by including feeder ID as a random effect. The first approach directly modeled pST as a probability following a binomial distribution. In this approach, we assumed that the pST value from larger groups were estimated with greater certainty and thus weighted pST by group size. We assumed that larger groups had lower uncertainty in their pST estimate due to less measurement error in their social network edge weights(i.e. with more individuals, there are more potential pairwise associations, which improves our ability to detect social assortment). This approach however does not directly take into account the estimated uncertainty of pST. Hence, for the second approach, we assumed that the logit transformation of pST followed a Gaussian distribution. With this assumption we could

compute the standard error (logit-se) of each pST estimate on the logit scale as the range of the logit-transformed 95%CI divided by 3.92. We then used an inverse variance weighting approach, a common method in meta-analyses (Sanchez-Meca and Marín-Martínez 1998; Lee et al. 2016), to take into account the error made on pST. We fitted a LMM using the logit-pST with the observations weighted by the inverse of the logit-transformed error of the pST ($1/\text{logit-se}^2$). As some pST estimates were 0, we added 0.00001 to all pST-estimates to enable logit-transformation of pST.

3.3 Results

3.3.1 *Feeder visits*

A total of 360,264 visits by 153 individuals were detected at feeders across the winter season. There was a statistically significant ($z = -5.191$, $p < 0.001$) but biologically negligible negative effect of temperature on individual feeder visits across the study period (average daily temperature slope = -0.007, standard error = 0.001), with only 17 visits difference between -40°C and 6°C (Appendix B Figure 3.15). Due to brief battery failures, visits were not recorded from two feeders 10A and 11A during periods “AP2/DP1” and “DP4”, respectively

3.3.2 *Social transmission plasticity and temperature*

Social transmission rates varied greatly across the season (pST range 0 - 0.93, Appendix B Table 3.6, Appendix B Figure 3.14). In 15 out of 29 instances, the pST was estimated as 0 which indicates that the pattern of rediscovery within groups was due to asocial learning. As predicted, we found a significant negative relationship between pST and

average daytime temperature, indicating that when temperatures were colder, the transmission of information about food presence followed the underlying social networks more closely (Figure 2A). Both statistical approaches (i.e., binomial and Gaussian models) support a strong negative relationship between pST and temperature (Table 1), indicating that this finding was robust across different underlying model assumptions. Neither modeling approach showed a significant relationship between pST and diffusion period number, indicating that social transmission use was not driven by a seasonal or order effect (Table 3.1, Figure 3.2B).

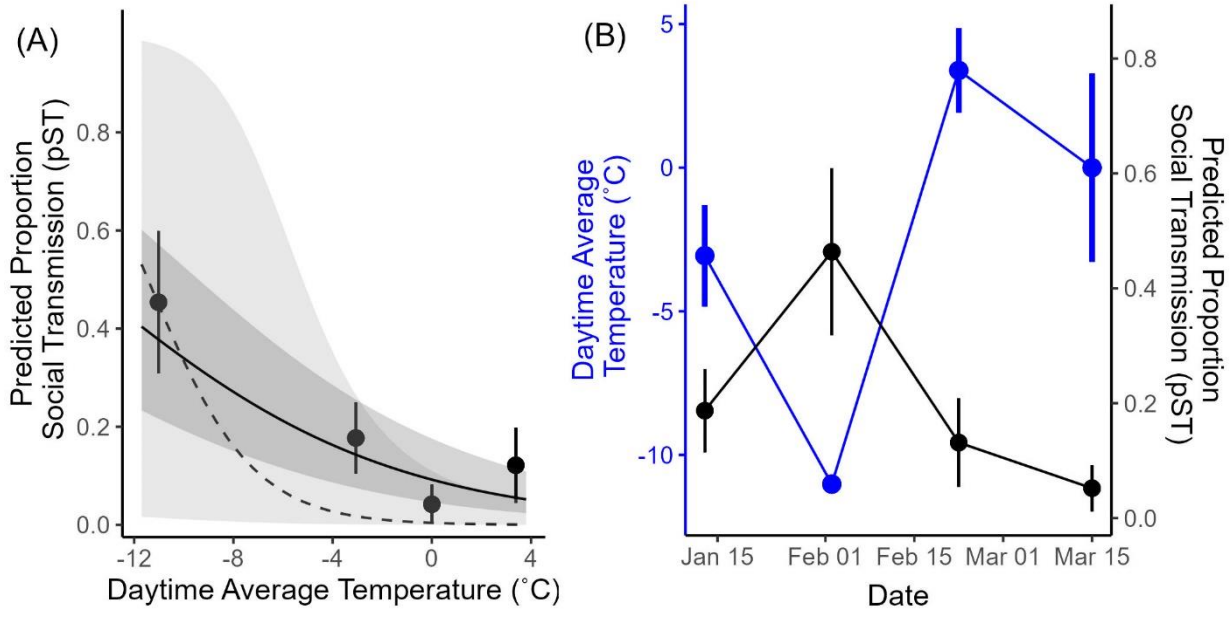

Figure 3.8. The relationship between pST and average daytime temperature directly (A) and over time (B). Both outer y-axes show the pST, with black points and error bars representing the mean +/- standard error of the estimated pST across feeders during each diffusion period. The left y-axis in B indicates temperature range, with blue points and error bars representing the mean +/- standard error of daytime average temperature. Lines and grey areas in A represent the model predictions from models in Table 3.1. The full line and dark grey ribbon

stand for the binomial model while the dashed line and light grey ribbon are for the logit transformed model. Lines in B are simply linking the points for easier visualization.

Table 3.7. Model outputs for the relation between pST and daytime average temperature (N=29). The binomial GLMM weighted by group size is shown on the left. The model using logit-transformed pST with estimation error carried forward is shown on the right.

	Binomial pST weighted by group size				**pST logit transformed with inverse variance weighting**			
Predictors	*Estimate*	*SE*	*z-value*	*p*	*Estimate*	*SE*	*t-value*	*p*
Intercept	-1.85	0.50	-3.68	<**0.001**	-4.57	3.95	-1.16	0.259
Daytime Avg. Temp.	-0.16	0.02	-6.93	<**0.001**	-0.48	0.19	-2.49	**0.019**
Diffusion period (DP)	-0.17	0.13	-1.36	0.174	-0.39	1.31	-0.30	0.766
Random Effects								
Residual	1				5.95			
Feeder	0.88				8.96			

3.4 Discussion

In this study, we investigated whether plasticity in social information use was related to environmental variation affecting the cost/benefit ratio of social vs asocial information. We predicted that the reliance on social transmission should increase as temperatures decreased based on the assumption that the cost of asocial learning would be relatively high at lower temperatures due to increased energetic costs. Our results provide support for this, as the wild groups of black-capped chickadees in our study exhibited rapid and reversible plasticity in social information use in relation to changes in winter temperature. Specifically, social information use was lowest under relatively mild winter conditions (higher temperatures), and groups increased their use of social information as temperatures decreased. Below, we discuss our results in relation to other studies investigating social information use across measures of environmental harshness and highlight key directions for future work.

Here, we show that black-capped chickadees in our study population increased their relative reliance on social information use as mean daily temperatures decreased. This result is consistent with our assumption that the cost of gathering asocial information about the profitability of the feeders would increase with decreasing temperatures, leading to a higher relative reliance on social information. Given that our study design involved re-discovery of food at known feeder locations, first-hand sampling of a feeder may not be expected to represent a biologically important cost. However, previous work in the same population indicates that sampling known feeder locations is costly as most individuals avoid personal sampling of empty feeders (Haave-Audet et al. 2024). This implies that for many individuals, sampling of empty feeders is either costly or yields no net benefit. However, individuals that did sample the empty feeders experienced a significant benefit in the form of higher annual survival (Haave-Audet et al. 2024). Taken together, these results suggest that asocial

sampling is costly in this population, and that only individuals in better condition can afford to sample (Haave-Audet et al. 2024).

Given that energy demands of small birds in winter are known to increase with decreasing temperature (Grossman and West 1977; Cooper 2002; Broggi et al. 2004, 2007), the general costs of asocial learning should increase with decreasing temperatures. Thus, our finding that the use of social information about food increases with decreasing ambient temperatures is consistent with the prediction that social learning should be more frequent when asocial learning is costly (Boyd and Richerson 1988; Laland 2004; Kendal et al. 2018). Additionally, the absolute value of social information may increase at lower temperatures. Theory predicts that social learning can work as a variance-sensitive strategy to minimize starvation risk (Caraco and Giraldeau 1991; Koops and Giraldeau 1996; Barta and Giraldeau 2000), which is critical for survival for small birds in winter (reviewed in Brodin 2007). Specifically, under conditions of higher starvation risk (e.g., lower temperatures), higher reliance on social information reduces starvation risk because it reduces variance in food discoveries (Caraco and Giraldeau 1991; Barta and Giraldeau 2000). Thus, the shift to increased social information use at lower temperatures observed in the current study may reflect the increased cost of acquiring asocial information and/or the increased benefits of exploiting social information.

At first glance, our results appear to contrast with the result of previous work that has looked at variation in social information use across gradients in environmental harshness (Heinen et al. 2021, 2022). In those studies, Heinen and colleagues (2021, 2022) found that high elevation populations of mountain chickadees, that experience harsher environmental conditions, have a relatively lower use of social information compared to low elevation populations. However, we suggest that environmental harshness can be defined by different

environmental covariates such as low temperatures (as in our study), or as low predictability (e.g., Heinen et al. 2021, 2022). Although proxies for overarching environmental harshness like altitudinal differences are commonly used (Croston et al. 2017; Hermer et al. 2018; e.g., Heinen et al. 2021; Isaksson et al. 2024), it is important to recognize that environmental harshness *per se* is not predicted to exert a specific effect on the relative use of social versus asocial information; the predicted effect will instead depend on the specific dimension of environmental harshness being considered. For example, while lower temperatures are expected to increase the cost of asocial information acquisition and favour higher use of social information, less predictable environments should favour asocial information use because rapidly changing conditions mean that the value of social information deteriorates faster (Boyd and Richerson 1988; Feldman et al. 1996; Aoki et al. 2005). As high elevation mountain chickadees experience more rapid and severe changes in precipitation and snow cover than the low elevation population (Kozlovsky et al. 2018), the results of the studies by Heinen and colleagues (2021, 2022) align with the prediction that reliance on social learning should decrease with increased environmental unpredictability. Thus, we suggest that the difference between the result of our study and the studies in the mountain chickadees may stem from a difference in what aspect of environmental harshness is captured in each study. In our study, we believe that snow fall/ snow cover is unlikely to have influenced the birds' decision to rely more on asocial or social information. Chickadees forage mainly in trees and shrubs (Grubb 1975; Robinson and Holmes 1982; Hill and Lein 1988; Van Buskirk and Smith 1989) and should therefore be mostly unaffected by snow cover. Furthermore, our study area had snow cover on the ground throughout the study period (JJW personal observation), and major precipitation events are relatively rare (climate.weather.gc.ca/historical_data). However, changes in food predictability and costs of thermoregulation are not mutually exclusive. Thus, it would be interesting to compare the

relative importance of different dimensions of environmental harshness, such as predictability and energy expenditure, in shaping social information use in the wild where both dimensions vary independently.

Our study focused on the influence of temperature on social information use. We selected temperature as a key variable of interest because it is known to influence energy expenditure in small wintering birds (Grossman and West 1977; Broggi et al. 2004, 2007) and because high quality measurements of temperature are readily available. We hypothesized that the higher costs of asocial learning resulting from higher energy expenditure at low ambient temperatures would favour higher relative use of social information. While our results are consistent with this hypothesis, an important next step is to investigate changes in the relative use of social information in relation to other environmental variables that also increase energy expenditure. For example, solar radiation and wind speed also influence individual energy expenditure in birds (Wolf and Walsberg 1996; Ancel et al. 2015), and therefore, we would predict that lower solar radiation and higher wind speeds would also favour increased use of social information. As the structure of the vegetation around the feeders varied, with some being more exposed than others, solar radiation and wind speed may have had a moderating influence on the effect of temperature on social information use in our study. Furthermore, as solar radiation and wind may vary more across shorter distances than temperature, they may have contributed to the heterogeneity in effects across feeders observed in our study. Considering additional environmental aspects that affect energy expenditure including solar radiation, and wind speed, will allow future studies to draw stronger inference about the causal effect of energy expenditure on relative use of social information.

Although we interpret the observed changes in social information use across diffusion periods as a response to changes in ambient temperatures, we also considered two potential alternative explanations. First, changes in social information use may have been driven by temporal (i.e., seasonal) effects, rather than temperature. For example, if chickadees increased reliance on social information in preparation for the winter season, they should have exhibited the highest reliance on social information in the first diffusion period in January as this is well into the winter season with a decrease towards the end of the season in expectation of spring. However, we found no support for a temporal effect on social information use (Figure 3.2B). Second, previous studies have found that chickadees increase foraging rates with decreasing temperature (Arteaga-Torres et al. 2020; Haave-Audet et al. 2024). Variation in feeder use may influence the opportunities for temporally clustered events that meet our criteria for modSRI. Thus, one potential concern is that the variation in traffic at the feeders could generate variation in social network edge weights and hence, the NBDA estimates used in our study. However, we did not observe strong temperature-related differences in foraging rates in the present study (Appendix B Figure3.15). Further, our analysis controlled for variation in feeding rates in our estimation of pST by including it as a moderator for asocial learning in the NBDA. Thus, we accounted for the potential influence of differences in individual feeder use on the relative reliance on asocial and social information throughout the analysis. Therefore, the temperature-related effects on social information use cannot be explained by either season or foraging rate, and we conclude that temperature remains the most likely proximate factor shaping variation in social information use across diffusion periods observed in this study.

Although our results are consistent with temperature as a key driver of variation in social information use in chickadees, the lack of a continuous gradient of temperatures means that we are unable to determine if that shift is a continuous linear shift or something

more akin to a threshold. By chance, one of the four diffusion periods observed had markedly lower ambient temperatures than the other three diffusion periods, meaning we cannot address whether the effect of temperature is linear, or whether there is a threshold effect. Furthermore, we were unable to evaluate interactions between temperature, individual feeder use, and period on social information use. As feeder visitation remained stable over time (Appendix B Figures 3.3-10) and across temperatures (Appendix B Figure 3.15), we found no indication of potential interaction effects. Further studies with data collected over a wider range of temperatures and with more replicates over time would be needed to evaluate both potential non-linear effects of temperature, as well as interaction effects.

Despite the opportunities to refine and expand upon the present study, our results suggest that changes in winter temperatures are associated with rapid plasticity of social information use. Winter temperatures are a major agent of selection for many species living in temperate zones, suggesting that the response could be adaptive. Our study looked at changes in social information use at the level of the population and is thus not appropriate for evaluating the direct consequence this plasticity has on survival. However, quantifying individual variation in plasticity of social information use would be a worthwhile next step towards understanding the adaptive value of social learning. We predicted an effect of temperature on the relative use of social information *a priori* based on the assumption that asocial information gain would be more costly at lower temperatures due to increased energy expenditure. We suggest that the key next step to understanding how challenging environments shape social information use is to test the relationship between social information use and other environmental cues that affect animals' energy expenditure (Schradin et al. 2023; Love and Wagner 2023; Makuya et al. 2023), such as solar radiation or wind speed.

3.5 Ethics

This study was conducted under the University of Alberta Animal Care and Use Committee (ACUC) permit: AUP00002210, Alberta Wildlife Research Permit and Collection Licenses: 56631, 56632,19-056, 20-056, 21-056, and Environment and Climate Change Canada Bird Banding Permit: 10963.

Appendix B

Section S1. Feeder visits: Within feeder, across DPs, daily feeder visits

The total number of feeder visits was highly variable among feeders and dates. The graphs shown in this section show the distribution of visits per day for each feeder. Due to battery failures, feeder 10A was missing data for diffusion period 1 and feeder 11A was missing data for diffusion period 4 (Figures 3.6 and 3.7). Figures 3.3-10 show the distribution of daily visits at each feeder, 02A – 16A respectively. An example of the distribution of feeder visits and corresponding daily average temperature is given in Figure 3.11.

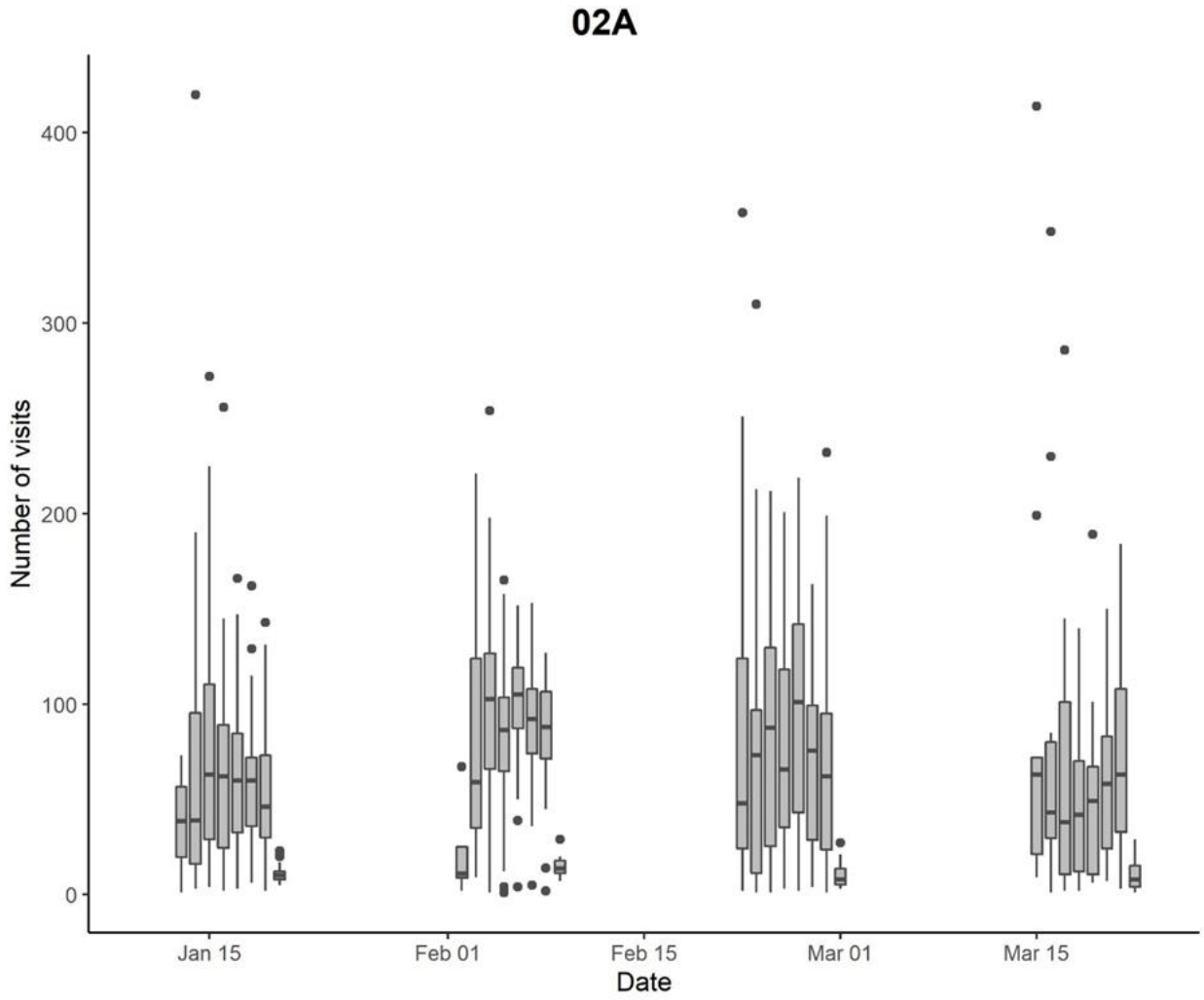

Figure 3.9. Distribution of daily visits to feeder 02A during each full period across the season. Tukey boxplots for each day show the median line, with the box around it representing the 25th (lower) and 75th (upper) percentiles. The vertical line indicates 1.5x the IQR and any points indicate values outside of that range.

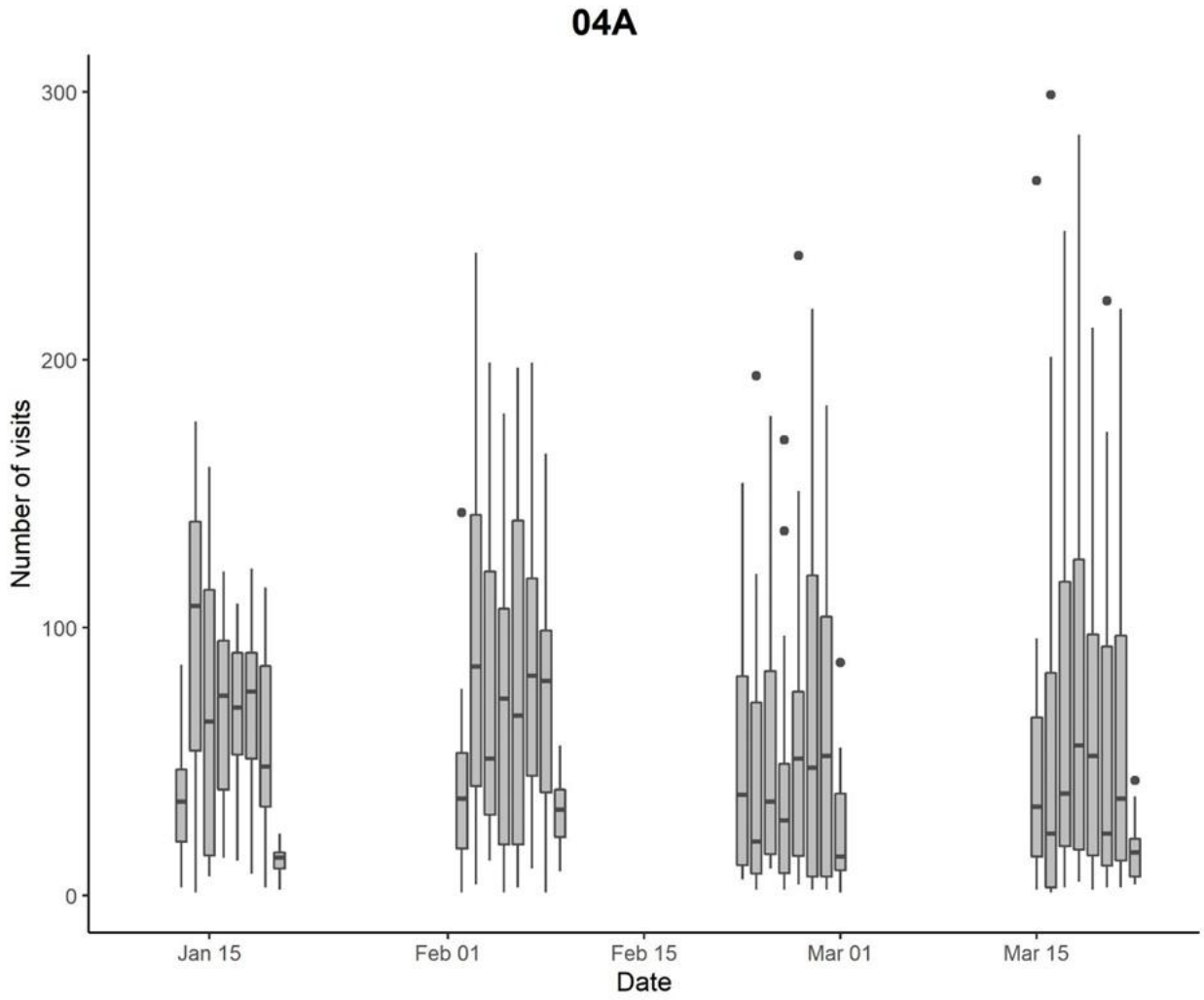

Figure 3.10. Distribution of daily visits to feeder 04A during each full period across the season. Tukey boxplots for each day show the median line, with the box around it representing the 25th (lower) and 75th (upper) percentiles. The vertical line indicates 1.5x the IQR and any points indicate values outside of that range.

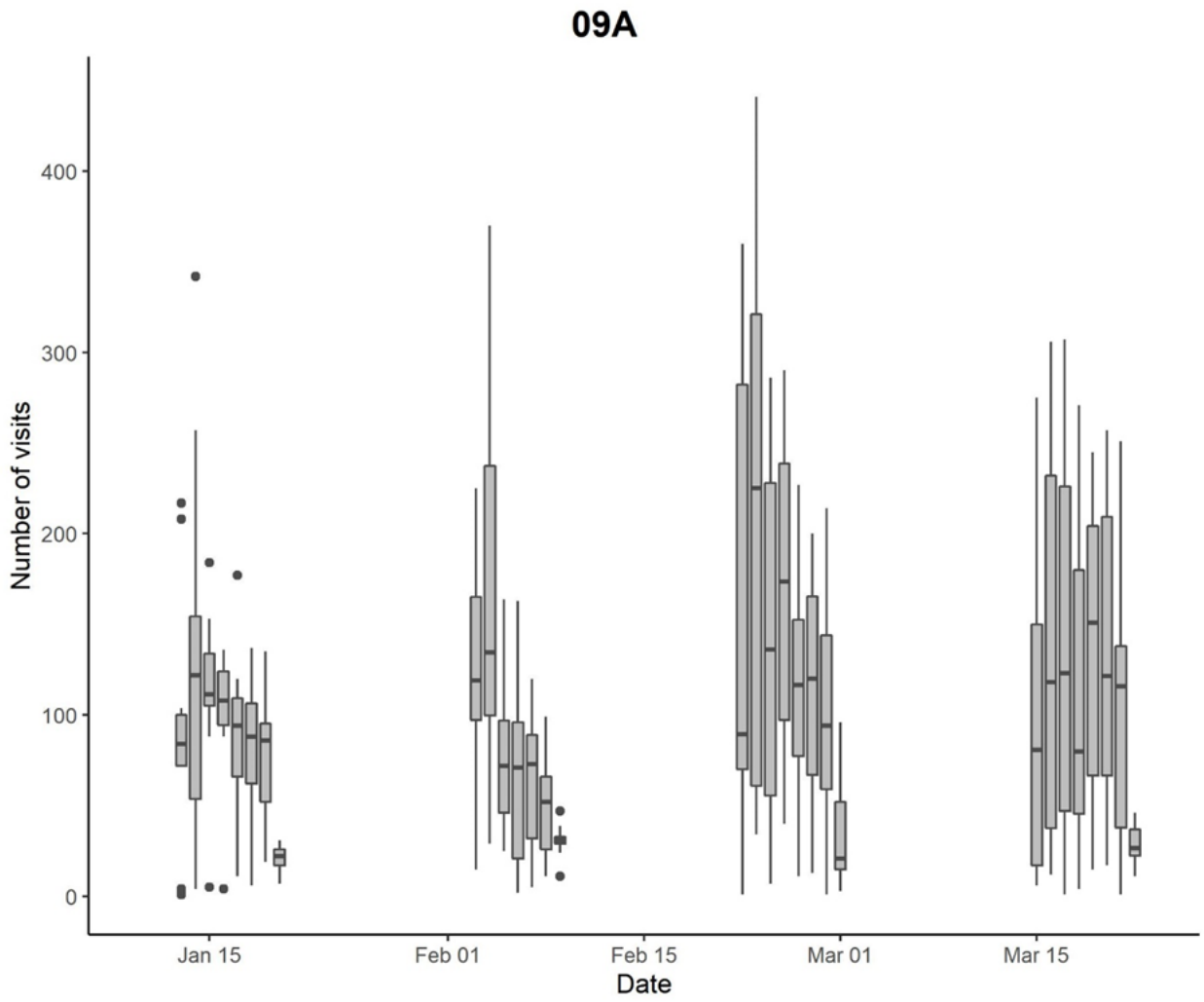

Figure 3.11. Distribution of daily visits to feeder 09A during each full period across the season. Tukey boxplots for each day show the median line, with the box around it representing the 25th (lower) and 75th (upper) percentiles. The vertical line indicates 1.5x the IQR and any points indicate values outside of that range.

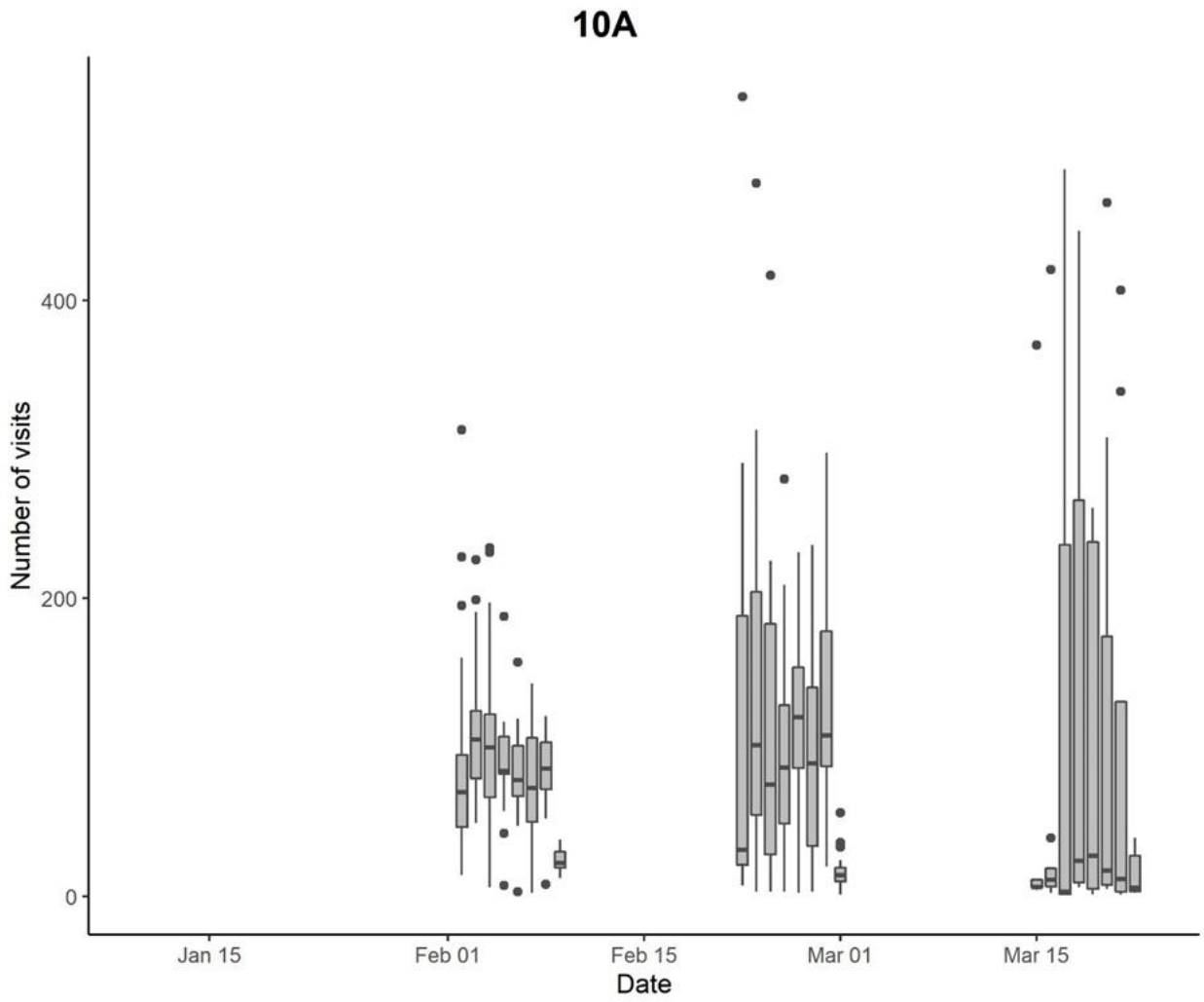

Figure 3.12. Distribution of daily visits to feeder 10A during each full period across the season. Tukey boxplots for each day show the median line, with the box around it representing the 25th (lower) and 75th (upper) percentiles. The vertical line indicates 1.5x the IQR and any points indicate values outside of that range.

