Foraging tactics and social networks in wild jackdaws

Submitted by Michael Kings to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Biological Sciences in March 2018

Number of pages: 181

Number of words (including all tables, legends and references): 36,097

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Abstract

Individual variation in asocial and social behavioural traits can affect patterns of social association. Resultant individual-level variation in sociality can be quantified using social network analysis. Social network analysis has recently been applied to the study of the evolution and development of social behaviour. Though captive systems have provided useful contributions to this endeavour, investigating the factors shaping social structure in wild populations affords superior ecological relevance. The characterisation of the social structure of wild animals has been greatly aided by improvements in automated data collection methods, particularly the miniaturisation of Radio-Frequency Identification (RFID) technology for the purposes of studying the social foraging behaviour of wild birds. In this thesis, I use RFID methods to examine the factors influencing between-individual variation in foraging routines (Chapter Two) and social network position (Chapter Three) in wild populations of a colonial corvid species, the jackdaw (*Corvus monedula*). I then relate social network position to reproductive success (Chapter Three) and investigate the developmental plasticity of jackdaw social behaviour by determining the effect of early life conditions on social network position (Chapter Four). Finally, I describe the fine-scale temporal dynamics of social foraging, the nature of accompaniment during paired foraging and the foraging benefits of social support (Chapter Five).

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Acknowledgements

Firstly, I would like to thank my primary supervisor Dr. Alex Thornton. Alex has been extremely generous with his time and has always managed to steer me in the right direction. My secondary supervisors have also been very helpful; Dr. Andy Radford in particular provided useful advice and input on research matters at all stages of the work.

My family has been very supportive and understanding over the last few years and I hope to repay the many favours that I surely now owe! I would also like to thank a close family friend, Dr. Hilary Reed, for her support and advice regarding the process of doing a PhD.

Without Dr. Guillam McIvor none of the work I have attempted in the last few years would have been possible. Guill helped me a great deal with the construction of the feeders that I used for data collection and was responsible for the majority of ringing and collection of life history information. Also, Victoria Lee, Richard Woods and Alison Greggor have provided invaluable practical help and general advice on PhD matters. Similarly, I would like to thank the masters students (particularly Amy Cooke, Emma Doyle, Jennifer Austin, Holly Fisher, Andy Szopa-Comley and Alex Hadleigh) and interns (Lisanne van Woerden, Noémie Régli, Victoire Dejardin, Elisa Fouillac, Rosa Amurrio and Cindy Maslarov) who have assisted with fieldwork. I would like to thank Paul Gluyas and the staff at Pencoose Farm, as well as Odette Eddy and Saint Stithians Church, for allowing us access to sites for fieldwork. I am also grateful for technical and practical advice and assistance from Martin Whitaker, Dave Cruse, Adam Stringer and Sam Lanyon.

As part of the South West Doctoral Training Programme (SWDTP) I have been able to gain experience working on other projects. I would like to thank Dr. Steve Bates for coordinating SWDTP activities for us at Exeter. I would also like to thank Dr. Joah Madden for supervising my first rotation project and Dr. Christophe Sarran for hosting me at the Met Office for my placement. I would also like to thank other Exeter SWDTP PhD students, particularly David Pascall and Emmanuelle Briolat for the advice and general camaraderie.

Being a member of the Centre for Ecology and Conservation has given me the chance to meet a wide range of Animal Behaviour researchers and collaborate on a range of projects. I have learned a lot from working with Dr. Helen Morrogh-Bernard, Dr. Lauren Brent, Dr. J.J. Valletta and Dr. Colin Torney and from discussing ideas with Professor Alistair Wilson, Dr. Alex Mesoudi and Dr. Dan Cox.

Finally, I would like to thank Professor Mark Viney. As my tutor during my undergraduate studies he convinced me to apply for PhD positions, I doubt I would have done so without his encouragement.

Declaration

No part of this dissertation has previously been submitted for any qualification. All work contained in this thesis was conducted under the supervision of Dr. Alex Thornton, Dr. Andy Radford and Dr. Andy Russell. All of the work is my own.

Chapter One: General Introduction

Background

Causes of individual variation in behaviour

Foragers must invest time and energy to locate resources, whilst minimising their exposure to predation and starvation risk (McNamara & Houston, 1987). Efficient foraging behaviour may therefore benefit fitness, so foraging behaviour should be expected to be under selection, driving the evolution of optimal foraging strategies (MacArthur & Pianka, 1966; Emlen, 1966). These assumptions form the basis of 'Optimal Foraging Theory' (OFT), which is a modelling approach focussed on gaining understanding of the evolution of foraging strategies under given environmental conditions. Early successes of OFT included the modelling of patch use dynamics (Charnov, 1976), prey choice (Krebs *et al*., 1977) and social association during foraging (Fretwell & Lucas, 1970). However, the optimality of a foraging strategy depends not only on environmental conditions but also the properties of the forager (McNamara & Houston, 1985). To successfully mitigate the risks of both predation and starvation, individuals should be flexible as to the degree of foraging risk they accept and their evaluation of the acceptability of foraging risk should be determined by their state (McNamara & Houston, 1987). State comprises the properties of an individual, either intrinsic (e.g. energy reserves) or extrinsic (e.g. territory size), that affect the costs and benefits of its behaviour (McNamara & Houston, 1996). Between-individual differences in behaviour are commonly observed and may be explained by consistent individual variation in state and a feedback between state and behaviour (Wolf & Weissing, 2010; Dingemanse & Wolf, 2010; Sih *et al*., 2015). These consistent between-individual differences are commonly referred to as ‘animal personality’ and have been observed in a range of behavioural traits, such as aggression and exploratory behaviour (Sih *et al*., 2004; Reale *et al*., 2007; Sih & Bell, 2008).

Several mechanisms may contribute to the generation of personality variation. Firstly, stable between-individual differences in state can exist due to differences in life history characteristics, such as sex (Wolf & Weissing, 2010). Secondly, a link between state and behaviour that features positive feedback can promote between-individual variation (Sih *et al*., 2015). For example, Rands and co-workers (2003) showed that initial differences in energetic requirements can lead to stable individual differences in foraging behaviour. Thirdly, consistency in social behaviour may be favoured if social partners are required to coordinate their action (Dall *et al*., 2004; Wolf *et al*., 2011). Furthermore, between-individual variation and within-individual consistency in social behaviour favours social responsiveness, whereby an individual takes into account the prior behaviour of its social partner when making social decisions (Wolf *et al*., 2011). Finally, differences in individuals’ expected future fitness should lead to between-individual variation in risk-related behaviours, such as aggression (Wolf *et al*., 2007). The higher an individual’s expected future fitness, the more risk-averse it should be expected to be (Wolf *et al*., 2007). Once personality variation is established, certain environmental or social conditions are required for its maintenance over evolutionary time. Spatio-temporal variation in environmental conditions can maintain behavioural differences, as different levels of environmental risk favour different degrees of risk-taking (Wolf & Weissing, 2010). Negative frequency-dependent selection (Maynard Smith, 1982), whereby rarer phenotypes possess a competitive advantage over their more common counterparts is likely also key to maintenance of between-individual variation in behaviour. A common model of social foraging features a population of ‘producers’ and ‘scroungers’, individuals that rely on asocial or social information respectively to discover foraging patches, and a mixture of social phenotypes is maintained due to negative frequency-dependent selection (Barnard & Sibly, 1981).

Though individuals may exhibit consistency in their frequency of expression of certain behaviours, behavioural plasticity may be favoured if it enables individuals to match their behaviour to the prevailing conditions. For example, resource availability alters the costs and benefits of ‘producing’ and ‘scrounging’ during social foraging (Giraldeau & Beauchamp, 1999) and individuals can benefit from learning to alter their tactics dependent upon the degree of resource competition (Morand-Ferron *et al.*, 2007; Morand-Ferron *et al*., 2010). The social environment can induce transient changes in behavioural consistency (Webster & Ward, 2011). Individuals may consistently differ in the extent to which their behaviour is plastic, meaning that plasticity itself may be a component of personality (Dingemanse *et al*., 2010; Dingemanse & Wolf, 2013). Personality and social behaviour are not fixed properties of an individual and can change predictably over the course of development (Stamps & Groothuis, 2010) or in response to stressors experienced during early life (Spencer, 2017). The alteration of behaviour resulting from early life conditions is an example of ‘developmental plasticity’. Developmental plasticity can be adaptive as it can enable a developing individual to adjust its behaviour to suit the environmental conditions it will be exposed to later in life (Snell-Rood, 2013). Developmental plasticity is observed in social behaviour and is often triggered by stress during early development (Spencer, 2017). In general, stress during early life tends to reduce social motivation and increases aggression (Spencer, 2017). The extent to which such changes in social behaviour are adaptive (i.e. ‘social programming’) is difficult to ascertain, but is an important direction for future research (Spencer, 2017).

Fitness consequences of social behaviour

Social interactions can have both positive and negative effects on an individual’s fitness. Being the recipient of direct social interactions, such as grooming, can benefit an individual through a number of mechanisms, such as dampening of the stress response (e.g. Kiyokawa *et al*., 2014; Ishii *et al*., 2016). Agonistic interactions resulting from interaction during resource competition also affect fitness. Winning contests establishes access to resources, so should benefit fitness (but see Verhulst & Salomons, 2004). Social interaction can also benefit an individual’s inclusive fitness (Hamilton, 1964) when behaviours benefit the fitness of kin. Sociality can affect a number of different outcomes that influence fitness, such as survival probability (Stanton & Mann, 2012), offspring survival (Silk *et al*., 2003), mating success (Formica *et al*., 2011) and reproductive success (Gilby *et al*., 2013). The structure of behaviours between affiliates, rather than merely their occurrence, can be an important determinant of fitness (Royle *et al*., 2012).

An individual’s tendency to make appropriate decisions regarding when, how and with whom to interact is referred to as its ‘social competence’ (Taborsky & Oliveira, 2012). Social partners and the nature of social relationships may change over time, necessitating flexibility in an individual’s social responses. Therefore, sociality is commonly assumed to be instrumental for the evolution of intelligence, as encapsulated by the ‘Social Intelligence Hypothesis’ (SIH: Humphrey, 1976). Comparative studies of brain size in mammals, particularly primates, provide some support for the SIH as brain size and social group size have been found to be correlated (Dunbar, 1992; Dunbar & Schultz, 2007). Further, recent experimental evidence suggests that social complexity, as approximated by social group size, can affect cognitive performance and in turn fitness (Ashton *et al*., 2018). However, mixed support from comparative analyses (Holekamp, 2007; deCassien *et al*., 2017; Sayol *et al*., 2017) suggest that sociality may not always correlate with brain size. In addition, large brain size is not a pre-requisite for the possession of sophisticated mechanisms of cognition (Emery & Clayton, 2004). The nature of social relationships, rather than merely the number of social partners, may be a key driver of the evolution of intelligence (Dunbar & Schultz, 2007). For example, members of a breeding pair may maximize their fitness by tracking the condition of their partner and adjusting their behaviour accordingly (Emery *et al*., 2009). Therefore, determining the cognitive load of behavioural interactions occurring within the pair bond should therefore be a key focus of social cognition research.

Cooperation comprises sets of interactions that produce net benefits for all of the participants (Noë, 2006). Cooperation can arise through a number of mechanisms, including mutualism, kin selection, direct reciprocity and indirect reciprocity (Nowak, 2006). Repeated interaction between familiar individuals engaged in a task featuring competition for limited resources can lead to the establishment of direct reciprocity (Axelrod & Hamilton, 1981). In some cases, direct reciprocity can place high cognitive demands on the participants, as it may require the collection, storage and utilization of information concerning a cooperative partner’s previous actions (McAuliffe & Thornton, 2015). Indirect (Nowak, 2006) and generalized reciprocity (Rutte & Taborksy, 2007) are mechanisms that are also capable of establishing dynamics of reciprocal exchange. These processes feature the indiscriminate engagement of individuals in cooperative acts based on reciprocity with members of their social group (Pfeiffer *et al*., 2005). As such, the requirement for individuals to monitor the cooperative tendencies of their social partners and tailor their behavioural responses to best suit interaction with a particular partner is relaxed. The potential for partner switching (‘partner-choice’), rather than the requirement to manage the outcomes of repeated interactions with a partner (‘partner-control’), may be integral to the maintenance of reciprocity between unrelated members of a social group (Noë, 2006; Schino & Aureli, 2017). A social group can therefore be seen as a market (Noë & Hammerstein, 1994; Noë & Hammerstein, 1995), wherein members compete for access to cooperative exchanges. The prevalence of ‘partner-choice’ processes in reciprocal exchange has been explored in wild primates, but the relative importance of ‘partner-choice’ and ‘partner-control’ cooperative dynamics is rarely examined in wild populations.

Social network analysis

Social network analysis (SNA) is a useful framework for the characterization of social structure. A social network comprises nodes and edges. In animal behaviour research, nodes in social networks are usually representative of individuals. Consequently, edges represent a behavioural link between two individuals, either in the form of an explicit interaction (e.g. grooming) or a spatio-temporal association. The simplest social networks have binary edges, whereby an edge merely indicates whether an interaction or association occurred between a pair of individuals. For a network of association, edges are undirected as there is no defined sender and receiver. Social networks of association can be created from records of group membership. In this case, it is assumed that all members of an observed group are associating, a criterion commonly referred to as the 'gambit-of-the-group' (Franks *et al*., 2010). In contrast, for networks of interaction, such as dominance networks, edges are directed owing to the existence of a definable actor and recipient and are typically constructed from direct observations of behaviour. Including the strength of social relationships, by using weighted rather than binary edges, can reveal subtle patterns of association and produce more accurate social networks (Croft *et al*., 2005; Lusseau *et al*., 2008; Franks *et al*., 2010; Croft *et al*., 2011; Voelkl *et al*., 2011). Finally, Individual variation in sampling effort is a common issue for social network data collected from wild populations and can be mitigated by calculation of 'association indices', which adjust edge weights to account for the participants' duration of observation during the sampling period (Cairns & Schwager, 1987).

SNA enables the description of three levels of social structure: gross social group structure, the structure of sub-groups and cliques within a social group and individual variation in social behaviour. Group-level properties are usually assessed through inspection of metrics such as *Density*. *Network Density* describes the proportion of possible edges that have been observed and indicates the sparseness of a social network. Life history characteristics of individuals, such as age or sex, may influence social network structure. For example, individuals of the same sex (e.g. Mourier *et al*., 2012) or personality type (e.g. Croft *et al*., 2005; Croft *et al*., 2009) may be more likely to associate with each other. This phenomenon is referred to as 'assortment' and can be formally tested through calculation of 'assortativity coefficients' (Newman, 2002; Newman, 2003; Farine, 2014). Individual-level network properties are assessed through inspection of metrics such as *Degree* or *Eigenvector Centrality*, which quantify an individual’s social network ‘position’. These metrics characterize centrality, which is the tendency of an individual to be peripheral or highly connected within its social group. *Degree* is a simple count of an individual’s number of associates and as such is a simple measure of an individual’s gregariousness. *Eigenvector Centrality* is an example of a network metric that incorporates indirect social relationships into the calculation of centrality. An individual can be highly central in its social network, according to *Eigenvector Centrality*, either by associating with highly central individuals or associating with a large number of individuals. As an individual’s *Eigenvector Centrality* is influenced by its gregariousness, *Degree* and *Eigenvector Centrality* may be correlated. Correlation of network metrics is likely to be common (Farine & Whitehead, 2015) and examining differences in an individual’s centrality dependent upon the measures employed (e.g. Lusseau *et al*., 2008) may be necessary to disentangle the multitude of social processes causing variation in social network position.

Statistical analysis of social network structure often requires the use of specialized models and procedures. Assessment of the determinants of gross social group structure can be achieved through use of matrix correlation (Mantel, 1967) and regression (Krackhardt, 1988; Dekker *et al*., 2007) procedures. The use of Generalized Linear Models (GLMs) and Generalized Linear Mixed Models (GLMMs) enables the investigation of the factors influencing individual social network position (Croft *et al*., 2011). Potential sampling bias and non-independence issues necessitate a reliance on permutation tests (Manly, 1997) for the determination of significance when examining the causes and consequences of network structure. Typically, the permutation test is achieved by comparison of a test statistic (e.g. Mantel Z value; assortativity coefficient, GLMM fixed effect coefficient) to a distribution of values extracted from networks of randomized data. Randomized networks can be created from a suitable null model, such as those created using Exponential Random Graph Models (ERGMs: Robins *et al*., 2007), or from permutation of the raw behavioural data prior to network generation. Performing the permutation on the raw data, prior to the generation of the network, is a powerful method as it can introduce restrictions on swaps (Croft *et al*., 2011; Farine, 2017). For instance, individuals can be swapped only within certain spatial or temporal limits to prevent the permutation procedure from generating spurious associations (Bejder *et al*., 1998; Farine, 2017).

A desire to understand the social processes that cause temporal change in social structure (e.g. Larson *et al*., 2018) has driven the development of specialized modelling procedures for this endeavour (Blonder et al., 2012; Pinter-Wollman *et al*., 2013). One such example is ‘Stochastic Actor-Oriented Models’ (SAOMs), which can be used to model change in network structure in great detail (Snijders *et al*., 2010). However, SAOMs may be difficult to fit to data from wild populations, due to consistency of both overall network size and participant identities being a necessity (Fisher *et al*., 2017). An alternative modelling framework is ‘Relational Event Models’ (REMs), which model temporal dynamics on the level of single interactions (Butts, 2008). Consequently, loss of information due to integration of data over sampling periods is avoided, so REMs are useful for modelling social dynamics that occur over short timescales, such as reciprocity (e.g. Tranmer *et al*., 2015).

Automated data collection

A common hindrance of investigation of social behaviour in the wild is collection of datasets of sufficient size and quality to warrant formal statistical analysis. Recent technological advances provide researchers with a range of methods for automated data collection from wild populations. These methods encompass automated recording of video and audio and automated determination of space use, such as through use of GPS tracking, social proximity sensing or Radio Frequency Identification (RFID) (Krause *et al.*, 2013; Dell *et al.*, 2014; Kays *et al.*, 2015). For an RFID system to be effective for monitoring the space use of wild populations, each individual must be fitted with a unique tag that can be read by an RFID reader (Bonter & Bridge, 2011). Typically, the RFID reader is fitted to an object that receives frequent visits from foraging individuals, such as a bird feeder. RFID tags are usually passive, so do not require a battery. As a consequence, RFID tags can be much smaller than alternative tracking solutions that require battery-powered tags (i.e. GPS) and are much cheaper (Bonter & Bridge, 2011). The miniaturisation of RFID technology makes it an attractive solution for the monitoring of the space use patterns of wild birds. The requirement for individuals to visit a specific location in order for their activity to be logged restricts the utility of RFID systems for detailed analysis of spatial ecology, such as determination of individuals' home range. However, RFID systems are particularly suited to determining patterns of social association, as many individuals can be fitted with tags and the readers can be active outdoors for long periods of time (e.g. Farine *et al*., 2015).

Datasets from automated collection methods are often large and detailed, requiring sophisticated forms of data processing and analysis. For instance, the generation of social networks from RFID data requires the detection of temporal association between individuals. This can be achieved by querying the data with a simple fixed threshold (i.e. 15 seconds) (Lauw *et al*., 2005; Krings *et al*., 2012). However, Psorakis and co-workers (2012) showed that machine learning methods (see Valletta *et al*., 2017), which detect clusters of activity in the data stream without recourse to arbitrary temporal thresholds, outperform simple methods. Social networks generated from RFID data have recently been used to determine the effect of various factors on social network position, such as personality (Aplin *et al*., 2012) and developmental stress (Boogert *et al*., 2014).

Study species and system

In this thesis, I use a system of automated data collection via RFID-enabled feeders (e.g. Farine *et al*., 2015) combined with social network analyses to understand the causes and consequences of social interactions in animal societies, using wild jackdaws (*Corvus monedula*) as a model system. Jackdaws are corvids, so are closely related to rooks, crows, ravens, jays and magpies. As such, jackdaws may possess advanced cognitive abilities, as has been observed for other Corvids (Emery & Clayton, 2004). Jackdaws form long-term pair-bonds and show strict monogamy (Henderson et al. 2000). Re-pairing occurs following a partner's death, but is rare under other circumstances (Röell, 1978). Food sharing and allopreening interactions may be key to the formation and maintenance of the pair bond (de Kort *et al*., 2006; von Bayern *et al*., 2007). The pair is the fundamental unit of jackdaw social structure and can be detected in patterns group activity, such as flocking (Jolles *et al*., 2013). Jackdaw groups exhibit a dominance hierarchy and dominance interactions, in the form of displacements and direct aggression, commonly occur during foraging (Verhulst & Salomons, 2004). Jackdaws are highly neophobic in a foraging context, though social association can facilitate transient reductions in neophobia (Greggor *et al*., 2016).

Pairs breed in natural cavities and often exhibit yearly site fidelity. Jackdaw pairs prospect in the spring and prepare nests for the breeding season, which begins in mid-April. Each pair produces one clutch per year and four or five eggs are typically laid (though clutch size can vary from one to seven). There is a 17 day incubation period following laying, during which time the female must attend to her eggs to ensure hatching. Laying and hatching are both sequential. Consequently, hatch order affects the extent to which sibling competition influences chick growth, with late-hatching chicks exhibiting high mortality rates (Arnold & Griffiths, 2003). Furthermore, sibling competition in the period after hatching, but before fledging, directly affects chick stress hormone levels (Greggor *et al*., 2017). Finally, chicks fledge approximately 35 days post-hatching and continue to associate with their parents in the weeks following fledging.

Research was conducted at two main breeding sites in west Cornwall, Pencoose Farm (N 50°11’55.37’’, W 5°10’7.48’’) and Stithians (N 50°11’25.98’’, W 5°10’49.00’’). Each site contained 40-50 nest boxes, which were occupied by breeding pairs during the spring and summer months. In total, there were approximately 1500 ringed birds. Ringing and collection of life history information was undertaken during the breeding season. Each ringed bird was fitted with three coloured rings and a metal ring bearing a British Trust for Ornithology (BTO) code. One of the coloured rings contained a unique Passive-Integrated Transponder (PIT) tag that could be read by RFID data loggers. Individuals that fledged from nest boxes at the breeding sites were ringed at fledging and adults were either ringed following trapping away from their nest or capture at the nest. Blood samples were taken during ringing and subsequently used for molecular sexing (Griffiths *et al.*, 1998). In addition, biometric recordings, such as tarsus length (Henderson, 1991) and wing length, were taken. The growth of chicks born in nest boxes was monitored until fledging. Each chick received a colour mark immediately post-hatching to enable its identification prior to ringing and chicks were weighed six or seven times, at approximately five day intervals, from the day of hatching until fledging.

Thesis structure

I used a system of RFID feeders to investigate the processes determining individual variation in asocial and social foraging patterns, relate social network position to fitness, quantify plasticity in social network position and describe patterns of turn-taking during paired foraging events.

Chapter Two

To determine the factors affecting between-individual variation in foraging routines, I extract measures of daily feeder usage and assess the effects of life history, morphometry and competition on individual’s feeding patterns. I go on to examine the repeatability of individual foraging behaviour.

Chapter Three

I examine the relationship between social network position and fitness in jackdaws. Firstly, I investigate the relationship between individual characteristics and social network position using social networks of association generated from feeder visit data. Using these social networks, I then relate network position during the breeding season to reproductive success.

Chapter Four

I use social networks of association from feeder visit data to investigate the effect of developmental conditions, as indicated by measures of sibling competition and growth rate, on juvenile social network position.

Chapter Five

I first quantify the value of foraging with a partner by inspecting the duration of solo and paired visits to feeders. I then describe the patterns of queuing that occur when multiple jackdaws visit feeders together and model the turn-taking dynamics underlying queuing interactions between associates.

Chapter Six

I summarise the main findings from chapters 2-5, raise broader questions regarding the nature of jackdaw social structure, identify possible methodological improvements and suggest topics for future work.

Note

Each data chapter is written as a separate piece of work. Consequently, certain information (i.e. general methods) may be repeated. I apologise for any inconvenience this may cause to the reader.

Chapter Two: Individual variation in daily foraging routines of wild jackdaws

Abstract

Individuals must adjust their foraging behaviour to suit the environmental and social conditions they encounter. Mitigation of the risks associated with foraging can induce predictable temporal patterns of foraging effort referred to as foraging routines. Daily foraging routines have been identified in groups of passerines, but the mechanisms underlying between-individual variation in foraging routines have received little attention due to methodological constraints. Recent advances in Radio-Frequency Identification technology have enabled detailed investigation of the foraging routines of wild birds. We used a system of automated feeders to record the daily patterns of foraging visits of wild jackdaws to supplementary food sources over a two year period. Individuals mainly differed in the extent to which they used supplementary food, but also differed in their tendency to concentrate activity in the mornings and the length and number of feeder visits per day. Life history characteristics, such as age and sex, and morphometrics were not robust predictors of each of the aspects of feeder usage. Individual identity accounted for the greatest proportion of between-individual variation in supplementary food use, but repeatability of individual foraging behaviour was low. Consequently, jackdaws vary in their tendency to exploit novel sources of supplementary food, but are inconsistent in their quantity of daily usage and the timing and duration of their feeding visits. Given the existence of appreciable individual variation in supplementary food usage, the extent to which this variation is determined by

individual quality and its relation to fitness are promising avenues of further research.

Introduction

Starvation and predation risk can shape the evolution of foraging behaviour (McNamara & Houston, 1987; Lima & Dill, 1990; Houston *et al.*, 1993). The inherent trade-off in investment in the avoidance of starvation and predation selects for increased efficiency in allocation of foraging effort (Houston *et al.*, 1993). Starvation risk is influenced by the state of the forager, so foragers should increase foraging effort and reduce vigilance as their condition declines (McNamara & Houston, 1987). In diurnal birds, there are periodic changes in condition over the course of the day; condition is worst at dawn following inactivity overnight and improves as the bird forages throughout the day. Consequently, birds should display consistent daily foraging routines (McNamara *et al.*, 1994; Houston & McNamara, 1993), a prediction that is supported by experimental work on captive (Dall & Witter, 1998; Polo & Bautista, 2006) and wild (Ratikainen & Wright, 2003; Macleod *et al.*, 2005; but see Bonter *et al.*, 2013) groups.

Individuals consistently differ in ‘personality’ traits, such as aggression and boldness, which influence foraging behaviour (Sih *et al*., 2004). This between-individual variation reflects differences in responses to risk that are repeatable (Bell *et al.*, 2009), heritable (Dochtermann *et al.*, 2015) and consistent across contexts (Dingemanse *et al.*, 2010). Personality influences foraging behaviour by affecting the tendency to explore unfamiliar surroundings (Dingemanse *et al.*, 2002), sample novel food sources (Greggor *et al.*, 2016) and engage in social interactions during foraging (Aplin *et al*, 2013; Aplin *et al.*, 2014; Aplin *et al.*, 2015). Quinn and co-workers (2012) investigated the relationship between exploration behaviour and the negotiation of predation and starvation risk during foraging in great tits. Exploration behaviour and traits related to social dominance (age, sex) predicted individuals' tolerance of foraging risk (Quinn *et al.*, 2012).