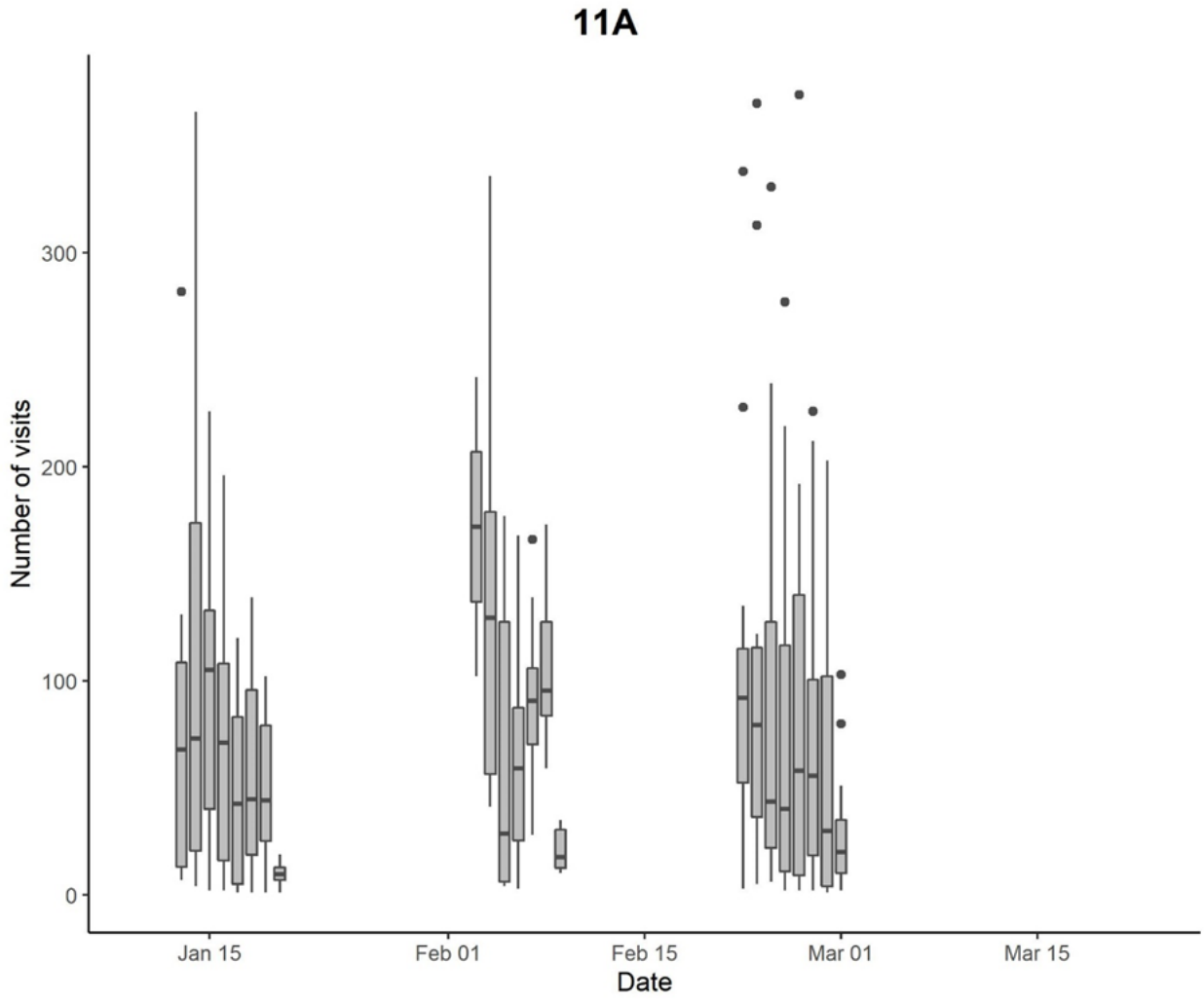

Figure 3.13. Distribution of daily visits to feeder 11A during each full period across the season. Tukey boxplots for each day show the median line, with the box around it representing the 25th (lower) and 75th (upper) percentiles. The vertical line indicates 1.5x the IQR and any points indicate values outside of that range.

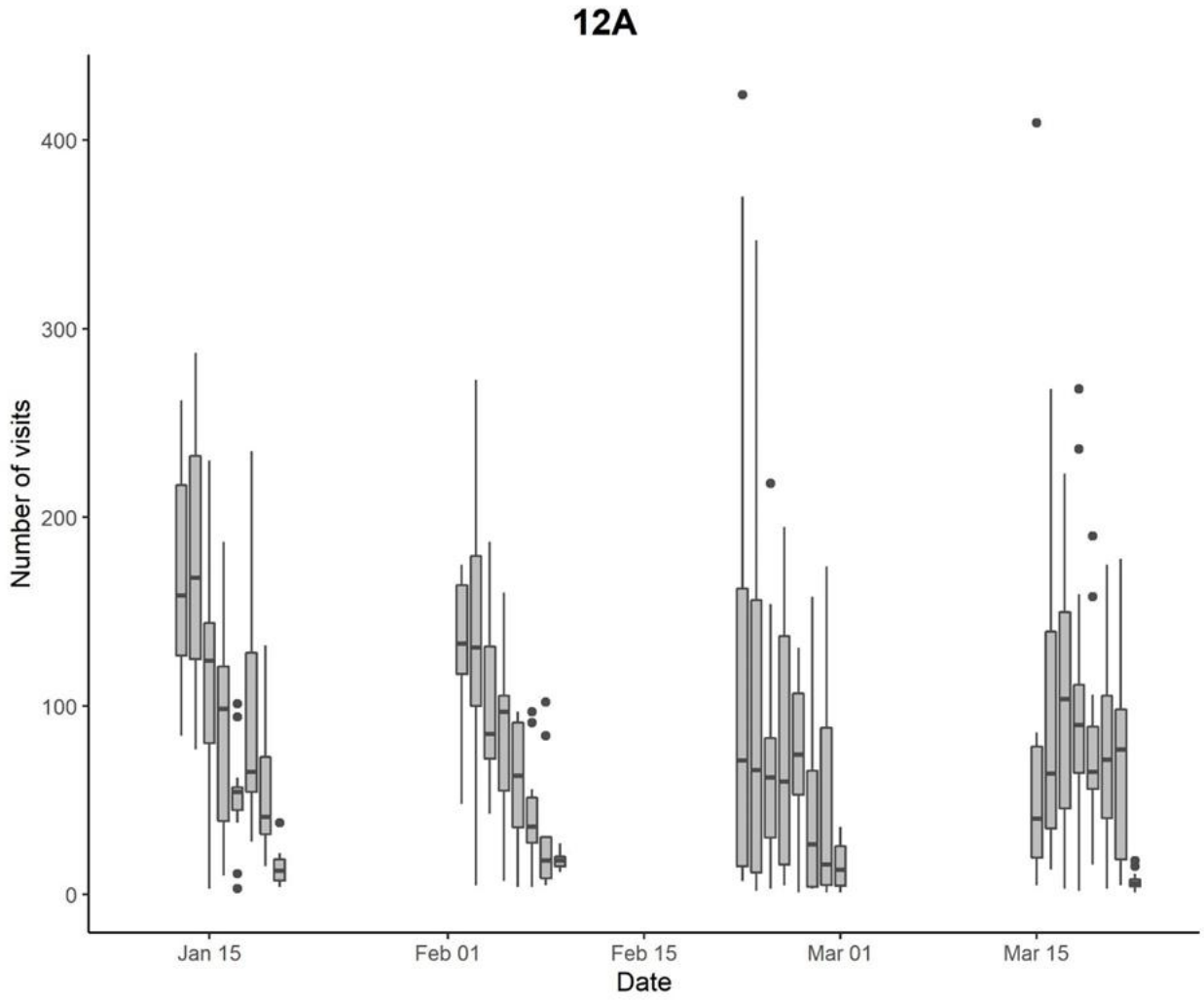

Figure 3.14. Distribution of daily visits to feeder 12A during each full period across the season. Tukey boxplots for each day show the median line, with the box around it representing the 25th (lower) and 75th (upper) percentiles. The vertical line indicates 1.5x the IQR and any points indicate values outside of that range.

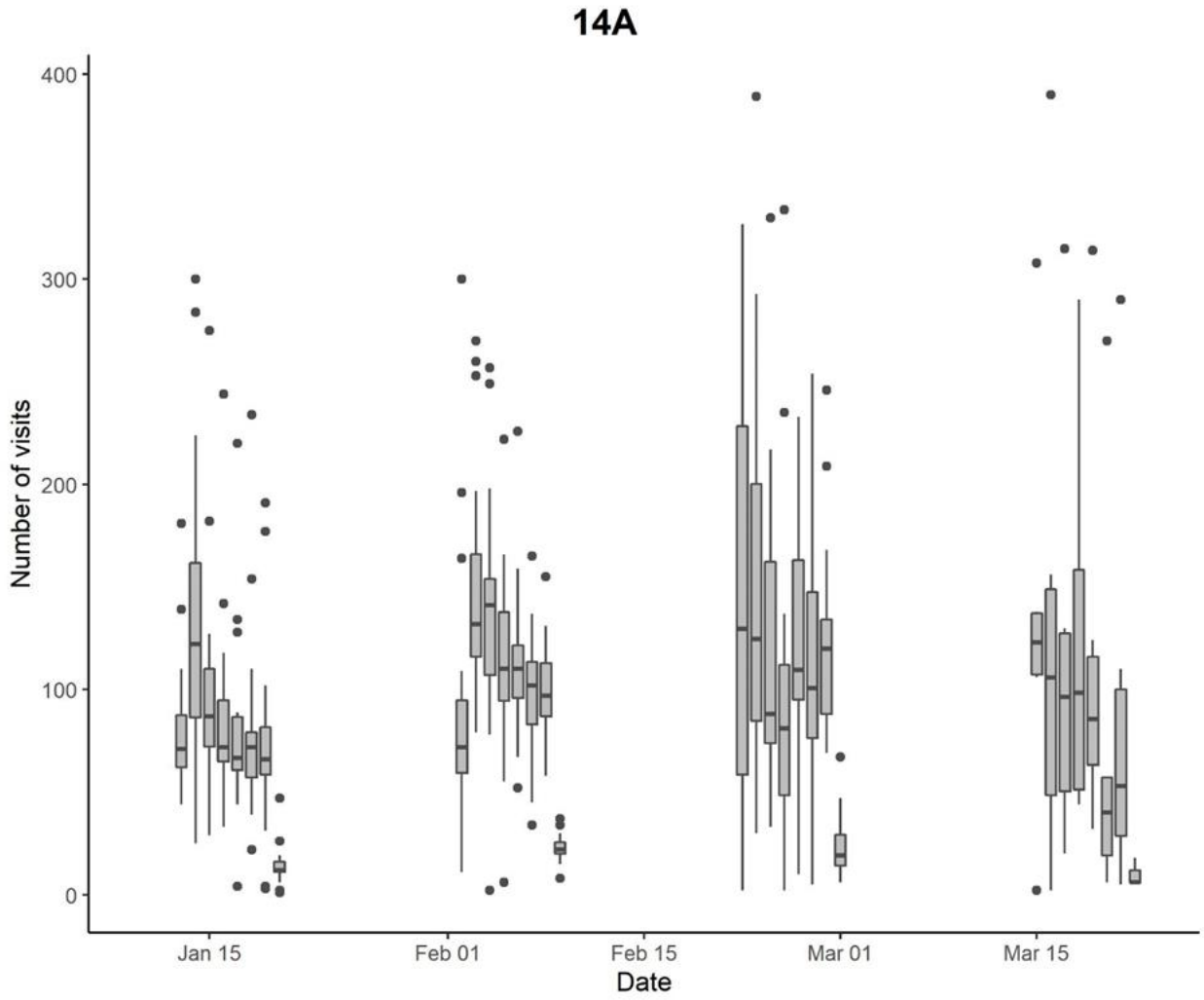

Figure 3.15. Distribution of daily visits to feeder 14A during each full period across the season. Tukey boxplots for each day show the median line, with the box around it representing the 25th (lower) and 75th (upper) percentiles. The vertical line indicates 1.5x the IQR and any points indicate values outside of that range.

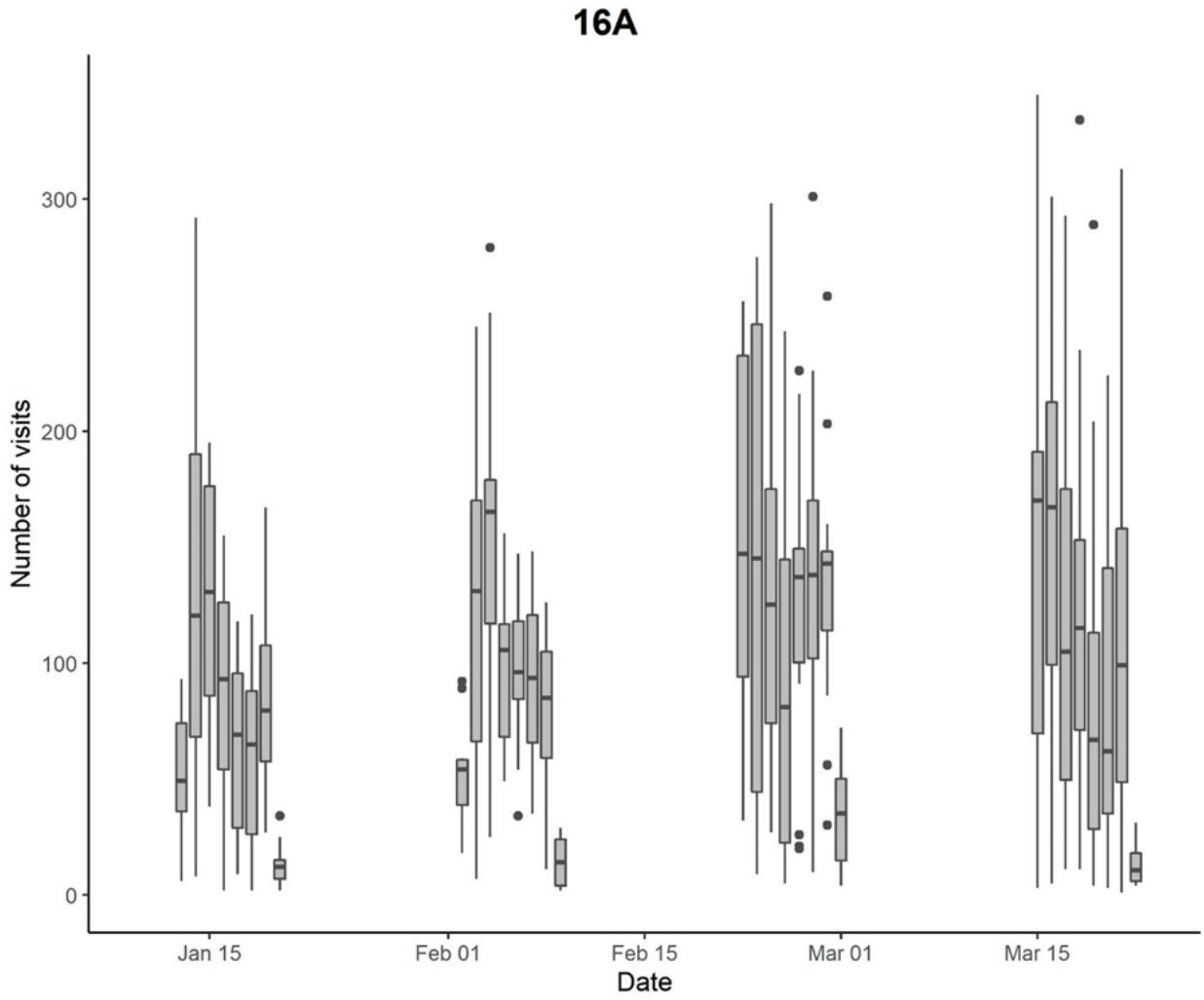

Figure 3.16. Distribution of daily visits to feeder 16A during each full period across the season. Tukey boxplots for each day show the median line, with the box around it representing the 25th (lower) and 75th (upper) percentiles. The vertical line indicates 1.5x the IQR and any points indicate values outside of that range.

Section S2. Weather data

The Edmonton International Airport (Lat: 53.308, Long: -113.568) is located approximately 15 km from the University of Alberta Botanical Garden. Through the website linked in the main text, we downloaded hourly weather data, including temperature in Celsius, for the entire season December 2020 – April 2021. Data was downloaded for each month and combined in R to a single weather data set. The average daytime temperature, used in the main analysis, was calculated as the average of all hourly temperature measures from the nearest one hour before the first detection of a chickadee to one hour after the last detection of a chickadee on the refilling day for each period, see Table 3.2. The average daily temperature was calculated as the mean of hourly measurements within each date (Figure 3.11B).

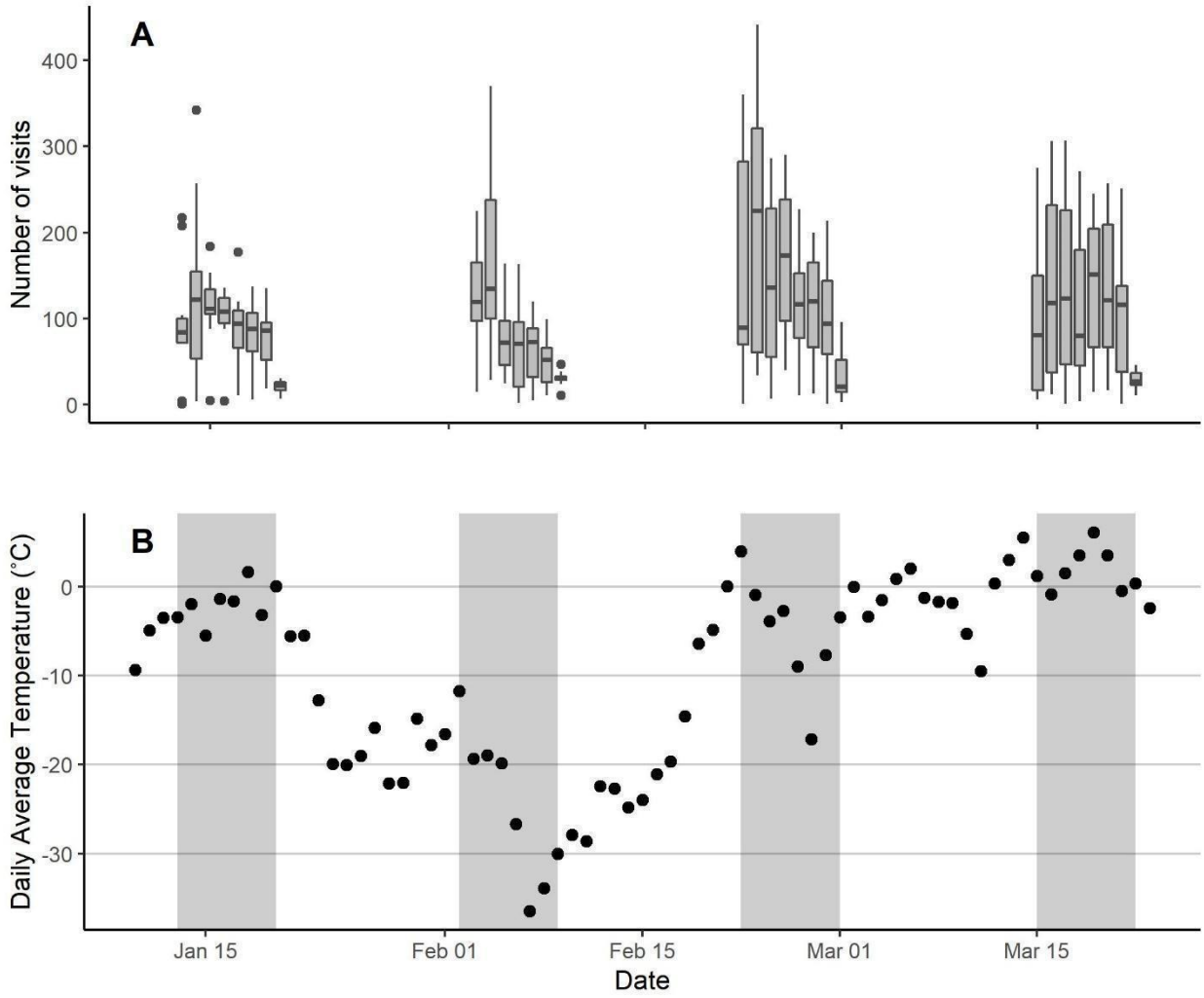

Figure 3.17. Daily number of feeder visits (A) and temperature (B) over the period for which we investigated feeder rediscovery diffusion (x-axis). (A) An example of visitation data at a feeder, here feeder 09A (see Appendix B section 1, Figures S1.1-8 for each individual feeder). Tukey boxplots for each day show the median line, with the box around it representing the 25th (lower) and 75th (upper) percentiles. The vertical line indicates 1.5x the IQR and any points indicate values outside of that range. (B) The daily average temperature across the season. The shaded areas show when feeders were full (DP1-4, main text).

Table 3.8. Daytime average temperatures, with range, for each of the refill days when birds could rediscover the feeder.

Date	Diffusion Period	Temperature (˚C)	Temperature range (min, max)
2021-01-13	1	-3.1	-7.0, -0.8
2021-02-02	2	-11.0	-11.4, -10.6
2021-02-22	3	3.4	0.7, 5.5
2021-03-15	4	0.0	-3.5, 5.5

Section S3. Feeder fidelity

To assess the degree to which each feeder represented independent units, we evaluated feeder fidelity of individual chickadees. First, we extracted the number of feeders that each individual visited and ranked them based on the number of visits made to each. Then we used a generalized linear mixed effects model to test whether the number of feeder visits differed between the 1^{st}, 2^{nd}, *etc.*, feeder visited most. The model was constructed assuming a poisson error distribution due to the count structure of the number of feeder visits. We included bird ID and "AP/DP" period as random effects to account for repeated measures for individuals and over time.

The chickadees in this study showed strong feeder preference. Out of 153 individuals detected throughout the study period, 73 individuals visited two feeders or more, and 26 out of those visited three or more (Figure 3.12). Individuals that visited multiple feeders exhibited strong preference for one feeder, visiting that one significantly more than any other feeders ($Chi^2 = 62046.9$, $df = 5$, $p < 0.001$, Figure 3.12).

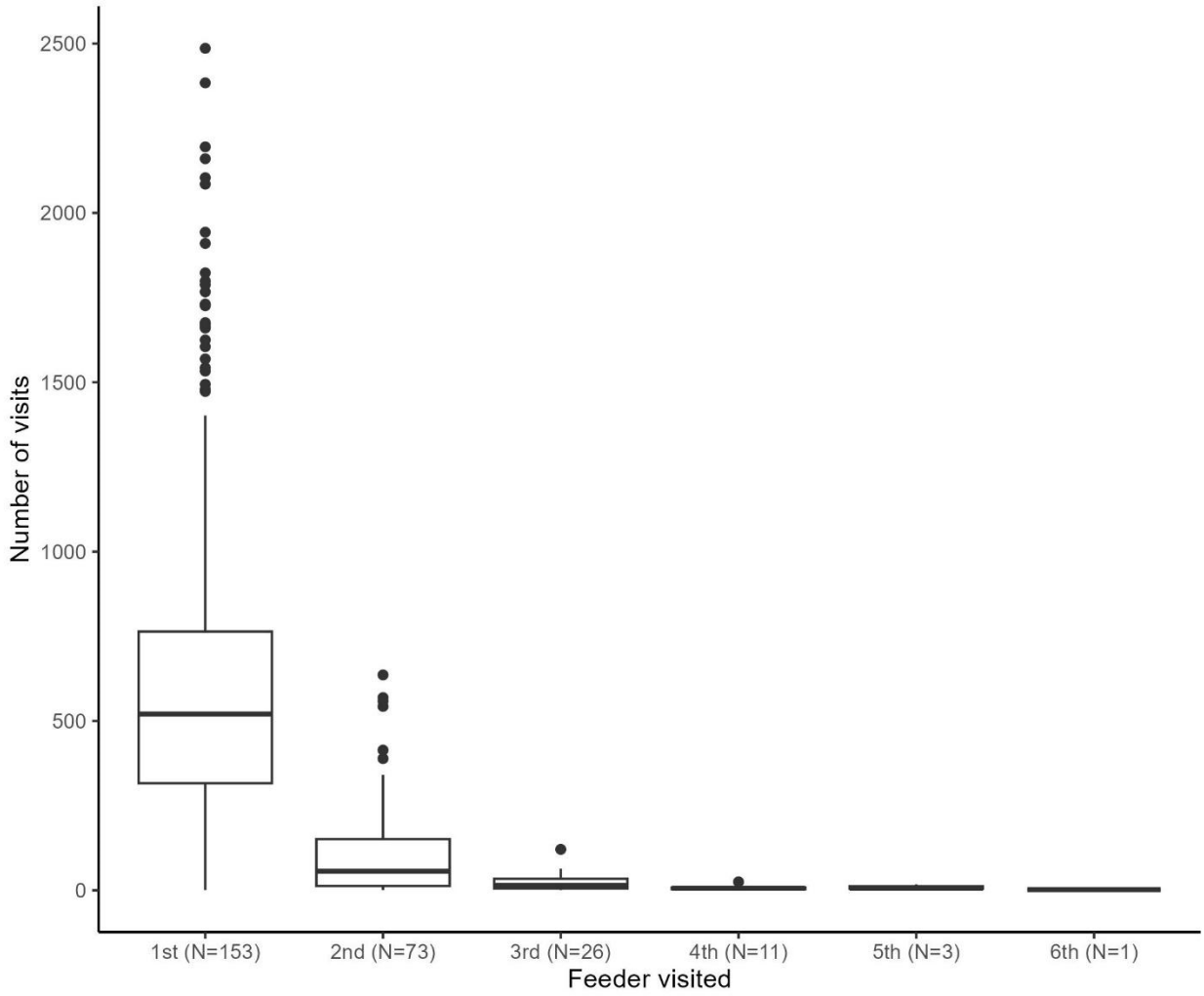

Figure 3.18. Average number of visits by individuals to each of the feeders they visited. The y-axis shows the number of visits, x-axis indicates which number of feeders an individual visited and the number of individuals that visited that number of feeders. The thick horizontal line indicates the median number of visits in each category, the box represents the 25ht to 75th percentile range. The vertical line indicates 1.5x the IQR and the points illustrate values outside the IQR.

Although the birds in our study showed clear feeder preferences, many birds were not restricted to using a single feeder, meaning that the groups in our data were not completely independent of each other (Figure 3.12). The additional variation in our social network

estimates and diffusion data stemming from the slight overlap in feeder use by individuals reduce the power of our analyses which makes our estimates conservative.

Section S4. Social network - modSRI

The saturated stream of feeder visitations in our data was too dense to use the commonly used *Gaussian mixture model* (GMM) and was identifying inappropriate grouping events. Figure 3.13 provides an example of the first 6 grouping events identified by the GMM using the *gmmevents* function in the *asnipe* package (version 1.1.17, Farine 2013).

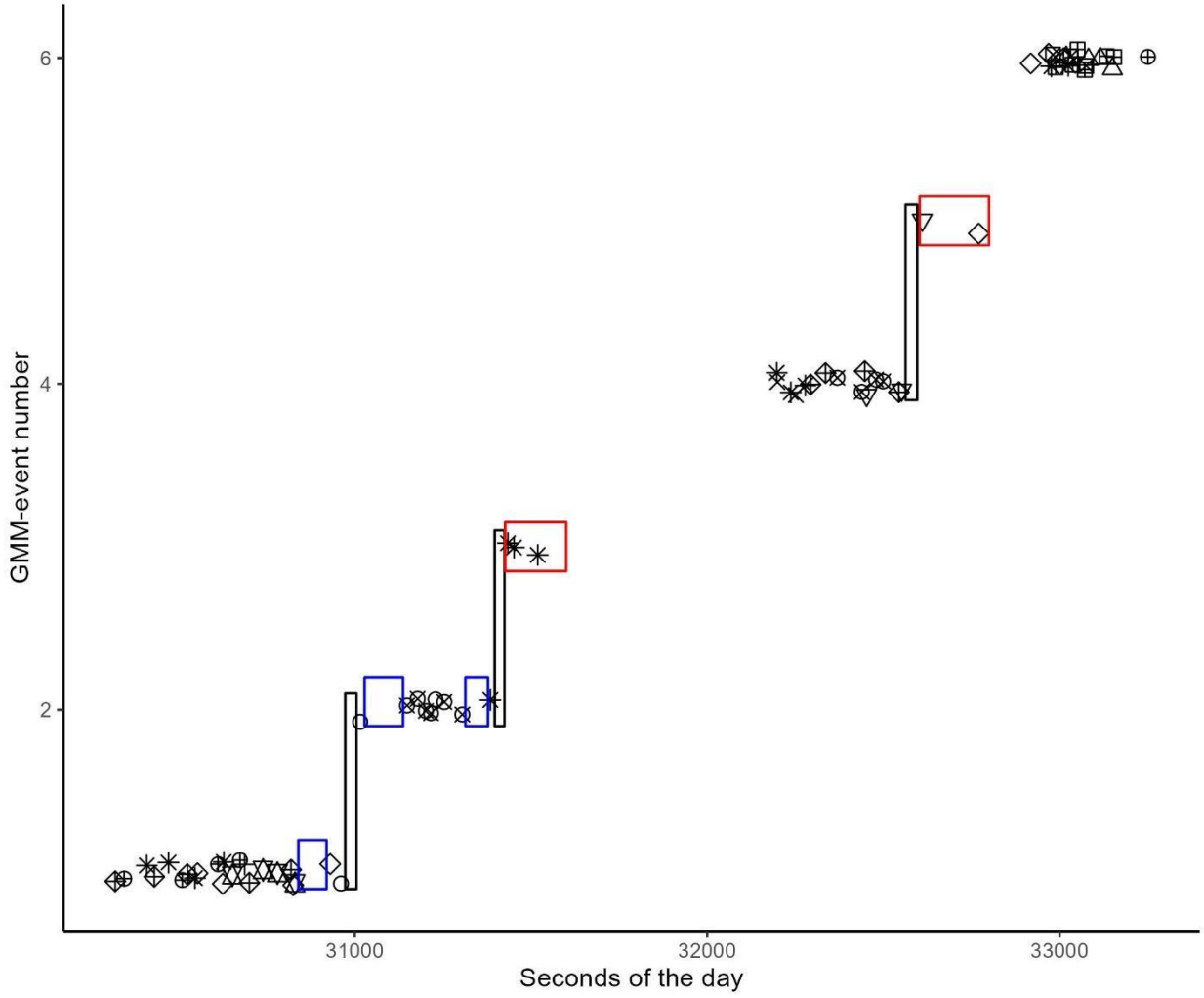

Figure 3.19. Example of the first 6 out of 84 identified grouping events at feeder 11A on 23rd Dec 2020, using the commonly used *Gaussian mixture model* approach (package asnipe reference). The y-axis indicates the number of the grouping event, the x-axis indicates the seconds of the day. Each type of shape represents an individual. The blue rectangles indicate

prolonged inter-individual visit interval within a grouping event. The black rectangles indicate short inter-event periods. The red rectangles highlight grouping events that are biologically unclear as the first individual within is closer to the previous grouping event than some intra-group intervals (blue) in earlier events.

The original *Simple Ratio Index* (Cairns and Schwager 1987) is suitable when the data has high coverage of interactions between subjects, and when the subjects recorded constitute the sample of interest, here the set of individual birds detected using a feeder during a given "Full" period.

The original version of SRI is calculated using the following equation (3.1):

$$\frac{x}{x + y_{ab} + y_a + y_b}$$

(3.1)

where *x* represents when birds A and B of a dyad are seen together in the same group, y_{ab} represents when A and B are seen in different groups, y_a is when bird A is detected in a group but not bird B, and finally, y_b represents when bird B was detected but not bird A (Cairns and Schwager 1987). The SRI thus defines an association between individuals as how often they were detected in the same grouping event in relation to all detected grouping events. To accommodate the potentially saturated stream of visitations on some days at some feeders, we instead defined a co-occurrence between bird A and B in a dyad as whether they were detected at the feeder within +/- 20 seconds of each other. To accommodate this definition of a co-occurrence between individuals in the SRI calculation we used the following modified equation (modSRI equation: 3.2):

$$\frac{x_{ab} + x_{ba}}{y_a + y_b}$$

(3.2)

where x_{ab} represents the number of times when bird B was detected at least once within 20 seconds of bird A, x_{ba} represents the number of times bird A was detected at least once within 20 seconds of bird B, y_a represent the total number of detections of bird A during the association period, and y_b is the total visits by bird B for the association perid.

Section S5. Results using 30s modSRI threshold

We checked whether the results were sensitive to our definition of a proximity event by repeating the modSRI calculations and subsequent analyses using a +/- 30 seconds threshold instead of 20 seconds. Results are shown in table 3.3.

Table 3.9. Model outputs for the temperature – pST relation, similar to Table 1 in the main text, from models that had the dyadic association strength in the underlying networks estimated using a +/- 30 second threshold.

	Binomial pST weighted on group size				**pST logit transformed with inverse variance weighting**			
Predictors	*Estimate*	*SE*	*z-value*	*p*	*Estimate*	*SE*	*t-value*	*p*
Intercept	-1.69	0.46	-3.70	**<0.001**	-3.85	4.02	-0.96	0.348
Daytime Avg. Temp	-0.15	0.02	-6.71	**<0.001**	-0.49	0.20	-2.50	**0.019**
Diffusion period (DP)	-0.21	0.13	-1.62	0.105	-0.72	1.33	-0.54	0.593
Random Effects								
Residual			1				6.53	
Feeder			0.60				8.76	

Section S6. Social network – Group size

The group of birds using each feeder was largely distinct from those using neighbouring feeders except for occasional floaters. Table 3.4 gives a summary of the number of individuals using each feeder during the association period (AP). Table 3.5 gives detailed information about group sizes during both AP and the diffusion period (DP) as well as the number of individuals in the DP that were also in the AP at the same feeder.

Table 3.10. Group size mean, minimum, and maximum for each period (Association period [AP]/ Diffusion period [DP]) across all feeders.

Period (AP/DP)	*Mean Group Size*	*Min. Group Size*	*Max. Group Size*
AP1/NA	27.9	13	42
AP2/DP1	20.6	14	33
AP3/DP2	19.8	12	29
AP4/DP3	23.4	16	36
NA/DP4	16.7	8	22

Table 3.11. Summary of group sizes and RFID matches between the association period and the diffusion period. The proportion of IDs from DP in AP was calculated as the number of RFID matches from DP in AP divided by the group size during association.

Feeder	Group size in Association Period (AP)	Diffusion period (DP)	Group size in DP	Nb. IDs in DP from AP	Prop. IDs in DP from AP
02A	42	1	33	27	0.64
04A	27	1	19	16	0.59
09A	13	1	14	12	0.92
11A	29	1	26	21	0.72
12A	22	1	17	15	0.68
14A	33	1	20	20	0.61
16A	23	1	15	15	0.65
02A	33	2	29	25	0.76
04A	19	2	21	18	0.95
09A	14	2	16	13	0.93
11A	26	2	12	11	0.42
12A	17	2	12	10	0.59
14A	20	2	25	20	1.00
16A	15	2	16	14	0.93
02A	29	3	36	25	0.86
04A	21	3	22	18	0.86

09A	16	3	16	14	0.88
10A	27	3	29	22	0.81
11A	12	3	25	11	0.92
12A	12	3	22	11	0.92
14A	25	3	21	19	0.76
16A	16	3	16	13	0.81
02A	36	4	22	18	0.50
04A	22	4	20	18	0.82
09A	16	4	18	13	0.81
10A	29	4	14	12	0.41
12A	22	4	17	16	0.73
14A	21	4	8	7	0.33
16A	16	4	18	15	0.94

Section S7. Social transmission: s-values and pST

Table 3.12. NBDA output values.

Feeder	Diffusion period (DP)	(s) [95CI]	pST [95CI]
02A	1	0.74 [0 - 5.17]	0.32 [0 - 0.66]
02A	2	0.72 [0 - 4.61]	0.31 [0 - 0.66]
02A	3	0 [0 - 0.21]	0 [0 - 0.15]
02A	4	0 [0 - 2.77]	0 [0 - 0.42]
04A	1	0.38 [0 - 14.89]	0.21 [0 - 0.66]
04A	2	1.49 [0 - 13.81]	0.41 [0 - 0.77]
04A	3	4.15 [0.41 - 62.72]	0.6 [0.19 - 0.87]
04A	4	0 [0 - 3.36]	0 [0 - 0.38]
09A	1	0 [0 - 2.51]	0 [0 - 0.53]
09A	2	53.33 [4.54 - 586]	0.93 [0.69 - 0.95]
09A	3	0.89 [0 - 8.96]	0.29 [0 - 0.72]
09A	4	0.03 [0 - 3.22]	0.01 [0 - 0.38]
10A	3	0 [0 - 0.25]	0 [0 - 0.2]
10A	4	0 [0 - 1.13]	0 [0 - 0.26]
11A	1	0.44 [0 - 2.85]	0.21 [0 - 0.52]
11A	2	18.94 [0 - 208]	0.64 [0 - 0.8]
11A	3	0 [0 - 3.35]	0 [0 - 0.61]

12A	1	4.04 [0 - 80.99]	0.5 [0 - 0.81]
12A	2	0 [0 - 1.21]	0 [0 - 0.29]
12A	3	0 [0 - 0.92]	0 [0 - 0.41]
12A	4	1.14 [0 - 8.92]	0.28 [0 - 0.66]
14A	1	0 [0 - 1.42]	0 [0 - 0.43]
14A	2	14.42 [2.71 - 158]	0.89 [0.67 - 0.98]
14A	3	0 [0 - 0.4]	0 [0 - 0.28]
14A	4	0 [0 - 1.67]	0 [0 - 0.18]
16A	1	0 [0 - 3.04]	0 [0 - 0.44]
16A	2	0 [0 - 1.51]	0 [0 - 0.5]
16A	3	0.1 [0 - 3.05]	0.09 [0 - 0.59]
16A	4	0 [0 - 1.96]	0 [0 - 0.49]

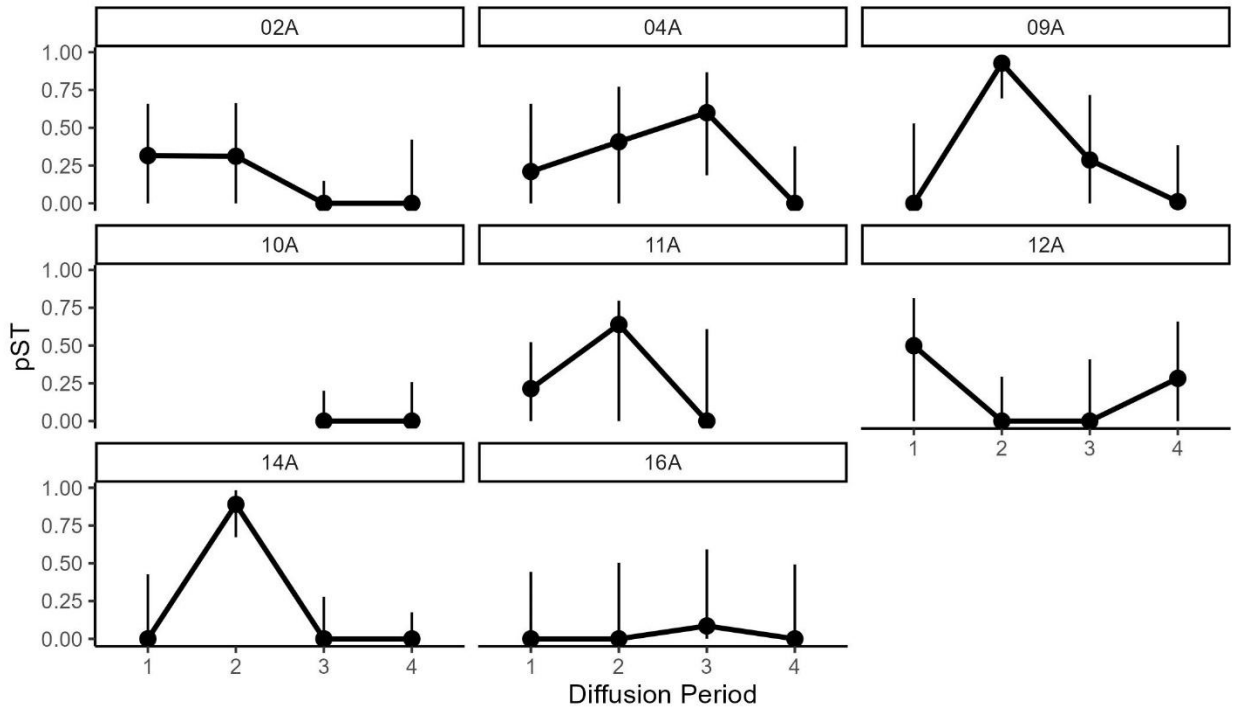

Figure 3.20. Change in pST over time within feeder. The y-axis indicates the pST value and the x-axis indicates the diffusion period. Each panel represents the feeder indicated in the banner above it. The points show the estimated pST value within the vertical line representing the 95% CI.

Section S8. Feeder visits across temperature

Ambient temperature during the study period did not have a substantial effect on feeder visitation rates (Figure 3.15).

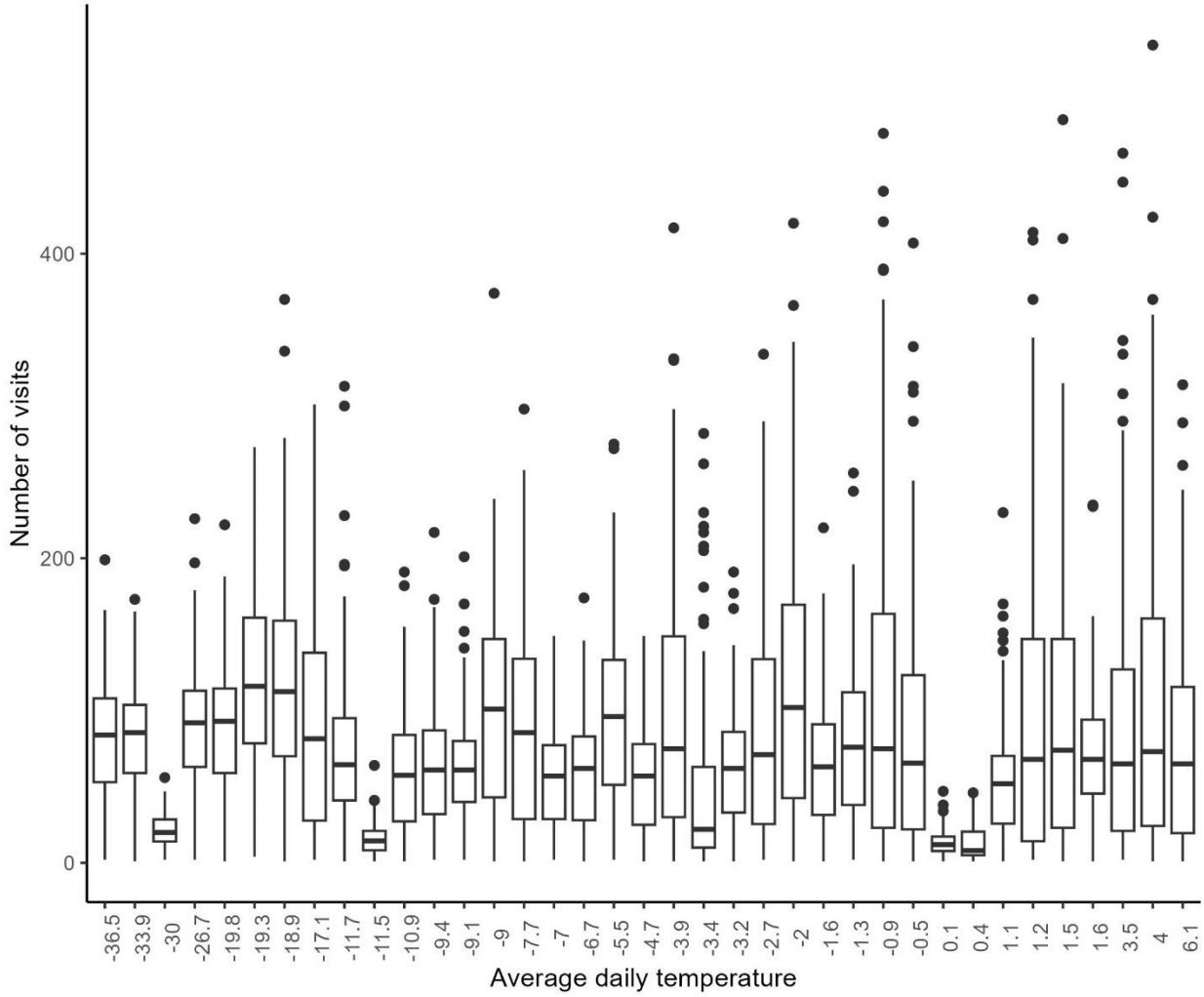

Figure 3.21. Individual average number of visits to a feeder across the season. The y-axis shows the number of visits, and the x-axis shows the temperature. The thick horizontal line indicates the median number of average visits at each daily average temperature, the box represents the 25ht to 75th percentile range. The vertical line indicates 1.5x the IQR and the points illustrate values outside the IQR.

Chapter 4

Information gain predicts network centrality, but the effect varies with acquisition method

This chapter is being prepared for submission to Journal of Animal Ecology.

4.1 Introduction

Most group living animals form social networks whose structure is mainly driven by non-random interactions between individuals, shaped by their social decision making (Krause and Ruxton 2002; Krause et al. 2007). The position an individual holds within a network can have important ecological implications, such as influencing their reproductive success (Silk 2007; McDonald 2007; Ryder et al. 2008; Cameron et al. 2009; Brent et al. 2013; Page et al. 2017; Beck et al. 2021), survival (Silk et al. 2009; Stanton and Mann 2012), access to information (Krause et al. 2007, 2009; Aplin et al. 2012; Brent 2015; Jones et al. 2017; Evans et al. 2020, 2021; Romano et al. 2022) and exposure to pathogens (Krause et al. 2007, 2009; Evans et al. 2020, 2021; Romano et al. 2022). Within these networks, individual sociality and, by extension, the social network structure are predicted to depend on a trade-off between the cost and benefits of social transmission, such as information vs pathogen transmission (Krause and Ruxton 2002; Romano et al. 2022). The spread and access to social information is considered to be a driving factor in social evolution (overview in Rogers 1988; Whiten 2005, 2017; Boyd et al. 2011). However, while it is known that social network structure can influence how information is transmitted between individuals (Mann et al. 2012; Aplin et al. 2012, 2015a; Hobaiter et al. 2014; Atton et al. 2014; Brent 2015; Firth et al. 2016; Kulahci et al. 2016; Firth 2020), the potential social network consequences of an individual obtaining new information are still largely understudied (but see Kulahci et al. 2018; Kulahci and Quinn 2019).

Many individual-level factors can influence the position an individual holds in a network (review in Wascher et al. 2018; see also Cantor et al. 2021), including sex and age (Lusseau and Newman 2004; Canteloup et al. 2021; Gomes et al. 2022), personality (Godfrey et al. 2012; Aplin et al. 2015b), social rank (Canteloup et al. 2021; Gomes et al. 2022), social history (McDonald 2007), and developmental conditions (Boogert et al. 2014). It was

recently suggested that an individual's state of knowledge about the environment could also influence its position within the social network (Kulahci et al. 2018; Kulahci and Quinn 2019). As information is crucial for adaptive behavioural responses in a variable environment, an individual that gains novel information may become a valuable social partner thus leading to an increase in its network connectedness (Kulahci et al. 2018; Kulahci and Quinn 2019). Although it has been shown that central individuals tend to have better access (increased exposure) to information within their network (Aplin et al. 2012; Kulahci et al. 2016), little is known about how information gain influences individuals' subsequent network position.

In a recent study, it was shown that lemurs that learned a novel problem-solving task received more affiliative interactions from conspecifics after the task was removed (Kulahci et al. 2018). This suggests a persistent positive effect of obtaining information that is new to the group on individual social centrality (Kulahci et al. 2018). In contrast, house sparrows, *Passer domesticus,* received more aggressive interactions when they performed well at solving tasks on their own but not when their success was experimentally manipulated (Preiszner et al. 2015). Preiszner et al. (2015), tested the effect of two aspects of problem-solving performance on social interactions: inherent differences in performance, and perceived differences in performance. First the inherent differences in problem-solving were measured in three extractive foraging tasks. Then some were trained on a fourth task. Finally, the authors experimentally induced difference in problem-solving performance by having a focal sparrow observe four simultaneous demonstrators that varied in perceived problem-solving performance. Variation in demonstrator performance was achieved by presented each demonstrator with a version of the fourth task that was either i) no task present ii) container impossible to open, iii) container always open, or iv) opening mechanism worked the way the sparrows were trained on (Preiszner et al. 2015). Preiszner et al (2015) found that individuals

that did well in the first three problem-solving tests received more aggressive interactions than low performing conspecifics. In contrast, the experimentally induced perceived differences in performance did not predict aggressive interactions among group members (Preiszner et al. 2015). This was also true under scenario iv), which would be viewed as a successfully solved task by the observer. Thus, additional factors related to information acquisition besides direct display of an individual's state of knowledge seem to play an important role in the social evaluation of the demonstrator by its conspecifics.

Previous studies of information gain and network position have predicted that individuals who gain information will experience an increase in their social centrality within the network (Kulahci et al. 2018; Kulahci and Quinn 2019), because information should always be a good resource (McNamara and Dall 2010). However, considering that network dynamics are determined by more than a single factor, the effects of individual information gain on their network position might not be so straightforward. For example, more central individuals may enjoy more benefits, such as exposure to information, but higher centrality may also have higher costs, such as increased pathogen exposure (Romano et al. 2022) or increased social competition (Forkman and Haskell 2004; Ratcliffe et al. 2007). If individuals gain centrality via information gain, we may expect that they will only remain in their new position if they can cope with the increased cost. Alternatively, individuals might be pushed away from the more central position gained from information acquisition not due to costs but simply because their status as a source of information is not reinforced. This could lead to transient effects of individual information gain on social network position in a "15 minutes of fame" scenario. In other words, if an individual discovered novel information once by chance and became more central its centrality would decrease with time since it does not continue to provide any new information (no reinforcement of information acquisition). Therefore, an individual that gains network centrality via information acquisition will only enjoy the

benefits until the increased costs of social competition and/or the lack of reinforcement of their knowledgeable phenotype knocks the individual back down in centrality.

The aim of this study was to investigate how different types of individual information gain might influence the social phenotype of individuals in the black-capped chickadee *Poecile atricapillus*, an animal known to experience fission-fusion group dynamics throughout their lives. Specifically, we ask whether individual acquisition of foraging information is predictive of an individual's future social network position. Additionally, we ask whether the relation between individual information gain and social network position are persistent or transient within a season. To answer these questions, we investigated four repeated re-discoveries of supplemental feeders in eight wild groups of black-capped chickadees between the end of December 2020 and mid-March 2021 (Figure 4.1). Black-capped chickadees are well suited for testing these questions because they form social groups with clear dominance hierarchies during winter (reviewed in Ratcliffe et al. 2007) which can act as a stabilizing factor on individuals' network position. A previous study showed that the repeatability of two measures of social network centrality in the black-capped chickadee are roughly 0.4 (Jones et al. 2019). This suggests that despite there being a clear dominance structure in the flocks, there is still room for factors such as information acquisition to influence individual social network position.

We used radio frequency identification (RFID) technology to construct daily social networks for five days after each refilling event and evaluated immediate and delayed effects of how an individual's informed phenotype affected its social position. We considered two aspects of an individual's informed phenotype. First, an individual's general propensity for maintaining updated information, which we assumed should be a long-term informed trait and thus a stable, consistent, knowledge indicator. Second, we looked at how quickly an individual rediscover a newly refilled feeder. Quick discovery of the feeders after refilling

can be due to frequent sampling of the feeder (i.e. general information gathering strategy), or simply by chance and even by social learning. We thus consider the time to rediscover a feeder by a given individual to be a more labile, inconsistent, knowledge indicator. Our prediction was that being informed, regardless of whether it is expressed via the stable or the variable indicator, would be positively correlated with social connectedness. We also predicted that the consistent indicator should have a stable positive correlation with social connectedness through time, whereas the effect of the inconsistent indicator would decrease over days. We use mixed-effects regression models to evaluate whether individual information gain predicts an individual's social network position at both short and long timescales.

4.2 Material and Methods

4.2.1 Data collection

We studied a population of black-capped chickadees at the University of Alberta Botanical Garden (UABG) in Devon, Canada (Lat: 53.407, Long: -113.758) between December 30th, 2020, and March 22nd, 2021. At this site, chickadees visited eight custom-made feeders distributed at least 270 meters apart. Each feeder was equipped with an RFID-reader (Priority 1 Design, Australia). Prior to the study period (Dec-Mar) individuals were captured and fitted with passive integrated transponder (PIT) tags with a unique identification code for each individual (Arteaga-Torres et al. 2020). Every time an individual accessed the feeder, we recorded the PIT-tag code (bird id), the date, and the time of the visit (to the nearest second). We used this information to estimate information gathering traits and social group structure.

The feeders were continually filled with black oil sunflower seeds from September 2020 until the start of the study period on December 30th, after which they were filled and emptied at regular intervals. Throughout the study period, the feeders were repeatedly kept empty for 2 weeks and then full for 1 week, henceforth referred to as empty and full periods (Figure 4.1). This schedule was repeated four times, referred as rounds 1 to 4 for each feeder, and all feeders were emptied and refilled on the same dates.

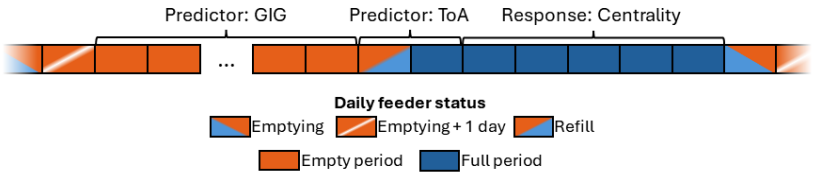

Figure 4.22. Schedule for one treatment round. Each square is one day. The ellipsis in the center of the empty period indicates days that were omitted in the figure to save space in the figure, but the total empty period was 13-14 days. GIG = General information gathering, and ToA = Time of acquisition.

4.2.2 Informed traits: High quality information maintenance & time of acquisition

We estimated three traits that were assumed to represent two distinct aspects of an individual's potential to be a source of information. The first two traits are related to the stable informed phenotype. These two traits were estimated during the empty periods to assess an individual's' propensity to invest time and energy on gathering and maintaining high quality asocial information on food availability. For this, we calculated the proportion of days during the empty periods that the individual visited the feeder (i.e. persistence of investment in asocial information) as well as the daily average number of visits on the days it visited the feeder (i.e. intensity of investment in asocial information). We refer to these traits as the "General Information Gathering" traits (GIG, Figure 4.1). For calculating these traits,

we excluded visits on the days that the feeders were refilled or emptied, henceforth shoulder dates, as feeder visit behaviours could not be standardized during these days. We also excluded one additional day after the feeders were emptied (Figure 4.1). The additional day was excluded because individuals tended to visit the feeders more on the two first days of the empty periods (Appendix C Figure 4.3), which might lead to inflated estimates of both traits. To evaluate whether excluding the additional day would influence any downstream results, we tested the correlation of individual visitation rates during the empty period between a subset of the data excluding only the shoulder dates, and one subset that excluded the shoulder dates plus one extra day. Excluding the extra day did not change our measure of individual visitation behaviour. Individual visitation measures during the empty period were highly correlated across subsets of the data (Pearson's $R = 0.99$, $t = 63.05$, $p<0.001$, Appendix C Figure 4.4). Thus, we calculated the GIG traits based on the subset excluding the additional day at the start of the empty period.

The third trait we estimated was the time taken by an individual to start using the feeder after it was refilled. This trait is an indication of the time needed for an individual to acquire the information that the feeder has been refilled, referred to as time of acquisition (ToA). This trait, however, captures both asocial and social information gathering since as soon as one individual discovered the feeder was refilled, this information could be learned socially by its conspecifics. We calculated ToA for each individual as time elapsed (in seconds) from the moment the feeder was refilled until the first visit by the individual before the end of the day after the refill (Figure 4.1). The refill time varied between feeders as they were refilled successively on the refill days. We excluded the inactive nighttime period to not inflate the values for the individuals that visited for the first time on day two. We calculated the inactive nighttime period by subtracting the last visit to a feeder on the day the feeders were refilled from the first visit to a feeder on the day after the feeders were refilled, using

pooled visitation data across feeders within each full period. Thus, the excluded nighttime period was the same for all feeders within a period. The end of the day after the feeders were refilled was similarly calculated as the last visit registered across feeders within each period. Since feeder were filled consecutively on the same day at the beginning of each full period and in a different order each time, the maximum potential value of ToA was not the same for any feeder across periods. In addition, the amount of time between refilling and the night period also differed between feeders and periods. Consequently, we mean-centered and scaled ToA (to have an SD = 1) within each period for each feeder. This step would make ToA comparable between feeders and periods.

4.2.3 Social network centrality

Individual chickadees were mainly associated with one feeder during the study period allowing us to consider individuals using one feeder as a group. Since individuals in our study regularly visited the feeder continuously throughout the day, we were unable to identify grouping events using *Gaussian mixture model* (Psorakis et al. 2012) which are otherwise commonly used to infer social associations in free ranging groups of animals (Farine et al. 2012; Aplin and Morand-Ferron 2017; Evans et al. 2018). We thus estimated the strength of connection between individuals using a modified version of the *Simple Ratio Index* (SRI) (Cairns and Schwager 1987). We defined an association index as how often two individuals were detected within +/- 20 seconds of each other, divided by the sum of visits to the feeder by both individuals. This modified SRI index (henceforth modSRI) ranges from 0 to 1 and was quantified for each dyad at a feeder on a daily basis during the full periods, to build a daily weighted social network for each feeder (Appendix C section S2).

Because feeder visitation could not be standardized on the days the feeders were either filled or emptied, we did not construct social networks for those days. Furthermore, since the time

of acquisition trait was calculated across the first two days of each full period, i.e. the refill day plus one day, we also did not build social networks during those days to avoid artificially confounding time of acquisition with social network structure. Thus, the first two days and the last day of each full period were thus excluded from social network observations and analysis (Figure 4.1). To investigate change in individual centrality measures over time, each daily network at a feeder within a full period included all individuals detected at that feeder at least once during the full period.

From the networks we extracted two direct measures of an individual's social centrality: its degree and strength. We also calculated three indirect measures of an individual's social centrality: betweenness-, eigenvector-, and harmonic centrality. Individual degree is the number of connections an individual has, and the strength is the sum of an individual's connection weights (Croft et al. 2008), here the modSRI. For information transmission, degree can be seen as how many individuals the focal individual has the potential to spread/acquire information to/from, whereas strength can be viewed as the likelihood of information passing to/from the focal individual to direct contacts depending on the frequency of interactions between them. Betweenness centrality is the number of times that an individual is on the shortest path between two other individuals in the network (Freeman 1977). Betweenness centrality gives an estimate of how important an individual is for geodesic transmission of, in our case, information throughout the network (Croft et al. 2008). We also quantified each individual's eigenvector centrality, which is a measure of relative connectedness or how well connected an individual is relative to how well connected everyone else is in the network (Bonacich 1972, 1991, 2007). Finally, we quantified harmonic centrality for each individual. Harmonic centrality describes how close an individual is to reaching every other individual in the social network, i.e. how many other individuals it needs to go through to reach any given individual (Rochat 2009). An individual

that requires fewer intermediaries to reach any given individual in the group is more central according to this measure. Its calculation is derived from the equation for closeness centrality but is more appropriate for unconnected networks (Rochat 2009), which we have in our data. Unconnected networks, in our case, are networks that include individuals that are not connected to any other individuals (Appendix C Figures 4.5 – 4.34). Group size as well as individual centrality measures varied within feeders across periods and between feeders (Appendix C Table 4.2, Appendix C Figures 3.35 – 3.42).

4.3 Statistical methods

All data processing and analyses were performed in R (R Core Team 2020).

4.3.1 Correlation and repeatability of informed traits

To assess the degree to which our measures of informed phenotypes estimate distinct traits, we evaluated the correlation between them using the *Hmisc* package (5.1-1, Harrell Jr 2023). Simply estimating the correlation between the measurements at the observation level conflate the among- and within individual correlations among the traits but allows us to estimate an overall relation among traits. We also assessed whether individuals were consistent in their informed phenotypes by evaluating the repeatability of the three informed traits using the rptR package (Stoffel et al. 2017). As the functions in the package use a mixed-effects model structure (LMM/GLMM) to estimate repeatabilities, we first constructed models and evaluated model assumptions to choose the appropriate repeatability function. For each repeatability test, we included the informed trait as the response variable, with individual and feeder included as random effects, assuming a Gaussian error distribution. The proportion of days an individual visited during the empty period was square root transformed and the average number of daily visits during visiting days of the empty period was log-

transformed. All mixed effects models in this study were constructed and evaluated using the *lme4* and *lmerTest* packages (Bates et al. 2015; Kuznetsova et al. 2017). Model assumptions were tested and assessed visually using the *performance* package (Lüdecke et al. 2023).

4.3.2 Correlation and repeatability of social network centralities

Daily networks and individual network centralities were constructed and estimated using the *igraph* package (Csárdi and Nepusz 2006). Several studies, including on black-capped chickadees (Jones et al. 2019), have shown that individuals display a significant degree of consistency in their social network position (Blaszczyk 2018; Jones et al. 2019). Estimating how much variation in social network position that is due to an individual's social personality should facilitate interpretation of the effect of information gain on individual network position. To describe the consistency of individual social phenotypes, we evaluated repeatability of the social traits. To estimate repeatability, we need multiple observations per individual, so we created a subset of the data that included likely group members within a full period, defined as individuals with degree scores above 0 for more than one day during the full periods. We fitted a model for each centrality measure separately with the centrality measure as the response variable and individual as a random effect. We calculated the adjusted repeatability by including group size as a fixed effect. We included group size in our models because group size is known to influence centrality estimates. In addition, we included period number and feeder as additional random effects to account for the grouped structure of our data. Betweenness centrality was calculated as 0 for 47.6% of observations in the subset of our data that considered whether individuals were likely stable members of the group at a given feeder. Due to the severe saturation of 0s in this measurement of betweenness, we were unable to include it in any further analysis and it was removed from the study. We fitted models with a Poisson error distribution for degree centrality, since it is a

count variable, and we used Gaussian error distributions for strength, eigenvector, and harmonic centrality. Harmonic centrality was square root transformed prior to the analysis to meet model assumptions. In addition, to establish the similarities among different centrality measures, we estimated Pearson's correlations among our four measures using the same method as described for the information traits above.

4.3.3 *Social network centrality in relation to information acquisition*

To investigate whether the informed phenotypic traits could affect individuals' social centrality, we used a mixed effects model approach. For each centrality measure, we modelled the centrality estimate as a function of the three informed traits. We also included days into the full period [1-5], group size, sex, and age [0-4] as fixed effects while bird id, feeder, and period number were fitted as random effects. We included an interaction between the number of days into the full period and each of the three informed traits respectively to assess whether the influence of the informed traits on social centrality varied over time. We also included the interaction between the proportion of days an individual visited during the empty period and the average number of daily visits during those days. The interactions represent the total number of visits during the empty period and thus allowed us to estimate the effect of just visiting a lot no matter how often. Degree centrality was modelled assuming a Poisson error distribution due to the count nature of this measure. Strength, eigenvector, and harmonic centralities were modelled assuming Gaussian error distributions following square root transformations to respect model assumptions. We assessed the impact of the multi-level variables age, days into the full period, and the interaction between days into the full period and the informed traits using the *Anova* function from the *car* package (Fox and Weisberg 2019).

4.4 Results

4.4.1 *Informed traits*

Individuals showed clear variation in the proportion of days during the empty period that they visited the feeder and in their daily average number of visits during those days (Appendix C Figure 4.43). The proportion of days during the empty period that an individual visited and the daily average number of visits to the feeder that the individual made during those days were significantly correlated (Pearson's $R = 0.42$, $p < 0.001$). However, the moderate strength of the correlation indicates that despite being related the two phenotypic measures still capture different aspects of the informed trait. Thus, we include both measures in the analysis on whether information gain predicts individual centrality measures.

The informed traits measured in this study were significantly correlated. The two GIG traits were weakly correlated with time of acquisition (proportion of days visited - ToA: $r = -0.31$, $p < 0.001$; average visits on visit days - ToA: $r = -0.24$, $p < 0.001$). Time of acquisition was negatively correlated with both of the GIG traits such that the smaller the time of acquisition, the higher the GIG trait values. Thus, individuals that visit the feeders both regularly (i.e. proportion of days) and intensively (i.e. average number of visits on visit days) during the empty periods tend to be the individuals that visit the feeders earlier after being refilled.

Individuals showed low to moderate, repeatability in proportion of days visited ($R = 0.28$, $SE = 0.05$, $CI = [low: 0.19, high: 0.38]$, $p < 0.001$), and daily average visits on days visited ($R = 0.2$, $SE = 0.05$, $CI = [0.10, 0.28]$, $p < 0.001$). Repeatability was low but significantly different from zero in the time they first approached the feeder after it was refilled ($R = 0.05$, $SE = 0.04$, $CI = [low: 0.00, high: 0.13]$, p-value = 0.017).

4.4.2 *Individual centrality measures*

All four centrality measurements were significantly correlated with one-another (Appendix C Table 4.2). Degree, strength, and eigenvector centrality were highly correlated while harmonic centrality was moderately correlated with the other measures (Appendix C Table 4.2). All centrality measures were also significantly repeatable at the individual level with degree (R [+-SE] = 0.21 [0.036], CI= [0.156, 0.291], p-value < 0.001), strength (R [+-SE] = 0.314 [0.045], CI= [0.229, 0.404], p-value < 0.001), and eigenvector (R [+-SE] = 0.343 [0.042], CI= [0.262, 0.428], p-value < 0.001) centrality showing moderate repeatability and harmonic (R [+-SE] = 0.058 [0.014], CI= [0.033, 0.087], p-value < 0.001) centrality being weakly repeatable.

4.4.3 *Informed phenotypes and individual centrality*

The initial models that included the interaction between the informed phenotypic traits and days showed that only the interaction between ToA and number of days was significant (Appendix C Table 4.4. for evaluation of the interaction using Anova and Appendix C Table 4.5. for output of full interactive model). Thus, we re-ran the models including only the ToA – Days interaction and no interaction between the GIG traits and days and we present the results from these models below (Table 4.1).

All three informed traits were significant predictors of all four centrality measures (Table 4.1). For both of the GIG informed traits, the more an individual expressed either of them, the more central the individual was during the full periods. The interaction between the GIG traits shows a negative correlation with all four centrality measures (Table 4.1) such that the effect of either trait on the centrality measure decreases the more both traits are expressed. The ToA trait was negatively correlated with the centrality measures such that individuals with lower-than-average ToA, i.e. quicker to discover, were more central.

The interaction between ToA and number of days into the full period was statistically significant for all four centrality measures, indicating that the effect of ToA on individual centrality varies over time (Anova in Appendix C Table 4.6). All interactions of ToA and days >1 into the full period are significantly different from the ToA – Day 1 value, except for the ToA – Day 2 interaction for Eigenvector (Table 4.1). The interaction ToA effect was strongest at Day 1 with the effect diminishing successively across days, illustrated by the decrease in slope for the relation between the ToA and each centrality measure across days in Figure 4.2.