Social foragers can enhance their foraging efficiency by exploiting the cues of foraging conspecifics. Social information use can reduce search costs (Giraldeau & Dubois, 2008), but the value of social information declines as the frequency of its use by other foragers increases (Boyd & Richerson, 1988) and the inherent frequency-dependence of cue use maintains between-individual variation in foraging strategies. The distribution and nature of food sources can also influence the value of social information and consequently the balance of social foraging strategies in a population. When resources can be monopolized a greater prevalence of social information use is to be expected (Giraldeau & Beauchamp, 1999) and there is evidence that foragers can adjust their degree of social information use to best exploit the prevalent foraging conditions (Morand-Ferron *et al.*, 2007; Morand-Ferron *et al*., 2010). Determining the impact of social conditions on foraging dynamics requires data of high temporal resolution that captures the properties of individual feeding bouts.

Recent advances in automated tracking technologies have facilitated the study of the space use patterns and social interactions of wild populations in fine spatio-temporal detail (Krause *et al.*, 2013, Kays *et al.*, 2015, Dell *et al.*, 2014). The study of foraging routines in birds has been greatly enhanced by the miniaturisation of Radio-Frequency Identification (RFID) technologies, specifically the creation of small leg-rings equipped with unique RFID tags and the incorporation of RFID tag readers into bird feeders (Bonter & Bridge, 2011). The use of RFID technology enables unparalleled temporal resolution in estimates of foraging activity, but as yet automated studies of foraging routines have been confined to a small number of species (Bonter *et al.*, 2013; Quinn *et al.*, 2012; Crates et al., 2016; Milligan *et al.*, 2017). Milligan and co-workers (2017) investigated between-individual variation in the usage of automated feeders by wild tits; individuals differed in their quantity of feeder usage and the dynamics of their feeder visits. Dominance related measures (age, sex) influenced aspects of tit feeder usage, but there was no effect of personality (Milligan *et al*., 2017). The influence of morphometric traits directly related to dominance (i.e. body size) on patterns of individual supplementary food usage has not yet been examined.

I studied the daily foraging routines of RFID-tagged jackdaws using a system of automated feeders. Jackdaws will exploit novel food sources and exhibit variation in personality traits related to foraging, particularly responses to novelty (Greggor *et al.*, 2016). Social context affects individual responses to novelty (Greggor *et al.*, 2016) and jackdaws engage in both affiliative (de Kort *et al.*, 2006; Wechsler, 1989; von Bayern *et al.*, 2007) and agonistic (Henderson & Hart, 1995; Verhulst & Salomons, 2004; Verhulst *et al.*, 2014) interactions during foraging. Adult jackdaws are long-term monogamous (Henderson *et al.*, 2000) and continue to associate with their offspring following fledging (Henderson & Hart, 1993). Jackdaws groups are comprised of multiple family units and the size and structure of groups varies across seasons (Kubitza *et al*., 2015). We analysed the visits of individual jackdaws to automated feeders to describe jackdaw daily foraging routines, determine the repeatability of foraging behaviour and quantify the effect of life history characteristics, morphometry and social factors on aspects of feeder usage. I predict that Juveniles exhibit greater quantity of supplementary food usage than adults. I also expect that competition has a differential effect on feeder visit duration dependent upon age and sex, such that greater competition reduces feeder visit duration for juveniles (of both sexes) and adult females, but does not have a discernible effect on the foraging behaviour of adult males. Finally, feeder visit duration is expected to be highly repeatable at the level of the individual and to be shorter for juveniles than adults and shorter for females than males.

Materials and Methods

Study population

Data were collected from jackdaws in and around two nest-box colonies in west Cornwall: Stithians (N 50°11’25.98’’, W 5°10’49.00’’) and Pencoose Farm, TR3 7DN (N 50°11’55.37’’, W 5°10’7.48’’) during 2015, 2016 and January-March 2017. Approximately 1500 ringed jackdaws visit the two sites and there are between 40 and 50 available nest boxes installed at each site. Pairs of jackdaws prospect in the spring and build nests in the nest boxes in preparation for the breeding season. They lay a clutch of eggs in April/early May and after laying there is a three week incubation period during which the female incubates the eggs and is fed by the male (Henderson & Hart, 1993). This is followed by a 30-35 day period following hatching when chicks remain in the nest box and are fed by both parents, though the male retains the primary provisioning role (Henderson & Hart, 1993). Following fledging, parents and offspring continue to associate. The breeding sites continue to be frequented by jackdaws for several weeks post-fledging, after which activity diminishes, though ringed jackdaws return sporadically to the breeding area over autumn and winter (personal observation).

Ringing and collection of life history information occurs during the breeding season. At ringing, each individual is given a metal ring with a BTO code and three coloured rings, of which one contains a Passive-Integrated Transponder (PIT) tag. Chicks were ringed at fledging and adults were ringed after trapping at or near the nest. During ringing, blood samples were taken for molecular sexing (Griffiths *et al.*, 1998) and tarsus length (to 0.1mm) was recorded as an estimate of body size. Chicks ringed in their nest box and then observed up to one year from ringing were classed as juveniles; otherwise individuals were classed as adults.

Ethical Statement

Home Office (PPL 80/2371) and British Trust for Ornithology (C6079, C5752, C5746) licenses covered bird ringing and the experimental work and procedures adhered to the guidelines of the Association for the study of Animal Behaviour (ASAB) and the University of Exeter Biosciences Ethics committee (2014/577).

Automated feeder usage data

Three feeders, each equipped with a data logger, were placed at Stithians, two feeders were placed at Pencoose Farm and three feeders were placed between the two sites. Feeders were filled with mixed corn *ad libitum* and were operational from 05:30 to 20:30 each day. The readers were equipped with two antennae, arranged one behind the other on a feeding perch, such that a bird standing on the front antenna would have access to food, while a bird standing on the back antenna behind a feeding bird would have to queue for access to food (Fig.1). The antennae in each feeder were connected to an IBT EM4102 RFID data logger, powered by six C-cell batteries. When a ringed bird stood over an antenna, it's unique PIT-tag ID code, the current time and date and the antenna ID were logged every 100ms until the bird left (Table S1).

Data processing

The data from the RFID readers was processed to identify individual visits to the feeders. A visit was defined as a period of time on the feeder without a change in individual occurring. If five seconds or more elapsed between PIT-tag reads, this was counted as a new visit. Twelve statistics were extracted from the visit data to summarise each individual's daily activity. Total time on feeder, mean time on feeder, standard deviation in time on feeder, central time on feeder (relative to sunrise), standard deviation in time between visits (as proportion of day length), earliest visit (relative to sunrise), latest visit (relative to sunset), number of visits, shortest visit, longest visit, mean change in time on feeder, mean difference in time between visits (as proportion of day length) were calculated. The time of day of measures were given relative to sunrise or sunset times, extracted from UK National Almanac Office data (HMNAO: www.gov.uk/HMNAO). Daily statistics were only evaluated if an individual had more than one visit in a particular day (necessary for calculating standard deviations). Additionally, data points were only included for individuals for which full life history information was known (N = 336 individuals).

Statistical Analysis

Principal Component Analysis

Fig. 1: Feeder equipped with an RFID reader. Two antennae are mounted on the feeding perch in primary (1) and secondary (2) positions. The feeder is filled with mixed corn.

To mitigate colinearity in daily statistics and to capture aspects of foraging behaviour that may constitute combinations of daily statistics, I applied principal component analysis to the set of daily statistics. The first five components explained 94.3% (34.6%, 19.5%, 18.9%, 12.1% and 9.2% respectively) of the variation in the daily statistics (Table 1). Each of the first five components had an eigenvalue greater than one (Table 1), so met a common selection criterion (Kaiser, 1992). The fifth component only marginally exceeded the selection criterion and explained less than 10% of variance, so was omitted from further analysis. Inspection of the loadings for each component (Table S2) supports the interpretation of the first four components representing overall quantity of feeder usage, concentration of feeder usage in the mornings, tendency to make many short visits throughout the course of the day and bingeing infrequently respectively.

Table 1: Eigenvalues and proportion of variance explained for each principal component.

	PC1	**PC2**	**PC3**	**PC4**	**PC5**
Standard deviation	2.04	1.53	1.51	1.21	1.05
Proportion of Variance	0.346	0.195	0.189	0.121	0.0919
Cumulative Proportion	0.346	0.541	0.731	0.852	0.944

Linear Mixed Models (LMMs)

To examine the influence of individual life history characteristics, season and social context on how individuals used the feeders, I applied linear mixed effects models (LMMs) to the component scores of each of the first four principal components. LMMs were fitted using the lme4 package (Bates *et al*., 2013) in R (R Core Team, 2017). For each model, feeder nested within site, subject and date were fitted as random effects. Age, sex, season, tarsus length and number of individuals using the feeder were included as fixed effects. Interactions of season with age and sex were also included to account for potential age and sex bias in feeder usage across seasons. Seasons were defined as five time periods, chosen to approximately match the key annual life history periods of the birds. The age-season and sex-season interactions were also included to account for potential demographic variation across seasons.

Model fit was assessed by visual inspection of residuals. Following inspection of residuals from LMMs fitted to untransformed data, Box-Cox transformations were applied (Gurka *et al.*, 2006). Model selection was performed using AIC comparison. For each component, a set of models was defined, the models were ranked according to AIC and retention of models for the final model set was determined through application of a nesting rule (Richards *et al.*, 2010). The best model and any models that were simpler, nested versions of the best model and differed in AIC value by less than six were retained (Richards *et al.*, 2010) and comprised the final model set. If multiple models were retained, Akaike weights were calculated for the models in the final set to aid model comparison (Burnham & Anderson, 2002). Measures of absolute model fit were determined from conditional and marginal r-squared values for LMMs calculated using the R package ‘MuMIn’ (Bartoń, 2016). Percentage of variance explained by each random effect was calculated to aid comparison of the explanatory value of the random effects (Appendix: Random Effects Tables). Individual-level repeatability was calculated for models of within and across seasons

(Dingemanse & Dochtermann, 2013; Milligan *et al.*, 2017) using the R package 'rptR' (Stoffel *et al.*, 2017).

Results

Descriptive Statistics

In total, 336 individuals visited the feeders, of which 241 were adults and 95 were juveniles. The majority of feeder visits were short, lasting no longer than a few seconds (Fig. 2) and occurred during the breeding and post-breeding seasons (Table. 2) and visits from male jackdaws accounted for 60% of the time that individuals of known sex used the feeders.

PC1

The best model for the first component included age, sex, tarsus and number of individuals per day (Table S3). Juveniles used the feeders less than adults in general, females exhibited greater feeder usage than males and larger individuals used the feeders more (Fig. 3). As the number of individuals using the feeder increased, individual feeder usage declined (Fig. 3). Total variance explained by the model was 25.2% (conditional R-squared) and fixed effects explained 4.87% of total variance (marginal R-squared) (Table S6; Nakagawa & Schielzeth, 2013) and there was low (0.1-0.3) but not negligible individual-level repeatability for feeder usage (Table S9; Nakagawa & Schielzeth, 2010).

PC2

The best model for the second component included age, season, number of individuals per day and the interaction between season and age (Table S4). Adults tend to use the feeders earlier in the day than juveniles and the greater the number of individuals using a feeder the greater the tendency of an

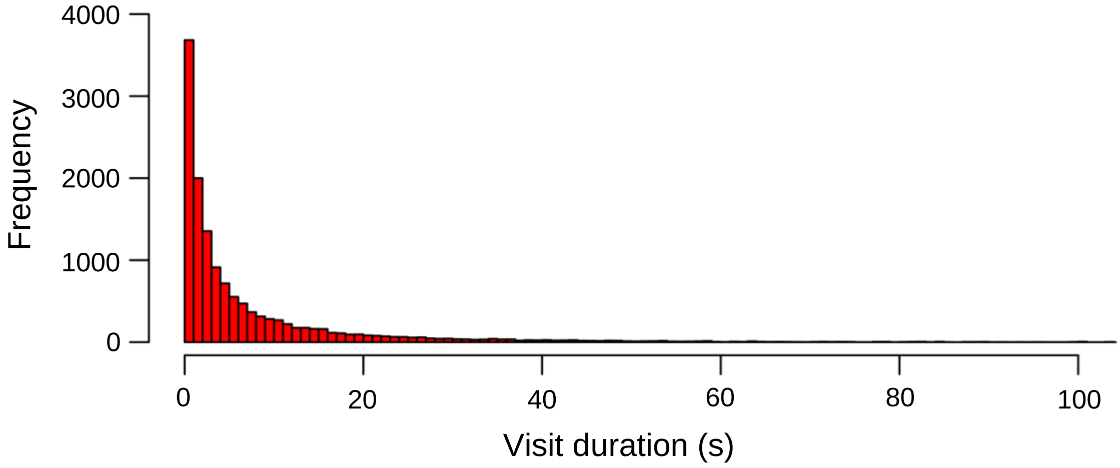

Fig. 2: Histogram of duration of feeder visits.

individual to use the feeder earlier in the day (Fig. 4). Total variance explained by the model was 23.9% (conditional R-squared), fixed effects explained 3.16% of total variance (marginal R-squared) (Table S7; Nakagawa & Schielzeth, 2013) and there was low but not negligible (0.1-0.3) individual-level repeatability for time of day of feeder usage (Table S10; Nakagawa & Schielzeth, 2010).

PC3

The best model for the third component included age, season, number of individuals per day and the interaction between season and age (Table S5). Juveniles and adults exhibited similar visit duration during the breeding season and autumn periods, but juveniles were more transient in the other seasons (Fig. 5). In general, the greatest transience was exhibited during the autumn and winter periods and transience in pre-breeding and post breeding season was lower than in the breeding season. The greater the number of feeder users

Table 2: Summary of feeder visits and time that feeders were occupied in each of the seasons

Season	Number of feeder visits	Time Feeders Occupied (s)	Percentage of total time (%)
Pre-Breeding	1313	9067	8.16
Breeding	6098	48188	43.4
Post-Breeding	3557	36696	33
Autumn	1092	8118	7.34
Winter	1800	8996	8.1

the greater the level of individual transience (Fig. 5). Total variance explained by the model was 25.4% (conditional R-squared), fixed effects explained 4.13% of total variance (marginal R-squared) (Table S8; Nakagawa & Schielzeth, 2013) and there was low but not negligible (0.1-0.3) individual-level repeatability for visit duration (Table S11; Nakagawa & Schielzeth, 2010).

Discussion

Variation between individuals in the daily foraging patterns of jackdaws is described by three components; individuals mainly differed in the extent to which they used supplementary food and differed somewhat in the timing and duration of their feeder visits. Individuals were rarely consistent in each of the aspects of feeder usage, as indicated by low individual repeatability in all models. Life history characteristics and morphometry explained only a small percentage of individual variation in total daily supplementary food usage, timing of usage and visit durations. Timing of feeder usage and visit duration

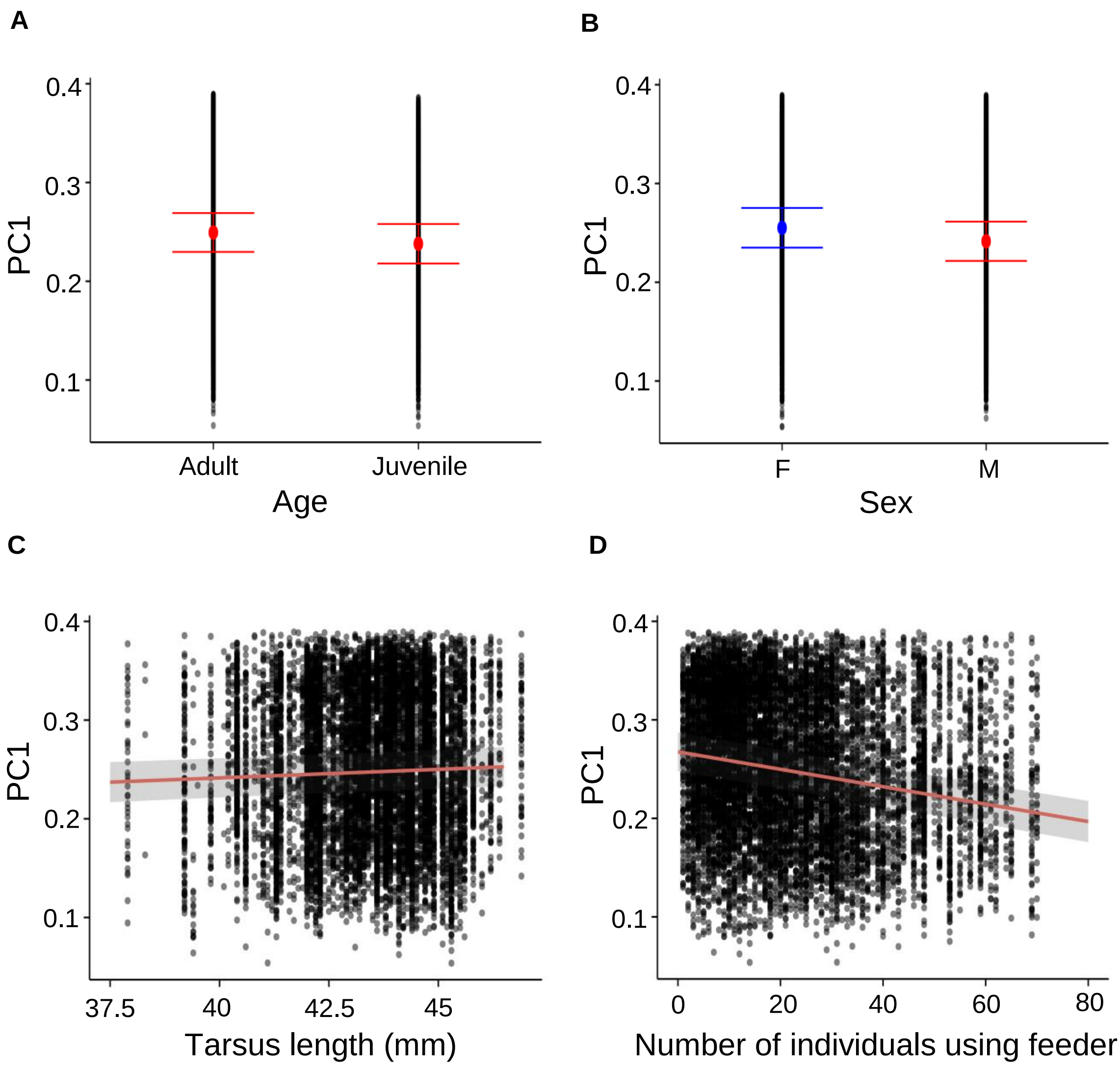

Fig. 3: Effect of age (**A**), sex (**B**), tarsus length (**C**) and number of individuals using a given feeder per day (**D**) on adjusted values (Box-Cox transformation) for the first principal component. Fitted values and 95% confidence intervals (colour) are overlaid on the raw data.

were both affected by age, season and the number of individuals using the feeder on a given day. Daily total feeder usage was also influenced by age and the number of feeder users, as well as sex and body size.

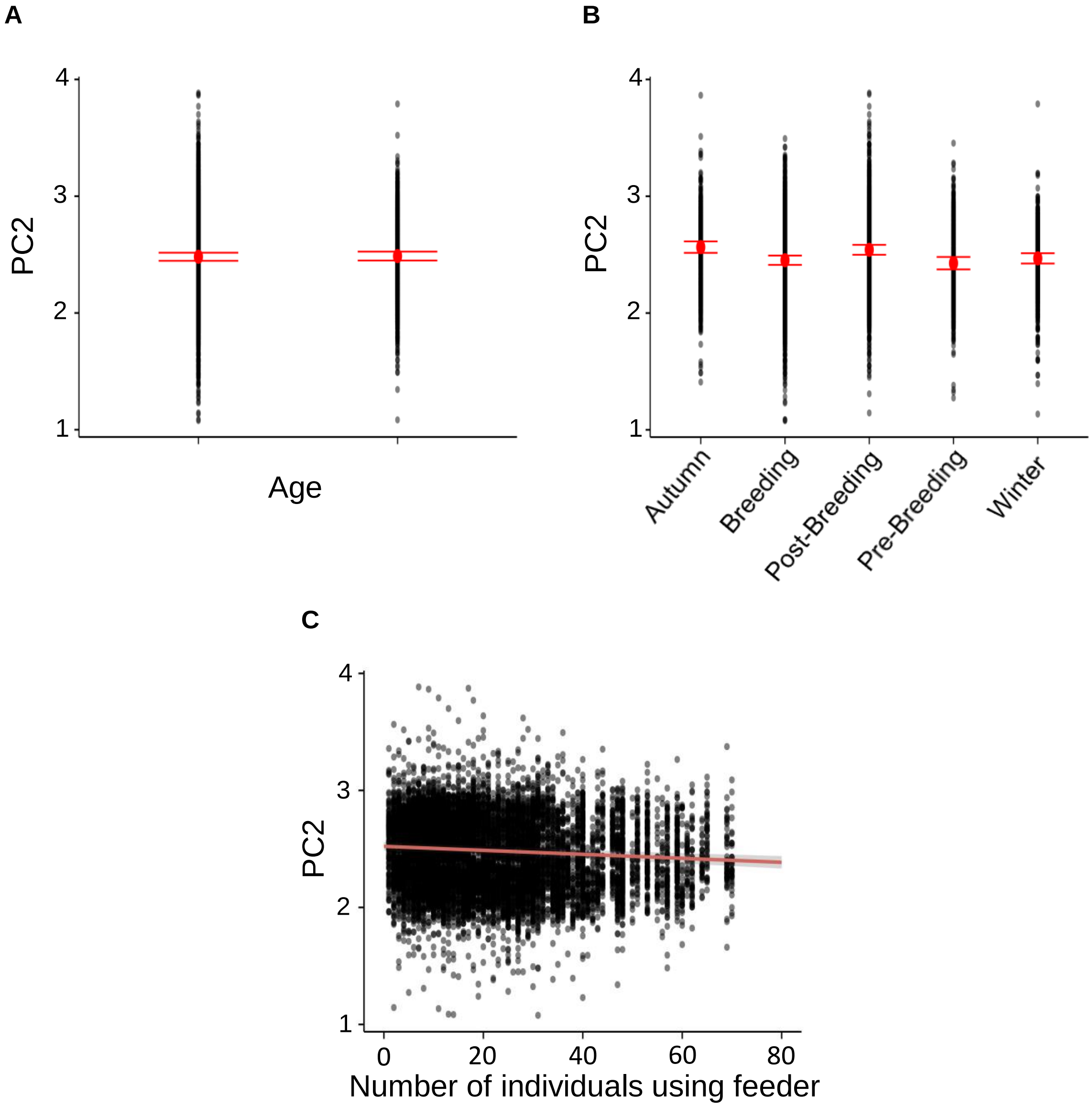

Fig. 4: Effect of age (**A**), season (**B**) and number of individuals using a given feeder per day (**C**) on adjusted values (Box-Cox transformation) for the second principal component. Fitted values and 95% confidence intervals (colour) are overlaid on the raw data.

Individuals differed more in quantity of daily feeder usage than in the timing or duration of visits to feeders. Predominant variation in total daily usage implies that some individuals utilized the feeders only sporadically, whilst for others the

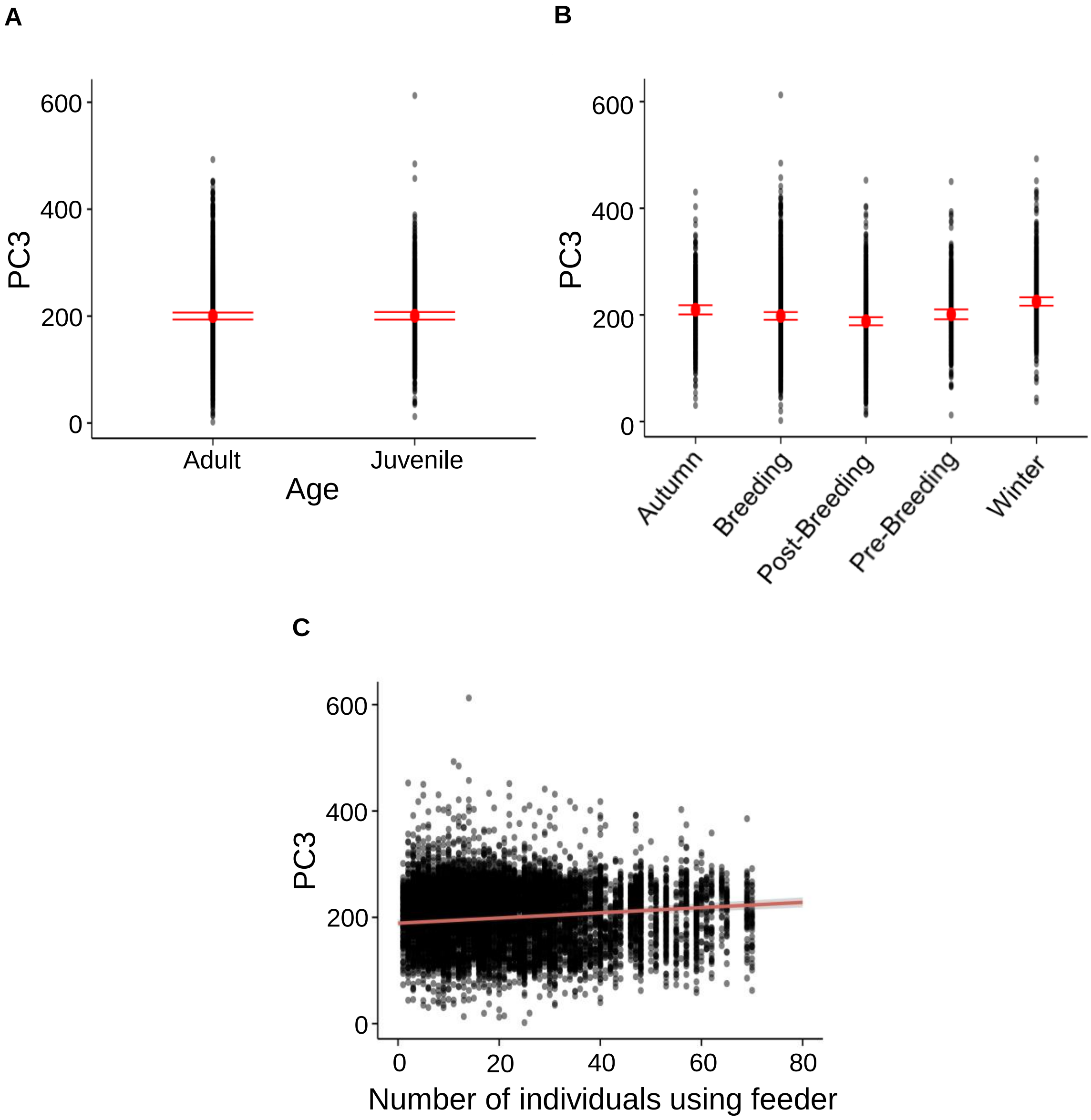

Fig. 5: Effect of age (**A**), season (**B**) and number of individuals using a given feeder per day (**C**) on adjusted values (Box-Cox transformation) for the third principal component. Fitted values and 95% confidence intervals (colour) are overlaid on the raw data.

consumption of supplementary food comprised a substantial portion of their diet. Usage variation is likely in part due to personality variation and differences in site fidelity. Jackdaws are known to be highly neophobic when presented with novel objects or food sources (Greggor *et al.*, 2016). Neophobia would influence the probability of an individual initially sampling a novel supplementary food source and subsequently becoming a regular user. Therefore, between-individual variation in neophobia may account for a proportion of the variation in supplementary food usage. However, low individual repeatability in feeder usage implies that individuals exhibit plasticity in the extent to which they bolster their diet with supplementary food from novel sources. Jackdaws also differ in their propensity to frequent the breeding sites at which the feeders were stationed. A few dozen individuals at each site are established breeders and visit a site throughout the year to maintain ownership of a nest box, but many more jackdaws visit the areas transiently during the breeding and immediate post-breeding periods. Differences in reliance on supplementary food between resident breeders and transient individuals may explain why jackdaws mainly differ in their tendency to use the feeders, rather than behavioural characteristics of their feeder visits.