Group size had a statistically significant association with all centrality measures with larger group sizes predicting higher centrality measures. Individual centrality measures were not related to the sex or age of the individuals (Table 4.1, Appendix C Table 4.5). Degree centrality was increased with the number of days into the full period. A similar but weaker pattern was shown between days into the full period and the strength, eigenvector and harmonic centrality measures (Table 4.1, Appendix C Table 4.5).

Table 4.13. Model outputs for social centrality measures in relation to informed phenotypic traits, including the interaction between the ToA and days into the full periods. ToA is mean-centred and scaled within period and feeder. A Poisson distributed GLMM was used for analysing Degree centrality whereas LMMs were used for the other three centrality measures. Reference categories for the categorical variables Day, Sex and Age are Day 1, Female, and Age 0, respectively. Statistically significant predictors are emphasized in bold.

	Degree				**Strength**				**Eigenvector**				**Harmonic**			
Predictors	*Estimate*	*SE*	*z-value*	*p*	*Estimate*	*SE*	*t-value*	*p*	*Estimate*	*SE*	*t-value*	*p*	*Estimate*	*SE*	*t-value*	*p*
(Intercept)	1.87	0.20	9.44	**<0.001**	0.92	0.15	6.26	**<0.001**	0.59	0.08	7.61	**<0.001**	11.96	1.17	10.22	**<0.001**
Prop. Days Visited (GIG)	0.25	0.07	3.69	**<0.001**	0.21	0.09	2.34	**0.019**	0.20	0.06	3.40	**0.001**	4.32	1.51	2.86	**0.004**
Avg. over Visit Days (GIG)	0.12	0.02	6.65	**<0.001**	0.12	0.02	5.16	**<0.001**	0.08	0.02	5.18	**<0.001**	1.10	0.39	2.86	**0.004**
Time of Acquisition (ToA)	-0.54	0.03	-20.93	**<0.001**	-0.35	0.02	-14.45	**<0.001**	-0.21	0.02	-13.55	**<0.001**	-4.01	0.41	-9.79	**<0.001**
Day 2	0.17	0.03	5.86	**<0.001**	0.01	0.03	0.21	0.837	0.03	0.02	1.33	0.185	0.92	0.55	1.67	0.095
Day 3	0.24	0.03	8.55	**<0.001**	0.05	0.03	1.51	0.132	0.05	0.02	2.40	**0.017**	0.99	0.55	1.79	0.074
Day 4	0.33	0.03	11.99	**<0.001**	0.05	0.03	1.44	0.150	0.07	0.02	3.29	**0.001**	1.86	0.55	3.36	**0.001**
Day 5	0.42	0.03	15.45	**<0.001**	0.12	0.03	3.65	**<0.001**	0.10	0.02	4.60	**<0.001**	2.85	0.55	5.16	**<0.001**
Group Size	0.35	0.02	20.19	**<0.001**	0.18	0.02	8.93	**<0.001**	0.05	0.01	3.90	**<0.001**	3.01	0.31	9.57	**<0.001**
Sex [Male]	0.00	0.09	0.04	0.966	-0.02	0.07	-0.29	0.772	-0.01	0.04	-0.28	0.778	0.23	0.67	0.34	0.733
Age 1	0.14	0.13	1.09	0.277	0.07	0.09	0.77	0.441	0.02	0.07	0.36	0.719	0.38	0.97	0.39	0.695

Age 2	-0.06	0.13	-0.47	0.641	-0.09	0.09	-1.00	0.319	-0.08	0.06	-1.18	0.238	-1.00	0.96	-1.05	0.295
Age 3	0.07	0.16	0.44	0.661	-0.01	0.12	-0.05	0.959	-0.02	0.08	-0.25	0.800	0.24	1.19	0.21	0.837
Age 4	0.11	0.22	0.51	0.608	0.08	0.16	0.53	0.595	0.02	0.11	0.23	0.818	1.50	1.62	0.92	0.355
Prop. Days Visited × Avg. over Visit Days	-0.19	0.05	-3.63	**<0.001**	-0.19	0.07	-2.83	**0.005**	-0.10	0.04	-2.39	**0.017**	-2.42	1.08	-2.24	**0.026**
ToA × Day 2	0.19	0.03	5.93	**<0.001**	0.10	0.03	3.17	**0.002**	0.05	0.02	2.20	**0.028**	1.79	0.55	3.23	**0.001**
ToA × Day 3	0.27	0.03	8.55	**<0.001**	0.15	0.03	4.62	**<0.001**	0.08	0.02	3.77	**<0.001**	1.95	0.55	3.53	**<0.001**
ToA × Day 4	0.35	0.03	11.28	**<0.001**	0.20	0.03	6.18	**<0.001**	0.11	0.02	5.29	**<0.001**	3.05	0.55	5.51	**<0.001**
ToA × Day 5	0.39	0.03	12.94	**<0.001**	0.23	0.03	7.18	**<0.001**	0.14	0.02	6.45	**<0.001**	2.97	0.55	5.37	**<0.001**
Random Effects																
Residual	1				0.17				0.07				50.42			
Bird ID	0.13				0.06				0.03				4.94			
Feeder	0.12				0.04				0.01				3.39			
Period	0.04				0.04				0.00				0.37			

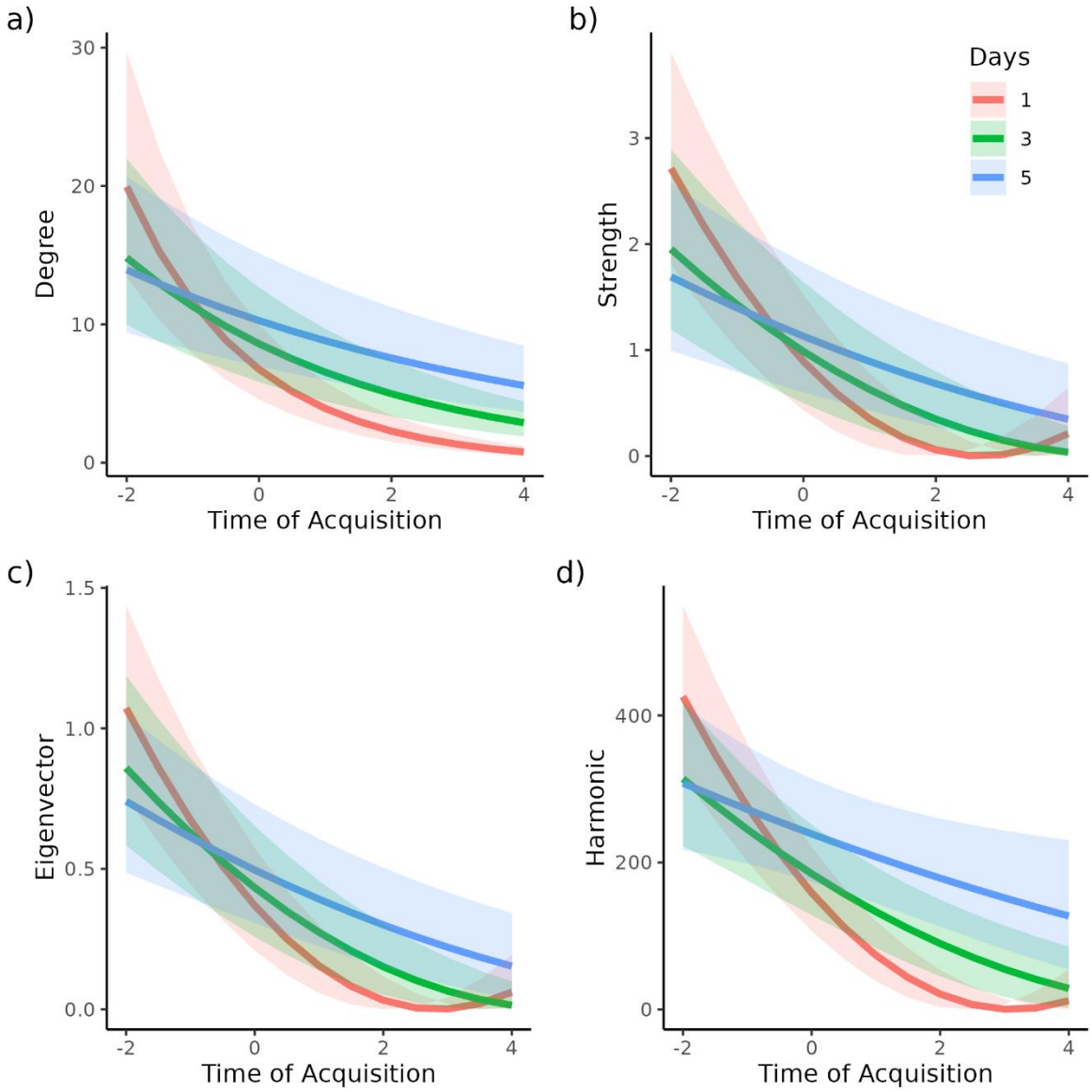

Figure 4.23. Change across days in the relationship between Time of Acquisition, ToA, and a) Degree, b) Strength, c) Eigenvector, and d) Harmonic centrality across days as estimated from mixed-effect models. Strength, Eigenvector centrality and Harmonic where square-root transformed in the models, but the graph shows back-transformed prediction on the original scale. The y-axis gives the centrality value and the x-axes show

the mean centered and scaled ToA. The red line indicates day 1, green indicates day 3, and blue indicates day 5. Days 2 and 4 were omitted for clarity.

4.5 Discussion

Individual information gain could substantially alter an individual's social environment by making them an attractive social partner and thereby increasing their centrality within their social network (Kulahci et al. 2018; Kulahci and Quinn 2019). However, the relationship between information acquisition and an individual's social centrality can be influence to different degrees by being a consistent or inconsistent source of information, as well as other factors such as social dominance interactions. Here, we investigated the link between asocial information gain and social centrality in wild groups of black-capped chickadees. We found that individuals that spend more time and energy to sample at a feeder when empty, as well as discover food sources more quickly tend to have higher centrality scores than individuals that do not. Furthermore, our results suggest that how an individual is informed influences its effect on centrality. We found that the more consistent informed phenotypic traits (GIG) had a stable effect on individual centrality. In contrast, the effect of the inconsistent informed trait (ToA) weakened over time (Figure 4.2). In addition, our results provide further support for consistency in individuals' social phenotypes.

All three informed traits estimated in this study were linked to an individual's social network position, thus supporting the hypothesis that being knowledgeable can have a positive effect on an individual's social centrality (Kulahci and Quinn 2019).

Individuals that were consistent in maintaining high quality information, as measured by the two general information gathering traits, were also more central. This result is in accordance with those individuals being valuable long-term social partners (Kulahci et al. 2018; Kulahci and Quinn 2019). In addition, being at the right place at the right time, as per our time of acquisition trait, can also temporarily boost an individual's centrality. We found that individuals were repeatable in whether they spend time and energy to maintain information about feeder status during the empty periods or not. This suggests that these traits are characteristic of generally informed individuals which should be considered valuable long-term social partners. The fact that both time and energy spent visiting the empty feeders predicted individual centrality measures across all days during the full periods further supports this conclusion. Similarly, individual centrality across days was also predicted by how quickly individuals visited the feeder after it was filled, with quicker individuals having higher centrality. However, this pattern weakened across the days of the full periods (Figure 4.2). A weakening pattern could stem from the network becoming more connected over time as flock members discover the feeder. However, as the temporal effect on social network position was trait specific to the ToA and not the GIG traits, it is unlikely that increased group connectedness was driving the decrease in effect of ToA on social network position over time. Furthermore, although the time until an individual first visited the feeder after it was refilled was significantly repeatable, the individual repeatability was estimated at ~5%. This indicates that there was a large within-individual environmental variation affecting who arrives earlier vs. later to the feeder. Together, these results are in line with our predictions about that stable versus variable informed phenotypic traits will have different impacts on individuals' social

phenotypes. In addition, the low repeatability of arrival time at the feeder combined with the vanishing effect of time of arrival on centrality over a few days support our original prediction of a “15 minutes of fame” effect.

The reduction of the ToA effect on centrality over a few days is due both to a decrease in centrality of early discovered (low ToA) and an increase of centrality in late discoverer (high ToA). One explanation for the decrease in the relation between time of acquisition and individual centrality is that the value of the information provided by individuals that arrive early will decrease over time. As more individuals arrive at the feeder and begin to use it consistently, more individuals are also demonstrating that the feeder is providing food. Alternatively, social factors such as dominance (Smith 1992; Ratcliffe et al. 2007) and social competition (Oh and Badyaev 2010) might act as stabilizing agents to mitigate the disruption to the social norm of the group caused by variation in individual information gain related to arrival time. Overall, our results strongly suggest that without reinforcement of the informed trait over time its importance for centrality decreases, and that centrality is not driven only by information acquisition and transfer.

Spending time and energy on maintaining updated information about environmental contingencies (e.g. availability of a food source) is seemingly only beneficial for centrality up to a point, as indicated by the negative effect of the interaction between the two general information gathering traits. While both of the stable informed traits had a positive relationship with individual centrality on their own, however, the interaction showed a negative modifying effect between them. The fitted model indicated that an individual that visited a feeder across multiple days would have higher centrality

compared to an individual that did not, but it would not increase in social centrality more by visiting many times within a day (Table 4.1). This result is consistent with a fundamental principal in associative learning in which early experiences have a stronger effect on establishing contingencies between stimuli (overview in Shettleworth 2010, pp. 124–127). For one chickadee observing another, learning the contingency between the expression of informed traits by a flock mate and that individual being a consistent source of information should be strongest initially with each consecutive exposure adding less strength to the association between the traits and the phenotype of the observed individual (Rescorla and Wagner 1972; Siegel and Allan 1996; overview in Shettleworth 2010, pp. 124–127). Alternatively, the value of the information produced by an individual visiting a feeder repeatedly during the empty period will decrease for observing conspecifics, i.e. they will observe an individual repeatedly demonstrate that the feeder is empty. Regardless of the underlying process, our results point to the presence of factors limiting the effect that individual information gain has on social network position, which has rarely, if at all, been considered previously.

The black-capped chickadees in our study exhibited moderate consistency in their degree, strength, and eigenvector social centrality measures, as expected from previous studies in Paridae (Aplin et al. 2015b; Jones et al. 2019). However, harmonic centrality was only weakly repeatable at the individual level. This likely reflects that black-capped chickadees form tight flocks during the winter (Smith 1992), such that most individuals within a daily social network will be directly connected to each other. This is further supported by the fact that approximately half of the betweenness scores were estimated at 0, indicating that about half of the individuals had direct contact with each other and

never needed to go through another individual to reach a given individual. Thus, although betweenness and harmonic centrality are important traits when considering information spread in groups of animals as they represent the shortest path for information to travel from one individual to another and the widest reach of information spread provided by any given individual, respectively, their use might be limited in tightly connected networks.

In conclusion, we found that an individual's informed phenotype does predict its social phenotype in this population of black-capped chickadee as we expected. However, the nature of the informed trait, whether it is stable or variable, impacts its predictive power of sociality over time. It would be important to consider the "15 minutes of fame" effect as well as the apparent diminishing return of information gathering effort on sociality in future studies. Finally, as both individual social phenotype, and individual information acquisition and use have been linked to variation in fitness, the connection between information gain and centrality could have indirect effects on each others' influence on fitness. Investigating the connection between information gain, social phenotype, and fitness could help identify important traits driving sociality.

4.6 Ethics approval

This study was conducted under the University of Alberta Animal Care and Use Committee (ACUC) permit: AUP00002210, Alberta Wildlife Research Permit and Collection Licenses: 56631, 56632,19-056, 20-056, 21-056, and Environment and Climate Change Canada Bird Banding Permit: 10963.

Appendix C

Section S1. Data handling for GIG informed traits

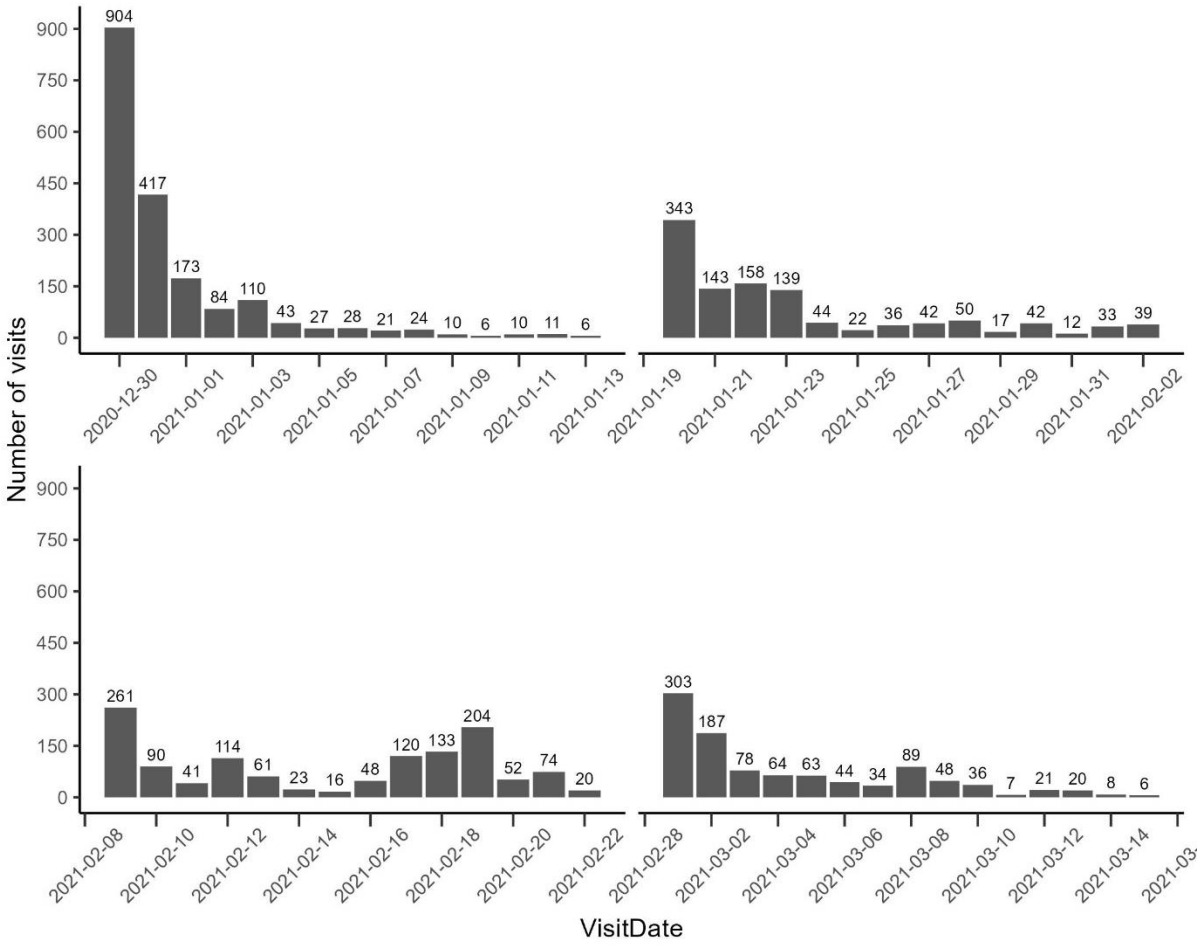

Figure 4.24. Daily feeder visits during each empty period across all feeders using data from all days, including shoulder dates. The graphs in order top-left to bottom-right show EMPTY periods 1-4 respectively. Y indicates number of visits, X show the dates, and the numbers atop each bar display the total number of visits for that date.

There is an inflation of visits at the start of each empty period which can skew our estimates of individual general information gathering trait. Excluding certain days of individual visitation data allows us to avoid introducing skewness in the measure caused by the inflation of visits. To investigate whether the visitation data excluding the shoulder dates plus one additional date at the start of the EMPTY period was different from the visitation data excluding only the shoulder dates, thus potentially influencing our measurements of the informed traits, we correlated individual visitation between these two subsets of visitation data (Appendix C Figure 4.4).

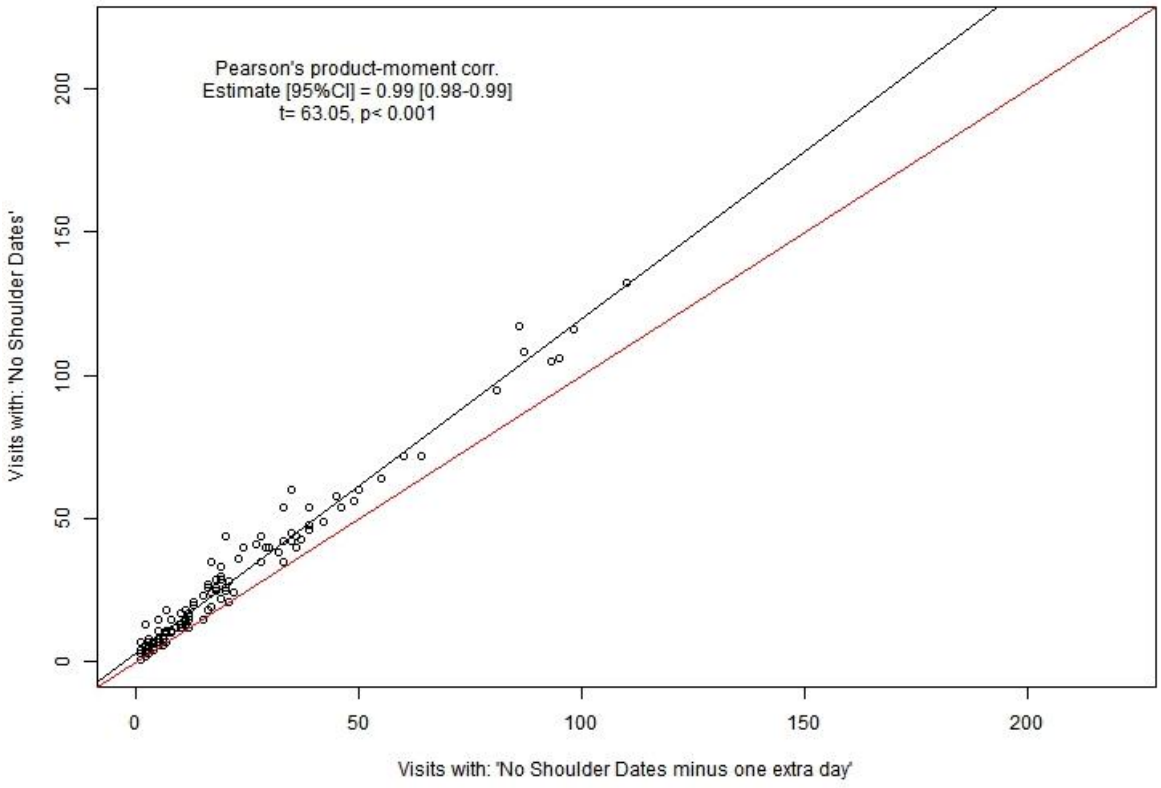

Figure 4.25. Correlation of individual feeder visits using data that excludes the shoulder dates of the EMPTY period and data that excludes the shoulder dates and one additional day at the start of the EMPTY period. The red line is a reference line indicating a 1:1 correlation and the black line indicates the correlation between the subsets of data.

Section S2. Social networks

The figures below are visual representations of the daily networks from which the individual centrality measures were taken. Each figure shows the five daily networks at a single feeder within a feeder = full period. The feeder, period, and date that the network belongs to are given above each network. Within each feeder and period (each figure), the number on each node represents the same individual across days. Grey lines represent

connections between individuals and their width are proportional to the strength of the connection between the individuals of the pair connected by the line (calculated as the modSRI * 10 for visibility).

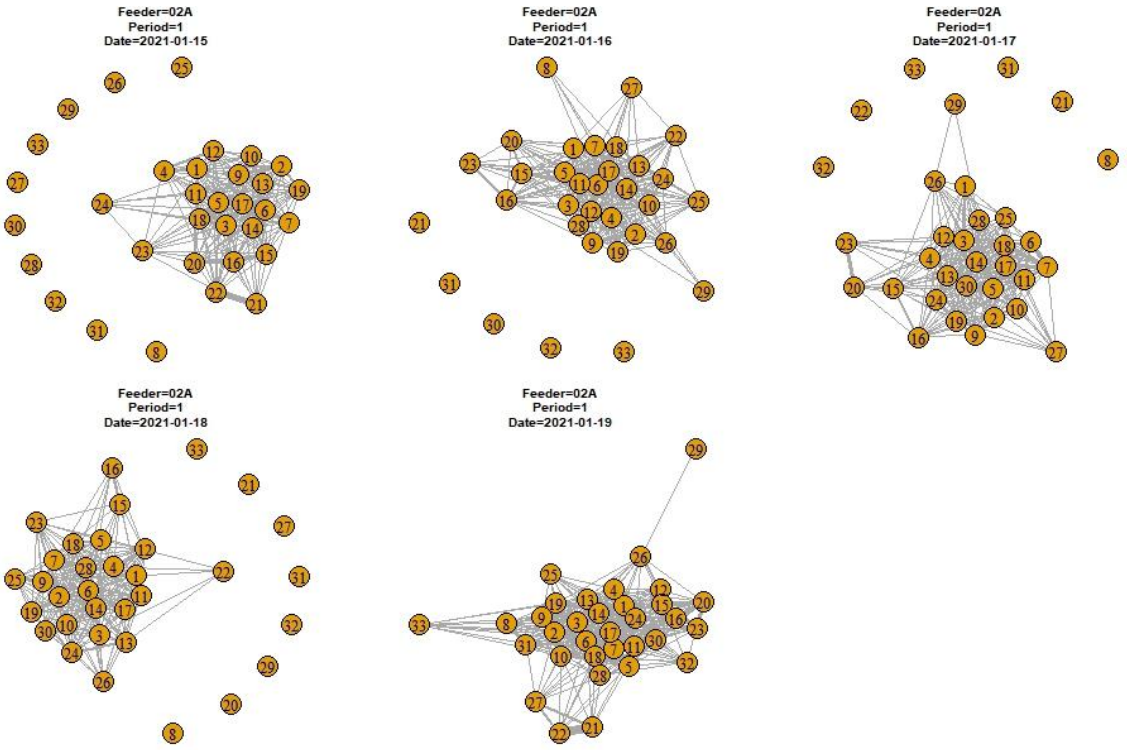

Figure 4.26. Daily social networks at feeder 02A during full period 1.

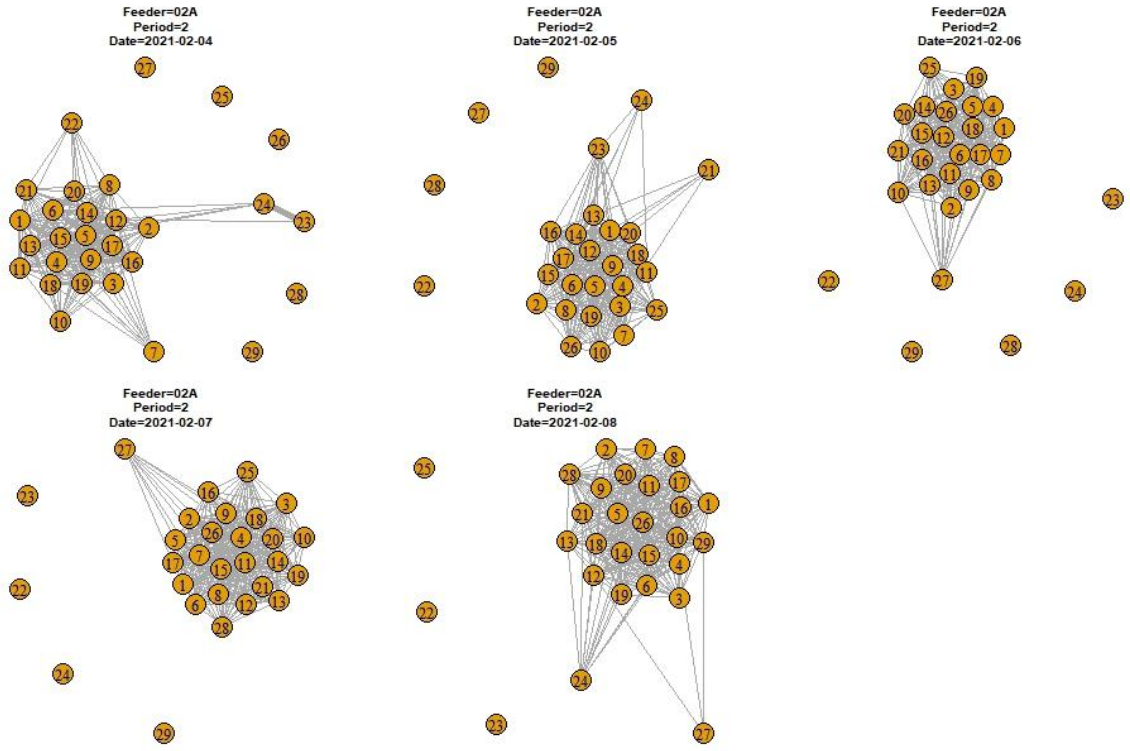

Figure 4.27. Daily social networks at feeder 02A during full period 2.

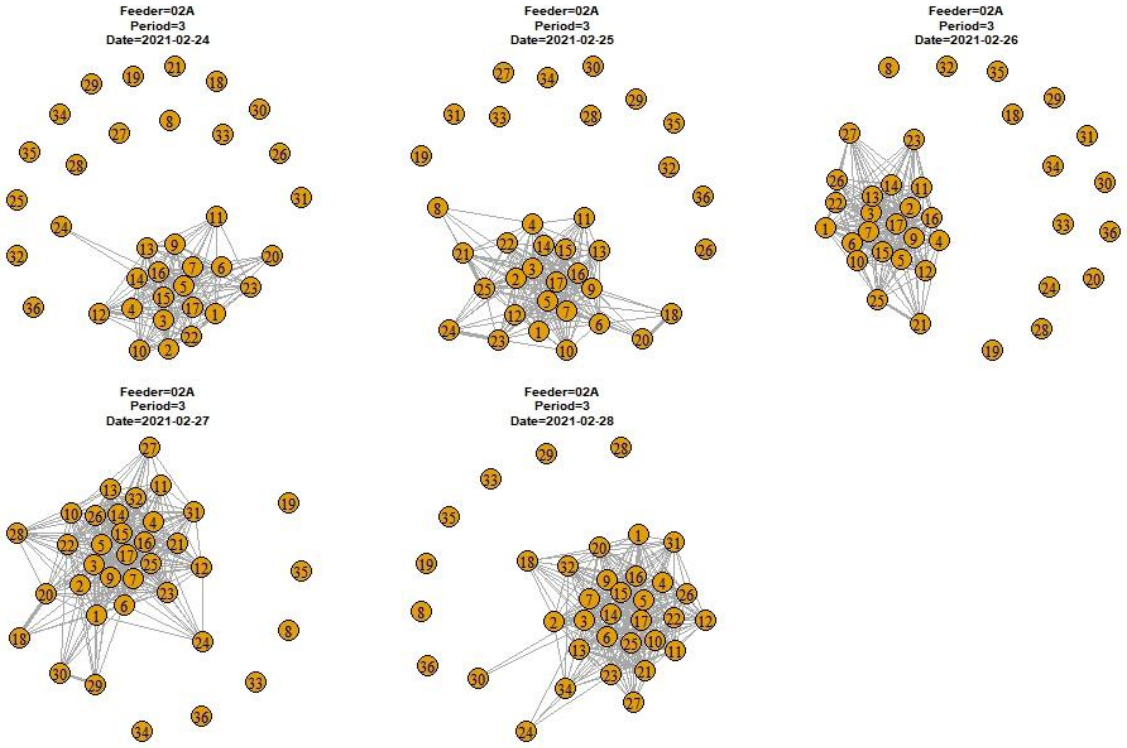

Figure 4.28. Daily social networks at feeder 02A during full period 3.

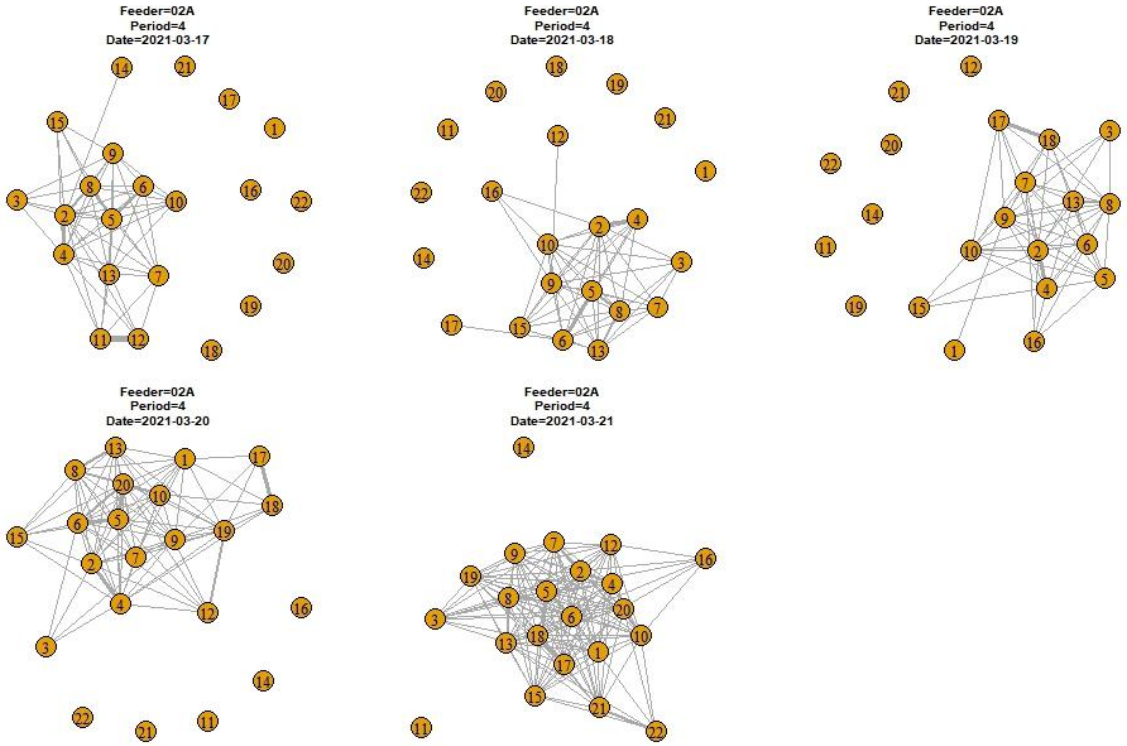

Figure 4.29. Daily social networks at feeder 02A during full period 4.

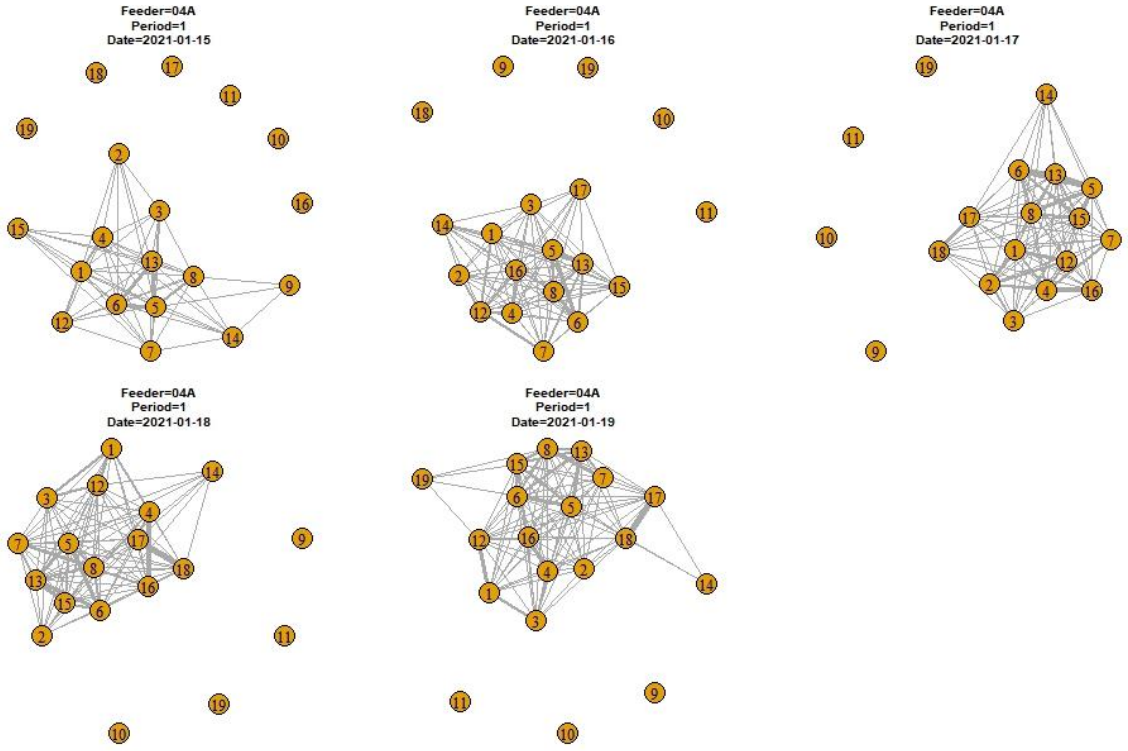

Figure 4.30. Daily social networks at feeder 04A during full period 1.

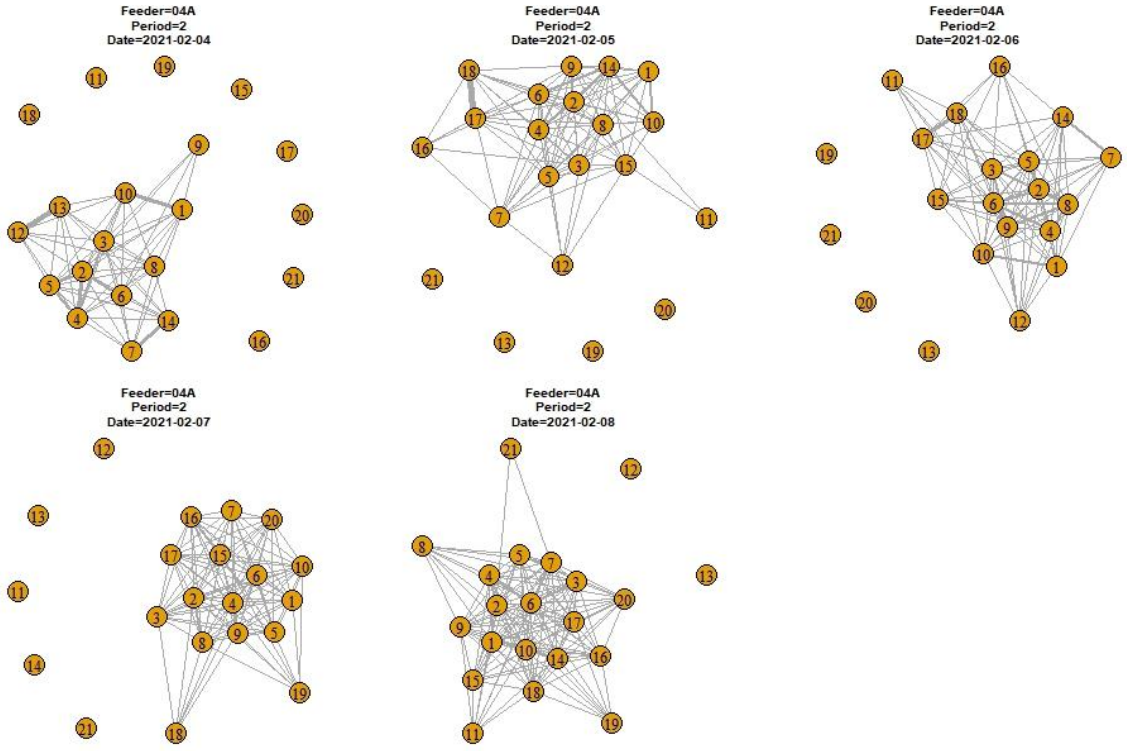

Figure 4.31. Daily social networks at feeder 04A during full period 2.

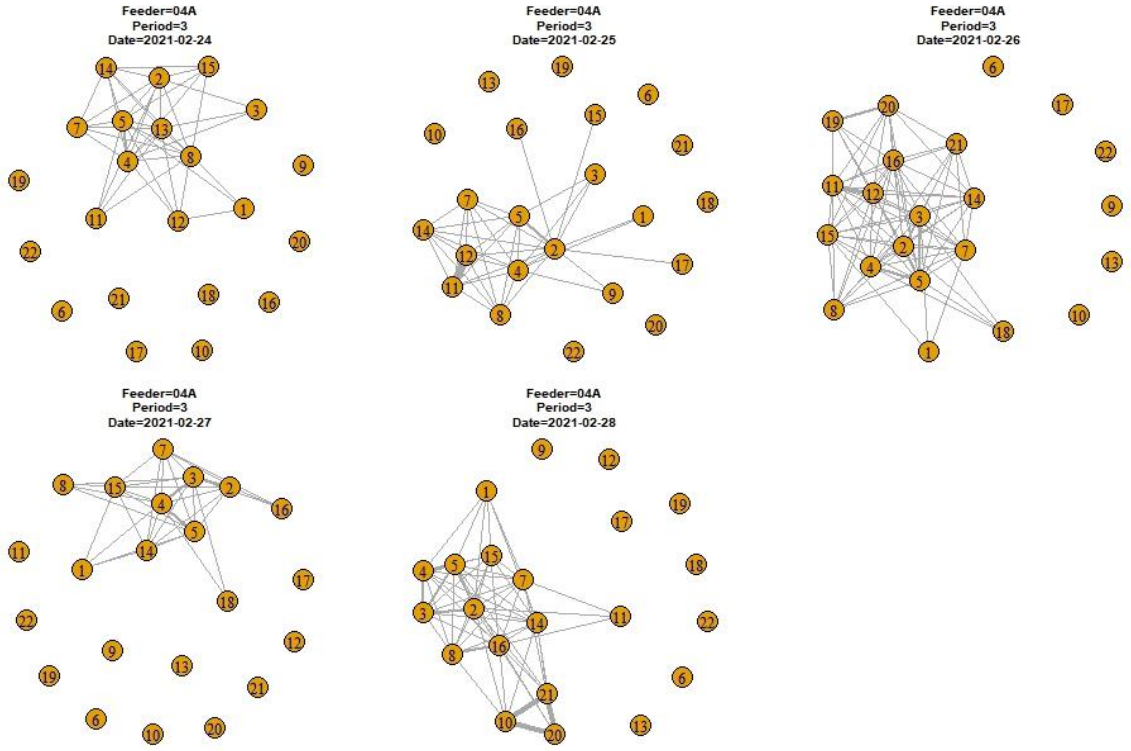

Figure 4.32. Daily social networks at feeder 04A during full period 3.

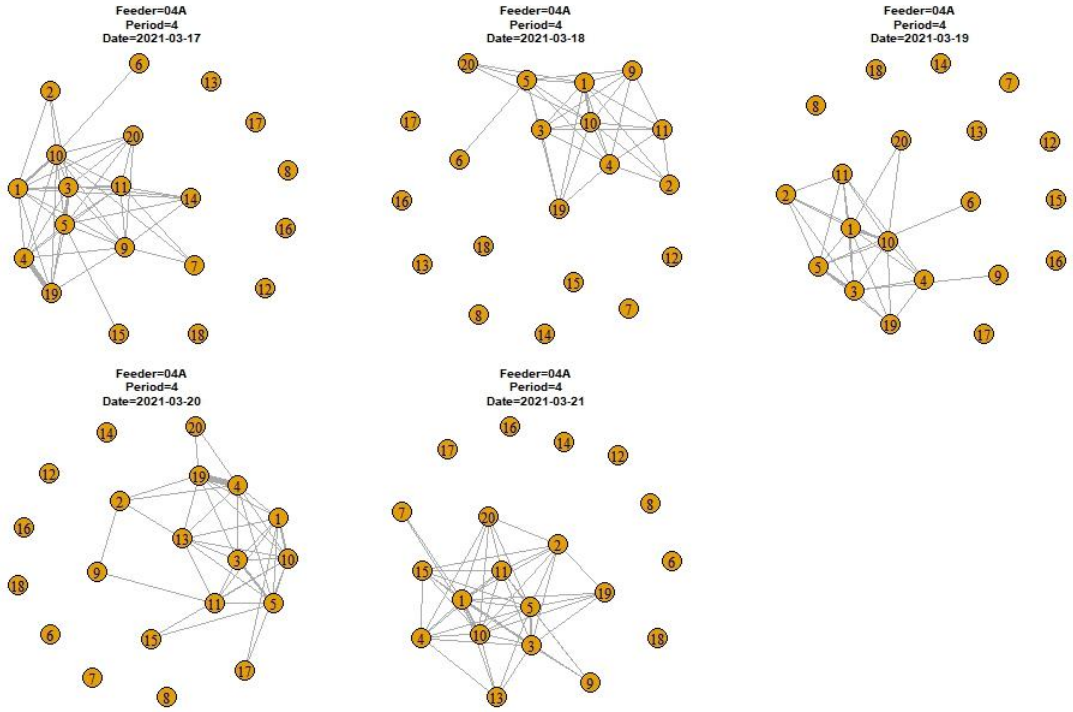

Figure 4.33. Daily social networks at feeder 04A during full period 4.

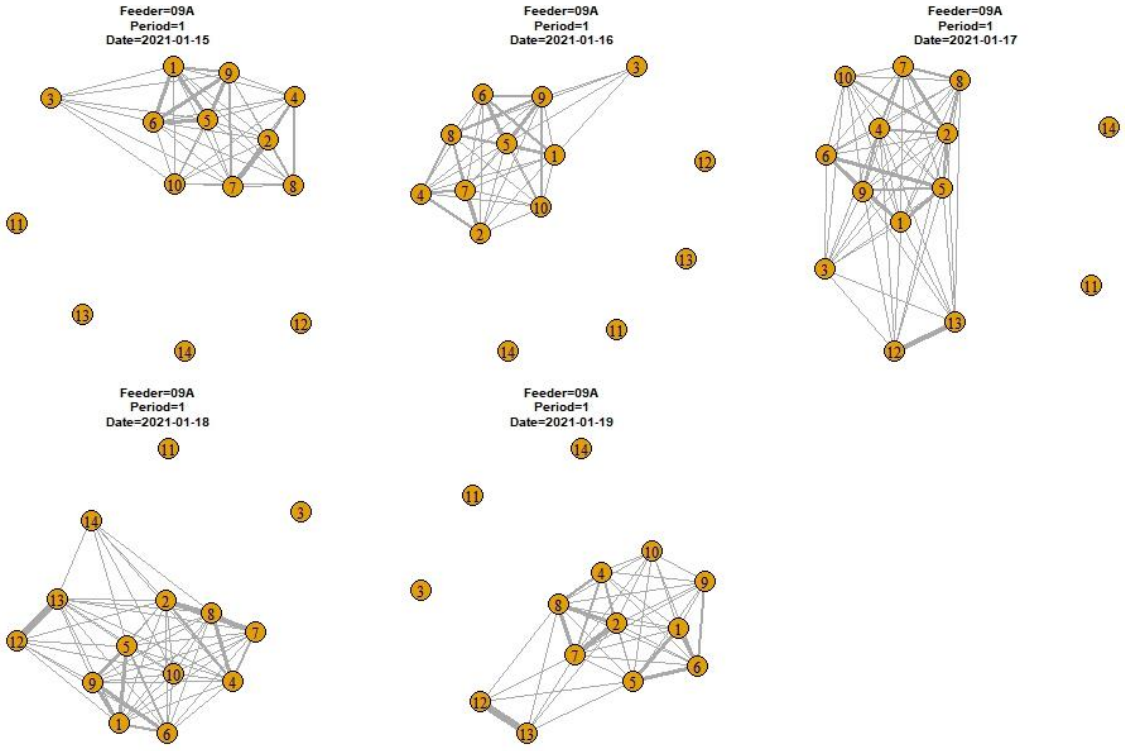

Figure 4.34. Daily social networks at feeder 09A during full period 1.

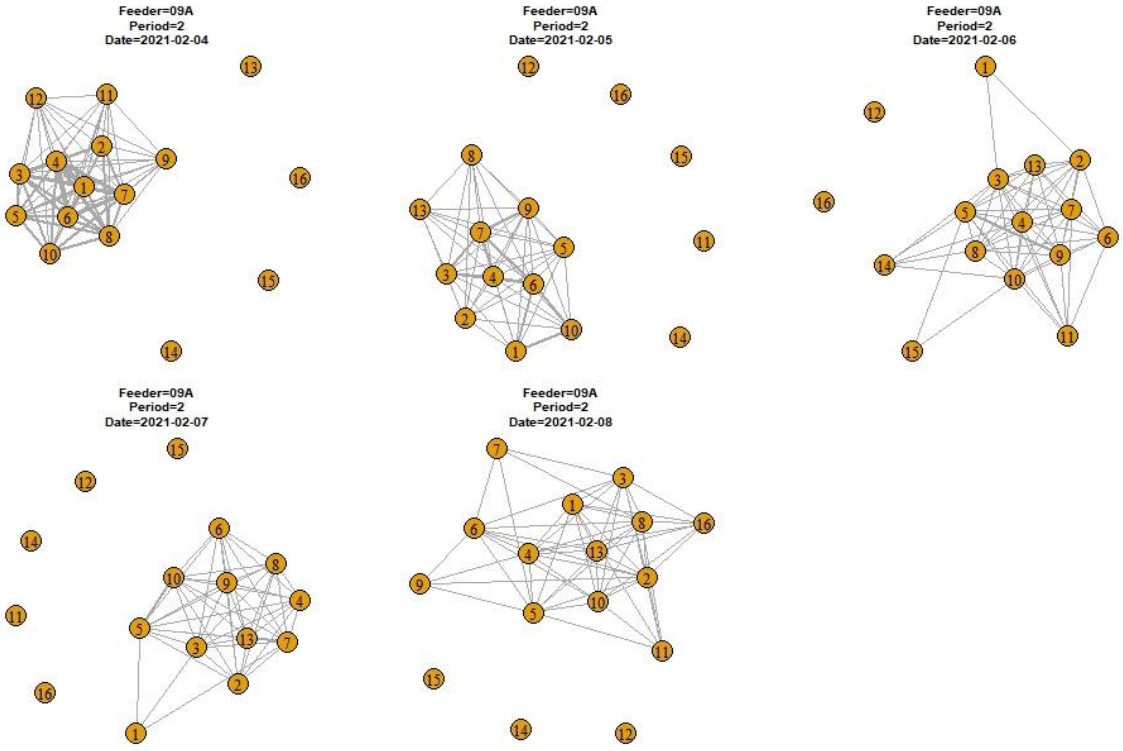

Figure 4.35. Daily social networks at feeder 09A during full period 2.

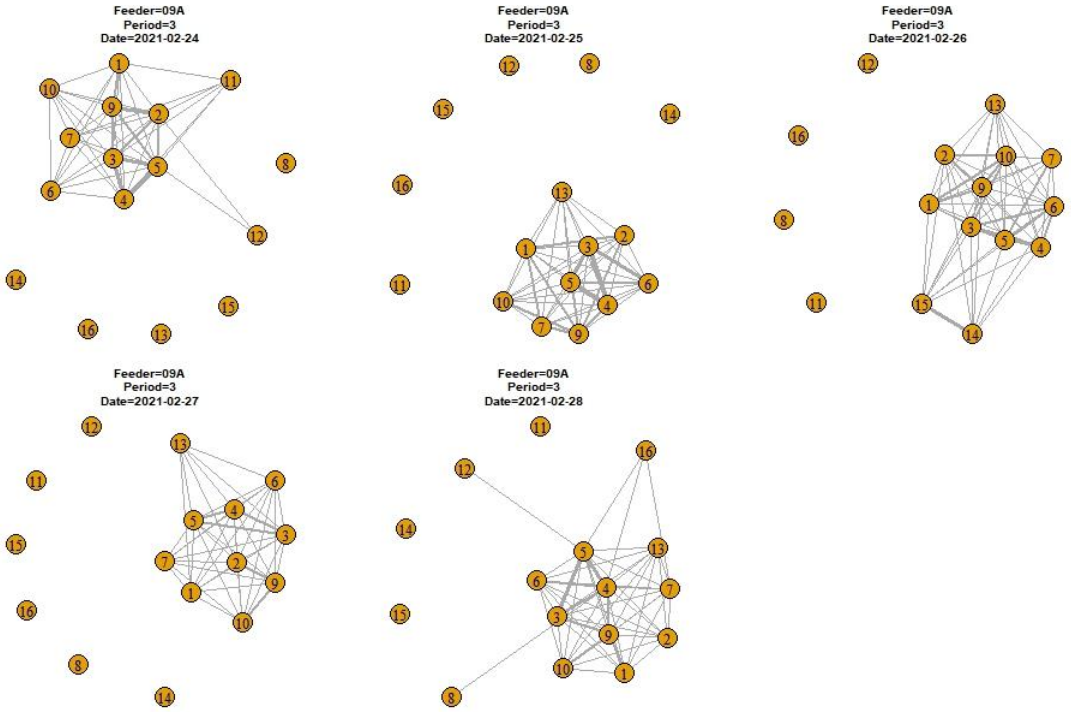

Figure 4.36. Daily social networks at feeder 09A during full period 3.

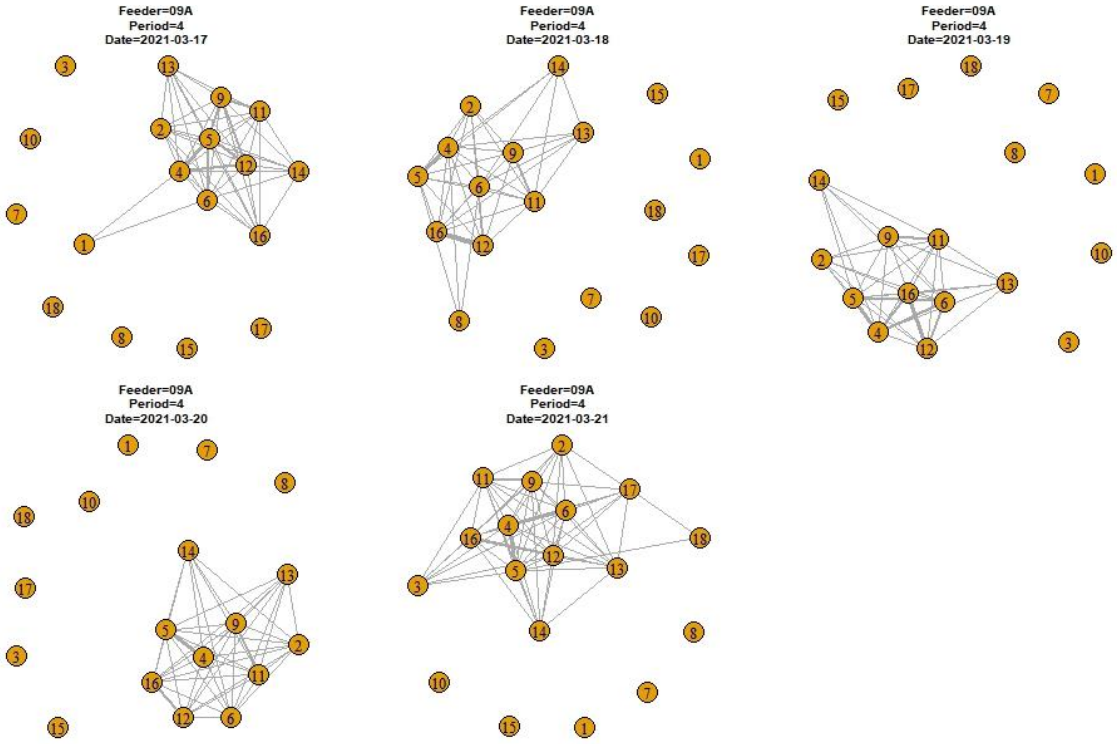

Figure 4.37. Daily social networks at feeder 09A during full period 4.

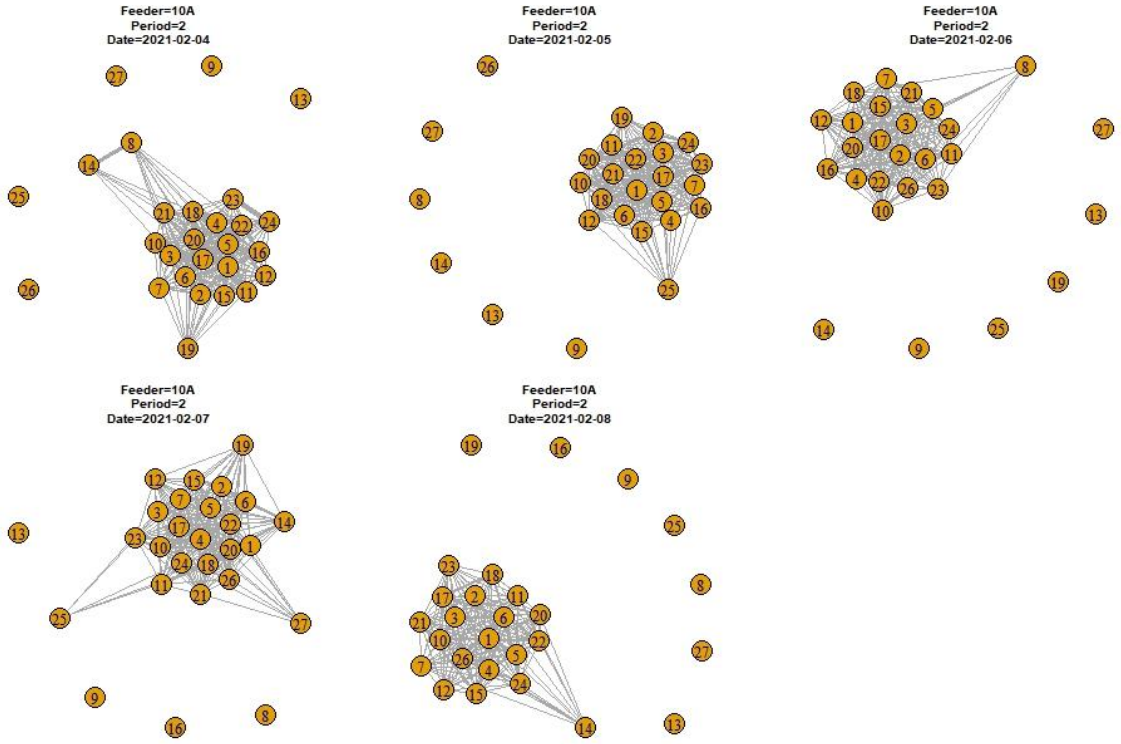

Figure 4.38. Daily social networks at feeder 10A during full period 2.

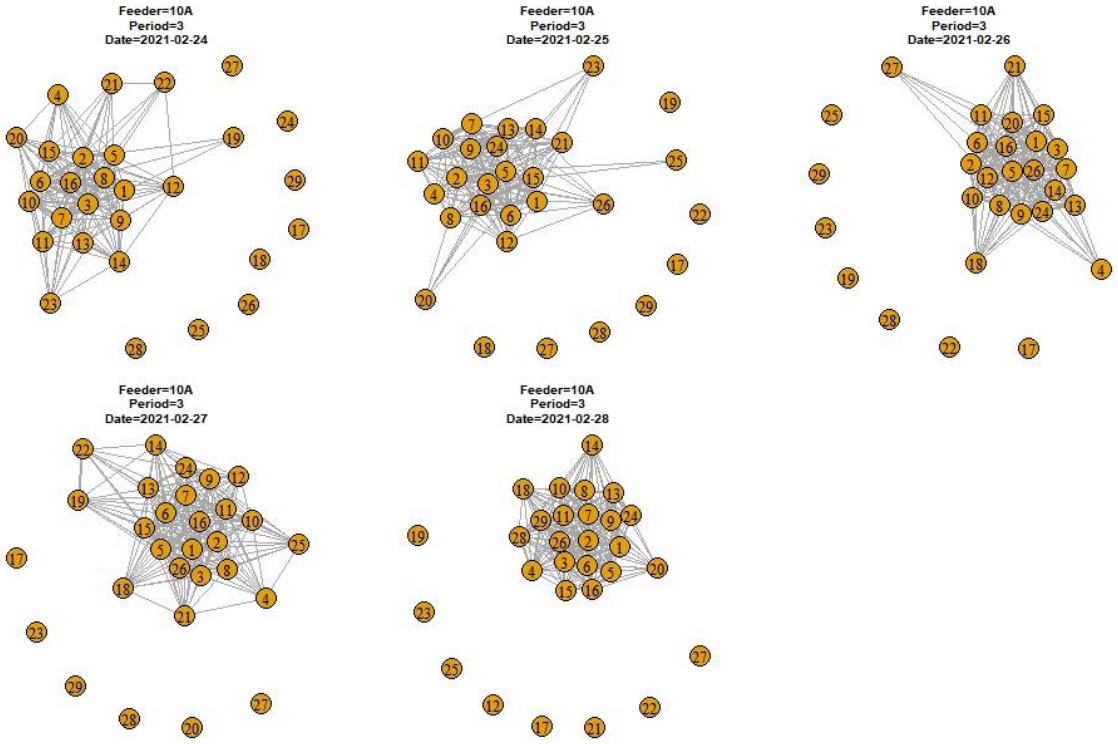

Figure 4.39. Daily social networks at feeder 10A during full period 3.

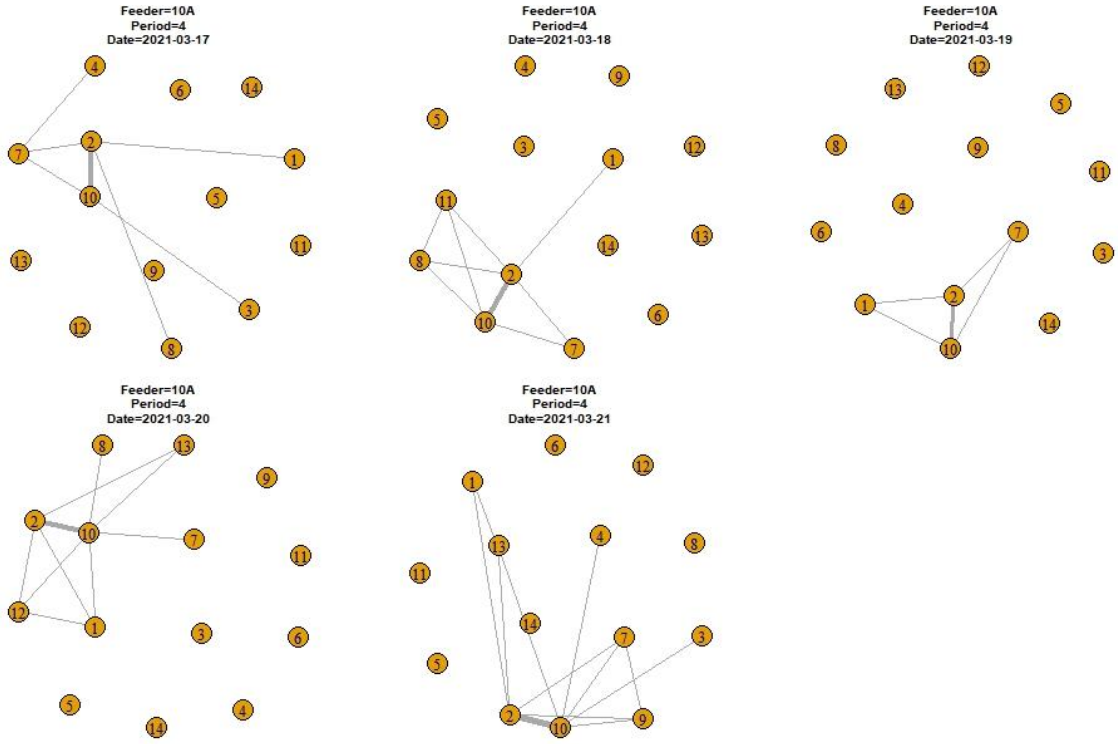

Figure 4.40. Daily social networks at feeder 10A during full period 4.

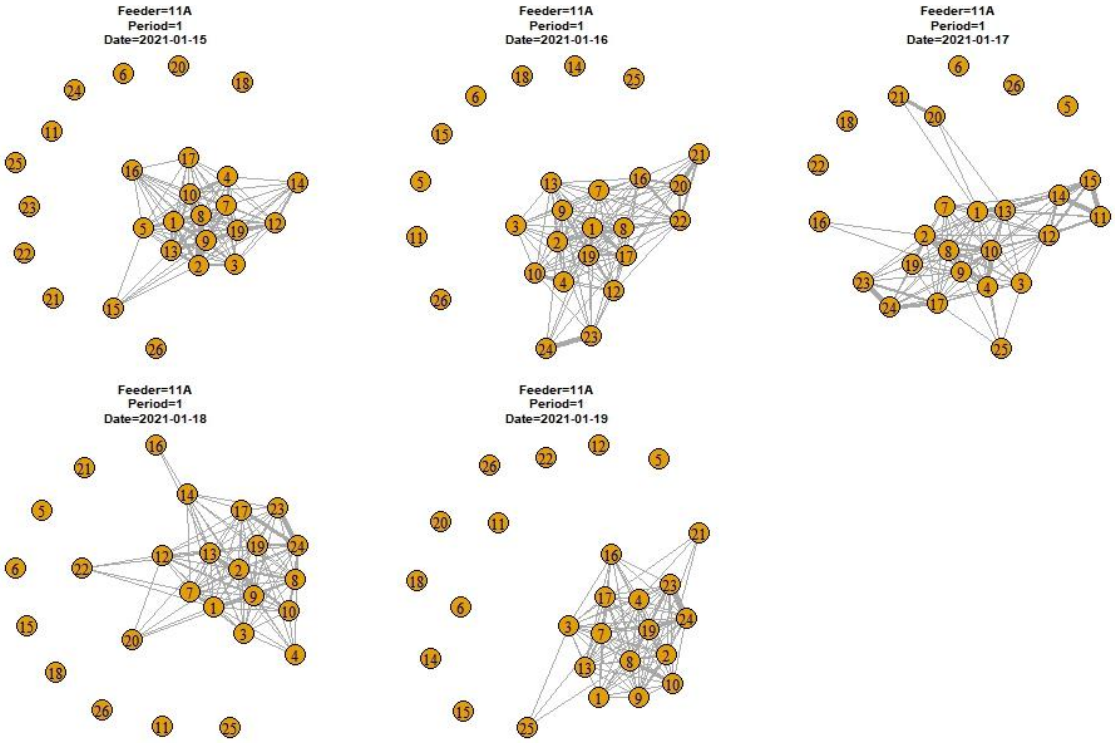

Figure 4.41. Daily social networks at feeder 11A during full period 1.