Season did not influence individual daily feeder usage, but did influence the timing and duration of feeder visits. The energetic requirements of survival during the autumn and winter may necessitate consistent foraging throughout the course of the day (Bonter *et al.*, 2013), but the lack of an effect of season on overall usage means that seasonal variation cannot simply be the result of increased foraging effort in response to restriction of foraging time (i.e. Lewis *et al.*, 2004). Therefore, seasonal effects are likely an artefact of day length variation. Additionally, individuals were no more consistent in the aspects of their feeder usage within seasons than across seasons, suggesting that characteristics related to individual identity, such as personality, are not robust predictors of supplementary food usage. Low repeatability may be indicative of plasticity resulting from social modulation of individuals' responses to foraging risk. Jackdaws are more likely to use a novel food source following observation of another individual sampling it (Greggor *et al.*, 2016); this social effect should depress individual repeatability.

Age and sex both influenced jackdaw supplementary food usage. The sexes differ in their provisioning role, especially during the breeding season, when females occupy the nest whilst offspring are reared and are largely dependent upon the male (Henderson & Hart, 1993). Females may therefore be expected to exploit supplementary food sources in the post-breeding period to recover their condition; female jackdaws did use the feeders more than males, but the lack of support for a sex-by-season interaction in models of feeder usage rules this out as an interpretation for sex differences in usage. Adults used supplementary food more than juveniles, but it may be difficult to distinguish between adult and juvenile feeder usage, because juveniles are often provisioned by their parents following fledging (Goodwin, 1986). It was not possible to identify food sharing interactions, so the age difference in usage may reflect the differing foraging roles of parents and offspring.

The supplementary food at each feeder could be monopolized. Jackdaw groups have stable dominance hierarchies (Verhulst & Salomons, 2004; Verhulst *et al.*, 2014) and rank influences access to food sources, especially when resources are clumped (Henderson & Hart, 1995). Larger individuals used the feeders more, suggesting that greater body size increases a jackdaw's ability to monopolize supplementary food at feeders. Juveniles are consistently subordinate to adults (Verhulst *et al.*, 2014), so displacement resulting from dominance interactions could explain why juveniles occupied feeders for shorter periods than adults. Juveniles also tended to use feeders later in the day than adults, which is consistent with a social dominance effect if the majority of jackdaw foraging activity tends to be concentrated in the mornings, as may be expected according to recent work on the dynamics of patch discovery (Farine & Lang, 2013). Elucidating the precise influence of social factors on the dynamics of feeder visits would require experiments incorporating automated restriction of feeder access (i.e. Firth *et al.*, 2015a; Firth *et al.*, 2015b). For example, the age, sex or body size composition of foraging groups could be manipulated to explicitly test the role of dominance in determining foraging dynamics.

In conclusion, jackdaws vary in the extent to which they use supplementary food and the timing and duration of their foraging visits. However, individuals are inconsistent in all aspects of their foraging behaviour and support for effects of age, sex and factors related to social dominance on usage is minimal. Future work would benefit from explicit manipulation of feeder access to establish the influence of social interactions on fine-scale foraging dynamics.

Supplementary Material

Table S1: Example of feeder data format.

Time-Date Stamp	Tag	Antenna	Year	Feeder	Site
524075027	010C1194F9	02	2016	HENDRA	STITHIANS
524075028	010C1194F9	01	2016	HENDRA	STITHIANS
524075029	010C1194F9	01	2016	HENDRA	STITHIANS
524075030	010C1194F9	01	2016	HENDRA	STITHIANS
524075051	010C10C2EE	01	2016	HENDRA	STITHIANS
524075052	010C10C2EE	01	2016	HENDRA	STITHIANS
524075053	010C10C2EE	01	2016	HENDRA	STITHIANS

Table S2: PCA loadings

	PC1	PC2	PC3	PC4	PC5
SUM_TIME	0.380047	-0.02562	0.088291	-0.39164	0.253965
NUM_VISITS	0.272412	-0.14987	0.212903	-0.49164	0.339704
MIN_TIME	0.044483	0.273332	-0.30322	0.336039	0.627546
MAX_TIME	0.463909	0.119362	-0.07928	-0.02176	-0.00862
AVGE_TIME	0.348721	0.264493	-0.26181	0.269665	0.218192
SR_T_MEAN	0.061732	-0.47263	-0.42706	-0.01132	0.002434
SR_START	-0.06415	-0.28006	-0.57253	-0.06096	-0.09434
SS_END	-0.14904	0.553736	0.115081	-0.05003	-0.11881
SD_TIME	0.43824	0.087754	-0.0518	0.043378	-0.38378
T_SPREAD	0.215414	-0.33665	0.391138	0.289561	0.143902
AVGE_TCH	0.407568	0.106057	-0.07862	0.103054	-0.43304
AVGE_TDIFF_SP	0.088618	-0.27794	0.307941	0.562226	0.008015

Table S3: Model selection table for the third principal component (PC1). GLMM coefficients are listed for each continuous predictor in a model, otherwise the presence of a categorical term is indicated by “Y”. Models are ordered according to Akaike Information Criterion (AIC) and model retention was based on comparison of AIC (ΔAIC) to that of the best model; the best model (lowest AIC) was retained by default as were simpler (i.e. fewer terms) models with a ΔAIC of two or less.

Model description	**Intercept**	**AGE(JUV)**	**SEX(M)**	**TARSUS**	**SEASON**	**DAY_INDIV**	**SEASON*AGE**	**SEASON*SEX**	**logLik**	**AIC**
AGE, SEX, TARSUS & DAY_INDIV	0.203	-0.0114	-0.0136	0.00173		-0.000885			12876.6	-25731.2
EVERYTHING	0.202	-0.00334	-0.0226	0.00179	Y	-0.00088	Y	Y	12887.7	-25729.4
EVERYTHING EXCEPT SEASON*AGE	0.206	-0.0108	-0.0225	0.00175	Y	-0.000872		Y	12883.5	-25729
NO INTERACTIONS	0.202	-0.011	-0.0136	0.00175	Y	-0.000867			12878.1	-25726.1
EVERYTHING EXCEPT SEASON*SEX	0.198	-0.00381	-0.0135	0.00179	Y	-0.000875	Y		12882	-25726
AGE,TARSUS,DAY_INDIV	0.211	-0.0112		0.00136		-0.000887			12869.9	-25719.8
AGE,SEX,DAY_INDIV	0.276	-0.0118	-0.0107			-0.000884			12869.6	-25719.2
NO INTERACTIONS, NO TARSUS	0.276	-0.0114	-0.0106		Y	-0.000867			12871	-25713.9
AGE,DAY_INDIV	0.27	-0.0116				-0.000886			12865.5	-25713
SEX,TARSUS,DAY_INDIV	0.197		-0.0131	0.00181		-0.000876			12864.9	-25709.8
SEX, TARSUS, SEASON, DAY_INDIV	0.196		-0.013	0.00182	Y	-0.000856			12867.6	-25707.2
DAY_INDIV	0.268					-0.000878			12853.7	-25691.5
AGE,SEX,TARSUS	0.192	-0.01	-0.0138	0.00168					12765.8	-25511.7

Table S4: Model selection table for the third principal component (PC2). GLMM coefficients are listed for each continuous predictor in a model, otherwise the presence of a categorical term is indicated by “Y”. Models are ordered according to Akaike Information Criterion (AIC) and model retention was based on comparison of AIC (ΔAIC) to that of the best model; the best model (lowest AIC) was retained by default as were simpler (i.e. fewer terms) models with a ΔAIC of two or less.

Model description	Intercept	AGEJUV	SEXM	TARSUS	SEASON	DAY_INDIV	SEASON*AGE	SEASON*SEX	logLik	AIC
AGE, SEASON, DAY_INDIV, (SEASON*AGE)	2.6	-0.00383			Y	-0.00171	Y		-2134.9	4303.9
EVERYTHING EXCEPT SEX	2.54	-0.00345		0.00157	Y	-0.00171	Y		-2134.4	4304.8
EVERYTHING	2.53	-0.00214	0.0257	0.00139	Y	-0.00171	Y	Y	-2130.9	4307.9
SEASON, DAY_INDIV	2.6				Y	-0.00173			-2143.5	4310.9
TARSUS, SEASON, DAY_INDIV	2.52			0.00182	Y	-0.00174			-2142.7	4311.5
AGE, SEASON, DAY_INDIV	2.6	0.0039			Y	-0.00173			-2143.4	4312.8
NO INTERACTIONS, NO SEX	2.52	0.00464		0.00186	Y	-0.00173			-2142.6	4313.3
EVERYTHING EXCEPT AGE	2.52		0.0266	0.00158	Y	-0.00174		Y	-2139.4	4314.7
NO INTERACTIONS	2.52	0.00498	0.00673	0.00166	Y	-0.00174			-2142.5	4315

Table S5: Model selection table for the third principal component (PC3). GLMM coefficients are listed for each continuous predictor in a model, otherwise the presence of a categorical term is indicated by “Y”. Models are ordered according to Akaike Information Criterion (AIC) and model retention was based on comparison of AIC (ΔAIC) to that of the best model; the best model (lowest AIC) was retained by default as were simpler (i.e. fewer terms) models with a ΔAIC of two or less.

Model description	Intercept	AGEJUV	SEXM	TARSUS	SEASON	DAY_INDIV	(SEASON*AGE)	(SEASON*SEX)	logLik	AIC	ΔAIC	Retained?
AGE, SEASON, DAY_INDIV, SEASON*AGE	199	-5.84			Y	0.493	Y		-53402.4	106838.7	0	Y
AGE, TARSUS, SEASON, DAY_INDIV, SEASON*AGE	219	-5.93		-0.449	Y	0.494	Y		-53401.3	106838.7	0	
NO SEASON*SEX	219	-5.9	0.884	-0.472	Y	0.493	Y		-53401.3	106840.6	1.9	
EVERYTHING	223	-5.92	-4.93	-0.483	Y	0.495	Y	Y	-53398.3	106842.7	2.1	
AGE, TARSUS, SEASON, DAY_INDIV	221	0.0168		-0.524	Y	0.502			-53415.5	106859.1	16.4	
NO INTERACTIONS	221	0.0365	0.543		Y	0.502			-53415.5	106861	1.9	
AGE, SEASON, SEASON*AGE	201	-5.66			Y		Y		-53441.7	106915.4	54.4	

Random effects summary

Table S6: PC1 LMM random effects

Random effect	**Variance**	**% Variance**
ID	0.00055	10.54852321
DATE	0.000164	3.145377829
FEEDER	0.000194	3.720751822
SITE	0.000206	3.950901419
YEAR	0	0
Residual	0.0041	78.63444572

Table S7: PC1 LMM random effects

Random effect	**Variance**	**% Variance**
ID	0.00447	4.283677
DATE	0.0164	15.7164
FEEDER	0.00133	1.274562
SITE	0.0000792	0.075899
YEAR	0.0000704	0.067466
Residual	0.082	78.582

Table S8: PC1 LMM random effects

Random effect	**Variance**	**% Variance**
ID	239.3	7.502743377
DATE	411.31	12.89575169
FEEDER	52.13	1.634425459
SITE	0	0
YEAR	6.04	0.189371375
Residual	2480.72	77.7777081

Repeatability tables

Table S9: PC1 repeatability summary

SEASON	YEAR	R	SE	CI (LOW)	CI (HIGH)
BREEDING	2015	0.112	0.021	0.072	0.155
BREEDING	2016	0.176	0.024	0.132	0.222
BREEDING	ALL	0.139	0.017	0.108	0.172
POST-BREEDING	2015	0.229	0.029	0.17	0.288
POST-BREEDING	2016	0.183	0.037	0.109	0.254
POST-BREEDING	ALL	0.21	0.026	0.159	0.258
AUTUMN	2015	0.172	0.048	0.08	0.263
AUTUMN	2016	0.258	0.076	0.103	0.405
AUTUMN	ALL	0.2	0.042	0.118	0.279
WINTER	2015	0.235	0.068	0.098	0.374
WINTER	2016	0.168	0.037	0.1	0.246
WINTER	ALL	0.182	0.033	0.117	0.246
PRE-BREEDING	2015	0.186	0.143	0	0.496
PRE-BREEDING	2016	0.163	0.036	0.093	0.233
PRE-BREEDING	ALL	0.156	0.035	0.09	0.224
	2015	0.153	0.018	0.12	0.188
	2016	0.151	0.019	0.116	0.19
	ALL	0.151	0.015	0.122	0.181

Table S10: PC1 repeatability summary

SEASON	YEAR	R	SE	CI (LOW)	CI (HIGH)
BREEDING	2015	0.06	0.016	0.033	0.091
BREEDING	2016	0.048	0.012	0.025	0.074
BREEDING	ALL	0.049	0.01	0.032	0.069
POST-BREEDING	2015	0.057	0.018	0.022	0.097
POST-BREEDING	2016	0.118	0.03	0.062	0.177
POST-BREEDING	ALL	0.072	0.016	0.042	0.104
AUTUMN	2015	0.099	0.04	0.025	0.182
AUTUMN	2016	0.065	0.046	0	0.165
AUTUMN	ALL	0.084	0.03	0.029	0.143
WINTER	2015	0.105	0.051	0.015	0.218
WINTER	2016	0.112	0.03	0.054	0.171
WINTER	ALL	0.101	0.026	0.054	0.155
PRE-BREEDING	2015	0.079	0.118	0	0.382
PRE-BREEDING	2016	0.09	0.028	0.034	0.149
PRE-BREEDING	ALL	0.091	0.028	0.041	0.15
	2015	0.057	0.011	0.037	0.078
	2016	0.059	0.011	0.039	0.079
	ALL	0.046	0.007	0.033	0.06

Table S11: PC1 repeatability summary

SEASON	**YEAR**	**R**	**SE**	**CI (LOW)**	**CI (HIGH)**
BREEDING	2015	0.117	0.02	0.077	0.157
BREEDING	2016	0.081	0.016	0.05	0.111
BREEDING	ALL	0.088	0.013	0.064	0.113
POST-BREEDING	2015	0.101	0.023	0.06	0.149
POST-BREEDING	2016	0.113	0.028	0.059	0.168
POST-BREEDING	ALL	0.109	0.018	0.073	0.144
AUTUMN	2015	0.146	0.045	0.06	0.244
AUTUMN	2016	0.147	0.063	0.035	0.278
AUTUMN	ALL	0.142	0.036	0.073	0.215
WINTER	2015	0.129	0.055	0.02	0.234
WINTER	2016	0.081	0.026	0.034	0.134
WINTER	ALL	0.072	0.022	0.03	0.119
PRE-BREEDING	2015	0.005	0.087	0	0.285
PRE-BREEDING	2016	0.074	0.025	0.026	0.125
PRE-BREEDING	ALL	0.073	0.026	0.029	0.13
	2015	0.106	0.015	0.077	0.135
	2016	0.091	0.014	0.065	0.118
	ALL	0.09	0.011	0.07	0.112

Chapter Three: Causes and consequences of variation in jackdaw social network position

Abstract

Social structure can affect individual fitness and shape the evolution of social behaviour. Individuals vary in their position within the structure of their social group and this variation arises due to properties of individuals, such as personality traits, and a relationship between life history and social behaviour. Social network position formally quantifies an individual’s patterns of social interaction within the context of its social group’s structure, has been shown to co-vary with ‘personality’ traits and life history characteristics and can predict fitness. I investigated the causes and fitness consequences of variation in social network position during the breeding season in a wild population of jackdaws (*Corvus monedula*). Social networks were generated from records of visits of adult jackdaws fitted with Passive-Integrated Transponder (PIT) tags to automated feeders equipped with Radio-Frequency Identification (RFID) readers. I found a sex difference in social network position, with male jackdaws typically being more central in the social network than females. Greater network centrality was also associated with increased reproductive success in both sexes. However, the relationship between network position and fitness was complex, depending upon both sex and the specific social network metric investigated. The complexities of the relationship between social network position and fitness in jackdaws warrant further detailed investigation of the social processes driving variation in jackdaw social network position.

Introduction

An individual’s social environment may have notable effects on its fitness (Goodnight *et al*., 1992; Moore *et al*., 1997; Wolf *et al*., 1999). To maximize fitness, individuals must make appropriate decisions regarding when and how to interact with conspecifics (Taborsky & Oliveira, 2012). Individuals vary in their propensity to engage in social interactions (Sih *et al*., 2004; Wolf & Weissing, 2012; Wolf & McNamara, 2013) and an individual’s social phenotype can be highly repeatable (e.g. Aplin *et al*., 2015) and may be considered a ‘personality’ trait (Krause *et al*., 2010; Wilson *et al*., 2013). Patterns of social behaviour may also differ depending upon life history characteristics, such as age (Stamps & Groothuis, 2010), sex (Schuett *et al*., 2010) or social context (Webster & Ward, 2011). The diversity of individual social phenotypes within a social group therefore influences social structure. In turn, social structure can dictate the fitness consequences of an individual’s social behaviour (e.g. Farine *et al*., 2015). Understanding the evolutionary trajectory of social behaviour therefore requires consideration of the relationship between an individual’s fitness and its position within the structure of its social group.

Social network analysis is a useful framework for evaluating social structure. Animal social networks usually display non-random structure (Croft *et al*., 2008), such that individuals vary in their position within the network. Certain individuals are peripheral, engaging infrequently in social interactions, whilst others are more active socially, so are more central (e.g. Flack *et al*., 2006; Wey & Blumstein, 2010; Madden *et al*., 2011). Several causes of inter-individual variation in network position have been identified (Pinter-Wollman *et al*., 2013). Changes in social behaviour can occur as an individual ages, creating a link between life history stage and network position (e.g. McDonald, 2007; Turner *et al*., 2018). Network position can also vary according to sex (e.g. Wey *et al*., 2013) and social rank (e.g. Sueur *et al*., 2010). Finally, Individual network position can be determined by ‘personality traits’ (e.g. Aplin *et al*., 2012), which may in part explain why network position has been found to be both repeatable (Aplin *et al*., 2015) and heritable (Lea *et al*., 2010; Brent *et al*., 2013). Consequently, social network position may be under selection, so knowledge of the relationship between network position and fitness is required to understand the selection pressures acting on social structure.

Agonistic and affiliative social interactions can have direct fitness consequences. For instance, Silk and co-workers (2003) found that more frequent participation in grooming interactions benefited adult females due to an increased probability of offspring survival. Inspection of social network position can reveal indirect relationships between sociality and fitness (Brent, 2015), such as the influence of social connectivity on an individual’s exposure to disease (e.g. Hamede *et al*., 2009; Weber *et al*., 2013), that may not be determinable from an analysis restricted to the level of the dyad. A link between social network position and survival, either of an individual or its offspring, has been found in several species. Brent and co-workers (2013) found that both interaction and association patterns predicted fitness in rhesus macaques (*Macaca mulatta*), with more central individuals in a network of proximity benefitting due to increased probability of offspring survival. The fitness consequences of social network position may also depend upon life history characteristics. For example, Stanton and Mann (2012) discovered that greater network centrality predicted future survival of juvenile male bottlenose dolphins (*Tursiops* sp.), but did not find such a relationship for females. The potentially complex relationship between life history, network position and fitness necessitates the collection of detailed life history and social association data from wild populations.

Automated data collection can enable the collection of large datasets of fine-scale individual space use (Bonter & Bridge, 2011; Krause *et al.*, 2013; Dell *et al.*, 2014; Kays *et al.*, 2015). The generation of robust social networks from these datasets is then achieved by the application of machine learning techniques (Psorakis *et al*., 2012; Psorakis *et al*., 2015; Valletta *et al*., 2017). The state-of-the-art for such practices has been established from analysis of the association patterns of wild great tits (*Parus major*) fitted with Passive-Integrated Transponder (PIT) tags during foraging visits to automated feeders (e.g. Farine *et al*., 2015). Farine and Sheldon (2015) used social networks generated from the automated feeder data to demonstrate that social network structure predicts great tit breeding patterns. Furthermore, variation in great tit social network position can be explained by personality traits (Aplin *et al*., 2013), individual network position is highly repeatable (Aplin *et al*., 2015) and it is related to an individual's probability of discovering and utilizing novel food sources (Aplin *et al*., 2012). Automated feeder data can generate social networks for wild populations in unprecedented detail, but to date has not been used to examine the relation between individual fitness and patterns of social behaviour.

I used a system of automated feeders to study the causes and consequences of variation in social network position in wild adult jackdaws. Jackdaws are highly social, semi-colonial birds of the corvid family (Roell, 1978). They frequently associate during foraging, so agonistic (Henderson & Hart, 1995; Verhulst & Salomons, 2004; Verhulst *et al.*, 2014) and affiliative interactions commonly occur (Wechsler, 1989; de Kort *et al.*, 2006; von Bayern *et al.*, 2007). Jackdaws are monogamous (Henderson *et al.*, 2000) and both members of a pair provision their offspring during the breeding season, though the male occupies the primary provisioning role (Henderson & Hart, 1993). Furthermore, parents continue to associate with their offspring in the months following fledging (Goodwin, 1986). I examined whether sex and body size influence social network position in adult jackdaws, the repeatability of network position at the level of the individual and the pair, and whether social network position during the breeding season predicts reproductive success, as quantified by the number of offspring surviving to independence. I predict that all aspects of network centrality are highly repeatable at the level of the individual. Furthermore, pair members have similar network position, such that there is high repeatability of network position at the level of the pair. Finally, I expect greater network centrality to be associated with increased reproductive output for both sexes.

Methods

Study population and automated feeders

The two breeding sites in west Cornwall (Stithians (N 50°11’25.98’’, W 5°10’49.00’’) and Pencoose Farm, TR3 7DN (N 50°11’55.37’’, W 5°10’7.48’’)) contained 40-50 nest boxes each, which jackdaw pairs occupied during the breeding season. Each nest box was monitored every 1-2 days during the breeding season, such that the number of eggs, chicks and fledged offspring from a box were accurately recorded. Adult jackdaws were ringed after trapping during the breeding and post-breeding time periods, using nest-box trap doors or large walk-in traps. Measurements of structural body size (tarsus length) and body mass were taken during ringing. Four rings were fitted, comprising three coloured rings, of which one contained a Passive-Integrated Transponder (PIT) tag, and a metal ring inscribed with a British Trust for Ornithology code. Blood samples extracted during foraging were subsequently used for molecular-sexing (Griffiths *et al.*, 1998) to confirm the sex of each individual, as jackdaws are sexually monomorphic. Three PIT tag-detecting feeders were placed at each of the breeding sites and were operational between April 2015 and March 2017. Feeders were active between 05:30 and 20:30, during which time jackdaws could feed on mixed corn *ad libitum*. When the feeding perch was occupied by a ringed jackdaw, bird's identity and the current date and time were recorded every 100ms by an IBT EM4102 RFID data logger powered by six C-cell batteries (see Chapter 2 for details).

Ethical Statement

Experimental work complied with the guidelines of the Association for the study of Animal Behaviour (ASAB) and the University of Exeter Biosciences Ethics committee (2014/577) and bird ringing procedures were covered by Home Office (PPL 80/2371) and British Trust for Ornithology (C6079, C5752, C5746) licenses.

Network Centrality Measures

I applied a machine learning technique (Psorakis *et al*., 2012; Psorakis *et al.*, 2015) to the raw data from the data loggers to detect associations between jackdaws. For each combination of associates, the 'simple ratio' index of association strength was calculated (Cairns & Schwager, 1987; Ginsberg & Young, 1992). The calculation was performed by dividing the number of feeding events in which both individuals were observed by the total number of feeding events both individuals participated in (Cairns & Schwager, 1987; Ginsberg & Young, 1992). These calculations were done for each of six sampling periods of sixty days, representing the major annual life history periods of adult jackdaws (Pre-Spring, Pre-Breeding, Breeding, Post-Breeding, Autumn, Post-Autumn). This generated six weighted, undirected social networks per site per year. The R package ‘asnipe’ (Farine, 2013) was used for the detection of feeding events and generation of social networks.

Multiple measures of centrality were calculated for each individual in each social network. The measures *Degree*, *Strength* (weighted degree), weighted *Betweenness*, weighted *Eigenvector Centrality* (Freeman, 1979; Friedkin, 1991) and *Social Differentiation* (Whitehead, 2008) were calculated for each individual in each network (Fig. 1). *Degree* and *Strength* are simple measures of gregariousness (Farine & Whitehead, 2015), quantifying an individual’s number of associates and the total strength of an individual’s associations respectively. *Eigenvector Centrality* is a measure that accounts for the centrality of individual’s associates; an individual can have high *Eigenvector Centrality* either by having high *Degree*/*Strength* or by associating with individuals with high *Degree*/*Strength*. *Betweenness* measures the number of shortest paths between vertices that pass through a vertex. Centrality measures typically quantify the number of connections originating from or passing through a node, so characterize the structure of a node’s neighbourhood (Bonacich, 1987). *Social Differentiation* quantifies the variation in strength of a nodes associations, so determines the extent to which a nodes interactions within its neighbourhood are uniform (Whitehead, 2008). *Social Differentiation* is calculated as the coefficient of variation of the strength of an individual’s associations and is a measure of whether the individual associates indiscriminately or with certain preferred individuals (Whitehead, 2008; Boogert *et al.*, 2014). All network centrality measures were normalized to control for variation in group size and were calculated using the R package ‘igraph’ (Csardi & Nepusz, 2006).