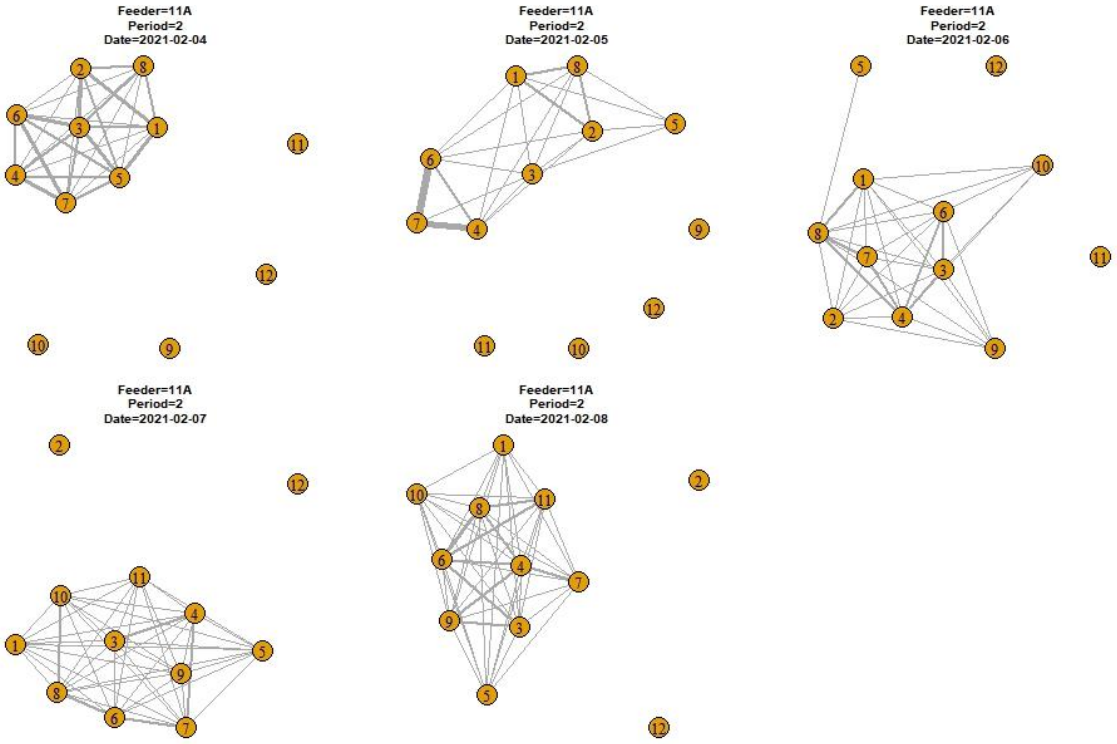

Figure 4.42. Daily social networks at feeder 11A during full period 2.

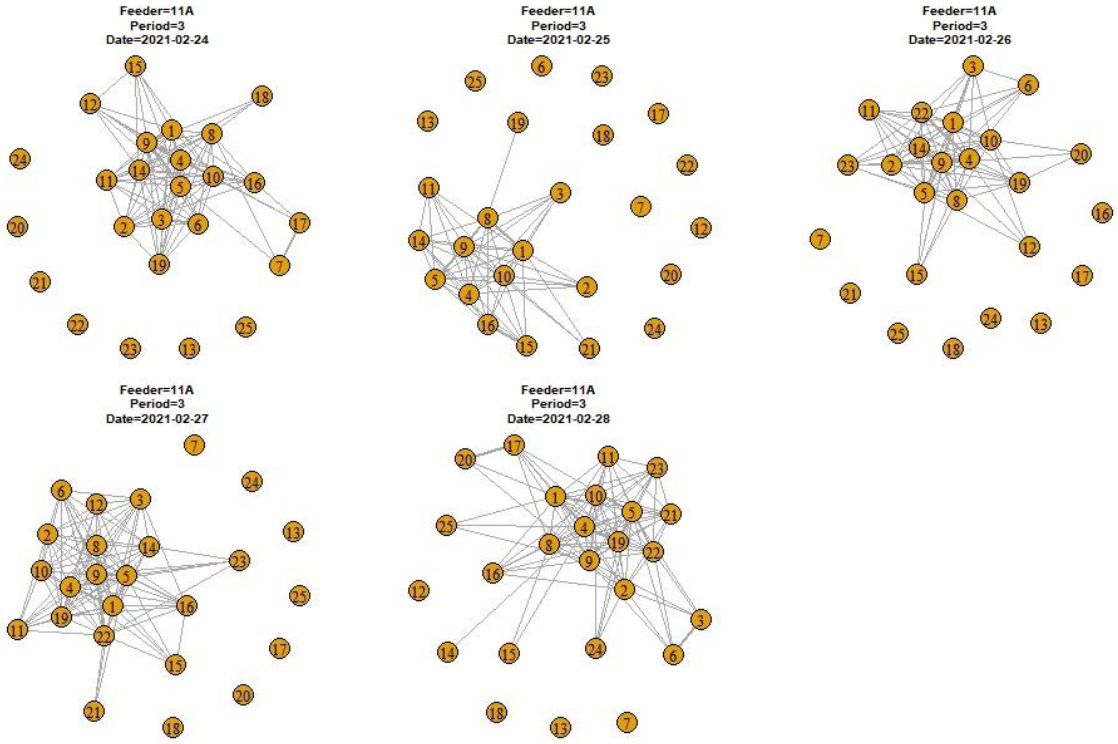

Figure 4.43. Daily social networks at feeder 11A during full period 3.

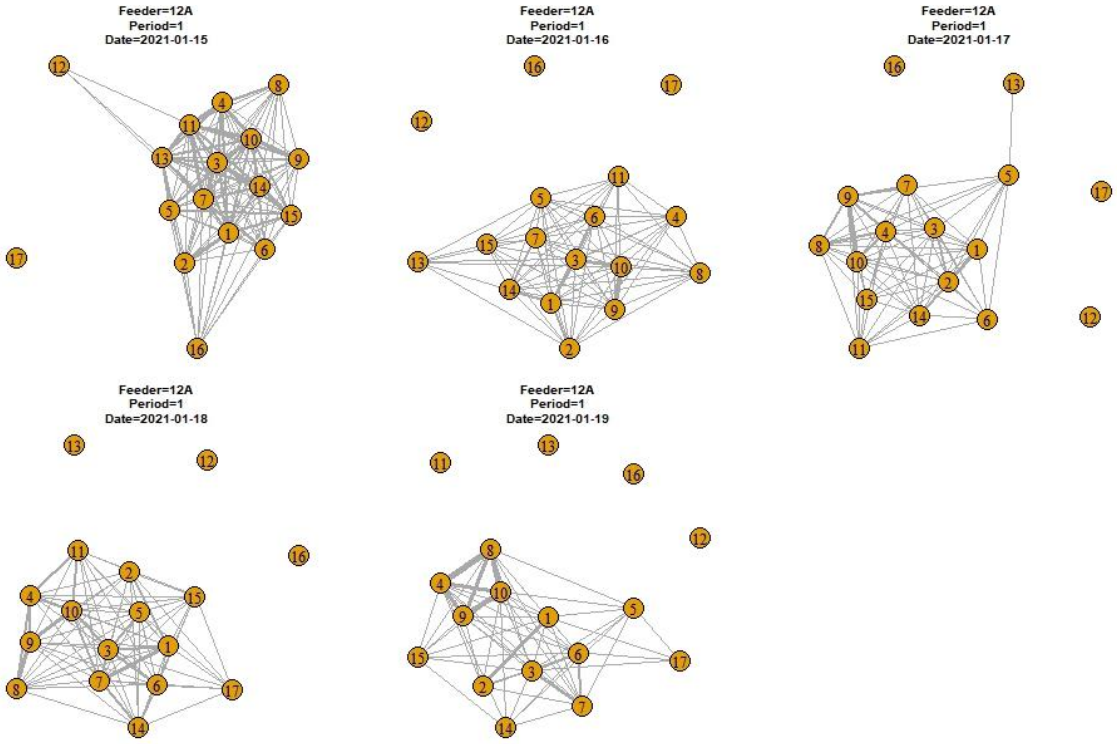

Figure 4.44. Daily social networks at feeder 12A during full period 1.

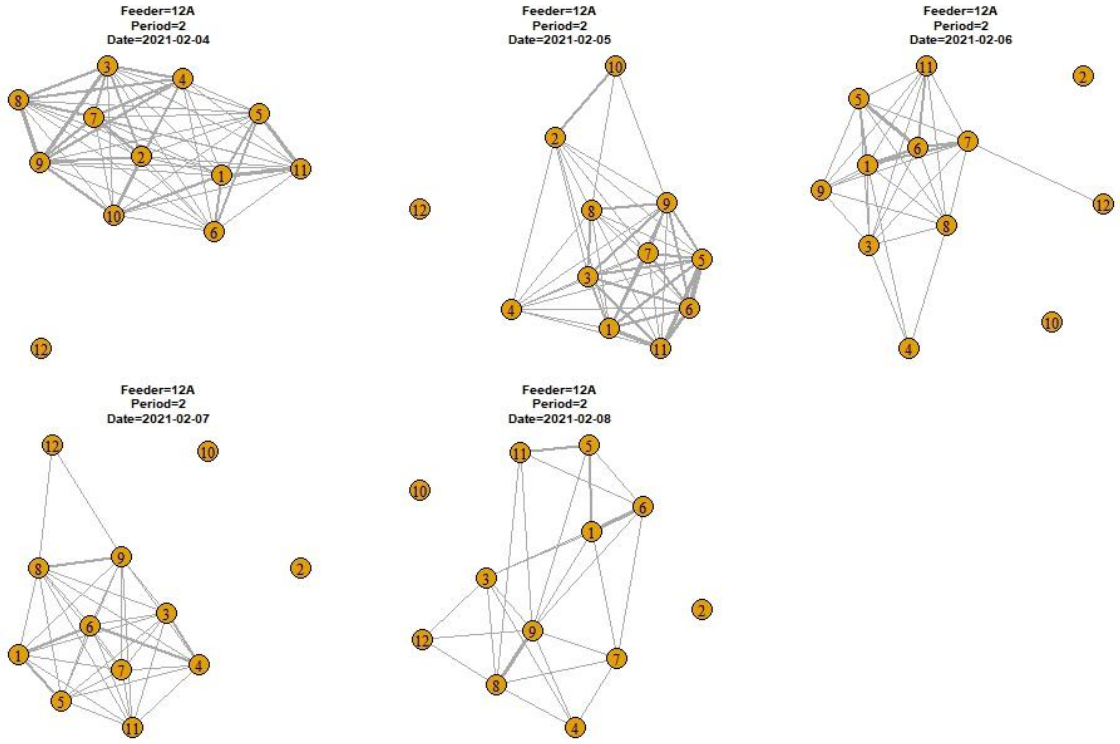

Figure 4.45. Daily social networks at feeder 12A during full period 2.

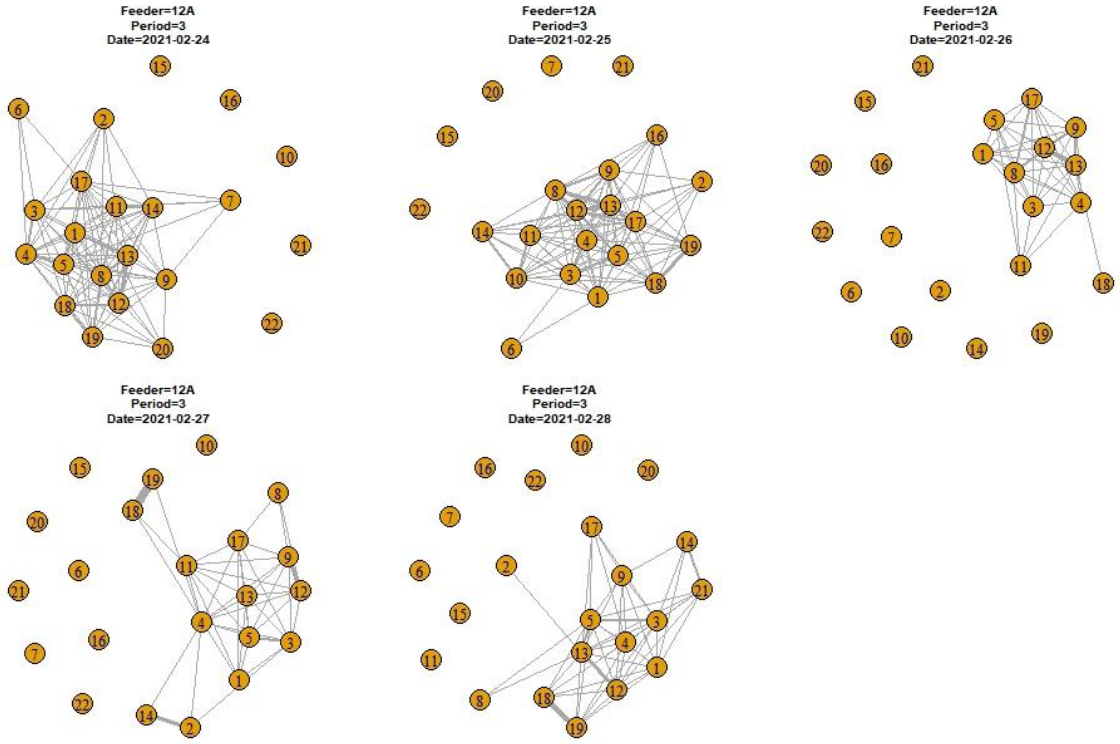

Figure 4.46. Daily social networks at feeder 12A during full period 3.

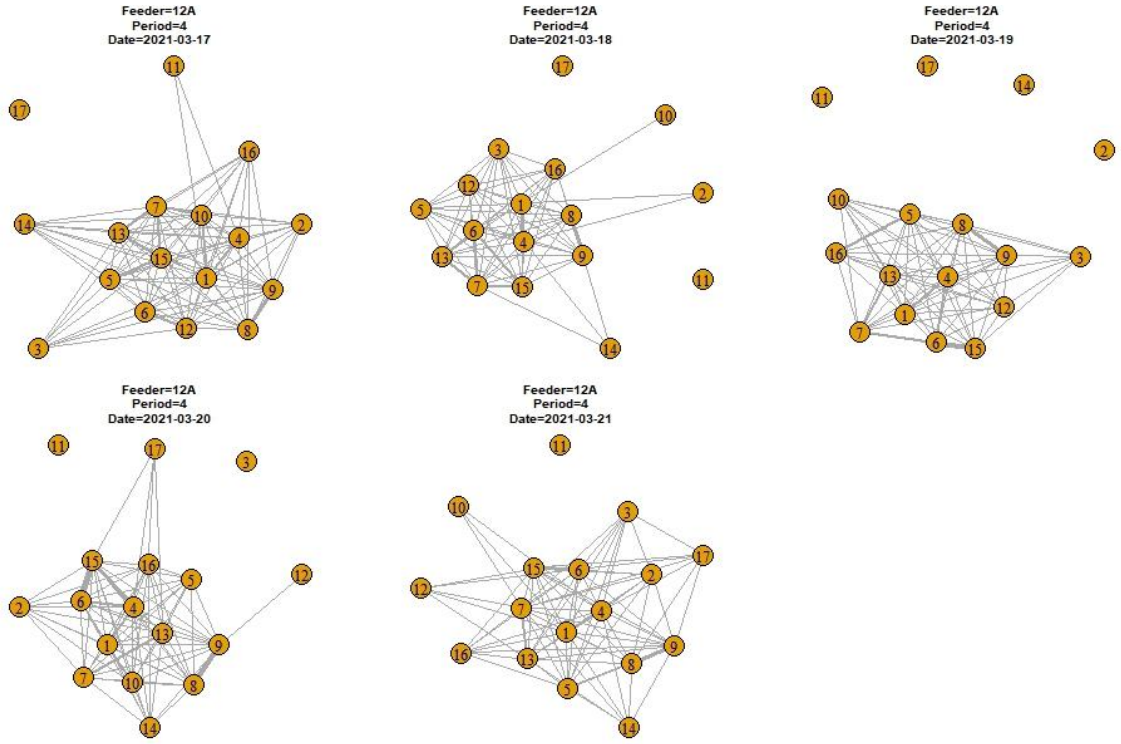

Figure 4.47. Daily social networks at feeder 12A during full period 4.

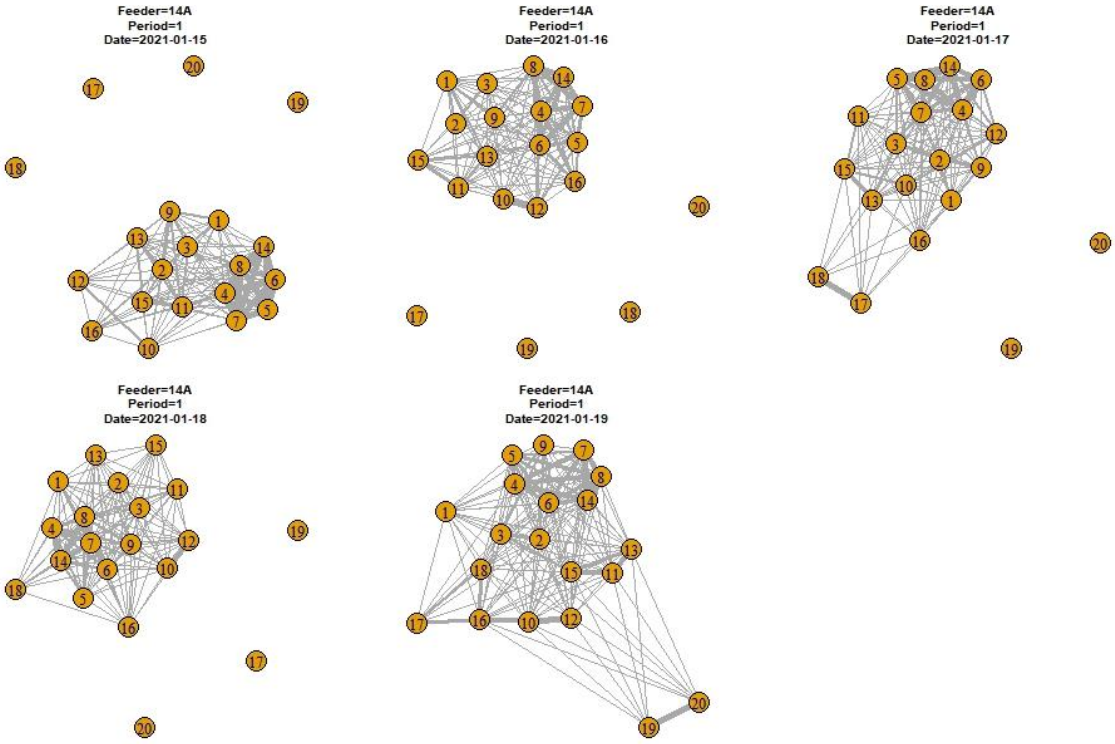

Figure 4.48. Daily social networks at feeder 14A during full period 1.

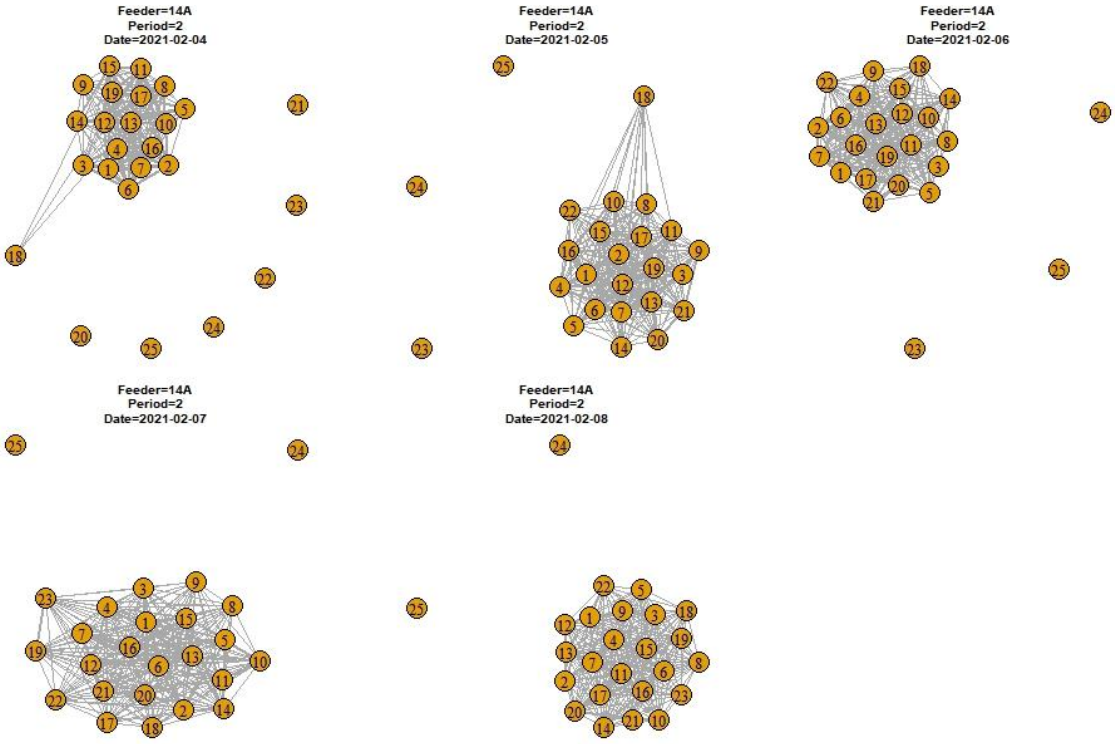

Figure 4.49. Daily social networks at feeder 14A during full period 2.

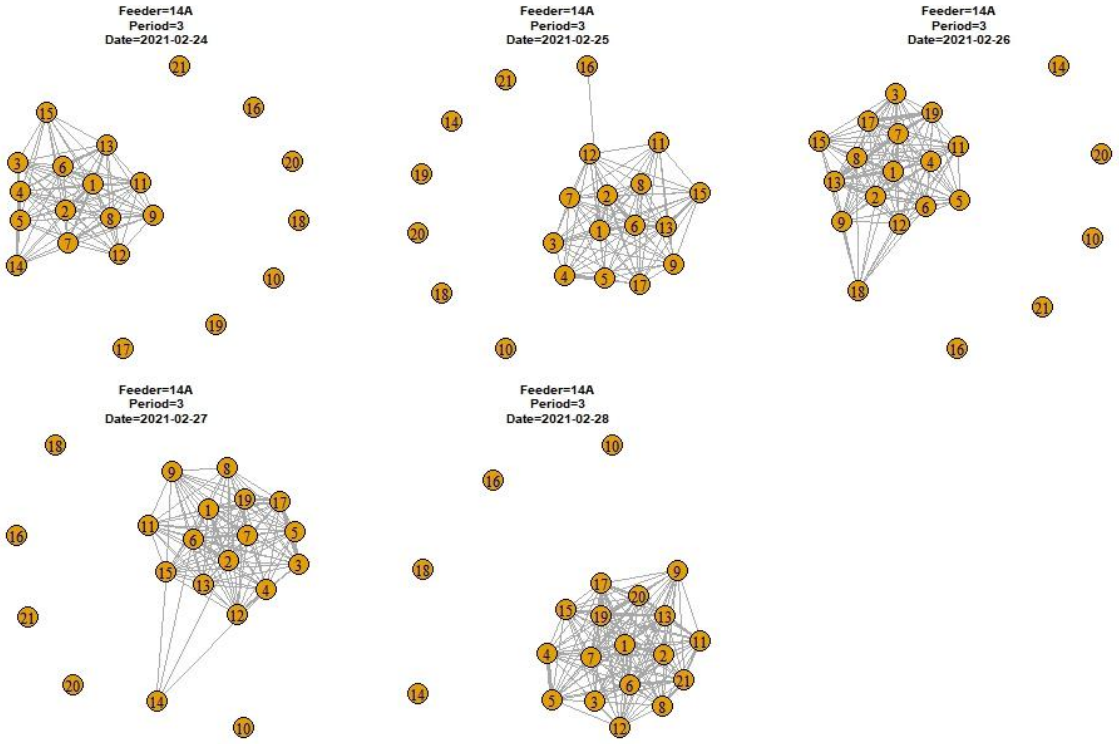

Figure 4.50. Daily social networks at feeder 14A during full period 3.

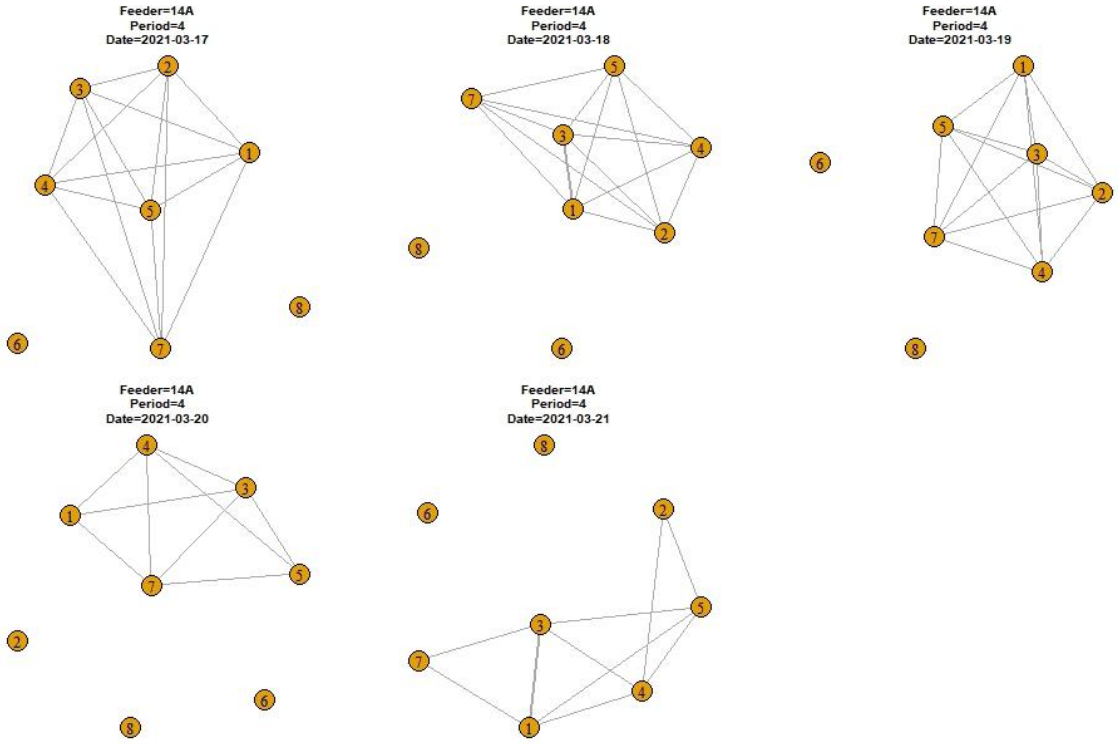

Figure 4.51. Daily social networks at feeder 14A during full period 4.

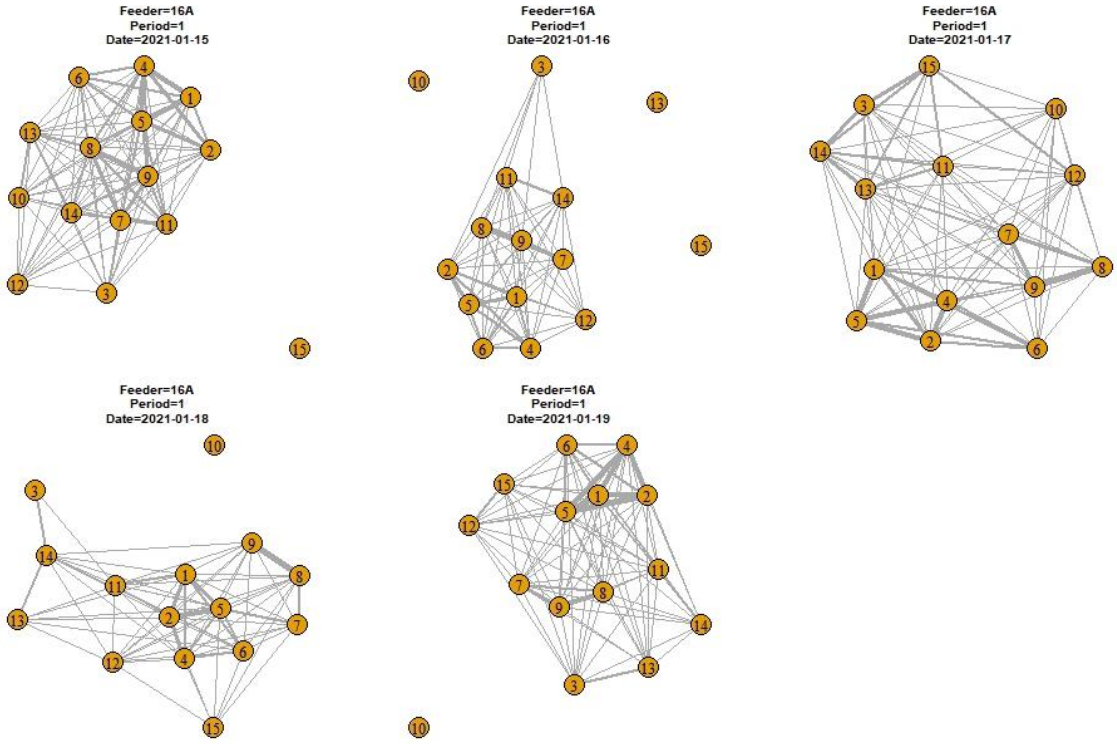

Figure 4.52. Daily social networks at feeder 16A during full period 1.

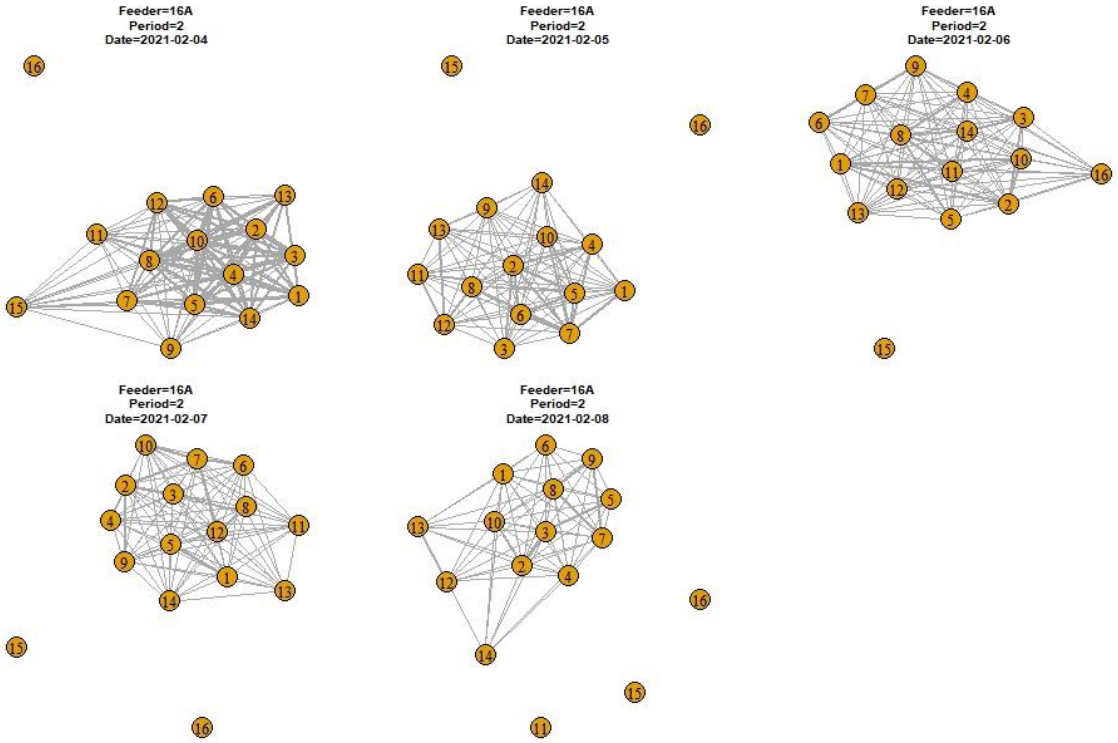

Figure 4.53. Daily social networks at feeder 16A during full period 2.