Linear Mixed Models (LMMs)

I used Linear mixed models (LMMs) to determine the effect of life history characteristics on social network position and the influence of social network position on reproductive success. Due to the non-independence of network data, which violates the assumptions of LMMs, the significance of fixed effects was assessed by permutation tests (Croft *et al*., 2011; Boogert *et al.*, 2014; Farine & Whitehead, 2015; Farine, 2017). A thousand permuted networks were generated for each sampling period via data stream permutation (Bejder *et al*., 1998) and centrality measures were extracted from the resulting networks. The permutation process consisted of swapping the feeding event memberships of a pair of individuals (one pair swapped per permutation), with swaps constrained to occur within the daily data stream of each feeder, causing randomization of associations between individuals whilst preserving the gross structure of the data (Bejder *et al.*, 1998; Whitehead, 1999; Whitehead *et al*., 2005; Sundaresan *et al*., 2009). LMMs were then fitted for each centrality measures using each permuted dataset and the fixed effects coefficients were extracted. P-values for each fixed effect were calculated by dividing the number of permuted LMM coefficients of greater (absolute) magnitude than the un-permuted LMM coefficient by the number of permutations performed (as per Equation 2 in Ruxton & Neuhäuser, 2013).

I used centrality measures as response variables in LMMs to determine the effect of life history on social network position. A separate LMM was therefore run for each centrality measure, with tarsus length (an estimate of skeletal body size: Henderson, 1991), sex and site fitted as fixed effects in each of the models. Individual identity and season nested within year were fitted as random effects. In addition, the repeatability of social network position at both the individual and

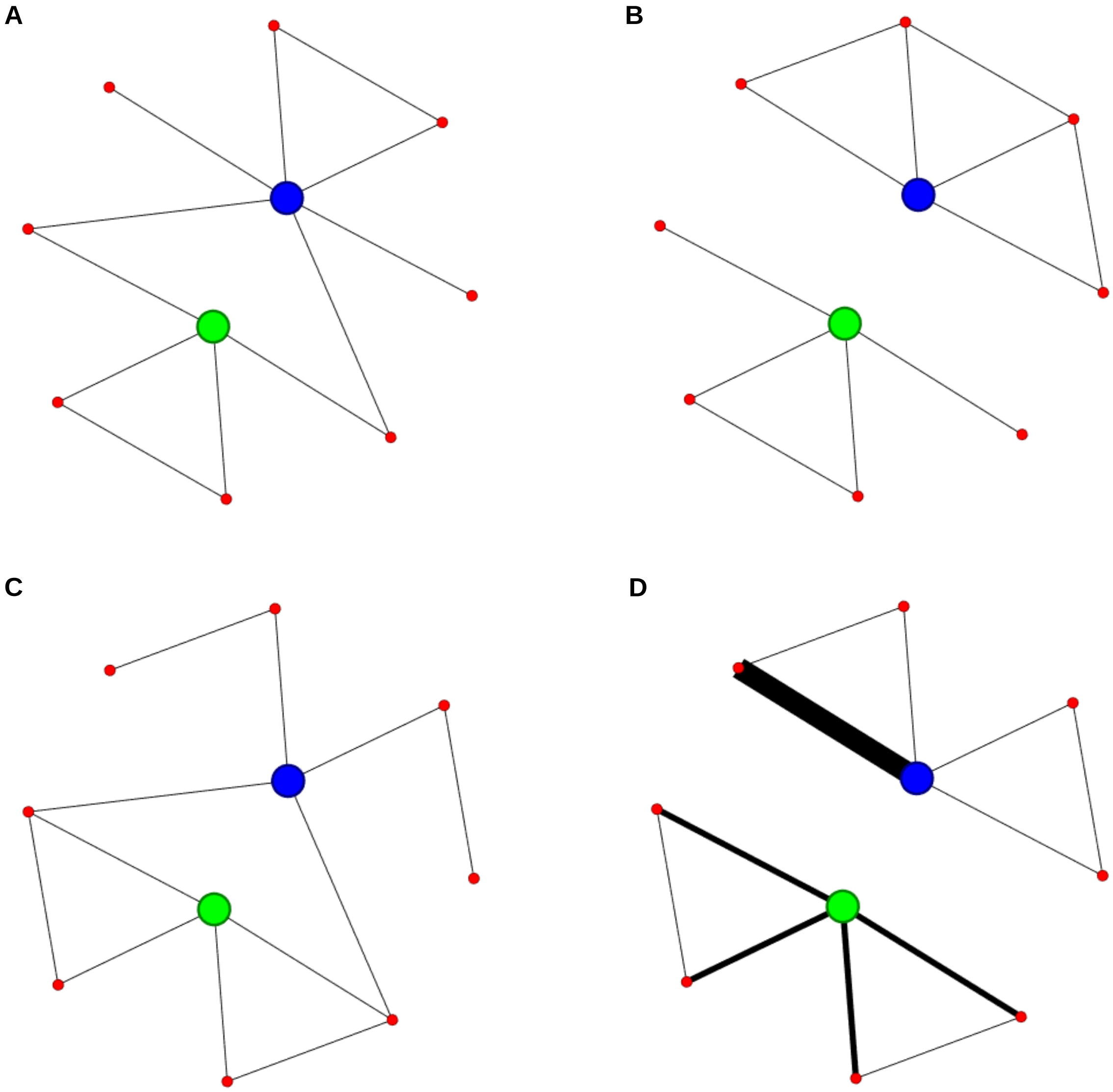

Fig. 1: Illustration of measures of network centrality and social differentiation. Each graph contains ten nodes and twelve edges; edge width indicates association strength. In each graph, the blue node possesses a higher value than the green node for the stated network metric. *Degree* and *Strength* (**A**) – The number of associates (*Degree*), or the total associative strength (*Strength*), for a given node. *Eigenvector Centrality* (**B**) – A node's total associative strength, weighted by the associative strength of its associates. *Betweenness* (**C**) – The number of shortest paths between two nodes that pass through a given node. *Social Differentiation* (**D**) – The coefficient of variation of a given node's edge weights.

pair level was determined from calculation of intra-class correlation (ICC) (Nakagawa & Schielzeth, 2010) using the R package rptR (Stoffel *et al*., 2017).

To determine the effect of social network position on reproductive success, I used centrality measures as fixed effects in LMMs. The centrality measures used were extracted from breeding season networks only. Reproductive success was quantified as the number of offspring successfully fledged in a given year. Separate analyses were run for males and females to boost the sample sizes by enabling the inclusion of individuals with an un-ringed partner and to avoid issues of pseudo-replication. Tarsus length, year and total time spent on feeders during the relevant breeding season were also fitted as fixed effects. Individual identity was fitted as a random effect. Measures of centrality are often correlated (Farine & Whitehead, 2015) and inspection of variance inflation factors (VIFs; Zuur *et al*., 2010) from LMMs containing the centrality measures indicated that *Degree*, *Strength* and *Eigenvector Centrality* were multi-collinear. Consequently, I removed *Degree* and *Strength* from the analyses and fitted *Eigenvector Centrality*, *Betweenness* and *Social Differentiation* as fixed effects.

Results

Adult social network position

There was no significant effect of sex or body size on any aspect of adult social network position (Supp. Mat. *Network Position LMM tables*). Individual identity explained a moderate proportion of the variation in *Degree, Social Differentiation*; whereas season and year explained a large proportion of the variation in *Strength* (Supp. Mat. *Network Position LMM tables*). *Social Differentiation* and *Degree* were highly repeatable at the level of the individual, whilst *Eigenvector Centrality* and *Betweenness* were moderately repeatable and *Strength* was not repeatable

(Table S6). Pair-level repeatability was low to moderate for *Social Differentiation*, *Degree and Eigenvector Centrality*, but low for other measures of network position (Table S7). The structure of social networks also appeared to differ between the two study sites, as there was a difference in *Betweenness* (*Betweenness* LMM: β = 0.00592, S.E. = 0.00251, t = 2.36, p (perm) = 0.026), though this effect was found to be non-significant after Bonferroni correction for multiple testing (adjusted p-value threshold = 0.0125).

Predictors of reproductive success

Larger males produced more fledged offspring (Fig. 2A; LMM: β = 0.0459, S.E. = 0.087, t = 0.527, p (perm) < 0.001), but body size was negatively related to number of offspring fledged for adult females (Fig. 3A; LMM: β = -0.141, S.E. = 0.103, t = -1.37, p (perm) < 0.001). A greater amount of time spent on feeders during the breeding season was associated with reduced reproductive success for females (Fig. 3B; LMM: β = -0.000695, S.E. = 0.00126, t = -0.55, p (perm) < 0.001) but not males (LMM: β = 0.000422, S.E. = 0.0106, t = 0.397, p (perm) = 1). Individuals' breeding success was also influenced by aspects of their social network position. Specifically, greater *Eigenvector Centrality* (Fig. 3C; LMM: β = 0.782, S.E. = 0.562, t = 1.39, p (perm) < 0.001) and *Betweenness* (Fig. 3D; LMM: β = 1.14, S.E. = 2.46, t = 0.463, p (perm) < 0.001) during the breeding season predicted greater numbers of fledged offspring for females. Greater *Eigenvector Centrality* was also linked to greater male reproductive success for males (Fig. 2B; LMM: β = 0.97, S.E. = 0.549, t = 1.77, p (perm) < 0.001), but in contrast to females, greater male *Betweenness* was associated with fewer numbers of fledged offspring (Fig. 2C; LMM: β = -1.41, S.E. = 4.52, t = -0.312, p (perm) < 0.001). For both males (LMM: β = 0.00883, S.E. = 0.403, t = 0.022, p (perm) =

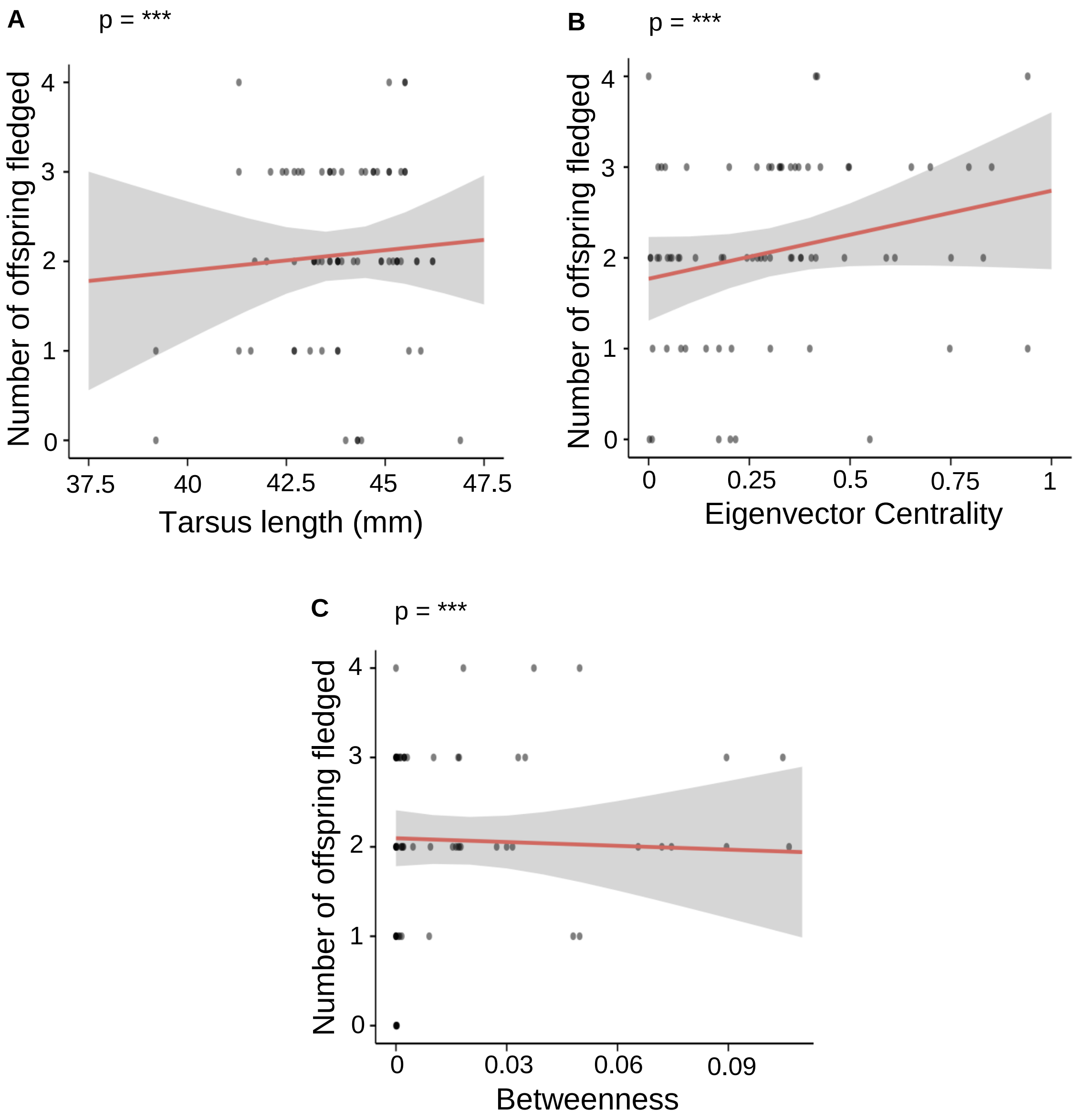

Fig. 2: Effect of tarsus length (**A**), *Eigenvector Centrality* (**B**) and *Betweenness* (**C**) and on number of offspring fledged by male jackdaws. *Eigenvector Centrality* and *Betweenness* scores were derived from a social network of association during the breeding season. Fitted values from GLMs and 95% confidence intervals (colour) are plotted over the raw data. The significance of effects, as calculated from permutation tests, is indicated symbolically (p<0.05: *; p<0.01: **; p<0.001: ***; p>0.05: N.S.).

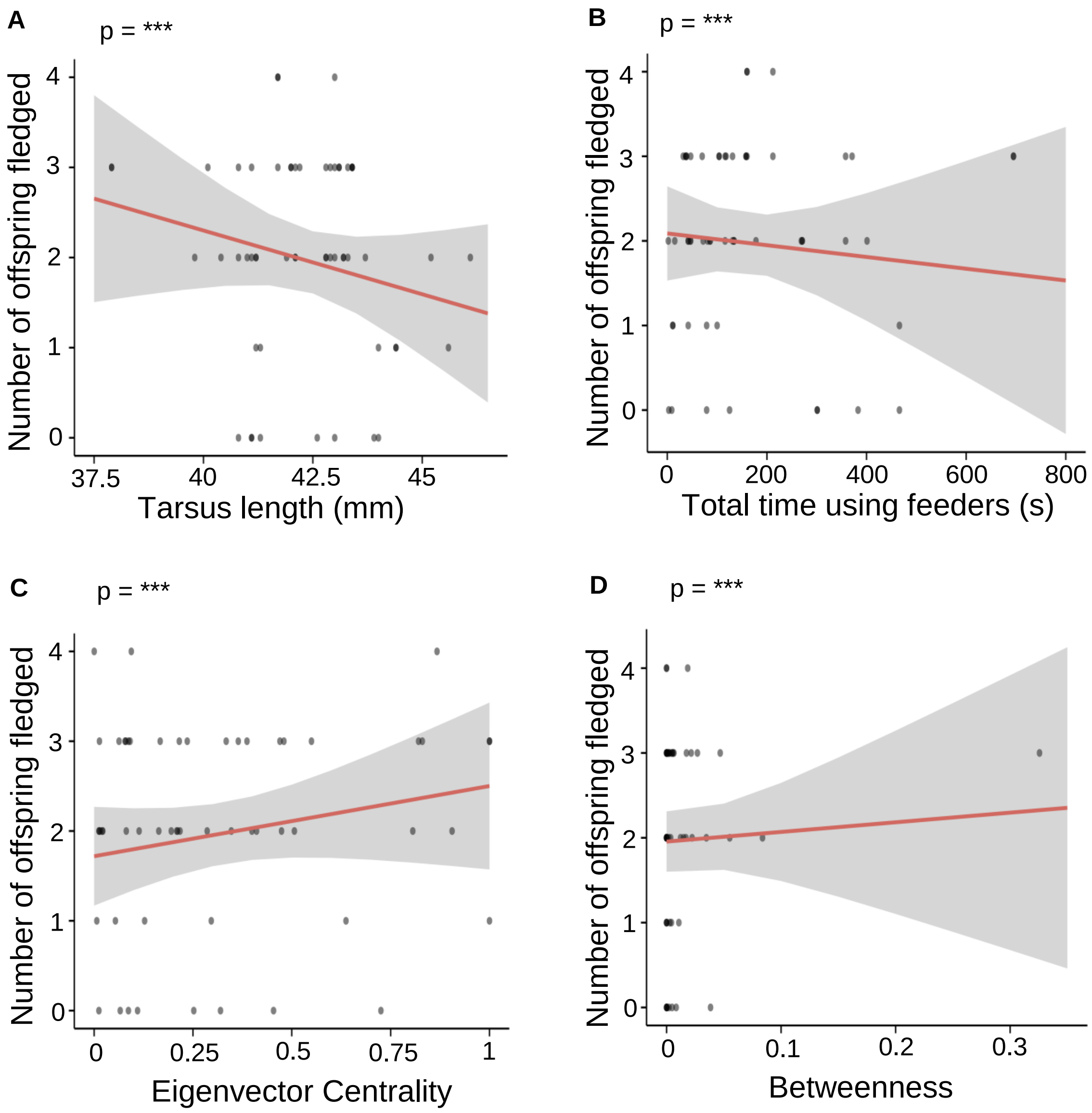

Fig. 3: Effect of tarsus length (**A**), total time using feeders (**B**), *Eigenvector Centrality* (**C**) and *Betweenness* (**D**) on number of offspring fledged by female jackdaws. *Eigenvector Centrality* and *Betweenness* scores were calculated from a social network of association for the breeding season. Fitted values from GLMs and 95% confidence intervals (colour) are plotted over the raw data. The significance of effects, as calculated from permutation tests, is indicated symbolically (p<0.05: *; p<0.01: **; p<0.001: ***; p>0.05: N.S.).

0.944) and females (LMM: β = -0.322, S.E. = 0.3, t = -1.07, p (perm) = 0.074), *Social Differentiation* was not linked to reproductive success. There were no significant differences between years in number of offspring fledged, but there were differences between sites (Table S8; Table S9). In addition, individual identity explained a large proportion of between-individual variation (75%) in female reproductive success and a substantial proportion (37.6%) of variation in male reproductive success (Table S8; Table S9).

Discussion

Jackdaws are amongst the most social of corvid species. Here I show that adult jackdaws' position within their social networks affects reproductive success for both sexes. Although an individual's position within the social network was unrelated to its sex and body size, individuals were relatively consistent in some aspects of their social network position, with both *Social Differentiation* and *Degree* showing moderate repeatability. Additionally, pair members shared some similarities in network position, though repeatability at the level of the pair was lower than for individuals. Network positions also influenced individuals' reproductive success, although the direction of effects was not always consistent between the sexes. While greater *Eigenvector Centrality* was associated with increased reproductive success in both sexes, greater *Betweenness* had positive effects on reproductive success for females and negative effects for males. Moreover, while larger males produced more fledged offspring, body size had the opposite effect for females. Females' success was also linked to their usage of feeders, with individuals that spent more time on the feeders producing fewer offspring.

My results highlight consistent differences between individuals in social network position. Individual identity explained a substantial portion of variation in social network position, particularly for *Degree* and *Social Differentiation*. While levels of individual repeatability for *Degree* were lower than those reported in a similar study of great tits (Aplin *et al.*, 2015), they were not negligible, suggesting that general gregariousness may be an innate property of an individual, likely determined by 'personality' (see Wilson *et al*., 2013). Repeatability was considerably higher for *Social Differentiation*, which measures an individual's tendency to differentiate between social partners. This outcome could be an indicator of variation in the strength of key relationships. Individuals that spend the majority of their foraging time with their partner would exhibit higher *Social Differentiation* than those that engage in transient associations, perhaps due to foraging alone or being unpaired. This interpretation is supported by the finding that the repeatability of *Social Differentiation* was non-negligible at the level of the pair, suggesting that aspects of partners' network position are coupled.

Sex was not a significant predictor of social network position, but social network position had differing effects on the reproductive success of males and females. For females, greater network centrality unequivocally leads to greater reproductive success. However, the direction of the effect on male fitness depends upon the measure of network centrality: *Eigenvector* centrality was positively correlated with reproductive success, while *Betweenness* had a negative effect. For males, it is therefore beneficial to be central and well connected within the social group, but not to be an individual that connects otherwise unconnected social units. This could indicate a benefit to participating primarily in within-group, rather than between-group, social interactions, perhaps due to the existence of stable dominance hierarchies in social groups. Sex-dependent effects of social network position on fitness, specifically mortality risk, have been found for dolphins (Stanton & Mann, 2012) and killer whales (Ellis *et al*., 2017). Differential effects of network position on fitness across sexes suggest that selection on sociality may operate differently in the two sexes, perhaps due to sexual selection (e.g. Oh & Badyaev, 2010). Understanding the underlying biological cause of the relationship between social network position and reproductive success in jackdaws will require further investigation of the nature of the social processes that each measure of centrality represents (i.e. Firth *et al*., 2017) and the interactions between measures (Brent, 2015; Farine & Whitehead, 2015).

My work also highlights the potential relationship between reliance on anthropogenic food sources and reproductive success. In some cases, supplementary food usage predicts poorer subsequent reproductive success (Plummer *et al*., 2013), though the opposite relationship has also been observed (e.g. Crates *et al*., 2016). I found that female jackdaws that spent more time on feeders in the breeding season produced fewer fledged offspring. Young jackdaw nestlings, like other passerines, cannot regulate their body temperature and are reliant on their mother for incubation, who in turn depends on her partner to supply her with food while incubating (Henderson & Hart, 1993). Extensive feeder usage by females during the breeding season could therefore be an indicator of time spent away from the nest, which likely has a negative effect on offspring condition (e.g. Rensel *et al*., 2010). Female reproductive success was also affected by body size, as smaller females fledged more offspring. Although this seems superficially counter-intuitive, it is worth noting that the measure of number of fledged offspring does not account for offspring quality (i.e. mass/size), so perhaps small females produce more chicks of lower quality (e.g. Smith *et al*., 1989). Given that female identity accounted for the majority of variation in reproductive success, it is highly likely that other, unmeasured aspects of females' individual characteristics, as well as the quality of their pair-bond partner, have important effects on their ability to successfully rear offspring.

In summary, I found consistent differences between individuals and sexes in jackdaw network position. My results also provide important insights into the determinants of fitness in a wild bird population, particularly the impact of social network position on reproductive success. These results have important implications for understanding the action of selection on variation in social behaviour in complex animal societies.

Supplementary Material

Network Position LMM tables

Table S1: Fixed and random effects summary for *Degree* LMM

Fixed Effect	**Coefficient**	**SE**	**t-value**	**p (perm)**
Tarsus	0.00133	0.00441	0.301	0.133
Sex (M)	0.0371	0.0147	2.52	0.725
Site	0.0439	0.0121	0.363	0.756

Random Effect	**Variance**	**% Variance**
ID	0.00796	25.2
Year	0.00288	9.1
Season	0.00361	11.4
Residual	0.0172	54.3

Table S2: Fixed and random effects summary for *Strength* LMM

Fixed Effect	**Coefficient**	**SE**	**t-value**	**p (perm)**
Tarsus	0.000412	0.000607	0.678	0.455
Sex (M)	0.00214	0.002	1.07	0.92
Site	-0.00116	0.00178	-0.65	0.693

Random Effect	**Variance**	**% Variance**
ID	0.0000556	0.873
Year	0.00371	58.2
Season	0.00196	30.8
Residual	0.000645	10.1

Table S3: Fixed and random effects summary for *Eigenvector Centrality* LMM

Fixed Effect	Coefficient	SE	t-value	p (perm)
Tarsus	0.00525	0.00549	0.955	0.096
Sex (M)	-0.00771	0.0182	-0.423	0.86
Site	0.0917	0.0157	5.83	0.259

Random Effect	Variance	% Variance
ID	0.00834	12.2
Year	0.00996	14.6
Season	0.0111	16.3
Residual	0.0388	56.9

Table S4: Fixed and random effects summary for *Betweenness* LMM

Fixed Effect	Coefficient	SE	t-value	p (perm)
Tarsus	0.000787	0.000868	0.907	0.267
Sex (M)	0.0049	0.00287	1.71	0.709
Site	0.00592	0.00251	2.36	0.026

Random Effect	Variance	% Variance
ID	0.000172	12.3
Year	0	0
Season	0.000128	9.14
Residual	0.0011	78.6

Table S5: Fixed and random effects summary for *Social Differentiation* LMM

Fixed Effect	**Coefficient**	**SE**	**t-value**	**p (perm)**
Tarsus	0.00184	0.0106	0.173	0.898
Sex (M)	-0.04	0.0354	-1.13	1
Site	0.0732	0.0301	2.43	0.132

Random Effect	**Variance**	**% Variance**
ID	0.036	19.8
Year	0.0000374	0.0205
Season	0.016	8.79
Residual	0.13	71.4

Repeatability tables

Table S6: Summary of individual-level repeatability for each measure of social network position.

Response Variable	R	SE	CI (LOWER)	CI (UPPER)
Social Differentiation	0.354	0.04	0.277	0.427
Eigenvector Centrality	0.182	0.045	0.099	0.275
Betweenness	0.137	0.037	0.072	0.214
Strength	0.006	0.008	0.001	0.031
Degree	0.299	0.055	0.187	0.405

Table S7: Summary of pair-level repeatability for each measure of social network position.

Response Variable	R	SE	CI (LOWER)	CI (UPPER)
Social Differentiation	0.121	0.054	0.021	0.235
Eigenvector Centrality	0.16	0.06	0.057	0.286
Betweenness	0.088	0.049	0	0.193
Strength	0.026	0.02	0	0.081
Degree	0.199	0.074	0.079	0.361

Reproductive Success LMM tables

Table S8: Fixed and random effects summary for male reproductive success LMM

Fixed Effect	**Coefficient**	**SE**	**t-value**	**p (perm)**
Site (STITHIANS)	-0.0818	0.23	-0.356	**<0.001**
Year (2016)	-0.291	0.203	-1.44	0.81
Tot_Time	0.000422	0.0106	0.397	1
Tarsus	0.0459	0.087	0.527	**<0.001**
EV_Centrality	0.97	0.549	1.77	**<0.001**
Betweenness	-1.41	4.52	-0.312	**<0.001**
Soc_Diff	0.00883	0.403	0.022	0.944

Random effect	**Variance**	**% Variance**
Name	0.308	37.6
Residual	0.511	62.4

Table S9: Fixed and random effects summary for male reproductive success LMM

Fixed Effect	**Coefficient**	**SE**	**t-value**	**p (perm)**
Site (STITHIANS)	-0.154	0.284	-0.543	**<0.001**
Year (2016)	-0.019	0.201	-0.094	1
Tot_Time	-0.000695	0.00126	-0.55	**<0.001**
Tarsus	-0.141	0.103	-1.37	**<0.001**
EV_Centrality	0.782	0.562	1.39	**<0.001**
Betweenness	1.14	2.46	0.463	**<0.001**
Soc_Diff	-0.322	0.3	-1.07	0.074

Random effect	**Variance**	**% Variance**
Name	0.8	75
Residual	0.267	25

Chapter Four: Developmental plasticity of jackdaw social network position

Abstract

Stress experienced during early development may have lasting effects on behaviour. Early life stress is linked to poor parental provisioning and high levels of sibling competition and can have profound effects on personality and social motivation, thereby influencing the patterns and nature of individuals' social interactions. Evidence for a lasting effect of developmental stress on patterns of social association has been found in captive systems, but to date this relationship has not been investigated in wild populations. Quantification of an individual's patterns of social behaviour is best achieved through examination of social network position. Social network position has important consequences for individual fitness and has been shown to be associated with personality, so is a crucial tool for the study of plasticity in social behaviour. I investigated the influence of developmental conditions on juvenile jackdaws' social network position using data collected from automated feeders. I found that sibling competition during early development is associated with more peripheral social network positions for juvenile jackdaws. Similarly, a juvenile's growth trajectory during early life decreases its network centrality and also reduces its tendency to favour particular social partners when associating at feeders. This is the first evidence of developmental plasticity of social network position in a wild population.

Introduction

Developmental conditions can have long-term effects on physiology, cognition and behaviour (Monaghan, 2008; Buchanan *et al*., 2013; Spencer, 2017). Inadequate nutrition (Metcalfe & Monaghan, 2001), parental separation (e.g. Rensel *et al*., 2010) and sibling competition (e.g. Greggor *et al*., 2017) are causes of stress during early life. Developmental stress can induce lasting changes in an organism's physiology (e.g. Criscuolo *et al*., 2008; Ahmed *et al*., 2014) and can have profound effects on social behaviour (e.g. Spencer & Verhulst, 2007), generally tending to decrease social motivation and increase aggression (Spencer, 2017). The great majority of research into the downstream behavioural consequences of early life stress has been conducted in captivity, so the effects of developmental conditions on the behaviour of wild animals are poorly understood. Studying the social effects of developmental stress in natural conditions is necessary to determine whether stress-induced changes in social behaviour are adaptive.

Tracking the effect of early life stress on social behaviour requires investigation of individuals' patterns of social association and interaction. Social network analysis enables the assessment of an individual's patterns of social behaviour whilst taking into account its social group structure (Croft *et al*., 2008). Individual social network position can be quantified in a number of ways, each capturing a different aspect of sociality (Brent, 2015). For example, summation of an individual's number of social relationships (*Degree*) or total social time (*Strength*) provide simple measures of gregariousness (Wey *et al*., 2008). More sophisticated measures of network position (e.g. *Eigenvector Centrality, Betweenness*), that incorporate indirect social relationships, can indicate an individual's importance for the transmission of disease (e.g. Hamede *et al*., 2009; Weber *et al*., 2013) or information (e.g. Aplin *et al*., 2012) through its social group. Finally, social network position has been found to correlate with fitness measures in a range of species (e.g. McDonald, 2007; Formica *et al*., 2011; Stanton & Mann, 2012; Gilby *et al*., 2013), so developmental plasticity of network position may have notable fitness consequences.

Recent evidence suggests that social network position can be affected by developmental conditions (Boogert *et al*., 2014). Boogert and co-workers (2014) used a system of automated feeders, equipped with Radio-Frequency Identification (RFID) apparatus (see Bonter & Bridge, 2011), to record the feeding bouts of captive zebra finches (*Taeniopygia guttata*). Robust social networks of association at feeders were generated from data collected from the RFID data loggers using a machine learning method (Psorakis *et al*., 2012; Psorakis *et al.*, 2015) and the social network positions of juvenile zebra finches treated with avian stress hormone (Corticosterone) were compared to those of a control group (Boogert *et al.*, 2014). Boogert and co-workers (2014) found that stressed juveniles were less likely to associate with their parents and associated indiscriminately with a greater number of individuals, resulting in occupation of more central social network positions. This study established a clear link between developmental stress and social network position in a captive setting, but this relationship has yet to be investigated in wild populations.

To determine how early life conditions influence social network positions in free-ranging populations, I analysed longitudinal changes in the social network positions of wild jackdaws (*Corvus monedula*). Social interactions are likely to play a critical role in governing jackdaws' access to resources. For instance, jackdaws are typically highly neophobic when confronted with novelty in a foraging context, but social information may allow individuals to overcome neophobia and take advantage of novel foraging opportunities (Greggor *et al.*, 2016). Social interactions also occur during foraging, particularly dominance interactions (Henderson & Hart, 1995; Verhulst & Salomons, 2004; Verhulst *et al.*, 2014) and food sharing between partners (de Kort *et al.*, 2006; von Bayern *et al.*, 2007). However, despite their importance, little is known about how patterns of social association develop, and whether they may be influenced by early life conditions. Jackdaw pairs show long-term monogamy (Henderson *et al.*, 2000) and lay a single clutch each year, with asynchronous hatching (Arnold & Griffiths, 2003). Corticosterone levels are greater in chicks from larger clutches, presumably as a result of elevated competition (Greggor *et al.* 2017). Given evidence from captive studies on other species linking stress levels in early life to later social network positions (e.g. Boogert *et al*., 2014), we may therefore predict that clutch size has knock-on effects on individual's social associations later in life. Similarly, social network position may be related to measures of individual quality such as growth rates and mass at fledging. Following hatching, chicks are provisioned by their parents for approximately thirty days before fledging and once fledged, juvenile jackdaws continue to associate with family members for several weeks (Goodwin, 1986). To determine if developmental conditions influence juveniles' future social network position or their patterns of association with family members and non-relatives, I analysed visits of individuals fitted with leg rings containing RFID tags (Bonter & Bridge, 2011) to a system of automated feeders. I predict that greater sibling competition and poorer nutrition during early development are linked to decreased strength of juvenile-kin associations post-fledging. I also expect that greater sibling competition and poorer nutrition during early development are linked to lesser gregariousness and a reduced tendency to concentrate social time with few key individuals.

Methods

Study population and automated feeders

I collected data from free-living jackdaws in the vicinity of two breeding sites in West Cornwall (Stithians: N 50°11’25.98’’, W 5°10’49.00’’ and Pencoose Farm: N 50°11’55.37’’, W 5°10’7.48’’)) . The sites are frequented by approximately 1500 ringed jackdaws and 40-50 pairs breed in nest boxes at each of the sites. Chicks from nest boxes were ringed at 25 days following hatching, which is approximately ten days before fledging occurs. All other ringed birds (including adults and post-fledging juveniles) were ringed after trapping using large walk-in traps or remote-controlled trap doors on nest-boxes. Each chick was weighed approximately ten times in the period between hatching and ringing. During ringing, each individual was fitted with a metal ring engraved with a British Trust for Ornithology (BTO) code and three coloured rings. One of the coloured rings contained a unique Passive-Integrated Transponder (PIT) tag that could be detected by antennae fitted to the feeders. Additionally, blood samples were taken to enable molecular sexing (Griffiths *et al.*, 1998) and body size measurements (wing length, tarsus length, weight) were recorded at ringing.

Feeders were positioned in close proximity to the nest-box colonies and were active between April 2015 and March 2017. Feeders recorded visits between 05:30 and 20:30 and were filled with mixed corn *ad libitum*. Each feeder had a perch that could be occupied by two birds at a time, such that an individual occupying the secondary position, furthest from the food, could not access the food if the primary position was taken. Both positions were covered by antennae that attached to an IBT EM4102 RFID data logger, which was powered by six C-cell batteries. When a feeding position was occupied by a ringed bird, its unique PIT-tag ID code, the current time and date and the antenna ID were logged every 100ms until it departed.

Ethical Statement

Experimental work complied with the guidelines of the Association for the study of Animal Behaviour (ASAB) and the University of Exeter Biosciences Ethics committee (2014/577). Additionally, bird ringing procedures were covered by Home Office (PPL 80/2371) and BTO (C6079, C5752, C5746) licenses.

Growth Trajectories

I fitted growth curves to each individual's weight observations to determine growth trajectories during the thirty days following hatching. Sigmoidal growth curves, characterized by three parameters (Fig. 1A), were fitted to each individual's weights in R using the package 'grofit' (Kahm *et al.*, 2010). I used a non-parametric technique based on fitting cubic splines, as this provides the best estimates of maximum growth rate (Kahm *et al.*, 2010). Estimates of maximum growth rate and weight at fledging were determined for each individual.

Social Network Position Measures

I applied a machine learning method (Psorakis *et al*., 2012; Psorakis *et al.*, 2015) to detect instances of grouped feeder visits by multiple jackdaws. Six sampling periods of sixty days in length were defined to coincide with the key annual life history periods (Pre-Spring, Pre-Breeding, Breeding, Post-Breeding,

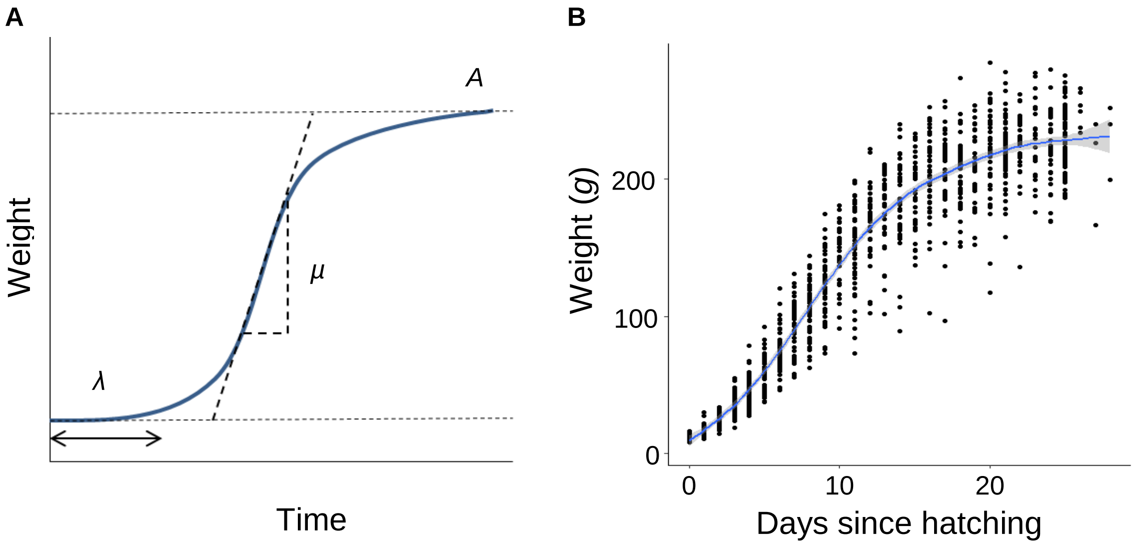

Fig. 1: Description of chick growth curves. Illustration of the model of sigmoidal growth fitted to each individual's weight observations (**A**); individual growth curves comprise three parameters, the lag phase (*λ*), estimated maximum growth rate (*μ*) and estimated final weight (*A*). Overall pattern of jackdaw chick mass change following hatching (**B**); line of best fit with 95% confidence interval from generalized additive model fitted to 1257 observations from 128 individuals.

Autumn, Post-Autumn) and an individual-level social network was generated for each season in each year. The association strength between two individuals in a sampling period was calculated by summing the time that the pair spent in the same feeding groups and dividing this value by the total time both individuals spent at feeders; this provides a measure of association between two individuals that controls for individual differences in foraging effort ('simple ratio' association index, Cairns & Schwager, 1987). The order of arrival at feeders was discounted in the calculation of association strength; consequently, the collection of association strengths for each possible pair in a sampling period comprised a weighted, undirected social network. Detection of feeding events and social network generation were performed using the R package ‘asnipe’ (Farine, 2013).

To enable assessment of individual network position, I calculated four measures of centrality (Freeman, 1979; Friedkin, 1991) and a measure of variation in association strength (‘*Social Differentiation*’; e.g. Boogert *et al.*, 2014) for each individual in each network (Chapter Three: Fig. 1). Multiple measures of centrality were chosen to capture different aspects of an individual’s network position (Chapter Three: Fig. 1). *Degree* and *Strength* (weighted Degree) are measures of gregariousness (Farine & Whitehead, 2015), but are simple measures of an individual’s network centrality that do not take into account the network position of an individual’s associates. Consequently, I also calculated weighted *Eigenvector Centrality*, which is a measure that accounts for the centrality of individual’s associates. An individual can have high *Eigenvector Centrality* either by having high *Degree*/*Strength* or by associating with individuals with high *Degree*/*Strength*. An individual’s network position can also be determined from analysis of the possible paths between nodes. Weighted *Betweenness* quantifies the number of shortest paths between vertices that pass through the vertex of interest and is important for identification of individuals that tie together disparate parts of the network. Finally, I also calculated *Social Differentiation*, which is a measure of whether an individual associates indiscriminately or with a few key individuals and is the coefficient of variation of an individual’s edge weights (Whitehead, 2008; Boogert *et al.*, 2014). Network centrality measures were calculated using the R package ‘igraph’ (Csardi & Nepusz, 2006) and the resulting values were normalized to control for group size variation between periods.

Linear Mixed Models (LMMs)

To assess the influence of developmental conditions on individuals’ subsequent patterns of association, I ran LMMs on each of the measures of network position. Age class, sex, estimated weight at fledging, maximum growth rate, tarsus length, number of siblings laid, number of siblings fledged and site were fitted as fixed effects. Individual identity nested within family and season nested within year were fitted as random effects. As network data violates the data independence assumptions of LMMs, the significance of fixed effects must be assessed by permutation tests (Croft *et al*., 2011; Boogert *et al.*, 2014; Farine & Whitehead, 2015; Farine, 2017). Permuted networks were generated for each season by data stream permutation, which constituted swapping individuals’ visits within the daily records of each feeder. In each permutation this process randomized associations between individuals whilst preserving the inherent spatio-temporal structure of the overall dataset (Bejder *et al.*, 1998; Whitehead, 1999; Whitehead *et al*., 2005; Sundaresan *et al.*, 2009). For each sampling period, a thousand permuted networks were generated by swapping the feeding event membership records of two randomly selected individuals. This resulted in a thousand permuted datasets for which LMMs were fitted as for the un-permuted dataset and the fixed effects coefficients were then extracted. Significance testing was performed by extracting each fixed effect coefficient for both the un-permuted LMM and the permuted LMMs and implementing a one-tailed significance test by calculating the number of permuted coefficient values of greater (absolute) magnitude than the un-permuted coefficient divided by the number of permutations performed (see Equation 2 in Ruxton & Neuhäuser, 2013).

Results

Description of chick growth

The typical trajectory of chick growth is approximately sigmoidal, with an initial lag phase, followed by an increase in growth rate until the maximum rate of growth is reached and finally growth slows as chick weight stabilises near fledging (Fig. 1B).

Social network position

Chicks from larger clutches subsequently tended to associate with fewer individuals (Fig. 2A; *Degree* LMM: $\beta = -0.000312$, S.E. = 0.0133, t = -0.234, p (perm) = 0.03), but other individual characteristics did not influence *Degree* (Table S1). None of the life history characteristics, morphometrics or measures of developmental condition affected *Strength* (Table S2). Clutch size (Fig. 3A; *Eigenvector Centrality* LMM: $\beta = -0.0207$, S.E. = 0.0155, t = -1.33, p (perm) < 0.001), tarsus length (Fig. 3B; *Eigenvector Centrality* LMM: $\beta = -0.000979$, S.E. = 0.0104, t = -0.094, p (perm) = 0.049) and maximum growth rate (Fig. 3C; *Eigenvector Centrality* LMM: $\beta = -0.0141$, S.E. = 0.00411, t = -3.43, p (perm) = 0.032) all had significant negative effects on *Eigenvector Centrality* (Table S3). Furthermore, there was a significant decrease in juveniles' *Eigenvector Centrality* following the first year after fledging (Fig. 3D; *Eigenvector Centrality* LMM: $\beta = -0.0465$, S.E. = 0.0284, t = -1.64, p (perm) = 0.002). Tarsus length was the only predictor that had a significant effect on *Betweenness* (Table S4),

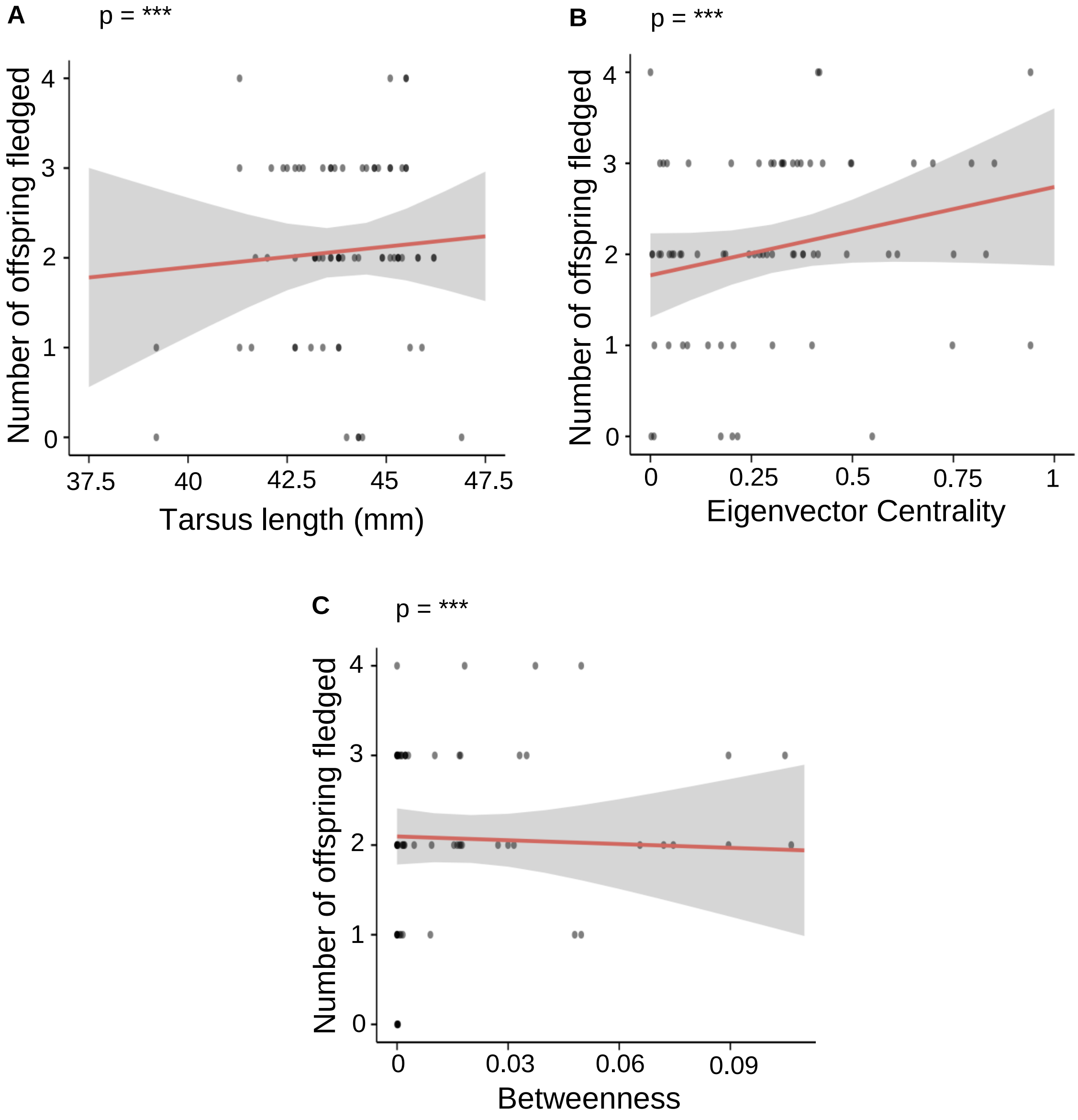

Fig. 2: Effect of tarsus length (**A**), *Eigenvector Centrality* (**B**) and *Betweenness* (**C**) and on number of offspring fledged by male jackdaws. *Eigenvector Centrality* and *Betweenness* scores were derived from a social network of association during the breeding season. Fitted values from GLMs and 95% confidence intervals (colour) are plotted over the raw data. The significance of effects, as calculated from permutation tests, is indicated symbolically (p<0.05: *; p<0.01: **; p<0.001: ***; p>0.05: N.S.).

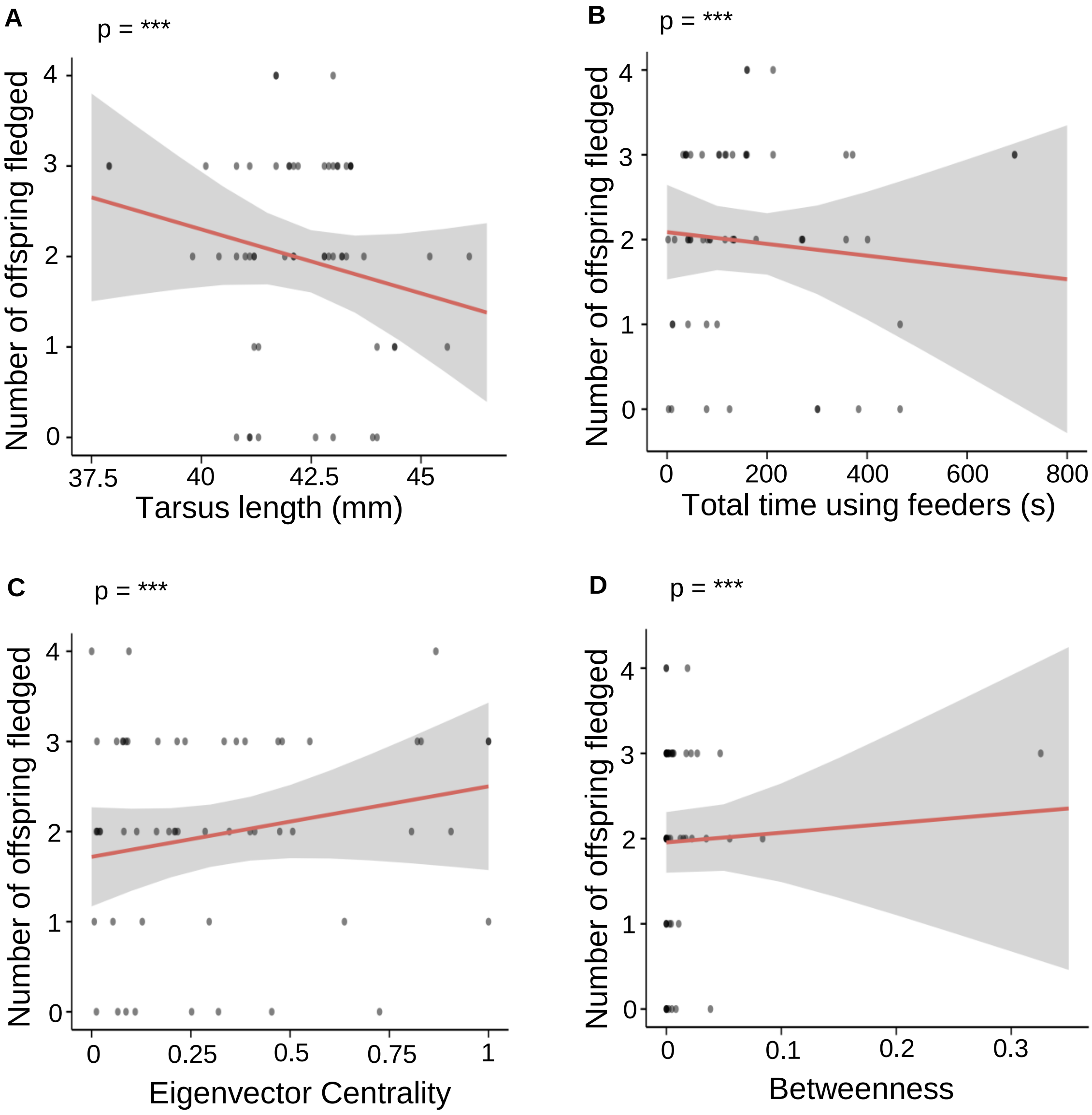

Fig. 3: Effect of tarsus length (**A**), total time using feeders (**B**), *Eigenvector Centrality* (**C**) and *Betweenness* (**D**) on number of offspring fledged by female jackdaws. *Eigenvector Centrality* and *Betweenness* scores were calculated from a social network of association for the breeding season. Fitted values from GLMs and 95% confidence intervals (colour) are plotted over the raw data. The significance of effects, as calculated from permutation tests, is indicated symbolically (p<0.05: *; p<0.01: **; p<0.001: ***; p>0.05: N.S.).

for which the effect was positive (Fig. 2B; *Betweenness* LMM: $\beta = 0.00159$, S.E. = 0.00291, t = 0.547, p (perm) = 0.028). Finally, greater maximum growth rate, though not any of the other predictors (Table S5), was associated with reduced *Social Differentiation* (Fig. 2C; *Social Differentiation* LMM: $\beta = -0.016$, S.E. = 0.00787, t = -2.03, p (perm) < 0.001).

Strength of association with relatives and non-relatives

Maximum growth rate in the period prior to fledging was a marginally non-significant predictor of strength of association between parents and offspring post-fledging, with there being a positive trend (*Parent-Offspring Association Strength* LMM: $\beta = 0.00191$, S.E. = 0.000991, t = 1.93, p (perm) = 0.05). Additionally, there was no evidence for a difference in association strength between paternal and maternal associations with offspring (Table S6). Juvenile associations with non-relatives were not influenced by juvenile age, sex or developmental conditions. Moreover, there was no difference in the strength of associations between juveniles and non-related adults of the same or different sex (Table S7).

Discussion

Developmental conditions in early life are widely assumed to influence individuals' later social interactions, but evidence from natural populations is lacking. I found that developmental conditions, life history characteristics and morphometry all influenced juvenile jackdaws' social network position. Nestling growth was approximately sigmoidal when inspected in aggregate, but there was clear individual variation in growth trajectories. The variation in growth and early-life conditions had important downstream effects. Overall, post-fledging juveniles exhibited a significant decrease in centrality of network position between the first and second years of life, but specific aspects of individual network positions were dependent on the conditions experienced in the nest. For instance, levels of sibling competition prior to fledging had important effects, with greater nestling clutch size associated with a reduction in centrality of network position post-fledging. Greater maximum growth rate during the pre-fledging period was associated with greater subsequent strength of association with parents, but reduced centrality and discrimination of associates within social networks. Juvenile body size has a complex effect on social network position, as larger juveniles have lower *Eigenvector Centrality* but also have higher *Betweenness*, suggesting that body size has differential effects on different aspects of social behaviour.