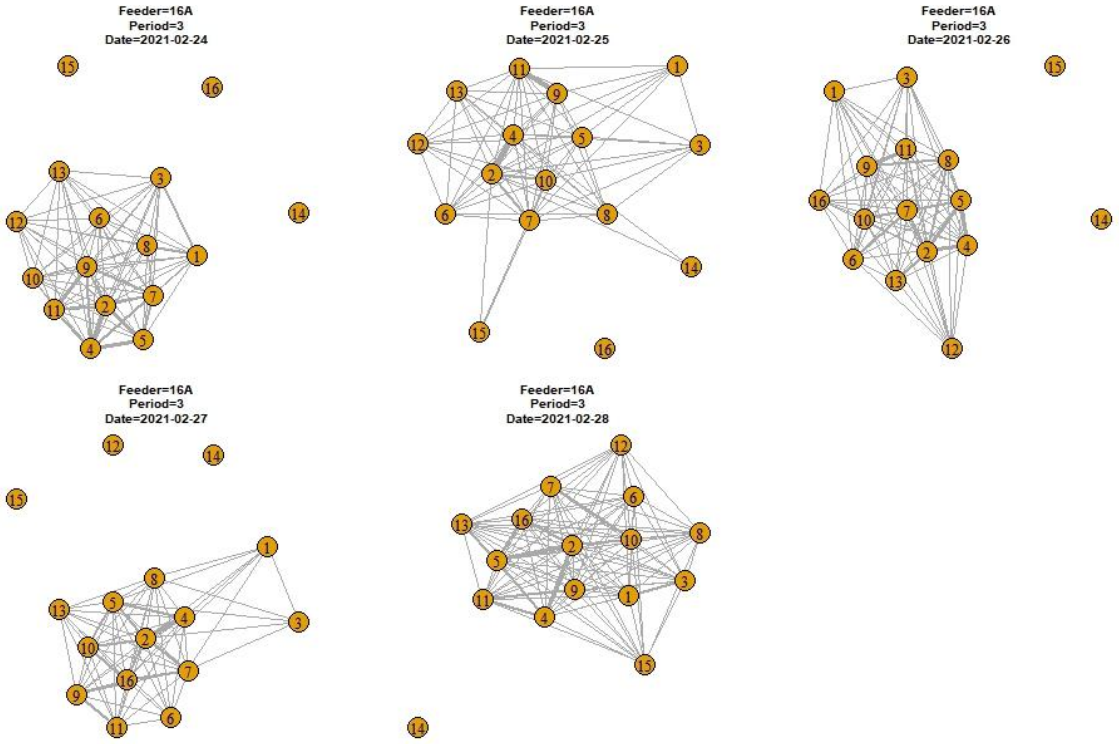

Figure 4.54. Daily social networks at feeder 16A during full period 3.

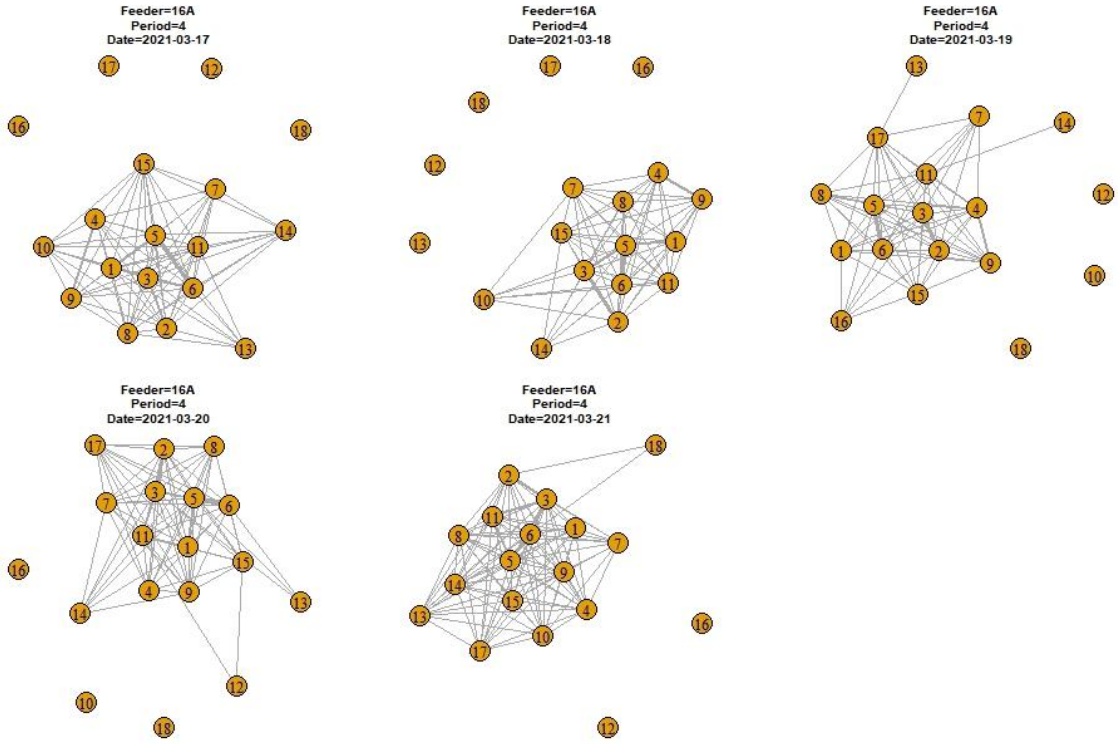

Figure 4.55. Daily social networks at feeder 16A during full period 4.

Table 4.14. Summary of estimated centralities for each feeder within each period. For each feeder – period combination the group size is given as well as the mean and range of the centrality measures.

Feeder	*Period*	*Group Size*	*Mean Degree [Min-Max]*	*Mean Strength [Min-Max]*	*Mean Betweenness [Min-Max]*	*Mean Eigenvector [Min-Max]*	*Mean Harmonic [Min-Max]*
02A	1	33	15.89 [0 - 31]	1.57 [0 - 3.88]	11.75 [0 - 69]	0.47 [0 - 1]	471.97 [0 - 859.63]
02A	2	29	18.04 [0 - 25]	2.14 [0 - 3.98]	10.35 [0 - 143]	0.63 [0 - 1]	341.54 [0 - 819.44]
02A	3	36	13.13 [0 - 28]	1.14 [0 - 3.04]	8.83 [0 - 77]	0.4 [0 - 1]	446.12 [0 - 1050.1]
02A	4	22	7.55 [0 - 19]	0.64 [0 - 2.06]	5.79 [0 - 39]	0.39 [0 - 1]	270.73 [0 - 678.33]
04A	1	19	9.07 [0 - 14]	1.1 [0 - 2.45]	4.62 [0 - 39]	0.5 [0 - 1]	213.91 [0 - 525.37]
04A	2	21	9.39 [0 - 18]	0.95 [0 - 1.97]	6.1 [0 - 40]	0.49 [0 - 1]	269.27 [0 - 589.08]
04A	3	22	4.65 [0 - 14]	0.4 [0 - 1.38]	3.83 [0 - 45]	0.31 [0 - 1]	194.71 [0 - 630.43]
04A	4	20	3.84 [0 - 12]	0.29 [0 - 1.01]	3.93 [0 - 31]	0.31 [0 - 1]	182.76 [0 - 601.93]
09A	1	14	6.94 [0 - 11]	1.09 [0 - 2.02]	2.91 [0 - 22]	0.59 [0 - 1]	121.6 [0 - 314.42]
09A	2	16	7.05 [0 - 12]	0.88 [0 - 2.97]	3.46 [0 - 32]	0.53 [0 - 1]	130.9 [0 - 337.12]
09A	3	16	6.03 [0 - 11]	0.82 [0 - 1.98]	2.86 [0 - 25]	0.48 [0 - 1]	122.8 [0 - 386.73]
09A	4	18	5.11 [0 - 12]	0.54 [0 - 1.55]	2.87 [0 - 32]	0.4 [0 - 1]	167.97 [0 - 607.1]
10A	2	27	14.92 [0 - 22]	2.06 [0 - 4.09]	7.64 [0 - 146]	0.6 [0 - 1]	247.15 [0 - 690.04]
10A	3	29	12.92 [0 - 22]	1.49 [0 - 3.48]	8.86 [0 - 100]	0.48 [0 - 1]	378.54 [0 - 917.61]

10A	4	14	1.23 [0 - 6]	0.09 [0 - 0.58]	1.1 [0 - 12]	0.16 [0 - 1]	176.36 [0 - 1003.2]
11A	1	26	8.12 [0 - 19]	0.91 [0 - 2.61]	6.18 [0 - 95]	0.4 [0 - 1]	245.31 [0 - 624.95]
11A	2	12	5.77 [0 - 9]	0.9 [0 - 1.95]	1.78 [0 - 18]	0.56 [0 - 1]	97.51 [0 - 399.5]
11A	3	25	7.02 [0 - 17]	0.6 [0 - 1.77]	7.13 [0 - 55]	0.36 [0 - 1]	332.23 [0 - 787.31]
12A	1	17	9.44 [0 - 15]	1.25 [0 - 3.31]	4.78 [0 - 65]	0.54 [0 - 1]	187.69 [0 - 416.07]
12A	2	12	6.57 [0 - 10]	0.97 [0 - 2.04]	2.97 [0 - 21]	0.62 [0 - 1]	117.66 [0 - 275.72]
12A	3	22	6.07 [0 - 16]	0.62 [0 - 2.19]	4.47 [0 - 46]	0.37 [0 - 1]	206.23 [0 - 626.08]
12A	4	17	9.39 [0 - 15]	0.98 [0 - 2.04]	6.36 [0 - 40]	0.57 [0 - 1]	263.46 [0 - 549.97]
14A	1	20	13.06 [0 - 19]	1.99 [0 - 3.78]	6.41 [0 - 52]	0.5 [0 - 1]	235.99 [0 - 479.93]
14A	2	25	17.84 [0 - 22]	2.63 [0 - 4.4]	4.67 [0 - 128]	0.69 [0 - 1]	188.64 [0 - 754.6]
14A	3	21	10.13 [0 - 16]	1.24 [0 - 2.79]	3.81 [0 - 64]	0.55 [0 - 1]	145.97 [0 - 430.51]
14A	4	8	3.2 [0 - 5]	0.28 [0 - 0.73]	1 [0 - 9]	0.53 [0 - 1]	74.31 [0 - 241.25]
16A	1	15	10.53 [0 - 14]	1.59 [0 - 2.94]	5.07 [0 - 47]	0.6 [0 - 1]	178.08 [0 - 313.17]
16A	2	16	11.47 [0 - 14]	1.71 [0 - 3.85]	3.65 [0 - 71]	0.68 [0 - 1]	145.42 [0 - 386.47]
16A	3	16	10.15 [0 - 14]	1.24 [0 - 2.75]	5.03 [0 - 49]	0.55 [0 - 1]	264.51 [0 - 766.9]
16A	4	18	8.84 [0 - 15]	0.82 [0 - 2.07]	5.17 [0 - 46]	0.47 [0 - 1]	272.07 [0 - 664.63]

The figures below (4.35-4.42) show the individual variation in centrality measures within each feeder across periods. All centrality measures have been standardized within feeder and period to improve visual comparisons between periods within a feeder. Standardization was done by dividing the estimated individual centrality measures with the group size within a given feeder and period.

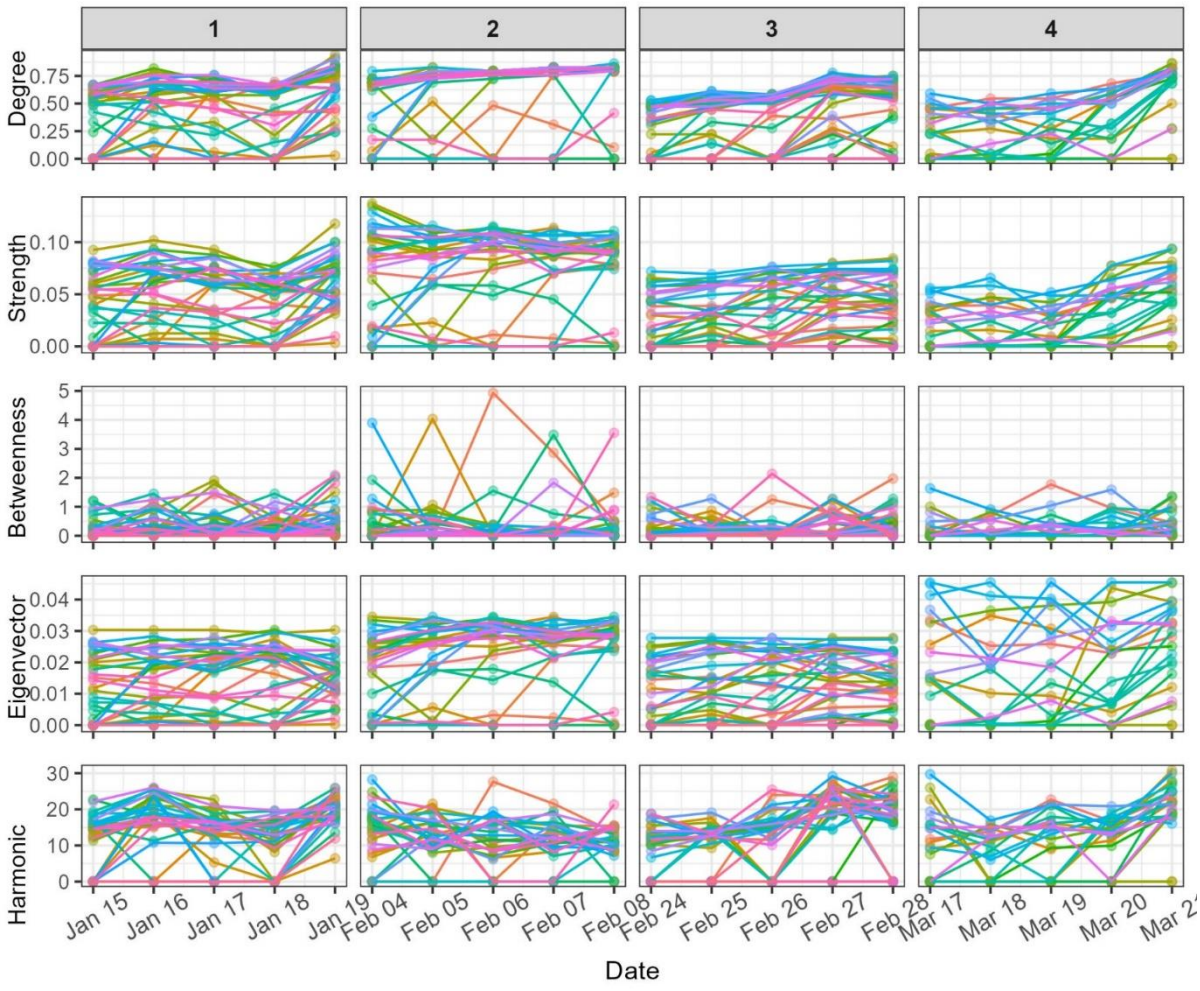

Figure 4.56. The variation in individual centrality measure over time at feeder 02A. All centrality estimates have been standardised between periods by dividing the estimates

with the group size within periods. Each row corresponds to a centrality measure and each column is a full period, denoted by the number at the top. Each colored line is an individual within a period. Colors do not represent the same individual between periods. The x-axis indicates the dates.

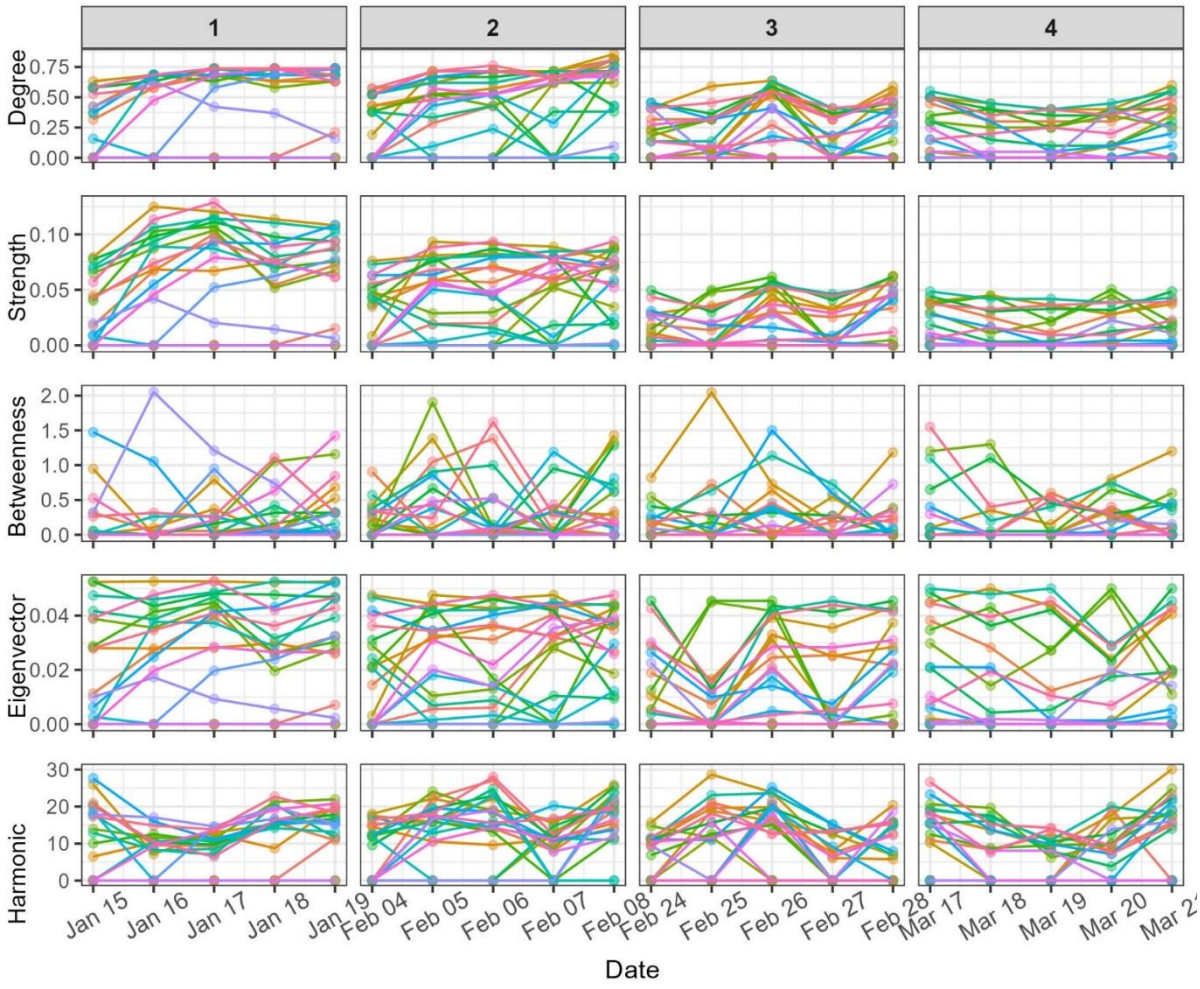

Figure 4.57. The variation in individual centrality measure over time at feeder 04A. All centrality estimates have been standardised between periods by dividing the estimates with the group size within periods. Each row corresponds to a centrality measure and

each column is a full period, denoted by the number at the top. Each colored line is an individual within a period. Colors do not represent the same individual between periods. The x-axis indicates the dates.

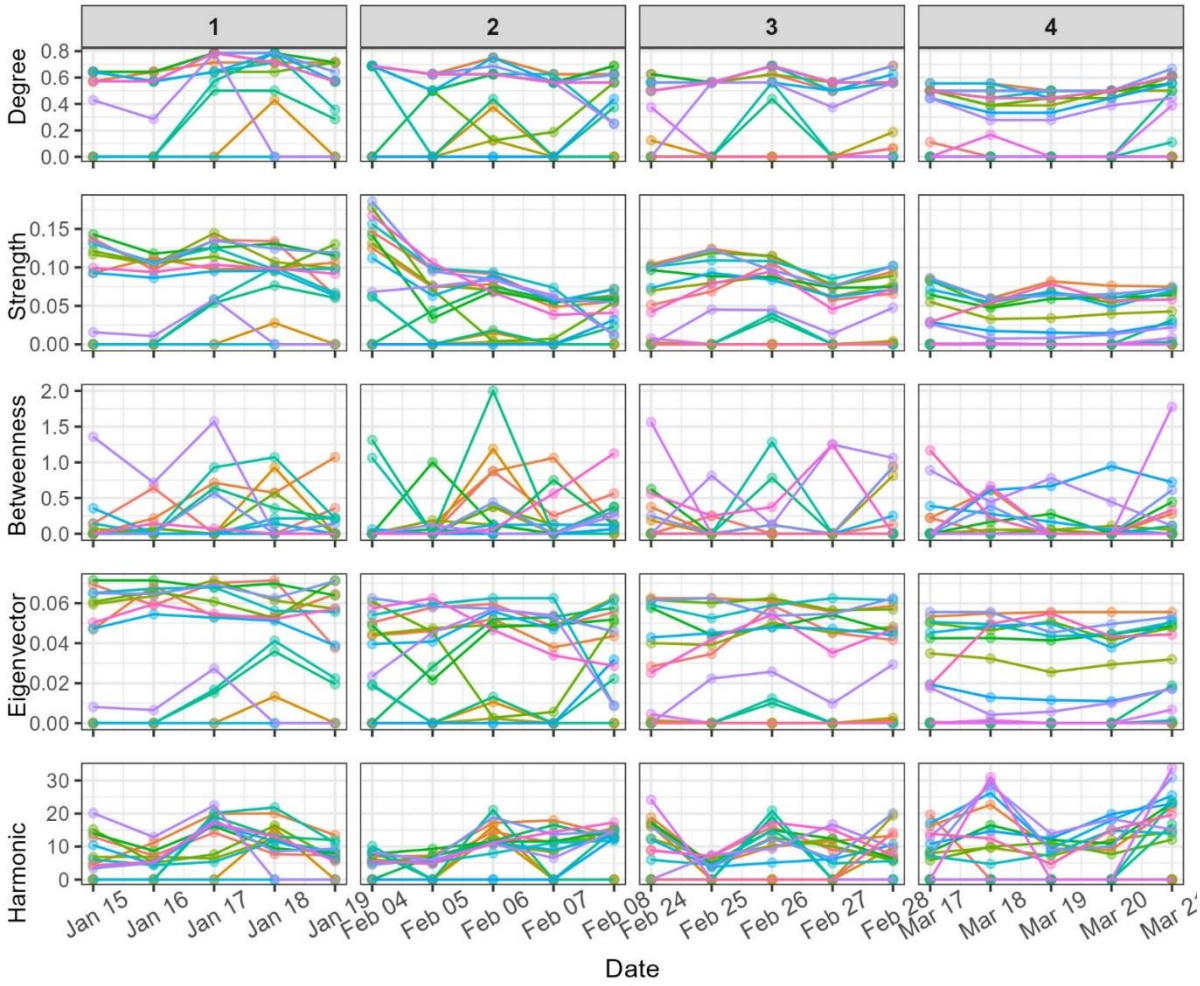

Figure 4.58. The variation in individual centrality measure over time at feeder 09A. All centrality estimates have been standardised between periods by dividing the estimates with the group size within periods. Each row corresponds to a centrality measure and each column is a full period, denoted by the number at the top. Each colored line is an

individual within a period. Colors do not represent the same individual between periods. The x-axis indicates the dates.

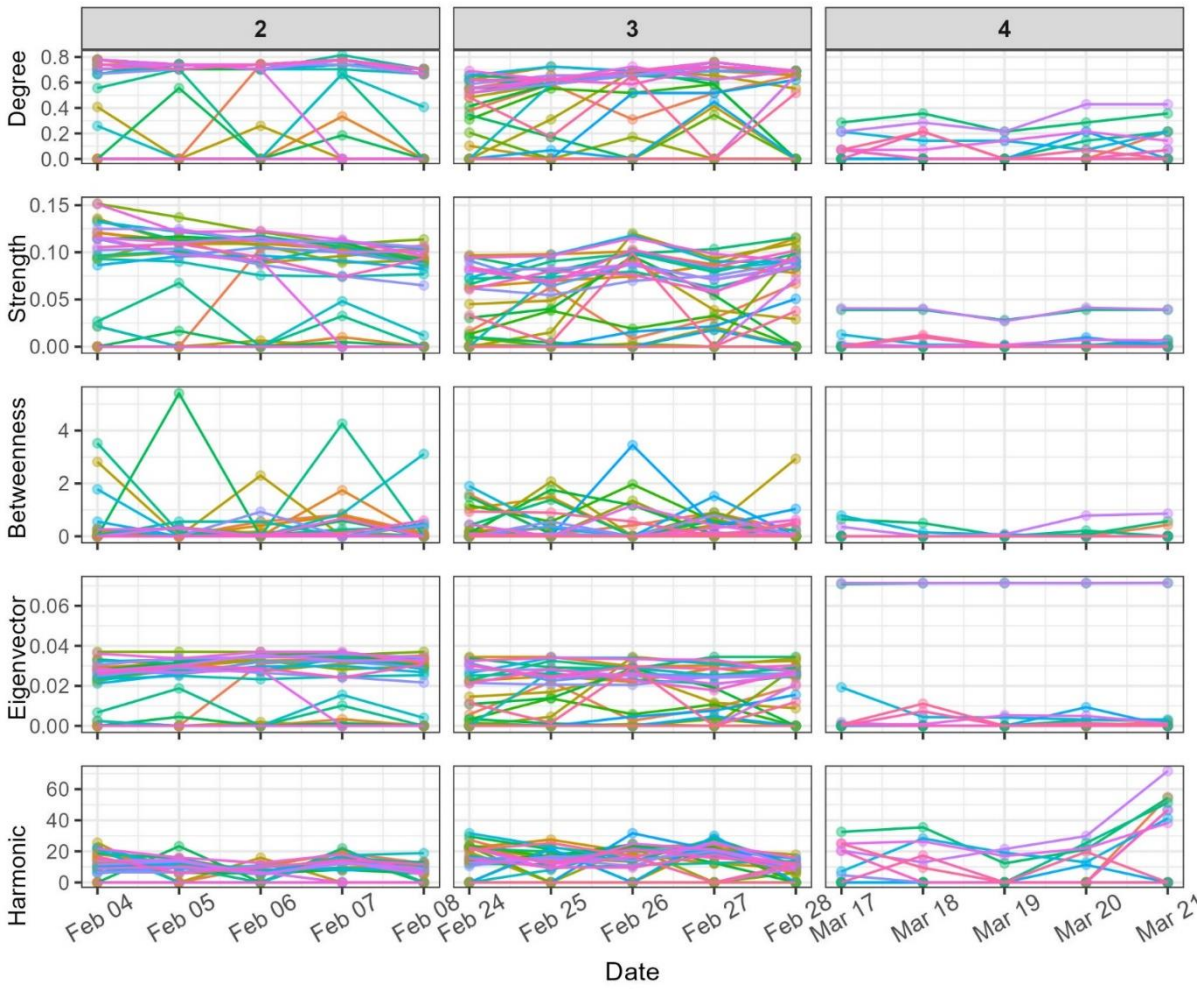

Figure 4.59. The variation in individual centrality measure over time at feeder 10A. All centrality estimates have been standardised between periods by dividing the estimates with the group size within periods. Each row corresponds to a centrality measure and each column is a full period, denoted by the number at the top. Each colored line is an

individual within a period. Colors do not represent the same individual between periods. The x-axis indicates the dates.

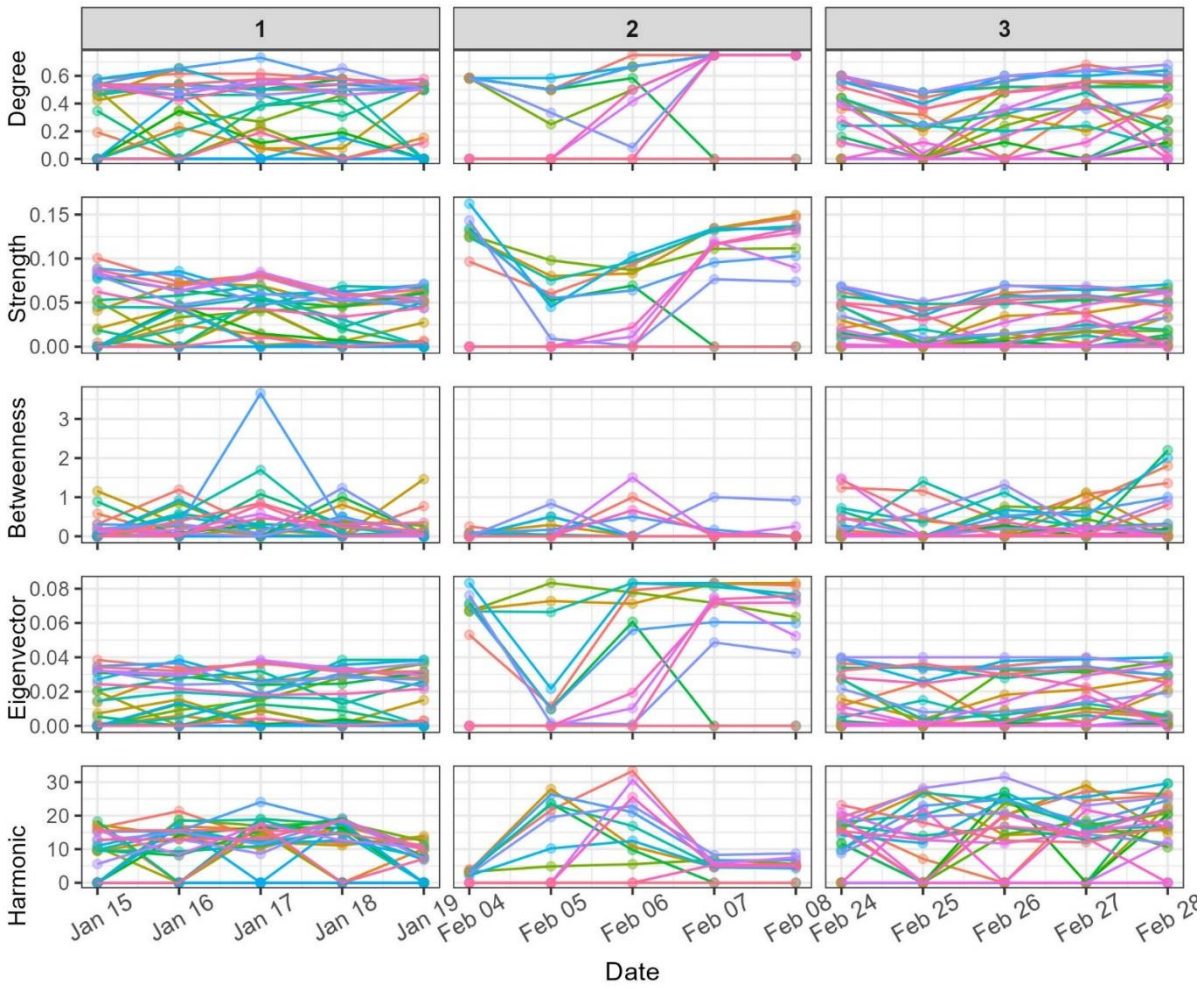

Figure 4.60. The variation in individual centrality measure over time at feeder 11A. All centrality estimates have been standardised between periods by dividing the estimates with the group size within periods. Each row corresponds to a centrality measure and each column is a full period, denoted by the number at the top. Each colored line is an

individual within a period. Colors do not represent the same individual between periods. The x-axis indicates the dates.

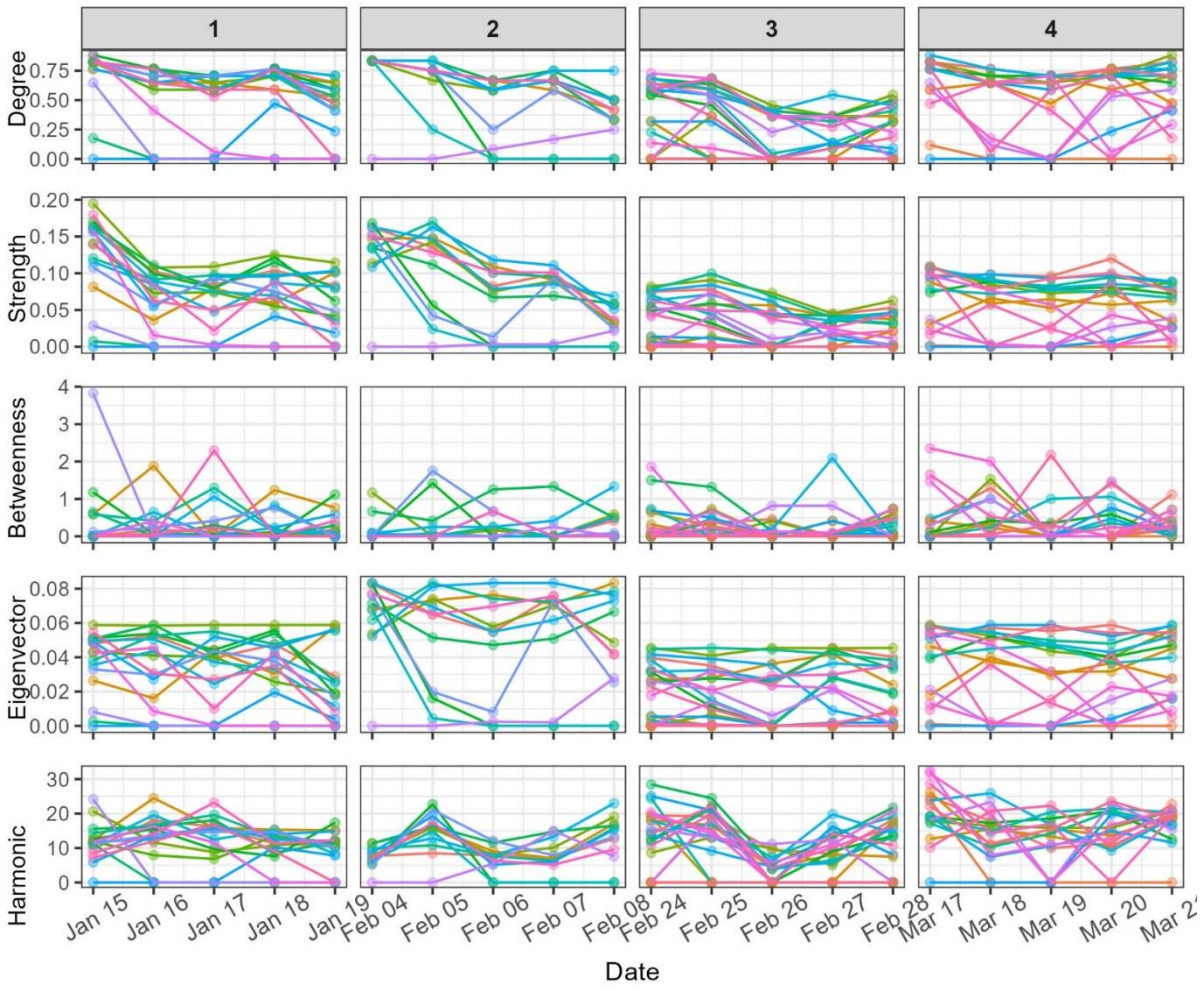

Figure 4.61. The variation in individual centrality measure over time at feeder 12A. All centrality estimates have been standardised between periods by dividing the estimates with the group size within periods. Each row corresponds to a centrality measure and each column is a full period, denoted by the number at the top. Each colored line is an

individual within a period. Colors do not represent the same individual between periods. The x-axis indicates the dates.