My results provide some support for the hypothesis that early-life stress levels can influence later social interactions in wild animal societies. Specifically, I found that greater levels of sibling competition affected juveniles' tendency to associate with conspecifics later in life. Chicks from larger clutches were more peripheral, associating with fewer individuals (lower *Degree*), though whilst significant this effect was weak, and having lower *Eigenvector Centrality*. The number of siblings successfully fledged had no influence on network position, suggesting that family structure before, but not after, fledging influences sociality. Greggor and co-workers (2017) found that stress titres positively correlate with sibling number in jackdaw chicks, indicating that sibling competition in the pre-fledging period causes early life stress in jackdaws. Social isolation is a common consequence of early life stress (Spencer, 2017), suggesting that early life stress reduces social motivation in jackdaws.

The finding that age had an effect on *Eigenvector Centrality* but not on the correlated measures *Degree* and *Strength* suggests that age had an effect on network position that cannot be explained by a change in general gregariousness. A decrease in the tendency of juveniles to associate with their parents as they begin to gain independence post-fledging could explain this phenomenon. A juvenile's *Eigenvector Centrality* is a product of its gregariousness and the gregariousness of its associates; a reduction in frequency of association with associates of notable centrality, such as parents, would cause a notable decline in *Eigenvector Centrality*, but may only have a negligible effect on other measures of network position.

Juveniles that experienced a higher maximum rate of growth as a result of parental provisioning during early life formed stronger associations with their parents following fledging. A high maximum growth rate may be evidence of compensatory growth, whereby poor initial development due to nutritional constraints is followed by a period of rapid catch-up growth (Metcalfe & Monaghan, 2001). Compensatory growth is an indicator of developmental stress and can have lasting effects on cognition (e.g. Fisher *et al*., 2006) and behaviour (e.g. Krause & Naguib, 2011). Greater association between parents and offspring at feeders may therefore represent extended parental care, whereby parents continue to aid the foraging of their offspring to mitigate the effects of poor provisioning during early development. Alternatively, high quality parents may be more likely continue to invest in their offspring following fledging, as a high maximum growth rate could also indicate high quality parental provisioning during early life. Aid during foraging in the period immediately following fledging can enhance juvenile survival probability (Heinsohn, 1991; Marchetti & Price, 1989), so high quality adults may benefit from sharing resources acquired foraging during the post-fledging period with their offspring. Further scrutiny of jackdaw growth trajectories, particularly the initial lag phase, is required to determine whether growth trajectory represents developmental stress or high parental quality in jackdaws.

Greater maximum growth rate during the pre-fledging period also reduced juveniles' tendency to discriminate when associating with conspecifics (lower *Social Differentiation*), meaning that they socialize with a range of associates without forming strong associations with certain favoured individuals. Boogert and co-workers (2014) found that developmental stress triggered reduction in *Social Differentiation* in juvenile zebra finches and this was associated with lower strength of association with parents, but higher centrality (*Degree and Betweenness*) owing to stressed juveniles' greater gregariousness. Juvenile jackdaws that had higher growth rates exhibited lower *Social Differentiation*, but had greater strength of association with their parents. This finding is somewhat counter-intuitive, as parents should be key associates of juveniles, so greater association with parents may be expected to introduce more variation in the association strengths within a juvenile's collection of ties, resulting in higher *Social Differentiation*. Consequently, juvenile *Social Differentiation* is not noticeably affected by the strength of association with parents in this study. However, the sampling periods I used may have been too broad to capture the dynamics of parent-offspring relationships and their effects on network position. The frequency of parent-offspring association may depend upon juvenile age and a detailed investigation of patterns of association in the days and weeks immediately following fledging may be necessary to elucidate whether associating with parents has social network ramifications.

Tarsus length, and therefore body size, had a complex effect on network centrality. Larger juveniles had higher *Betweenness*, meaning they were more prone to occupy network positions that bridged otherwise unconnected parts of the social network. A greater tendency of larger individuals to sample novel food sources may explain this effect. Aplin and co-workers (2012) discovered that higher *Betweenness* was linked to greater probability of patch discovery in great tits. If larger juvenile jackdaws are more likely to sample from a range of feeders, rather than concentrating their feeder activity in a single patch, then they may associate with a greater range of foraging groups and act as a tie between disparate parts of the social network. Larger juveniles also had lower *Eigenvector Centrality*, implying that they associated with less central individuals or were generally less gregarious. If size is a reliable indicator of developmental quality in jackdaws, then smaller juveniles may be adjusting their social foraging strategies (e.g. Farine *et al*., 2015) to seek out central individuals with whom to associate, so enhancing their *Eigenvector Centrality*. In cases where developmental factors influence multiple aspects of network position, exploring their relation to composite measures of network centrality (e.g. VanderWaal, 2014), perhaps derived through principal component analysis (Brent, 2015), may be required to determine biological significance of variation in network position.

In conclusion, growth trajectory, fledging body size and sibling competition during development all have a lasting effect on jackdaws' social tendencies over and above changes in social behaviour that occur as juveniles age. This is the first evidence for an effect of developmental conditions on social network position in a wild population. Further work should tie developmental plasticity to on other aspects the flexibility of social behaviour, such as stress-induced changes in social learning.

Supplementary Material

LMM tables

Table S1: Fixed and random effect summary for *Degree* LMM

Fixed Effect	**Coefficient**	**SE**	**t-value**	**p (perm)**
Age 1	-0.0169	0.0181	-0.931	0.089
Age 2	-0.0226	0.0365	-0.618	0.617
Age 3	-0.248	0.0991	-2.5	0.693
Sex (M)	0.029	0.0214	1.35	0.305
Tarsus length	0.00903	0.00847	1.07	0.073
Fledging weight	-0.000312	0.000608	-0.513	0.051
Maximum growth rate	-0.0102	0.00298	-3.41	0.169
Number of siblings laid	-0.00313	0.0133	-0.234	**0.03**
Number of siblings fledged	-0.021	0.0174	-1.21	0.599
Site (Stithians)	0.0736	0.0198	3.72	0.942

Random Effect	**Variance**	**% Variance**
ID	0.00174	4.72
Family	0.00325	8.82
Season	0.000361	0.980
Year	0.0109	29.6
Residual	0.0206	55.9

Table S2: Fixed and random effect summary for *Strength* LMM

Fixed Effect	**Coefficient**	**SE**	**t-value**	**p (perm)**
Age 1	0.000758	0.00379	0.2	1
Age 2	0.019	0.00747	2.54	1
Age 3	-0.0144	0.0183	-0.787	1
Sex (M)	0.00264	0.00318	0.832	1
Tarsus length	-0.000975	0.00127	-0.865	1
Fledging weight	-0.000781	0.0000848	-0.746	1
Maximum growth rate	-0.0000633	0.000488	-1.6	1
Number of siblings laid	-0.00287	0.00165	-1.74	1
Number of siblings fledged	-0.00138	0.00222	-0.624	1
Site (Stithians)	0.00212	0.00277	0.765	1

Random Effect	**Variance**	**% Variance**
ID	0.0000119	0.262
Family	0	0
Season	0.00238	52.4
Year	0.00132	29.1
Residual	0.000828	18.2

Table S3: Fixed and random effect summary for *Eigenvector Centrality* LMM

Fixed Effect	**Coefficient**	**SE**	**t-value**	**p (perm)**
Age 1	-0.0465	0.0284	-1.64	**0.002**
Age 2	0.00444	0.0564	0.079	0.704
Age 3	-0.269	0.145	-1.86	0.116
Sex (M)	0.0174	0.0283	0.612	0.073
Tarsus length	-0.000979	0.0104	-0.094	**0.049**
Fledging weight	0.000763	0.000768	0.993	0.365
Maximum growth rate	-0.0141	0.00411	-3.43	**0.032**
Number of siblings laid	-0.0207	0.0155	-1.33	**<0.001**
Number of siblings fledged	-0.0459	0.0207	-2.21	0.333
Site (Stithians)	0.0973	-0.0249	3.91	0.242

Random Effect	**Variance**	**% Variance**
ID	0.00296	4.57
Family	0.00129	1.99
Season	0.00277	4.28
Year	0.00959	14.8
Residual	0.0481	74.3

Table S4: Fixed and random effect summary for *Betweenness* LMM

Fixed Effect	**Coefficient**	**SE**	**t-value**	**p (perm)**
Age 1	-0.00112	0.0053	-0.211	0.685
Age 2	0.0412	0.0107	3.85	0.207
Age 3	0.00116	0.0316	0.037	0.95
Sex (M)	0.011	0.00729	1.51	0.81
Tarsus length	0.00159	0.00291	0.547	**0.028**
Fledging weight	-0.000382	0.000207	-1.84	0.129
Maximum growth rate	-0.000828	0.000995	-0.832	0.442
Number of siblings laid	-0.00987	0.00458	-2.16	0.495
Number of siblings fledged	0.00607	0.00593	1.02	0.884
Site (Stithians)	-0.00199	0.00659	-0.302	0.183

Random Effect	**Variance**	**% Variance**
ID	0.000251	7.31
Family	0.0004	11.6
Season	0	0
Year	0.000663	19.3
Residual	0.00212	61.7

Table S5: Fixed and random effect summary for *Social Differentiation* LMM

Fixed Effect	**Coefficient**	**SE**	**t-value**	**p (perm)**
Age 1	-0.0442	0.0524	-0.842	0.174
Age 2	-0.0696	0.103	-0.678	0.753
Age 3	-0.221	2.46	-0.9	0.343
Sex (M)	0.0219	0.0554	0.395	0.608
Tarsus length	-0.0172	0.0198	-0.87	0.302
Fledging weight	0.00222	0.00145	1.53	0.065
Maximum growth rate	-0.016	0.00787	-2.03	**<0.001**
Number of siblings laid	-0.0287	0.0294	-0.975	0.177
Number of siblings fledged	-0.0578	0.0385	-1.5	0.052
Site (Stithians)	0.0161	0.0453	0.354	0.683

Random Effect	**Variance**	**% Variance**
ID	0.0263	15.4
Family	0	0
Season	0.0235	13.7
Year	0.00449	2.62
Residual	0.117	68.3

Table S6: Fixed and random effect summary for *parent-offspring association strength* LMM

Fixed Effect	Coefficient	SE	t-value	p (perm)
Age 1	0.00337	0.113	0.475	0.292
Age 2	-0.00192	0.00709	-0.092	0.857
Sex (M)	0.00114	0.021	0.156	0.146
Rel (Mother)	-0.00247	0.00555	-0.445	0.54
Tarsus length	-0.000988	0.0029	-0.34	0.1
Fledging weight	-0.00012	0.000152	-0.79	0.277
Maximum growth rate	0.00191	0.000991	1.93	0.05
Number of siblings laid	0.000848	0.00308	0.275	0.817
Number of siblings fledged	-0.00432	0.00426	-1.01	0.332
Site (Stithians)	-0.0177	0.00694	-2.55	0.095

Random Effect	Variance	% Variance
ID	0	0
Family	0	0
Season	0.000217	31.6
Year	0	0
Residual	0.00047	68.4

Table S7: Fixed and random effect summary for *association strength of juveniles with non-related adults* LMM

Fixed Effect	**Coefficient**	**SE**	**t-value**	**p (perm)**
Age 1	0.00917	0.00257	3.57	0.792
Age 2	0.0227	0.00536	4.24	0.251
Age 3	0.0974	0.0183	5.33	0.256
Sex (M)	0.00137	0.00368	0.373	0.226
Sex_Diff (SAME)	-0.00273	0.00117	-2.34	0.257
Tarsus length	-0.0000179	0.00137	-0.013	0.169
Fledging weight	-0.0000601	0.0000956	-0.628	0.957
Maximum growth rate	0.00105	0.000501	2.1	0.768
Number of siblings laid	-0.00311	0.00199	-1.56	0.265
Number of siblings fledged	-0.00154	0.00259	-0.594	0.747
Site (Stithians)	0.0463	0.00297	4.92	0.498

Random Effect	**Variance**	**% Variance**
ID	0.00018	5.01
Family	0.0000105	0.292
Season	0.00135	37.6
Year	0	0
Residual	0.00205	57.1

Chapter Five: Structure and dynamics of jackdaw queuing interactions during foraging

Abstract

Turn-taking is a form of cooperation that can give rise to reciprocity between the participants. Turn-taking is a ubiquitous feature of human communication and has also been observed in the vocal communication and foraging behaviour of several animal species. Understanding both the dynamics of repeated cooperative interactions between a pair of co-operators and the process of partner choice is essential for diagnosing the forms of reciprocity that may underlie cooperative action. Until recently, methodological constraints restricted the study of turn-taking dynamics occurring during foraging to captive groups. Here, I use a novel application of Radio-Frequency Identification (RFID) technology to study the spatial arrangement pairs of wild jackdaws using automated feeders. I found that a substantial proportion of queuing interactions occurred between individuals of known affiliation, such as parents and offspring. Furthermore, queuing pairs were overwhelmingly likely to be of opposite sex, likely reflecting a preponderance of monogamous pairs engaging in paired feeding visits. In jackdaws, queuing could therefore be a reliable indicator of close affiliation and may be useful for predicting hitherto unknown social relationships. Finally, repeated turn-taking interactions between the same pair were an influential aspect of queuing dynamics, but partner-switching and whole-pair changes were also prevalent. This study provides the first evidence of turn-taking dynamics in the foraging behaviour of wild animals.

Introduction

Coordination of activities among different members of a group can benefit the individual participants (Clutton-Brock, 2009). In social foraging, synchronisation of activity can reduce an individual's predation risk (Hamilton, 1971) and provide an additional source of social time (Dunbar, 2009; Marshall *et al*., 2012). However, variation in individual behaviour during group activity is often observed, with individuals adopting certain behavioural roles, such as 'leaders' or 'followers' (King *et al*., 2009). An individual's role may be determined by its 'personality' (e.g. Aplin *et al*., 2014), social status (e.g. Nagy *et al*., 2010), or experience at the task at hand (e.g. Flack *et al*., 2012). These activity patterns occur at the level of the dyad as well as in larger social groups. Theoretical work on the behaviour of foraging dyads reveals that differences in energetic requirements (Rands *et al*., 2003; Rands *et al*., 2008) and dominance rank (Rands *et al*., 2011) may influence a pair's coordination of foraging activity. Competition over access to limited resources fosters conflict during social foraging, but conflict can be resolved by the adoption of turn-taking strategies (Crowley, 2001; Browning & Colman, 2004; Lau & Mui, 2008; Colman & Browning, 2009), whereby individuals alternate their access to a resource, thus avoiding conflict. Turn-taking dynamics occur in animal vocal communication (e.g. Takahashi *et al*., 2013) and have been observed during foraging (e.g. Harcourt *et al*., 2010; Fruteau *et al*., 2013) and provisioning (Johnstone *et al*., 2013) behaviours. Turn-taking during foraging has not been investigated in wild populations, though studying turn-taking in wild animals would enable examination of its importance for structuring social foraging dynamics in natural conditions.

Turn-taking can be viewed as a form of cooperation, due to the fact that it requires behavioural coordination and can result in net benefits for both participants (Noe, 2006; Franz *et al*., 2011). During a single turn-taking interaction, one of the individuals may have to incur an immediate cost, such as loss of time that could otherwise be invested in other foraging behaviours. This cost is incurred such that the individual's prospective long-term benefits are enhanced, but may also provide an immediate benefit for its partner. If the cooperators are kin, then an individual's sacrifice of its foraging time may not be to its detriment, due to the promotion of its inclusive fitness (Hamilton, 1964). For unrelated partners, the above criteria would conform to the common definition of reciprocal altruism (Trivers, 1971), so in some cases turn-taking dynamics may be a manifestation of reciprocity. There are several forms of reciprocity, which may differ in the cognitive demands they place on interactants (Hauser *et al*., 2009; McAuliffe & Thornton, 2015). Direct reciprocity requires the repeated interaction of a pair of associates, whereby each participant tracks the investment of the other and adjusts its behaviour accordingly. This process can generate cooperation strategies and patterns of dyadic turn-taking, but other mechanisms can also produce similar dynamics. For instance, generalized reciprocity features indiscriminate reciprocity between members of a social group and may have less stringent cognitive requirements than direct reciprocity, but can produce similar patterns of cooperation (Pfeiffer *et al*., 2005; Rutte & Taborsky, 2007).

In natural conditions, individuals will have the opportunity to cooperate with a range of social partners, making the evaluation of a partner's viability relative to that other potential partners important (Noë & Hammerstein, 1994; Noë & Hammerstein, 1995). The ability of an individual to alter whom it cooperates with can create a 'biological market' (Noë & Hammerstein, 1994; Noë & Hammerstein, 1995), whereby an individual has multiple options regarding the identity of its cooperative partner. The leverage afforded by the potential for partner switching disincentivises defection during cooperative interaction, thereby cultivating the conditions required for the maintenance of reciprocity (Barclay, 2011). Experimental investigation of exchanges in primates indicates that partner choice is likely crucial for the establishment of reciprocity (Schino & Aureli, 2017). An additional feature of biological markets can be the exchange of services. For example, individuals may exchange grooming for food (e.g. Scheid *et al*., 2008; Jaeggi & Gurven, 2013) or other benefits, such as support during agonistic interactions (e.g. Schino, 2007; Fraser & Bugnyar, 2012). Determining the mechanisms underlying seemingly reciprocal cooperative interactions occurring in wild populations is challenging as it requires knowledge of the nature and precise timing of interactions, as well as accurate identification of the participants.

Automated data collection techniques facilitate the quantification of spatial ecology at the level of the individual in unprecedented quality. In some cases, these datasets can also be used to infer patterns of social association and interaction. For example, Nagy and co-workers (2010) used automated analysis of pigeon (*Columba livia domestica*) feeding congregations to determine the structure of the group's dominance hierarchy, which they subsequently related to patterns of collective motion. The use of Radio-Frequency Identification (RFID) technology (Bonter & Bridge, 2011) has greatly advanced our understanding of the causes and consequences of association patterns in wild birds (e.g. Aplin *et al.*, 2013; Farine & Sheldon, 2015). However, determining the precise nature of the interactions underlying such associations from RFID data is challenging, usually requiring additional data, such as video recordings of the interactions occurring at feeders (e.g. Cole & Quinn, 2011). Here, I present a novel use of RFID technology to capture queuing interactions that occur during foraging.

I used a system of automated feeders equipped with the facility to simultaneously record the visits of multiple individuals to assess turn-taking dynamics in the foraging behaviour of pairs of jackdaws. Jackdaws are corvids, so belong to a family of species that have been shown to display sophisticated cognitive abilities rivalling those of certain primates (Emery & Clayton, 2004; Emery *et al*., 2007). Jackdaws are monogamous and association between pair members and more generally between kin are commonly observed. Specifically, parents continue to engage with offspring during foraging following the age of independence. Jackdaws engage in food sharing during foraging (de Kort *et al*., 2006). Furthermore, the application of relational event models (REMs; Butts, 2008), which are constructed in order to detect short-term turn-taking dynamics, has revealed that jackdaw food sharing commonly features reciprocation (Tranmer *et al*., 2015). Dominance interactions also regularly occur during foraging and jackdaw groups exhibit stable dominance hierarchies (Verhulst & Salomons, 2004; Verhulst *et al*., 2014). Specifically, parents continue to engage with offspring during foraging following the age of independence. I investigated whether queuing interactions provide evidence of close affiliation, the factors influencing an individual’s queuing role and the dynamics of repeated queuing interactions between pairs. I predict that social support reduces the occurrence of displacement during foraging, so increases the duration of feeding bouts relative to those of lone foragers. Foraging pairs will predominantly comprise individuals that are affiliated by kinship or breeding partnership. When pairs forage together, males are more likely to be observed occupying the primary feeding role (i.e. occupy the primary antenna on a feeder). Finally, I expect that the turn-taking dynamics of multi-participant foraging are primarily composed of within-pair swapping of the occupation of the primary foraging role, rather than partner-switching.

Methods

Study population and automated feeders

I investigated the foraging behaviour of wild jackdaws in and around two breeding sites in West Cornwall (Stithians: N 50°11’25.98’’, W 5°10’49.00’’ and Pencoose Farm: N 50°11’55.37’’, W 5°10’7.48’’)) . Approximately 1500 ringed jackdaws visit the sites and at each site pairs breed in the 40-50 nest boxes we have provided. Nestlings in nest boxes were ringed around the 25th day after hatching, which is approximately ten days before fledging. All other ringed birds (including adults and post-fledging juveniles) were ringed after trapping using large walk-in traps or remote-controlled trap doors on nest-boxes. Each individual was fitted with three coloured rings, one of which contained a unique Passive-Integrated Transponder (PIT) that could be detected by RFID antennae. A metal ring displaying a British Trust for Ornithology (BTO) code was also fitted to each individual during ringing. Finally, body size measurements (wing length, tarsus length, weight) and blood samples were also taken at ringing and the blood samples were subsequently used for molecular sexing (Griffiths *et al.*, 1998)

Eight feeders were active between April 2015 and March 2017. At each of the two main breeding sites three feeders were placed in the vicinity of the nest boxes. An additional two feeders were placed in the region between the two breeding sites. Feeders were filled with mixed corn *ad libitum* and were active between 05:30 and 20:30. The perch of each feeder contained two RFID antennae, arranged such that there were primary and secondary feeding positions. Individuals occupying the secondary position were unable to access food if the primary position was also occupied, meaning that the existence of queues during feeding events could be recorded. I used an IBT EM4102 RFID data logger, powered by six C-cell batteries, which is capable of simultaneously recording input from two antennae. For each occupied feeding position, the unique PIT-tag ID code, the current time and date and the antenna ID were logged every 100ms until the visiting bird departed. As these data were collected simultaneously for both feeding positions, the precise duration of queuing events was recorded, as well as the identities of the participants and their orientation. Queuing events were detected in the RFID dataset by processing the reader data to find instances where the two antennae recorded a different bird during the same second. A queuing event was defined as a feeding event during which both antennae were occupied by the same pair of individuals for at least two seconds. Queuing events of shorter duration were not included, as they may represent other forms of interaction, such as displacement resulting from a dominance interaction.

Ethical Statement

Ringing protocols were covered by Home Office (PPL 80/2371) and BTO (C6079, C5752, C5746) licenses. Experimental work conformed to the guidelines of the Association for the study of Animal Behaviour (ASAB) and the University of Exeter Biosciences Ethics committee (2014/577).

Analysis of Visit Duration

A simple rule was applied to identify individual feeding visits. A visit change was deemed to have occurred if individual identity changed or more than five seconds elapsed between recordings of the same individual at the feeder in question. The duration of solo feeding visits was compared to duration of queuing events by use of Linear Mixed Models (LMMs). Visit duration (in seconds) was the response term, a binary term indicating whether a feeding event was a solo visit or a queue was fitted as a fixed effect and the identity of the primary feeder was fitted as a random effect. I used the Kenward-Roger approximation (Kenward & Roger, 1997) to calculate the degrees of freedom for the LMM and enable calculation of a p-value for the fixed effect. This process was performed using the R package ‘pbkrtest’ (Halekoh & Højsgaard, 2014).

Transitivity and assortativity of jackdaw queuing

I used the records of primary and secondary individual identity during queuing interactions to generate a social network of jackdaw queuing interactions in order to investigate whether sex and tarsus influenced an individual’s queuing tendencies. The network was both weighted and directed, as visit duration was used to weight each queuing interaction and interactions had a clear direction (i.e. one primary individual joined by one secondary individual). To assess whether the global structure of the jackdaw queuing network was non-random I examined the transitivity of queuing interactions. For social networks of directed interactions, the structure of triads can reveal whether the pattern of interactions is indicative of a hierarchical social structure or random interaction. A preponderance of transitive triads (Fig. 1) is indicative of a hierarchy, whereas a large number of cyclic triads suggests that random processes govern network structure. Quantification of the ratio of transitive and cyclic triads in a network

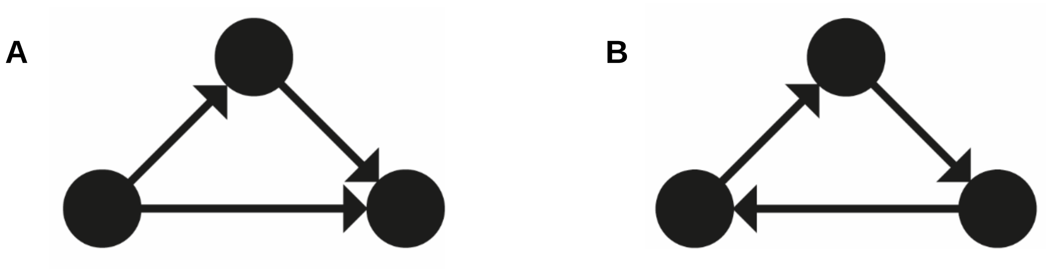

Fig. 1: Illustration of two examples of transitive (**A**) and cyclic (**B**) triads common to directed social networks of animal behaviour. The ratio of transitive to cyclic triads in a network reveals whether interactions conform to a linear hierarchy or occur as the result of a random process, with greater transitivity indicating greater order (Shizuka & McDonald, 2012).

provides a useful statistic for formally examining the global structure of directed networks (Shizuka & McDonald, 2012). As transitive triads tend to be more common in biological networks, this statistic is typically adjusted to a scale whereby zero represents the transitivity expected in a random network and a value of one represents total transitivity (see Shizuka & McDonald, 2012).

I calculated the adjusted transitivity metric for the jackdaw queuing network and determined its significance by comparison to a distribution of values calculated from a thousand permuted networks. Similarly, I tested the tendency of jackdaws to assort by sex and tarsus length when engaging in queuing interactions by calculation of assortativity coefficients (Newman, 2002; Newman, 2003; Farine, 2014). I used a version of the assortativity coefficient adapted for use with weighted networks, as inclusion of edge weights can enhance accuracy of assortment analyses (Farine, 2014). Standard errors of assortativity coefficients were estimated via jackknife procedure (Farine, 2014) and significance was assessed by comparison of the assortativity coefficient calculated for the un-permuted network to a distribution of coefficients calculated for a thousand permuted networks.

Queuing Network Position

I used several measures of social network centrality to quantify individuals' positions within the queuing network. The measures 'in-degree' and 'in-strength' quantified the number of partners an individual had queued behind and its overall time in the secondary position respectively. Conversely, 'out-degree' and 'out-strength' reflected the number of partners that had queued behind an individual and its overall time as the primary feeder during queuing events. Additionally, I utilized two measures of network centrality, weighted *Eigenvector Centrality* and weighted *Betweenness*, which incorporate indirect social relationships. An individual can have high *Eigenvector Centrality* by interacting with a lot of individuals, or by interacting with select individuals who themselves interact frequently. *Eigenvector Centrality* is an informative measure for directed networks, as it is closely related to measures of social rank (Hobson & DeDeo, 2015). *Betweenness* measures the number of connections between social group members that an individual mediates and can identify individuals that are key to joining otherwise unconnected components of the social network. I used General Linear Models (GLMs) to assess the effect of sex and body size on each aspect of individual network position. The significance of sex and body size effects was determined by comparison of coefficient values to distributions of coefficients from permuted networks (Farine & Whitehead, 2015; see Permutation Procedure).