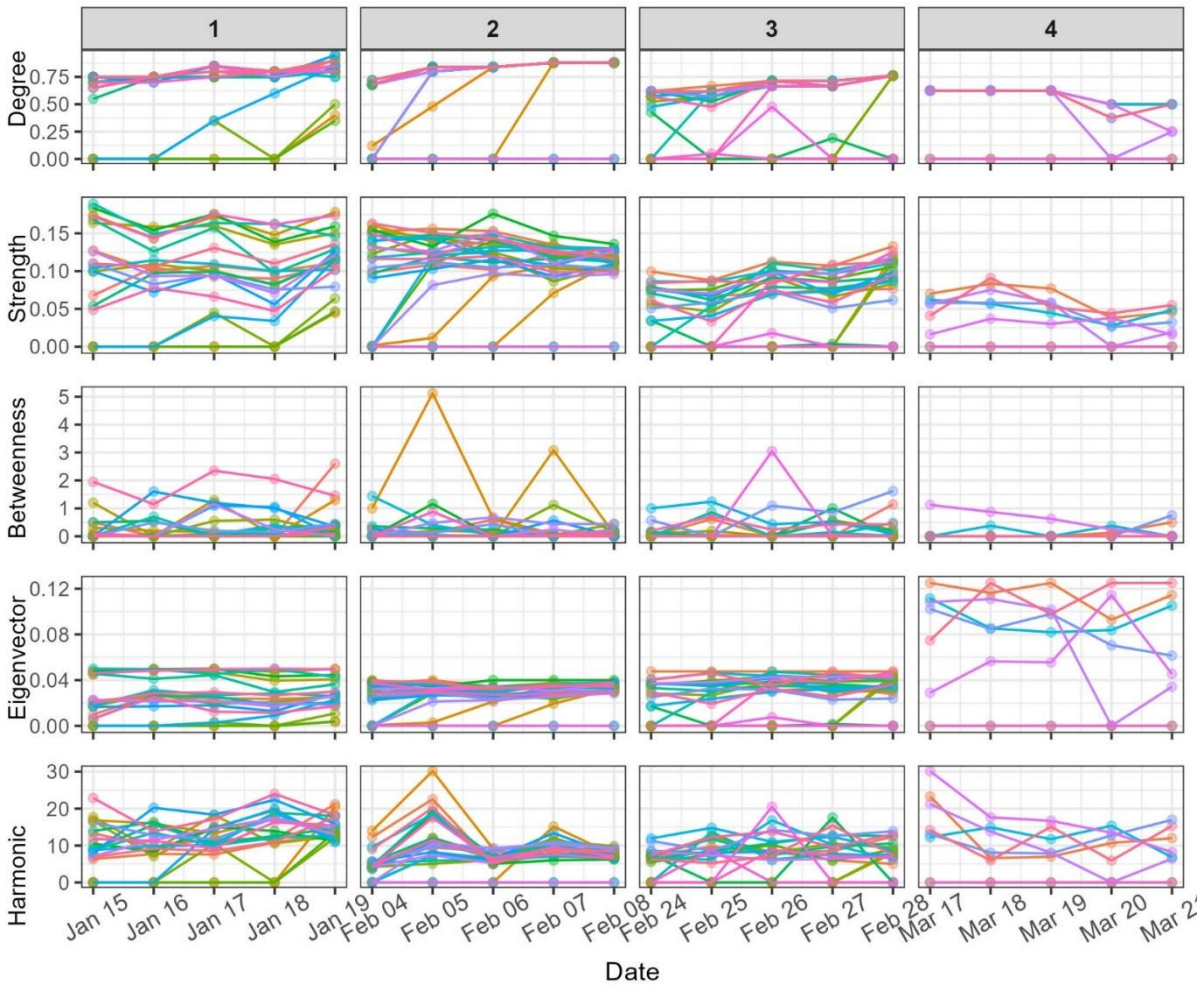

Figure 4.62. The variation in individual centrality measure over time at feeder 14A. All centrality estimates have been standardised between periods by dividing the estimates with the group size within periods. Each row corresponds to a centrality measure and each column is a full period, denoted by the number at the top. Each colored line is an

individual within a period. Colors do not represent the same individual between periods. The x-axis indicates the dates.

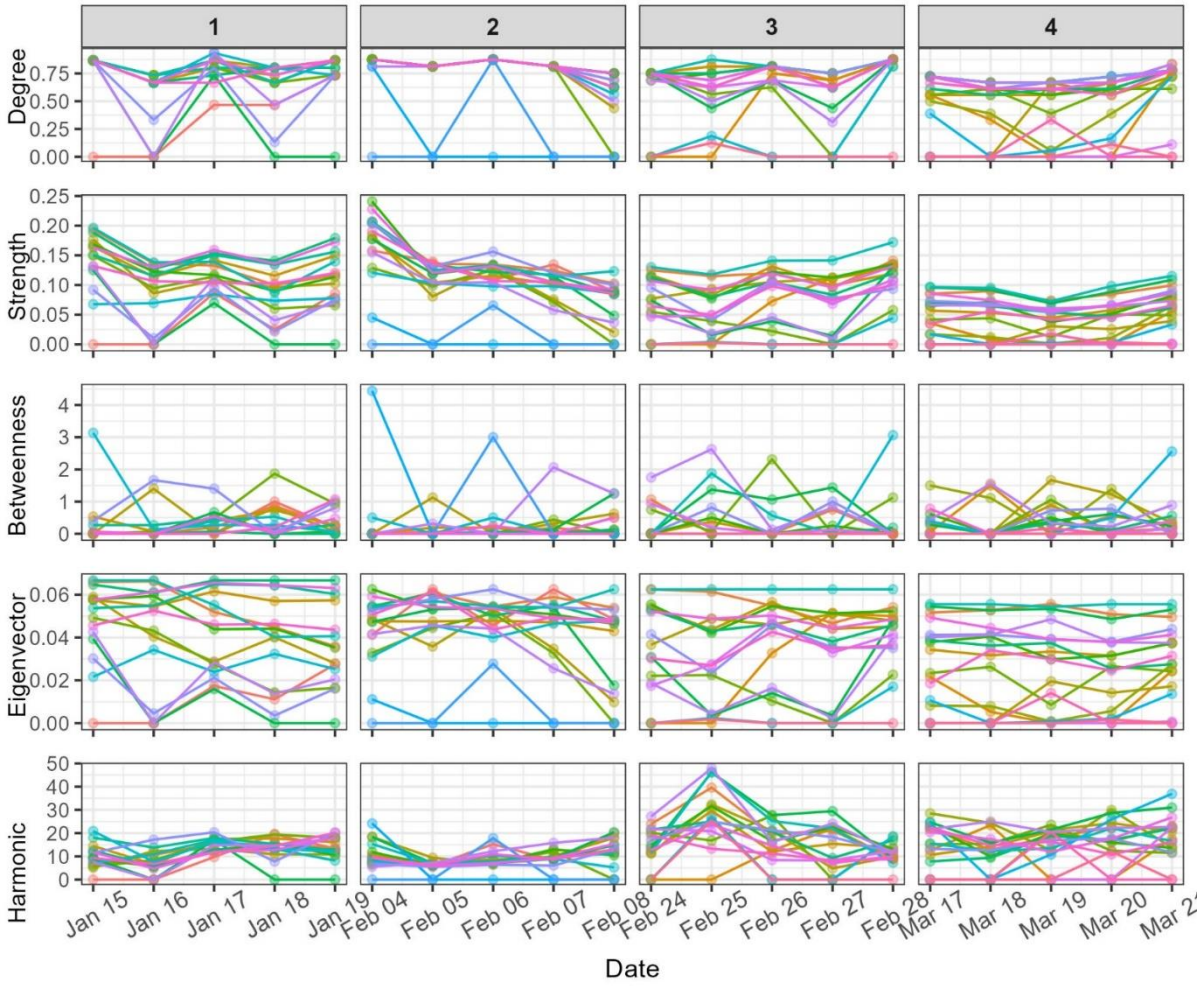

Figure 4.63. The variation in individual centrality measure over time at feeder 16A. All centrality estimates have been standardised between periods by dividing the estimates with the group size within periods. Each row corresponds to a centrality measure and each column is a full period, denoted by the number at the top. Each colored line is an individual within a period. Colors do not represent the same individual between periods. The x-axis indicates the dates.

Section S3. Informed traits

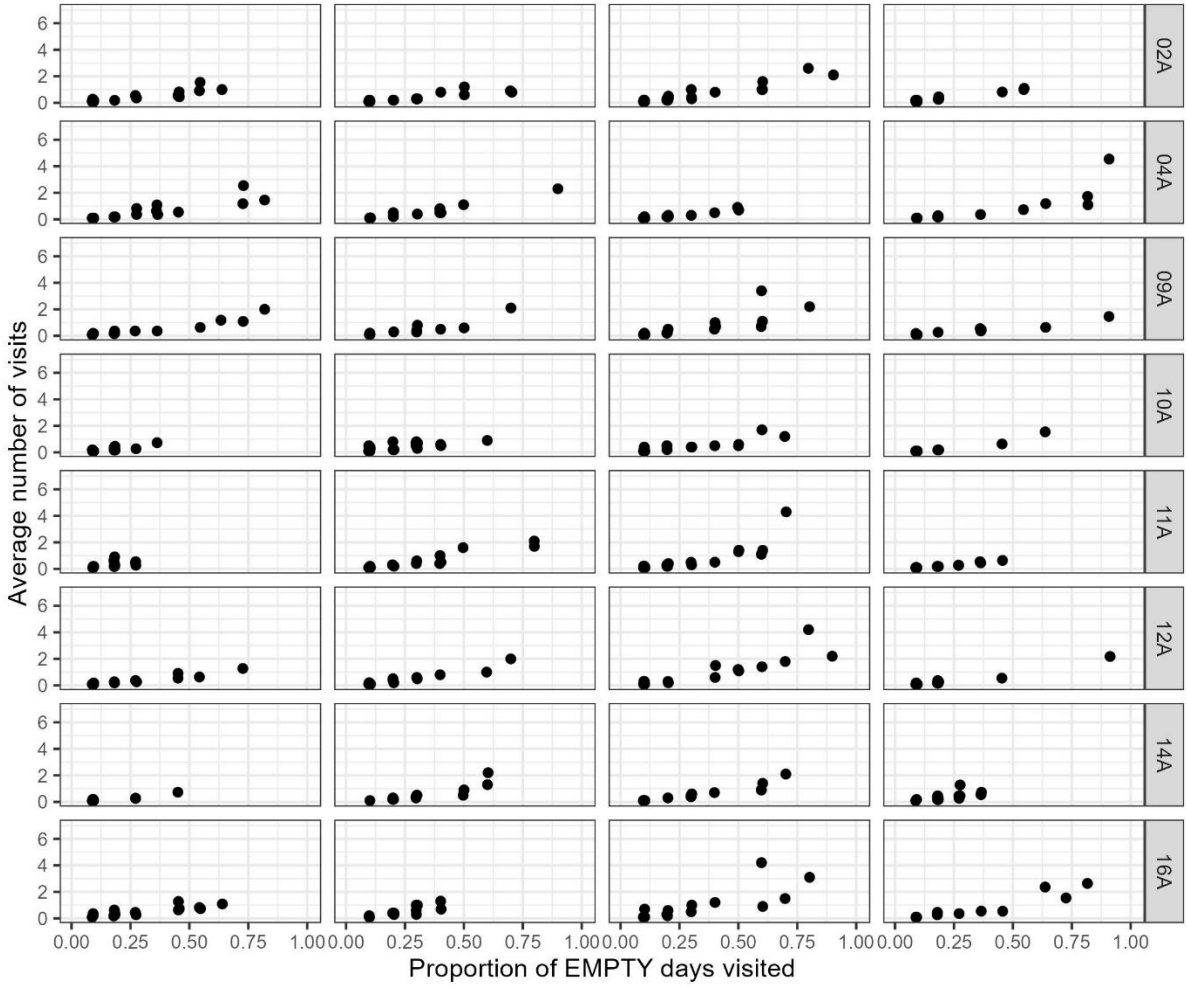

Figure 4.64. The proportion of days during the EMPTY periods that an individual visited a feeder (x-axis) in relation to the average number of visits the individual made during the days it visited (y-axis). Each column from left to right represent EMPTY periods 1-4, respectively, and each row represents the feeder labelled to the right. The black circles represent individuals. A small jitter was added to each individual value to improve visibility in the graph.

Section S4. Correlation of centrality measures

Table 4.15. Pairwise Pearson's correlation of centrality measures.

Correlated centralities		*Correlation Coefficient*	*p-value*
Degree	Strength	0.896	**<0.001**
Degree	Eigenvector	0.762	**<0.001**
Strength	Eigenvector	0.836	**<0.001**
Degree	Harmonic	0.645	**<0.001**
Strength	Harmonic	0.389	**<0.001**
Eigenvector	Harmonic	0.349	**<0.001**

Section S5. Model for relation between informed traits and centrality

Table 4.16. Anova outputs of the mixed-effects models for the relationship between the informed traits and individual social network position, including all interaction between the informed traits and days. ToA is scaled within period and feeder.

	Degree			*Strength*			*Eigenvector*			*Harmonic*		
	Chisq	*DF*	*p*	*Chisq*	*DF*	*p*	*Chisq*	*DF*	*p*	*Chisq*	*DF*	*p*
(Intercept)	91.87	1	**0.00**	40.04	1	**0.00**	57.38	1	**0.00**	96.65	1	**0.00**
Prop. Days Visited (GIG)	0.32	1	0.57	0.32	1	0.57	1.58	1	0.21	0.52	1	0.47
Avg. over Visit Days (GIG)	35.82	1	**0.00**	15.76	1	**0.00**	12.04	1	**0.00**	4.42	1	**0.04**
Time of Acquisition (ToA)	399.26	1	**0.00**	182.02	1	**0.00**	164.20	1	**0.00**	87.86	1	**0.00**
Days	95.15	4	**0.00**	3.28	4	0.51	6.18	4	0.19	6.14	4	0.19
Group Size	406.76	1	**0.00**	79.35	1	**0.00**	15.14	1	**0.00**	91.35	1	**0.00**
Sex	0.00	1	0.97	0.08	1	0.77	0.08	1	0.78	0.12	1	0.73
Age	3.81	4	0.43	4.80	4	0.31	3.73	4	0.44	4.50	4	0.34
Prop. Days Visited : Days	5.78	4	0.22	1.08	4	0.90	0.56	4	0.97	2.56	4	0.63

Avg. over Visit Days : Days	12.08	4	**0.02**	1.99	4	0.74	0.86	4	0.93	3.54	4	0.47
ToA : Days	172.87	4	**0.00**	52.75	4	**0.00**	47.50	4	**0.00**	35.84	4	**0.00**
Prop. Days Visited (GIG) x Avg. over Visit Days (GIG)	13.64	1	**0.00**	7.99	1	**0.00**	5.70	1	**0.02**	4.98	1	**0.03**

Table 4.17. Model outputs for the predictability of the three informed traits on the four centrality measures, including the interaction between the informed traits and days into the full period. ToA was mean centred and scaled within period and feeder. A Poisson distributed GLMM was used for analysing Degree centrality whereas LMMs were used for analysis of the other three centralities. Reference categories for the multilevel variables Day, Sex and Age are Day 1, Female, and Age 0, respectively.

	Degree				**Strength**				**Eigenvector**				**Harmonic**			
Predictors	*Estimate*	*SE*	*z-value*	*p*	*Estimate*	*SE*	*t-value*	*p*	*Estimate*	*SE*	*t-value*	*p*	*Estimate*	*SE*	*t-value*	*p*
(Intercept)	1.91	0.20	9.59	<**0.001**	0.95	0.15	6.33	<**0.001**	0.60	0.08	7.58	<**0.001**	12.35	1.26	9.83	<**0.001**
Prop. Days Visited (GIG)	0.07	0.12	0.57	0.572	0.10	0.17	0.57	0.570	0.14	0.11	1.26	0.210	2.13	2.94	0.72	0.469
Avg. over Visit Days (GIG)	0.18	0.03	5.98	<**0.001**	0.17	0.04	3.97	<**0.001**	0.09	0.03	3.47	**0.001**	1.49	0.71	2.10	**0.036**
Time of Acquisition	-0.54	0.03	-19.98	<**0.001**	-0.35	0.03	-13.49	<**0.001**	-0.21	0.02	-12.81	<**0.001**	-4.06	0.43	-9.37	<**0.001**

(ToA)																
Day 2	0.14	0.04	3.54	**<0.001**	-0.01	0.05	-0.18	0.856	0.02	0.03	0.45	0.651	0.24	0.91	0.26	0.792
Day 3	0.22	0.04	5.53	**<0.001**	0.02	0.05	0.41	0.680	0.04	0.03	1.10	0.270	1.08	0.91	1.19	0.235
Day 4	0.28	0.04	7.10	**<0.001**	0.01	0.05	0.14	0.889	0.05	0.03	1.59	0.113	1.40	0.91	1.54	0.124
Day 5	0.35	0.04	9.05	**<0.001**	0.08	0.05	1.44	0.150	0.08	0.03	2.21	**0.027**	1.91	0.91	2.10	**0.036**
Group Size	0.35	0.02	20.17	**<0.001**	0.18	0.02	8.91	**<0.001**	0.05	0.01	3.89	**<0.001**	3.01	0.31	9.56	**<0.001**
Sex [Male]	0.00	0.09	0.04	0.966	-0.02	0.07	-0.29	0.772	-0.01	0.04	-0.28	0.778	0.23	0.67	0.34	0.733
Age 1	0.14	0.13	1.09	0.276	0.07	0.09	0.77	0.441	0.02	0.07	0.36	0.719	0.38	0.97	0.39	0.695
Age 2	-0.06	0.13	-0.47	0.639	-0.09	0.09	-1.00	0.319	-0.08	0.06	-1.18	0.239	-1.00	0.96	-1.05	0.295
Age 3	0.07	0.16	0.44	0.662	-0.01	0.12	-0.05	0.959	-0.02	0.08	-0.25	0.800	0.24	1.18	0.21	0.836
Age 4	0.11	0.22	0.51	0.612	0.08	0.16	0.53	0.594	0.02	0.11	0.23	0.817	1.50	1.62	0.93	0.355
Prop. Days Visited x Day 2	0.13	0.16	0.80	0.425	0.06	0.23	0.25	0.802	0.05	0.15	0.32	0.748	3.60	3.99	0.90	0.368
Prop. Days Visited x Day 3	0.12	0.16	0.76	0.445	0.13	0.23	0.55	0.585	0.06	0.15	0.43	0.670	-0.24	3.99	-0.06	0.951
Prop. Days Visited x Day 4	0.28	0.16	1.73	0.084	0.19	0.23	0.82	0.410	0.08	0.15	0.54	0.590	2.66	3.99	0.66	0.506
Prop. Days	0.34	0.16	2.14	**0.032**	0.20	0.23	0.85	0.397	0.11	0.15	0.71	0.480	4.93	3.99	1.24	0.217

Visited x Day 5																
Avg. over Visit Days x Day 2	-0.06	0.04	-1.51	0.132	-0.05	0.05	-0.87	0.387	-0.03	0.04	-0.85	0.394	-0.84	0.94	-0.89	0.372
Avg. over Visit Days x Day 3	-0.04	0.04	-0.95	0.344	-0.05	0.05	-0.84	0.402	-0.01	0.04	-0.40	0.690	0.37	0.94	0.40	0.690
Avg. over Visit Days x Day 4	-0.08	0.04	-2.23	**0.025**	-0.06	0.05	-1.12	0.262	-0.01	0.04	-0.27	0.789	-0.29	0.94	-0.31	0.760
Avg. over Visit Days x Day 5	-0.12	0.04	-3.22	**0.001**	-0.07	0.05	-1.30	0.195	-0.02	0.04	-0.63	0.528	-1.17	0.94	-1.25	0.212
ToA × Day 2	0.19	0.03	5.44	<**0.001**	0.09	0.03	2.66	**0.008**	0.04	0.02	1.80	0.071	1.81	0.60	3.03	**0.002**
ToA × Day 3	0.27	0.03	8.09	<**0.001**	0.15	0.03	4.17	<**0.001**	0.08	0.02	3.53	<**0.001**	2.04	0.60	3.42	**0.001**
ToA × Day 4	0.34	0.03	10.60	<**0.001**	0.20	0.03	5.62	<**0.001**	0.11	0.02	5.05	<**0.001**	3.16	0.60	5.30	<**0.001**
ToA × Day 5	0.38	0.03	11.98	<**0.001**	0.23	0.03	6.48	<**0.001**	0.14	0.02	6.04	<**0.001**	2.99	0.60	5.01	<**0.001**
Prop. Days Visited (GIG) × Avg. over Visit Days	-0.19	0.05	-3.69	<**0.001**	-0.19	0.07	-2.83	**0.005**	-0.10	0.04	-2.39	**0.017**	-2.42	1.08	-2.23	**0.026**

(GIG)				
Random Effects				
Residual	-	0.17	0.07	50.55
Bird ID	0.13	0.06	0.03	4.93
Feeder	0.12	0.04	0.01	3.38
Period	0.04	0.04	0.00	0.37

Table 4.18. Anova outputs of the mixed-effects models reported in the main text for the relationship between the informed traits and individual social network position. These models include the interaction between ToA and days but not between the GIG traits and days. ToA is scaled within period and feeder.

	Degree			*Strength*			*Eigenvector*			*Harmonic*		
	Chisq	*DF*	*p*	*Chisq*	*DF*	*p*	*Chisq*	*DF*	*p*	*Chisq*	*DF*	*p*
(Intercept)	89.17	1	**0.00**	39.24	1	**0.00**	57.98	1	**0.00**	104.35	1	**0.00**
Prop. Days Visited (GIG)	13.63	1	**0.00**	5.49	1	**0.02**	11.58	1	**0.00**	8.18	1	**0.00**
Avg. over Visit Days (GIG)	44.27	1	**0.00**	26.58	1	**0.00**	26.82	1	**0.00**	8.17	1	**0.00**
Time of Acquisition (ToA)	438.10	1	**0.00**	208.89	1	**0.00**	183.49	1	**0.00**	95.91	1	**0.00**
Days	280.33	4	**0.00**	16.95	4	**0.00**	24.97	4	**0.00**	30.37	4	**0.00**
Group Size	407.50	1	**0.00**	79.67	1	**0.00**	15.22	1	**0.00**	91.58	1	**0.00**

Sex	0.00	1	0.97	0.08	1	0.77	0.08	1	0.78	0.12	1	0.73
Age	3.80	4	0.43	4.80	4	0.31	3.73	4	0.44	4.50	4	0.34
Prop. Days Visited (GIG) x Avg. over Visit Days (GIG)	13.16	1	**0.00**	8.02	1	**0.00**	5.72	1	**0.02**	5.00	1	**0.03**
ToA : Days	198.53	4	**0.00**	63.36	4	**0.00**	51.88	4	**0.00**	39.72	4	**0.00**

Chapter 5

Thesis discussion

The research that I have produced and presented in this thesis has focused on the links between social learning, information use, and the physical as well as the social environment. In *Chapter 2*, using populations of great tits living at two different elevations in the French Pyrenees, I found that social learning was not influenced by general differences in environmental harshness, assuming that differences in elevation are related to harshness. I suggested that the lack of a difference in social learning between populations may stem from social learning being similarly advantageous across environments. Consequently, the generalist great tit should modify its reliance on social information based on the context rather than general environmental conditions. Conversely, in *Chapter 3*, I found that a particular aspect of environmental harshness – temperature – could explain variation in the use of social information in the cold-adapted black-capped chickadee. I showed that within-season variation in social information use was negatively correlated with temperature in my study population. As colder temperatures infer higher thermoregulatory costs in endotherms, the results from *Chapter 3* suggest that increased social information use regarding foraging opportunities can be a risk-management strategy. By utilizing socially available information, individuals can avoid energetic shortfalls by ensuring access to food sources. In *Chapter 4*, I investigated whether producing socially available information had positive consequences on an individual's social centrality, which may provide additional survival benefits for

wintering residents. I found that being knowledgeable about food resources correlated positively with social network position in my study population of black-capped chickadees. However, the effect was variable in relation to whether the knowledgeable individual was consistent in maintaining accurate information or whether information was gained less reliably.

According to the 'harsh environment' hypothesis, environments that impose elevated challenges on animals' survival are predicted to favour cognitive abilities that can mitigate these effects (Pravosudov and Clayton 2002; Hermer et al. 2018). Until now, social learning had only been tested within the context of this hypothesis in one species of specialist scatter-hoarding species, the mountain chickadee (Heinen et al. 2021, 2022). This is despite the fact that environmentally induced changes in the relative cost of acquiring/using asocial or social information, as well as variation in environmental predictability, have been central concepts in the decision-making framework of social learning for decades (Boyd and Richerson 1988; Laland 2004; Kendal et al. 2018). Scatter hoarding specialists that have highly developed spatial learning and memory for storing and retrieving food caches (overview in Štorchová et al. 2010; and Pravosudov and Roth 2013) likely experience substantially different selective pressures in harsh environments, as compared to generalist species. A generalist should rather benefit from using any information they can acquire, asocial or social, to improve their chances for survival. However, when comparing great tits from harsh habitats to great tits from mild habitats, I found no significant difference in their social learning ability under a common garden paradigm (Isaksson et al. 2024). In *Chapter 2*, I suggested that social learning plasticity may have equalized the responses between high and low elevation individuals

in the common garden aviary. Testing the extent to which social information use is plastic in response to immediate environmental change is an important step for future research. However, in *Chapter 3*, I found that social information use by flocks of black-capped chickadees exhibited rapid and reversible plasticity in relation to variations in winter temperatures. Although the support for plasticity in social information use in my study comes from a specialist scatter hoarder, I expect to see a similar if not stronger pattern in the generalist great tit as they should be more tuned to exploiting any available information. The result of *Chapter 3* thus lend support to the suggestion that social learning plasticity could have equalized the social learning expression by great tits in *Chapter 2*. The next steps needed to confirm this would be to test the social learning performance of the great tits in the wild, rather than in a common garden paradigm.

Across *Chapters 2* and *3*, I considered the influence of environmental factors on social information acquisition and use with the assumption that social information use would increase in more challenging environments. However, environmental challenges or environmental harshness are broad concepts including multiple factors that may affect animals' learning and use of social information differently. In *Chapter 2*, I investigated a general environmental influence on social learning while assuming that harshness increased with elevation, and I did not find an effect. This could be due to the fact that harshness is multifaceted and that the diversity of factors constituting harshness interfered with and masked the effect of one another. Indeed, environmental factors that increase the costs of asocial information acquisition are predicted to promote the use of social learning while increased environmental stochasticity is predicted to favour asocial learning. The contrasting results of *Chapter 2* and *3*, suggest that instead of considering

general harshness, an important step for future research would be to separate and specify the environmental variables of interest.

In *Chapter 3*, I focused on a single aspect of harshness – cold temperature – that is known to cause increased energy costs for chickadees. Besides temperature, the environment remained fairly consistent over the winter without extreme shifts in precipitation (collaborators, personal communication), thus a rapid shift in energetic cost as a result of low temperatures was likely the main influence in *Chapter 3*. As theory predicted (Laland 2004; Kendal et al. 2018), the chickadees exhibited a higher level of social information use at lower temperatures when the energetic costs should have increased. In contrast, a population comparison in mountain chickadees showed that individuals from a harsh environment used social information less than individuals from a mild environment (Heinen et al. 2021, 2022). This result can be readily explained when considering that unpredictable environments also fall under the harshness umbrella as they restrict animals' chances of acquiring food. Low environmental predictability should promote asocial learning, rather than social learning, as information becomes outdated more quickly (Boyd and Richerson 1988). The high-elevation sites in the mountain chickadee studies rarely experienced daily average winter temperatures far below -6°C between 2012 and 2017, with an average of 4 days per year going below -10°C, but experienced frequent snowfall (Kozlovsky et al. 2018). Mountain chickadees are well adjusted to this range of temperature (Cooper 2002), but it would be harder to adjust to stochastic snowfall, so low environmental predictability is a more likely factor influencing social learning than asocial learning costs in this system. Conversely, when environmental predictability is low, individuals are more likely to be uncertain about the

best course of action at any given moment; theoretically, this should lead to an increased reliance on social information (Laland 2004). This aspect further confounds our ability to make accurate predictions of how environmental harshness will influence social learning.

Taken together, the recent progress made into the effects of extreme environments on social learning described above suggests that harshness has previously been defined too loosely. It is a compound concept, including a large diversity of environmental factors, and thus may make interpretation of social learning studies within this context difficult. It was recently suggested by Schradin et al (2023; See also Love and Wagner 2023; Makuya et al. 2023) that investigations of the effect of environmental extremes on behaviour should benefit from considering the difference between environmental harshness and environmental stress. In other words, whether the measured environmental variables represent general conditions that require energy conserving measures, environmental harshness, or brief environmental conditions that require increases in energy outputs, environmental stress. It is reasonable that predictions of environmental influences on social learning would benefit from being tested within these definitions of harshness and stress. Adding social learning as a way to conserve energy while foraging on top of other energy-saving mechanisms, such as hypothermia (Clark and Dukas 2000; Brodin 2007), should elevate the chances of winter survival in small birds. This aligns with the results of *Chapter 3*. Environmental stress, however, would likely represent factors that favour asocial learning. Indeed, an unpredictable environment, which is predicted to favour asocial learning, likely consists of multiple instances of environmental stress such as frequent blizzards. Based on the contrasting results of my studies in *Chapter 2* and *Chapter 3*, I conclude that investigations of cognitive ecology in

challenging environments would benefit from considering the "environmental harshness versus stress" framework. Considering the impact of environmental harshness, stress, and their combined effects on cognition would be extremely important to improve our understanding of observed behavioural variations in relation to variations in environmental conditions.

In *Chapter 4*, I found that consistent maintenance of high-quality information was a reliable predictor of an individual's social network position. However, I also found that inconsistent individual acquisition of information predicted individual network position, but that the relationship weakened over time. This short-lived boost in social centrality could have important survival consequences in rapidly changing environments. Higher network centrality has been linked to increased survival (Stanton and Mann 2012; Vander Wal et al. 2015; Lehmann et al. 2016; Bond et al. 2021; Philson et al. 2022) and gaining a short-term boost in centrality during, for example, a cold snap may be enough to keep an individual going until more favourable conditions return. In addition, an increase in the value of social information during harsh periods, as suggested by the increase in social information use in *Chapter 3*, could amplify the positive effects of information acquisition on social network position. In other words, individuals who are information producers may consequently gain more value as social partners in periods of increased environmental harshness. Further investigations are required to test this prediction. However, if this theory is supported, it may represent a previously unidentified survival aid for animals living in challenging environments.

Taken in concert, the studies presented in this thesis i) suggest that the influence of environmental challenges on social learning may be closely linked to species-specific

ecology, ii) show that social learning and information use are rapidly and reversibly plastic in relation to extreme environmental change, iii) emphasize how information gain and transmission may influence sociality, and finally, iv) propose a dynamic interaction between environmental harshness, social learning plasticity, and social structure as a substantial contributing factor in determining winter survival in *Paridae*. Further studies are required to disentangle the relationship between these components. While compound harshness is a good start, further investigation into the factors that make up harshness will give us deeper insight into what environmental aspects have shaped social learning. Of special interest is when asocial learning costs and environmental predictability clash or there is a change from one to the other, such as the seasonal transition from autumn storms (unpredictable) to cold winter nights (increased energetic costs). Furthermore, investigating the potential knock-on and feedback effects between social information use and sociality in relation to environmental harshness will be important from a population-dynamics viewpoint. In conclusion, this thesis has provided insight into the cognitive ecology of social learning and proposes novel avenues of research to improve our understanding of the processes that have shaped social learning across the animal kingdom.

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