Permutation procedure

The non-independence of network data and potential sampling biases that occur during data collection invalidate the use of traditional statistical tests to determine significance for network properties (Croft *et al*., 2011; Farine & Whitehead, 2015). Consequently, social network analysis typically relies on the use of permutation tests. For all statistical analyses of network properties, I calculated p-values by generating network metrics for the original, un-permuted network and comparing these values to distributions of values calculated for networks generated following permutation of the queuing data. I adapted a form of data-stream permutation (Bejder *et al*., 1998) based on a method developed for the permutation of focal follow data (Farine, 2017) to produce permuted networks. The original method employs swaps of group members to randomize the dataset prior to network generation and is constrained such that the gross spatio-temporal structure of the dataset is preserved (Farine, 2017). I randomized the sets of primary and secondary individuals independently using the R function *sample* to preserve each individual's total number of primary and secondary feeding position occupancies whilst randomizing its queuing partnerships. Permutation was applied separately to each of the six seasons within each year, where seasons were defined as sixty day periods that roughly aligned with the key annual life history stages of the birds. Additionally, permutation was applied separately for each breeding site. These restrictions were applied to ensure that spurious partnerships could not arise as a result of the permutation procedure, such as the partnership of two individuals only ever observed in different sites.

Relational Event Models (REMs)

Turn-taking dynamics often occur at a fine temporal scale. Social network analysis may be used to assess fine-scale reciprocity and turn-taking, provided the sampling regime used to generate the networks does not engulf the behavioural dynamics of interest. For example, Hemelrijk (1990) developed a method to detect evidence of reciprocity in group-level social network structure and demonstrated the feasibility of the method by applying it to the analysis of chimpanzee (*Pan troglodytes*) grooming exchanges. Similar, albeit more advanced, methods are still widely used and encompass the field of 'dynamic social network analysis' (Blonder *et al*., 2012; Pinter-Wollman *et al.*, 2013). Relational event models (REMs) are an alternative to dynamic network analysis that avoid potential sampling issues by modelling the occurrences of individual 'relational events', which are discrete interactions between a sender and receiver that occur at unique points in time (Butts, 2008).

I used REMs, fitted using the R package 'relevent' (Butts, 2008; Butts & Marcum, 2017), to determine support for the occurrence of three forms of turn-taking dynamics (Fig. 2) in jackdaw queuing interactions. I also used REMs to assess the effect of recency of queuing activity on an individual's tendency to later be observed queuing. Support for an effect of recency would mean that an individual is more likely to be observed queuing on multiple occasions when events are closely spaced in time. I fitted a separate REM for each site to prevent spurious partnership changes from being modelled. Temporal REMs were initially fitted, but exhibited poor fit, likely due to the large time differences between certain events. Consequently, ordinal REMs (Butts & Marcum, 2017) were fitted instead. Ordinal REMs do not explicitly model the duration between events as do temporal REMs. As such, the effect of 'recency' is not indicative of the probability of an event occurring given the time elapsed between events, but

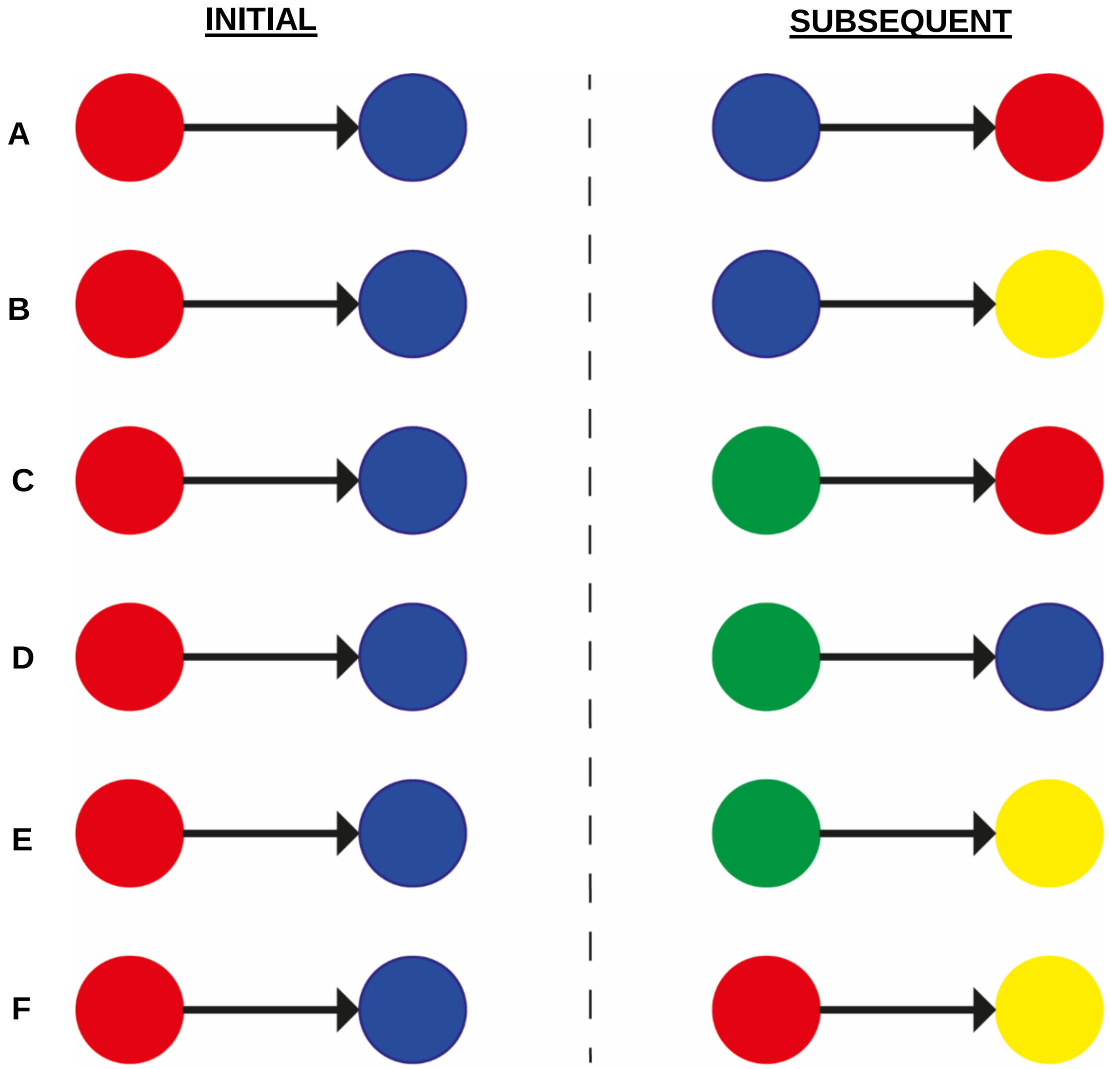

Fig. 2: Illustration of the six participation shifts that can occur during dyadic turn-taking (Gibson, 2003). The initial sender-receiver combination (red to blue) is followed by a subsequent sender-receiver pairing. The initial receiver can receive a turn as the sender ('turn-receiving': **A**, **B**) and this can be the result of a direct swap of the initial sender and receiver (**A**). An individual not observed in the initial interaction may claim the role of sender in the subsequent interaction ('turn-usurping'), with the initial sender (**C**), initial receiver (**D**) or another individual (**E**) being its receiver. Finally, the initial sender may maintain the role of sender in the subsequent interaction, though interacting with a different receiver ('turn-continuing': **F**).

rather the probability of a certain event occurring next in the event sequence REM coefficients represent event hazards, meaning that they indicate the relative likelihood of two types of event occurring. For a given form of turn-taking, the REM coefficient is the logged multiplier for the relative hazard of that turn-taking event and the other five forms of turn-taking. Therefore, evaluating the expression e^{coef} results in a value that indicates how many more times a given type of turn-taking event is likely to occur than the other forms.

I used a model selection procedure based on the inspection of the Akaike Information Criterion (AIC) to determine the best model from a set of candidate models. The best model and any simpler model with an AIC value within two of the best models AIC were retained (Richards *et al*., 2010). If multiple models were retained, support for each was calculated using Akaike weights (Burnham & Anderson, 2002). In addition to assessing relative model fit, I also calculated several statistics for assessment of absolute fit. I calculated the percentage of exact pairings predicted (Butts & Marcum, 2017) and compared these values to the prediction success expected from random choice of pairings. Finally, I calculated pseudo r-squared values for REMs (Nagelkerke, 1991; Tranmer *et al*., 2015) to assess model fit relative to null REMs.

Results

Summary Statistics

The duration of jackdaw feeding visits is significantly longer when an individual is accompanied by another individual than when foraging alone, with supported feeding bouts tending to last six seconds longer (Table S1; LMM: $\beta = 6.06$, S.E. $= 0.562$, $t = 10.8$, p (K-R) < 0.001), which is twice the duration of the mean feeder visit (mean visit duration = 3.1s). Feeding visits by single individuals were approximately ten times more common than events where two affiliates occupied the feeding perch simultaneously (828 paired feeder visits, 9916 solo). Multiple occupation of feeders was a strong indicator of close affiliation between individuals. Queuing events occurring between known pairs or family members accounted for at least 35% of the observed interactions. Furthermore, the majority of the interactions (approximately 75%) between individuals of unknown relation consisted of opposite sex pairings. Queuing network structure indicated that both sites feature a main component, comprising multiple individuals queuing with each other, and a number of separate dyads and triads (Fig. 3).

Transitivity and assortativity

The jackdaw queuing network featured a significantly greater than random proportion of transitive triads (t.tri = 0.8, p (perm) < 0.001; Fig. 4), demonstrating that there is a non-random structure to jackdaw queuing interactions. Queuing interactions between members of the opposite sex were more common than between members of the same sex (Table S2a; r = -0.48, S.E. = 0.0768, p (perm) < 0.001; Fig. 4). When queuing pairs consisted of a male and a female, both of the possible orientations (male primary, female primary) occurred with approximately equal frequency (Table S2b). Queuing was also more likely to occur for pairs with a greater disparity in tarsus length (r = - 0.18, S.E. = 0.0799, p (perm) = 0.01; Fig. 4).

Network Position

Males spent less total time (in seconds) occupying the secondary position when queuing than females (GLM: β = -50.4, S.E. = 24.2, t = -2.09, p (perm) = 0.013). Furthermore, larger individuals spent more time in the secondary position (GLM:

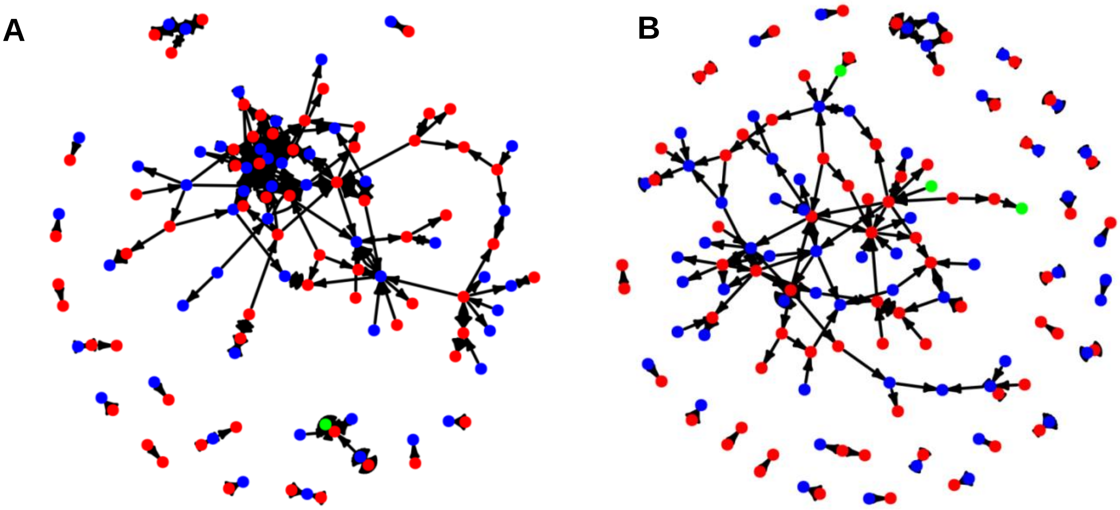

Fig. 3: Network diagrams of queuing interactions at the Stithians (**A**) and Pencoose (**B**) breeding sites. Node position is dependent upon centrality (Fruchterman-Reingold layout), with the most connected individuals closest to the centre of the diagram. Each queuing dyad is connected by a directed edge from the primary to the secondary feeder. Dyads that queued in both possible orientations display two edges of opposite arrow direction. Node colour indicates sex (blue = female, red = male, green = unknown).

β = 13.6, S.E. = 7.85, t = 1.74, p (perm) = 0.044). However, removal of an extreme value (Fig. 5) altered these results, such that neither the effect of sex (GLM: β = 14.4, S.E. = 15.5, t = -0.925, p (perm) = 0.595) nor tarsus (GLM: β = 1.39, S.E. = 5.05, t = 0.275, p (perm) = 0.934) remained significant. Furthermore, sex (GLM: β = -0.957, S.E. = 0.746, t = -1.28, p (perm) = 0.306) and tarsus length (GLM: β = 0.16, S.E. = 0.24, t = 0.661, p (perm) = 0.663) had no effect on the number of individuals that an individual queued behind and neither sex (GLM: β = 0.0131, S.E. = 0.72, t = 0.018, p (perm) = 0.979) nor tarsus length (GLM: β = -0.0593, S.E. = 0.233, t = -0.254, p (perm) = 0.751)

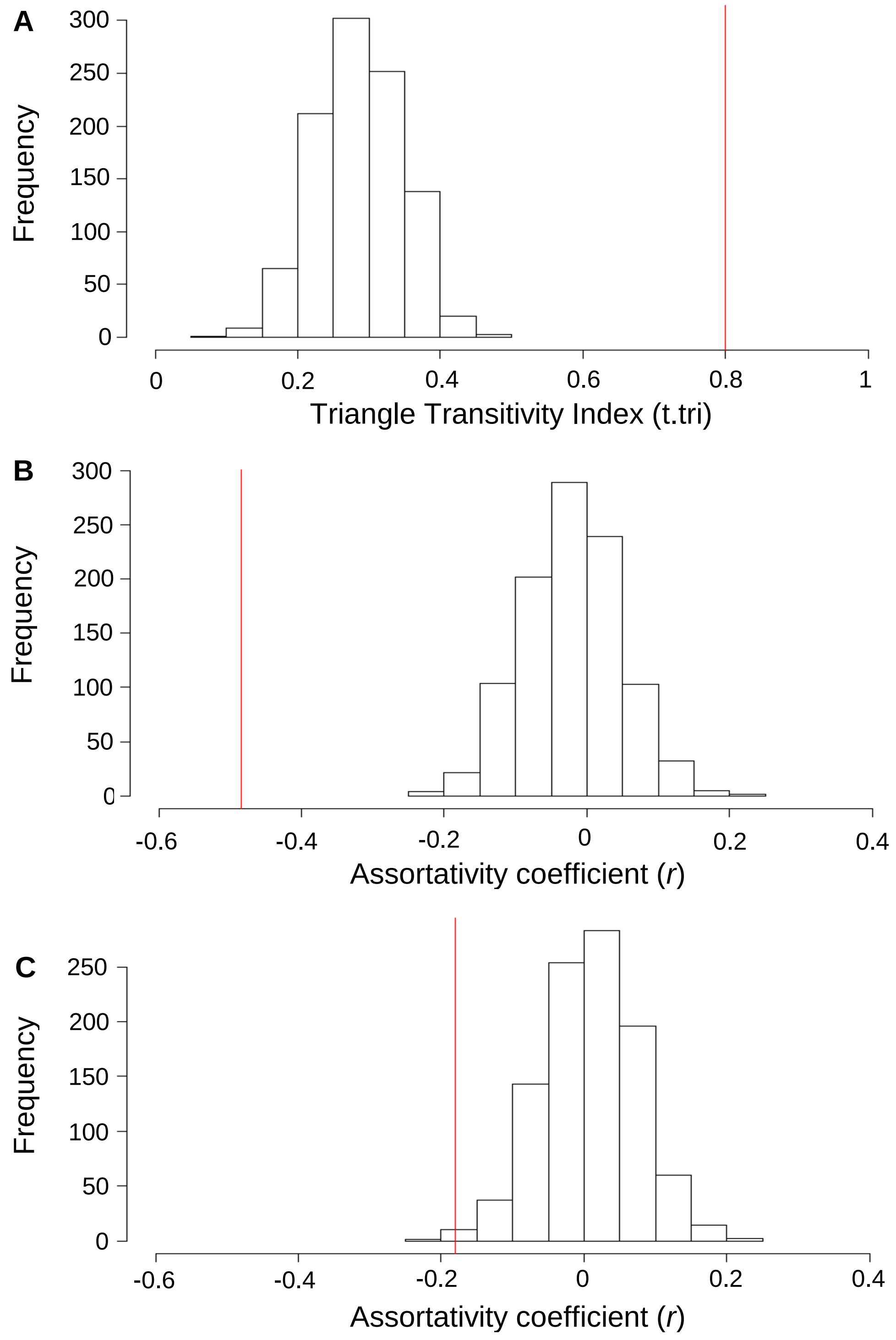

Fig. 4: Transitivity and assortativity of jackdaw queuing networks. Transitivity (**A**) and assortativity (**B**, **C**) coefficient values calculated for the un-permuted network (red lines) are displayed alongside the distributions of values extracted from a thousand networks generated following permutation of the queuing data. Assortativity was calculated for both sex (**B**) and tarsus length (**C**).

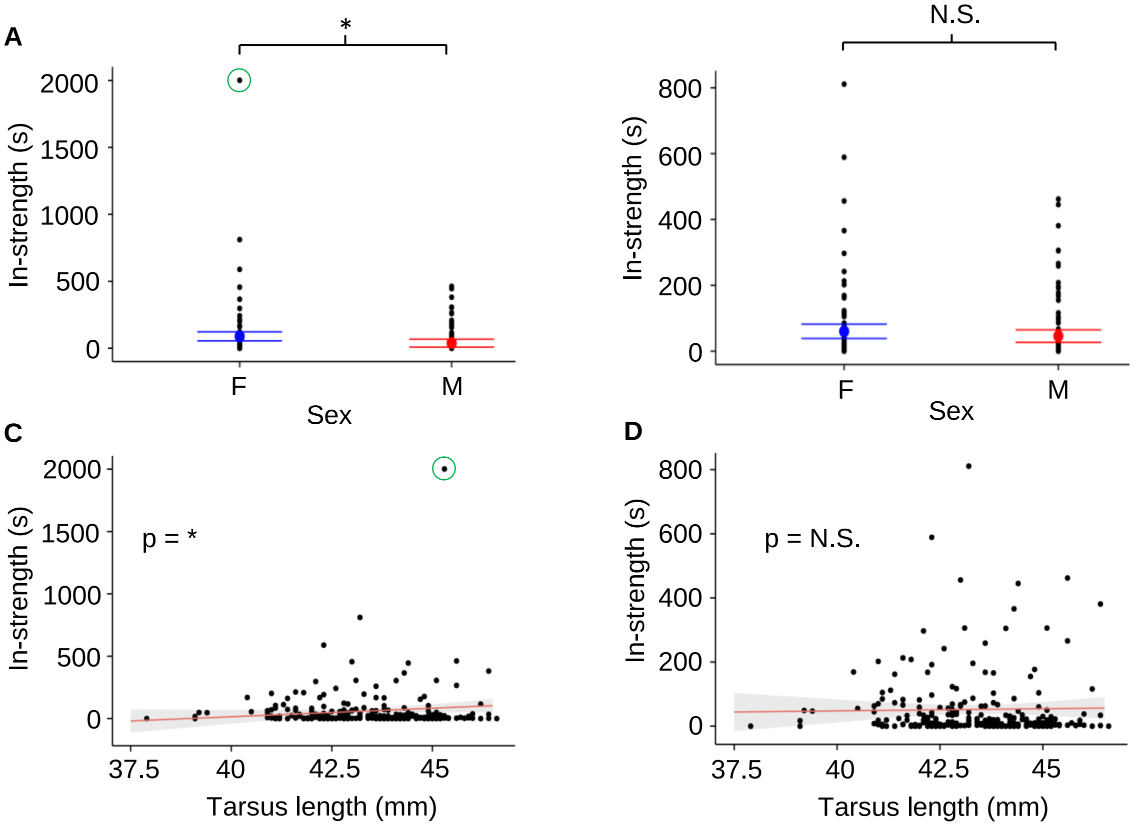

Fig. 5: Effect of sex (**A**, **B**) and tarsus length (**C**, **D**) on individuals' 'in-strength', which represents the total time spent in the secondary feeding position whilst queuing. Fitted values from GLMs and 95% confidence intervals (colour) are plotted over the raw data. Results from the original models (**A**, **C**) are plotted alongside results from models fitted following the removal of an extreme value (green circle; **B**, **D**). The significance of effects is indicated symbolically ($p<0.05$: *; $p<0.01$: **; $p<0.001$: ***; $p>0.05$: N.S.).

affected the number of individuals that queued behind an individual. Similarly, the amount of time spent as the primary feeder was not significantly affected by sex (GLM: β = 14.6, S.E. = 24.2, t = 0.606, p (perm) = 0.542) or tarsus (GLM: β = 0.0631, S.E. = 7.85, t = 0.008, p (perm) = 0.994). Finally, *Eigenvector Centrality* was not affected by sex (GLM: β = -0.0158, S.E. = 0.0103, t = -1.53, p (perm) = 0.502) or tarsus (GLM: β = 0.00642, S.E. = 0.00335, t = 1.91, p (perm)

= 0.527) and *Betweenness* was also not influenced by sex (GLM: β = 0.00012, S.E. = 0.000196, t = 0.611, p (perm) = 0.978) or tarsus (GLM: β = 0.0000115, S.E. = 0.0000636, t = 0.18, p (perm) = 0.993).

Relational Event Models (REMs)

REMs applied to queuing data from the two sites revealed that recent interactions have a strong influence on interaction dynamics and that turn-taking dynamics can explain some of the queuing patterns that occur at feeders (Table S9; Table S10). The strongest effect was observed for recency of interaction, as it was present in all of the best models for both sites. This means that the more recently that an individual interacted with a particular individual the more likely that those same individuals would be observed interacting in closely following events. In addition, turn-receiving and turn-usurping are prominent turn-taking dynamics in jackdaw queuing, as they featured in the best REM for each site. Furthermore, direct reciprocity (Fig. 2A) was more than twice as likely to occur as the alternative form of turn-receiving (Fig. 2B) and can be detected from visual inspection of pair's queuing interactions (Fig. 6). Turn-continuing was not present in the best REM from either site, but was present in the second best models at both sites, so did occur but was less prominent than other forms of turn-taking.

Model adequacy was assessed through inspection of prediction success and pseudo r-squared values. Overall, the REMs correctly predicted the exact pairing in the next event 10.6% and 7.46% of the time for Stithians and Pencoose respectively. In contrast, random choice of pairings would yield a prediction success of 0.0075% (116 individuals; Table S11) for Stithians and

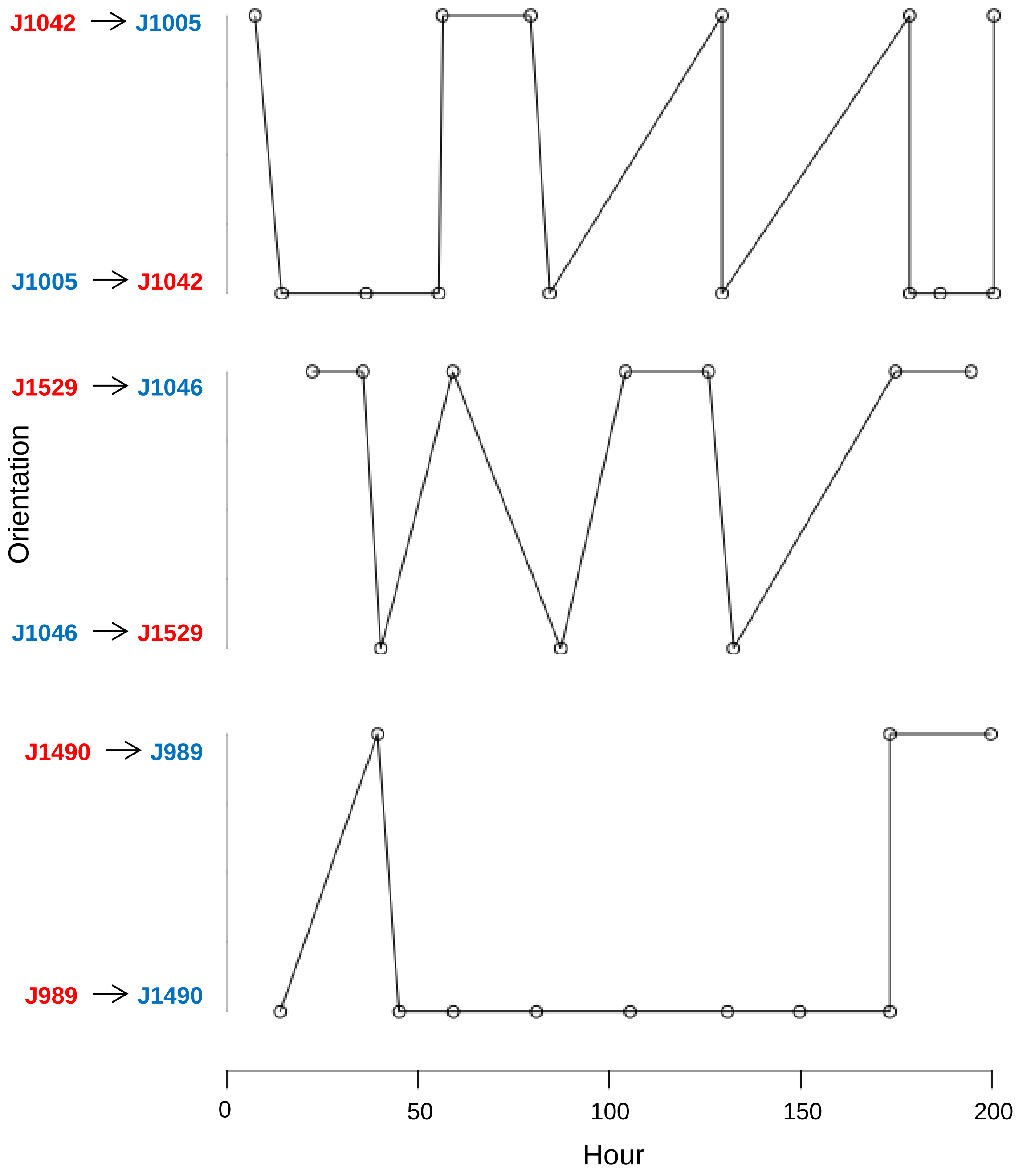

Fig. 6: Illustration of the diversity of queuing patterns exhibited by three male-female dyads foraging over the course of nine days. Each point represents a single queuing event and indicates the pair's orientation during that visit. Colours indicate an individual's sex (blue = female, red = male).

0.00561% (134 individuals; Table S11) for Pencoose. Finally, the Stithians and Pencoose REMs had pseudo r-squared values of 0.112 and 0.125 respectively.

Discussion

Turn-taking is a form of coordination that can enable resolution of conflict over resource acquisition, but is rarely investigated as a mechanism driving cooperative interaction during foraging. Here, I show that pairs of jackdaws queuing during foraging take turns to occupy the primary feeding role. An individual occupying the primary feeding role spent more time on the feeder during a visit than when foraging alone. A substantial portion of queuing interactions occurred between kin or known partners and of those interactions where the pair's affiliation was unknown, the majority consisted of interactions between members of the opposite sex. Sex also predicted an individual's tendency to be the secondary feeder during queuing events, as males tended to spend less time than females in the supporting role. Furthermore, larger individuals were more likely to occupy the secondary feeding position. Finally, pairs repeatedly visited feeders together and engaged in turn-taking, though other forms of social foraging dynamics were also present, including partner-switching and the displacement of foraging pairs by other dyads.

Queuing benefits the individual occupying the primary feeding role, as they remain feeding for longer per visit than when foraging alone. Accompaniment during foraging may provide benefits by reducing an individual's susceptibility to displacement by competitors, so may be favourable to foraging alone. However, the overwhelming majority of feeder visits were conducted by solo individuals, whilst queuing was to some extent restricted to family members or breeding pairs. Queuing events featuring different sex individuals were far more common than those between same sex individuals. Additionally, of the queues containing individuals of unknown affiliation, the vast majority featured members of the opposite sex. Therefore, queuing may be mostly likely to occur between breeding pairs. Consequently, queuing may be less common than solo feeder visits as it only occurs between closely affiliated individuals, such as breeding partners or kin. The greater duration of queuing events could therefore be due to the occurrence of food sharing and grooming interactions that are commonly displayed by closely affiliated jackdaws during foraging (de Kort *et al*., 2006). Finally, queuing data may have predictive value, enabling the inference of partnerships and family memberships in cases where confirmation of such relationships through behavioural observation is challenging.

Inspection of the prevalence of transitivity in queuing network structure shows that jackdaws discriminate when choosing a queuing partner. Furthermore, there is a form of queuing hierarchy, such that there are certain individuals that are almost exclusively occupants of the primary feeding position irrespective of their queuing partner, some that are always secondary and others that occupy either role dependent upon the queuing tendencies of their associate. Non-random transitivity is a common feature of animal social networks based on directed interactions, such as networks of grooming or aggression. Consequently, the queuing network shares similarities in structure with animal dominance networks (Shizuka & McDonald, 2012; Shizuka & McDonald, 2015), which are often characterized by the existence of a prominent linear hierarchy. Interestingly, the procedure I used to generate permuted networks produced networks of non-random transitivity, but random assortment by sex and body size. This indicates that the permutation procedure I employed preserved some aspects of network structure. The permutation procedure was specifically designed to preserve each individual’s total number of interactions as the primary and secondary individual, whilst randomizing the partnerships it was observed in. Therefore, simple patterns of feeding position usage may to some extent predict the linearity of the queuing hierarchy.

Body size differences influenced queuing patterns. The finding that queuing tended to occur between individuals with a disparity in tarsus length could be due to the occurrence of parent-offspring queuing, as the greatest difference in body size likely exists between adults and juveniles. Theoretical work has shown that the subordinate member of a pair of foragers may be the initiator in paired foraging activity, as a result of its greater energetic requirements (Rands *et al*., 2011). Consequently, juveniles may initiate parent-offspring queuing events, perhaps recruiting their parents to reduce the probability of their displacement from feeders by other adults.

Direct reciprocity, consisting of repeated queuing interactions between the same pair with alternation of the primary feeding role, was a feature of queuing interactions at both of the breeding sites. As such, partners may keep track of the configuration of prior queuing interactions and alternate their orientation to ensure both members benefit from cooperative foraging. Food sharing between jackdaws also features reciprocity and occurs among affiliates, which are not necessarily related or members of a breeding pair (de Kort *et al*., 2003; de Kort *et al*., 2006; von Bayern *et al*., 2007), so is perhaps a common occurrence in jackdaw foraging interactions. Reciprocity during foraging has clear benefits for closely affiliated individuals. For example, for strictly monogamous breeding pairs, future reproductive success may depend upon the maintenance of the condition of both partners (Emery *et al*., 2009). Therefore, successful breeding pairs should consist of individuals that monitor the condition of their partner and adjust their behaviour accordingly (Emery *et al*., 2009). Further investigation is required to determine if direct reciprocity during foraging only occurs between closely affiliated individuals, such as breeding partners or parents and their offspring, or is a more general feature of jackdaw social interaction.

Reciprocity between the same individuals was the most common form of turn-taking, whilst replacement of one pair by another distinct pair and partner switching were less prevalent. This finding could be a result of jackdaws' possessing a rigidly structured social group (Kubitza *et al*., 2015), with individuals displaying high fidelity to a small number of cooperative partners during foraging, such as family members, and tending not to mix with unfamiliar individuals. Though reciprocal turn-taking within pairs was twice as likely to occur as other forms of turn-taking, this estimate may actually be conservative, as demographic changes will have a differential effect on the occurrence of the different forms of turn-taking. The greater the demographic turnover, the greater the likelihood of whole-pair changes, as new individuals start to visit and interact at the feeders. This issue will be especially relevant to datasets containing large time intervals between some of the events and should be considered when deciding upon the modelling approach to employ. Finally, there was little support for queuing at feeders simply representing tolerance of a subordinate's presence by a feeding dominant individual. Queuing events did not tend to feature a single individual persistently occupying the primary role whilst others, perhaps acting as scroungers, took turns to queue in the secondary position. Consequently, jackdaw queuing predominantly features repeated interactions between consistent pairs and further work would benefit from examination of determinants of between-pair variation in queuing tendencies.

In summary, I used a novel application of RFID technology to capture the first evidence of turn-taking during foraging in wild animals. Jackdaw queuing interactions often occur between close affiliates and queuing behaviour could be utilized to infer jackdaw social relationships. Repeated queuing interactions between the same individuals are a common occurrence in foraging jackdaws and pairs often alternate which individual occupies the primary feeding role. Further work should scrutinize the social processes, such as the forms of reciprocity, underlying the observed turn-taking dynamics and the consistency of pairs' queuing dynamics.

Supplementary Material

Table S1: Visit duration LMM

FE	Coefficient	SE	t-value	p (K-R)
Intercept	11	0.269	40.9	
Support	6.06	0.562	10.8	**<0.001**

RE	Variance	% Variance
Individual	14.29	6.07
Residual	221	93.9

Table S2a: Assortment coefficients

Factor	r	SE	p (perm)
Sex	-0.484	0.0768	**<0.001**
Tarsus	-0.18	0.0799	**0.01**

Table S2b: Sex mixing matrix

	F	M	Total
F	0.092	0.37	0.462
M	0.367	0.171	0.538
Total	0.459	0.541	1

Network Position GLMs

Table S3: In-Degree GLM summary

Effect	Coefficient	SE	t-value	p (perm)
Sex (M)	-0.957	0.746	-1.28	0.306
Tarsus	0.16	0.24	0.661	0.663

Table S4: Out-Degree GLM summary

Effect	Coefficient	SE	t-value	p (perm)
Sex (M)	0.0131	0.72	0.018	0.979
Tarsus	-0.0593	0.233	-0.254	0.751

Table S5a: In-Strength GLM summary for original dataset

Effect	Coefficient	SE	t-value	p (perm)
Sex (M)	-50.4	24.2	-2.09	**0.013**
Tarsus	13.6	7.85	1.74	**0.044**

Table S5b: In-Strength GLM summary for dataset after removal of possible outlier

Effect	Coefficient	SE	t-value	p (perm)
Sex (M)	-14.4	15.5	-0.925	0.595
Tarsus	1.39	5.05	0.275	0.934

Table S6: Out-Strength GLM summary

Effect	Coefficient	SE	t-value	p (perm)
Sex (M)	14.6	24.2	0.606	0.542
Tarsus	0.0631	7.85	0.008	0.994

Table S7: Eigenvector Centrality GLM summary

Effect	Coefficient	SE	t-value	p (perm)
Sex	-0.0158	0.0103	-1.53	0.502
Tarsus	0.00642	0.00335	1.91	0.527

Table S8: Betweenness GLM summary

Effect	Coefficient	SE	t-value	p (perm)
Sex	0.00012	0.000196	0.611	0.978
Tarsus	0.0000115	0.0000636	0.18	0.993

Table S9: Relational Event Model (REM) selection table for the Stithians site. Four main types of dynamic (turn-receiving, turn-usurping, turn-continuing and recency) were included in the REMs. Models were ordered by Akaike Information Criterion (AIC). Model retention was based on comparison of model AIC values to the AIC of the best model (ΔAIC); the best model (lowest AIC) was retained as were simpler (i.e. fewer terms) models with a ΔAIC of two or less.

Coefficient values represent the likelihood of observing a given event relative to another (i.e. how many times more likely).

	Turn Receiving		**Turn Usurping**			**Turn Continuing**	**Recency**				
Model	**AB-BA**	**AB-BY**	**AB-XA**	**AB-XB**	**AB-XY**	**AB-AY**	**RRecSnd**	**RSndSnd**	**AIC**	**ΔAIC**	**Retained?**
Recency, TR, & TU	2.15	0.734	0.502	0.683	0.119		25.3	25.5	5287	0	Y
Everything	1.99	0.663	0.455	0.619	0.109	0.73	25.3	25	5288	1	
Recency, TU & TC			0.35	0.483	0.0829	0.579	28.5	23.8	5299	12	
Recency & TU			0.383	0.524	0.785		28.5	27.7	5300	13	
Recency, TR & TC	14.9	5.64				6.23	25.5	27.7	5384	97	
Recency & TR	14.7	5.42					25.5	26.6	5400	113	
Recency & TC						5.87	31.2	28.5	5579	292	
Just Recency							31.5	27.1	5595	308	
All p-shifts	2	0.00243	0.00271	0.00362	0.000809	0.00271			7071	1784	
TR & TU	176	0.212	0.239	0.32	0.0721				7303	2016	
TR & TC	2143	2.59				2.92			7439	2152	
Just turn-receiving	2101	2.54							7444	2157	
TU & TC			0.0963	0.129	0.029	0.0963			7729	2442	
Just turn-usurping			0.174	0.232	0.0523				7809	2522	
Just turn-continuing						2.48			8203	2916	

Table S10: Relational Event Model (REM) selection table for the Pencoose site. Four main types of dynamic (turn-receiving, turn-usurping, turn-continuing and recency) were included in the REMs. Models were ordered by Akaike Information Criterion (AIC). Model retention was based on comparison of model AIC values to the AIC of the best model (ΔAIC); the best model (lowest AIC) was retained as were simpler (i.e. fewer terms) models with a ΔAIC of two or less.

Coefficient values represent the likelihood of observing a given event relative to another (i.e. how many times more likely).

	Turn Receiving		**Turn Usurping**			**Turn Continuing**	**Recency**				
Model	**AB-BA**	**AB-BY**	**AB-XA**	**AB-XB**	**AB-XY**	**AB-AY**	**RRecSnd**	**RSndSnd**	**AIC**	**ΔAIC**	**Retained?**
Recency, TR, & TU	2.69	0.792	0.801	0.972	0.284		30.9	34.5	4442	0	Y
Everything	2.77	0.822	0.828	1	0.292	1.13	30.9	34.5	4444	2	
Recency & TU			0.52	0.629	0.181		33.1	34.1	4451	9	
Recency, TU & TC			0.495	0.6	0.172	0.677	33.1	33.8	4453	11	
Recency, TR & TC	8.67	2.7				3.74	31.2	35.5	4458	16	
Recency & TR	8.58	2.65					31.2	35.2	4460	18	
Recency & TC						3.67	35.5	37	4531	89	
Just Recency							35.5	36.6	4535	93	
All p-shifts	2.75	0.00189	0.00253	0.00315	0.00132	0.00253			6000	1558	
TR & TU	273	0.188	0.252	0.313	0.131				6098	1656	
Just turn-receiving	1959	1.35							6131	1689	
TR & TC	1978	1.36				1.81			6132	1690	
TU & TC			0.0846	0.105	0.0442	0.0846			6363	1921	
Just turn-usurping			0.154	0.192	0.0805				6404	1962	
Just turn-continuing						1.62			6559	2117	

Table S11: Summary of queuing datasets used for REMs.

	Stithians	**Pencoose**
Events	492	336
Individuals	116	134
Timespan	29/04/2015 to 11/04/2017	08/05/2015 to 24/12/2016

Chapter Six: General Discussion

In this thesis I have examined the factors influencing between-individual variation in asocial and social foraging behaviour, the relation of jackdaw social behaviour to fitness and the nature of interactions occurring during paired foraging. The discovery that jackdaw social network position is both plastic and predictive of reproductive success and that turn-taking dynamics occur during paired foraging gives rise to several avenues of further research. In this discussion, I outline the main findings from each data chapter, discuss the conclusions that can be drawn regarding jackdaw social structure, identify potential methodological improvements and suggest topics for future work.

Main findings

In Chapter 2 I found that between-individual variation in jackdaw feeder usage mainly consists of variation in time spent occupying feeders, rather than the timing of visits. Various life history characteristics, such as age, sex and tarsus length, were predictors of quantity and timing of feeder usage. However, low repeatability scores indicated that jackdaws are not consistent in their patterns of feeder usage. The greatest between-individual variation was found for overall feeder usage, suggesting there were unobserved individual characteristics, perhaps neophobia, influencing quantity of feeder usage. Knowledge of between-individual variation in patterns of feeder usage may be valuable for controlling for non-social causes of variation in patterns of social association.

In Chapter 3 I used machine learning methods to infer social associations from patterns of feeder visits by adult jackdaws and construct social networks. I then examined whether individual characteristics (sex and tarsus length) influence adult jackdaw social network position, but found no evidence for an effect. However, social network position does affect reproductive success for both adult males and females, though the nature of the relationship differs between sexes. The finding that social behaviour has differential effects on fitness was somewhat surprising considering that consistent sex differences in social network position were not found. These results suggest that there is not a simple correlation between social network position and fitness in jackdaws, but rather that the fitness value of social network position is modulated by individual characteristics, such as sex.

In Chapter 4 I used social network of association generated from feeder visit data to explore the factors influencing juvenile jackdaw social network position. I found that the social network position of juvenile jackdaws is affected by the conditions they experience during early life. Higher levels of sibling competition and greater maximum growth rate were found to be associated with juveniles occupying more peripheral social network positions. These findings are in line with experimental work conducted in captivity and this constitutes the first evidence of developmental plasticity of social behaviour in a wild population.

In Chapter 5 I showed that queuing during feeder usage may benefit feeding jackdaws, as visit duration is prolonged for queuing events relative to solo feeder visits. I found that queuing may be a reliable indicator of close affiliation, such as kin or pair-bond relationships. The prevalence of repeated interactions between closely affiliated individuals suggests that patterns of reciprocity and turn-taking may be a hallmark of foraging interactions featuring jackdaw partners or kin. Indeed, queuing events displayed turn-taking dynamics, of which direct reciprocity was found to be the most prevalent mechanism. This constitutes the first evidence of turn-taking in a wild population.

Causes and consequences of jackdaw social structure

Space use tendencies can influence social structure (e.g. Cantor *et al*., 2012; Shizuka *et al*., 2014) and *vice versa* (e.g. Nagy *et al*., 2010). Shared space use can produce patterns of social association, regardless of whether this association represents a meaningful social relationship (Whitehead & James, 2015). It may therefore be desirable to control for correlation in space use when calculating the strength of association between individuals and methods have recently been developed for this purpose (e.g. Whitehead & James, 2015). Alternatively, the effect of individual behavioural variation on resulting patterns of association can be actively investigated (e.g. Aplin *et al*., 2014). The influence of individual preferences for visit duration and time of day of feeder usage on social network structure in jackdaws could be a productive area of future research.

Though social network position is associated with fitness in a range of species, including jackdaws, deducing the social processes that cause variation in network position can be challenging. There may not be an intuitive link between the simplicity of a social process and the simplicity of the measure of network position that it influences (Firth *et al*., 2017b). For instance, an individual’s gregariousness, a simple measure of its tendency to directly associate, may predict its patterns of indirect social relationships (Firth *et al*., 2017b). Investigating the correlation between simple and complex network measures (Farine & Whitehead, 2015) may further elucidate this relationship. Furthermore, variation in social network position might be the outcome of the action of subtle social feedback processes. For example, Hobson and DeDeo (2015) showed that networks of aggression in monk parakeets (*Myiopsitta monachus*) form as a result of individuals updating their valuation of their social rank based on experience and altering their behaviour accordingly. Consequently, studying the feedback between network position and subsequent behavioural tendencies, perhaps through the use of dynamic social network analysis (Blonder *et al*., 2012; Pinter-Wollman *et al*., 2013), may be key to determining the causes of individual variation in social network position. The large longitudinal dataset of jackdaw social associations at feeders, alongside several years of jackdaw dominance data, feature sufficient temporal resolution and overall timespan to facilitate the study of gradual changes in social behaviour resulting from feedback processes.

Social network position has been found to be both repeatable (e.g. Aplin *et al*., 2015) and heritable (Lea *et al*., 2010; Brent *et al*., 2013). Considering that network position also exhibits individual-level variation, it is possible that aspects of social network position are shaped by natural selection (Kurvers *et al*., 2014; Croft *et al*., 2016). I found that *Social Differentiation* was the most repeatable aspect of jackdaw social network position. *Social Differentiation* refers to an individual’s tendency to be generally gregarious or associate with a few key individuals. This measure therefore has an intuitive relationship to underlying social personality, so variation in *Social Differentiation* may have a clear genetic basis. However, there was no clear relationship between *Social Differentiation* and reproductive success in jackdaws, so the selective pressures determining jackdaw *Social Differentiation* remain unclear. Alternatively, the tendency to exhibit aggression can be heritable (Dochtermann *et al*., 2015) and aggression frequently occurs during jackdaw dominance interactions (Verhulst

& Salomons, 2004). Examining the repeatability and heritability of individual position within networks of dominance and aggression in order to quantify strength of selection on social traits (e.g. Lea *et al*., 2010) could therefore be a productive avenue of future research. Interestingly, jackdaw social rank may feature forms of social rank ‘inheritance’ observed in certain mammals (Holekamp & Smale, 1991; Goldenberg *et al*., 2016). Röell (1978) observed that female rank is dependent upon the rank of their partner in jackdaws, although this observation was not subjected to formal statistical analysis. Studying social network position in jackdaw dominance networks could therefore enable the quantification of the relative contribution of genetic and non-genetic forms of ‘inheritance’ to the determination of social traits. As a consequence, this type of work could be a useful experimental investigation of gene-culture coevolution in animals (Cavalli-Sforza & Feldman, 1973; Feldman & Laland, 1996; Richerson *et al*., 2010).

Developmental plasticity of social behaviour is predicted to be adaptive under certain circumstances (‘social programming’), but this has not been examined experimentally (Spencer, 2017). In chapters two and three I showed that social behaviour is related to fitness in jackdaws and that early life conditions influence social behaviour. Adverse developmental conditions, such as poor nutrition or high levels of sibling competition during early life, generally reduce social motivation (Spencer, 2017). I found some evidence for this in jackdaws, as greater sibling competition and maximum growth rate were associated with the occupation of more peripheral social network position, though the strength of the detected effects was weak. Reduced network centrality, resulting from diminished social motivation, could be detrimental for fitness in jackdaws, as greater network centrality tended to be associated with greater reproductive success. Therefore, stressful conditions during early life could have a negative influence on fitness in later life in jackdaws. However, reduced social contact could also have fitness benefits, such as lesser exposure to socially-transmitted diseases (MacIntosh *et al*., 2012; Duboscq *et al*., 2016; Smyth *et al*., 2016). Finally, early life stress can cause a lasting increase in the tendency of an individual to display aggression during social conflict (Cumming *et al*., 2014; McCormick *et al*., 2015). Dominance interactions are a common feature of jackdaw foraging dominance is related to fitness in jackdaws (Verhulst & Salomons, 2004). Therefore, examining the effect of developmental conditions on aggression and the resulting fitness effects may provide a test of the adaptive value of 'social programming'.

The rate and timing of provisioning can be as influential as provisioning quality for determining the stress experienced by juveniles during development (Monaghan, 2008). Evidence of nutritional deficit during early life can be difficult to detect from biometry, as poor initial growth is often compensated by accelerated growth later in development ('compensatory growth': Metcalfe & Monaghan, 2001). However, compensatory growth likely has a negative effect on future viability and fitness (Metcalfe & Monaghan, 2003). For example, compensatory growth during early development is associated with poorer cognitive ability in adulthood (Fisher *et al*., 2006). Though maximum growth rate during development did predict aspects of jackdaw social network position, it was not possible to determine whether maximum growth rate was indicative of compensatory growth or higher quality parental provisioning. More detailed analysis of chick growth trajectories is required to make this distinction and should be a priority for future work. The parental response to poor pre-fledging provisioning is also a promising avenue of future research. Jackdaw parents continue to associate with offspring after fledging and poor quality parents may compensate for poor pre-fledging investment by increasing the frequency of their association with their offspring during post-fledging foraging. Paired foraging enables greater duration of visits to feeders, so parents may benefit their offspring by providing support during foraging.

As part of my investigation of the causes of variation in social network position, I examined repeatability of network position at the level of the pair. I found low-to-moderate repeatability for certain aspects of network position, suggesting that quantifying between-pair variation in position within a network could be a useful accompaniment to studies of individual variation. Pair-level repeatability could be evidence of hierarchical structure in jackdaw social networks, a phenomenon that to date has only been reported for certain mammals (e.g. Wittemyer *et al.*, 2005). Further work is required to determine the mechanisms by which pair-level network characteristics are generated. Homophily, whereby similar individuals are more likely to associate (McPherson *et al*., 2001), could produce these patterns if jackdaws with more similar social traits tend to form pairs (‘positive assortative mating’: Jiang *et al*., 2013). The investigation of pair-level social traits would also benefit from a focus on the effect of pair interaction on behavioural flexibility. The nature of interactions with a partner could have a transient effect on individual social behaviour (Dingemanse & Araya-Ajoy, 2015), or even drive the establishment of within-pair social roles (Bergmuller & Taborsky, 2010; Montiglio *et al*., 2013). I found clear between-pair variation in tendency to reciprocate queuing whilst foraging and the extent to which consistency of pair queuing behaviour reflects the adoption of ‘social roles’ in a foraging context would be an interesting topic for future work. Additionally, within-pair behavioural variation can influence reproductive output (e.g. Both *et* *al*., 2005), so the interaction of male and female ‘social personality’ is potentially related to fitness.

Collection and analysis of behavioural data from wild populations

Behavioural studies of wild animals necessarily feature the analysis of interactions between a subset of the overall population, as complete sampling coverage is rarely attainable. Unfortunately, characterization of social structure based on observation of a subset of individuals may not be accurate, particularly if individuals with a crucial social role are excluded from social networks (e.g. Flack *et al*., 2006). However, partial networks can be representative of broader social structure, though this may depend upon the particular network measures utilized (Silk *et al*., 2015). The use of methods that explicitly quantify sampling uncertainty when generating network ties (e.g. Hoppitt & Farine, 2017) may therefore be necessary for the generation of robust social networks for wild populations. Understanding the factors that drive sampling variation, such as the processes affecting variation in jackdaw feeder usage, is critical for ascertaining how representative a social network is of social structure. For example, if certain individuals are less likely to visit feeders due to greater neophobia, then the network structure derived from patterns of association at feeders may be more homogeneous than the actual social structure. As a result, selective exclusion of certain individuals due to task structure could then ultimately affect interpretation of the dynamics of processes occurring on the network, such as the spread of a novel foraging technique (e.g. Aplin *et al*., 2015).

A limitation of certain forms of automated data collection is the inability to explicitly define behavioural interactions (but see e.g. Nagy *et al*., 2010), which restricts the analysis of social behaviour to the examination of patterns of social association. In certain situations, patterns of association can be used to unequivocally detect particular behaviours. For example, in chapter five, I used an arrangement of multiple RFID antennae to detect queuing events occurring at feeders. In this case, spatial arrangement alone was sufficient to determine each individual's behavioural role during a queuing event. However, identification of other behavioural interactions, such as displacements resulting from dominance events, is more challenging. Recent work shows that dominance interactions occurring at automated feeders can be inferred from association data, though the calibration required to ensure accuracy may not be trivial (Evans *et al*., 2018). Determining the behavioural interactions underlying patterns of association could be essential for the interpretation of the causes of variation in individual social network position.

To ensure that observations of patterns of social foraging associations in the wild are representative social dynamics in natural conditions, attention should be paid to the effect of task structure on social foraging behaviour. The extent to which resources can be monopolized affects the value of social information during foraging, so may influence the mixture of social foraging tactics employed by members of a social group (Giraldeau & Beauchamp, 1999). This means that the structure of feeders, where food access can be monopolized, may inadvertently alter jackdaw social foraging dynamics. Careful examination of foraging behaviour in other contexts may therefore be needed to ensure that patterns of foraging behaviour observed at feeders, such as queuing, are representative of jackdaw social foraging under natural conditions. Alternatively, explicitly manipulating individual feeder access would enable the investigation of the role of certain individuals in determining social structure (e.g. Firth *et al*., 2017a) and the effect of task structure on patterns of association during foraging (Firth *et al*., 2015a; Firth *et al*., 2015b). Firth and co-workers (2015a; 2015b) created an active RFID-feeder system used it to explore the effect of limiting feeder access on social structure and the strength of key social relationships. Similar methods could easily be applied in our study system and would enable a range of innovative social behaviour experiments.

Future Work

Description of social structure is a vital first step prior to the investigation of the dynamics of information transmission through a social group (e.g. Allen *et al*., 2013; Claidière *et al*., 2013; Aplin *et al*., 2015). Recent development of analytical methods enables the determination of the value of social network structure for predicting patterns of information transmission (Franz & Nunn, 2009; Hoppitt *et al*., 2010). Social network position has been shown to predict acquisition of a novel foraging technique in captive ravens (Kulahci *et al*., 2016), but it would be useful to test whether social network position has a noticeable effect on information transmission in wild corvids.

Plasticity of social behaviour resulting from developmental conditions (i.e. ‘developmental plasticity’) has recently been tested experimentally (Boogert *et al*., 2014). Furthermore, developmental stress has been shown to affect cognition. Farine and co-workers (2015) experimentally adjusted the stress hormone levels of juvenile zebra finches and observed that greater stress increases the tendency of juveniles to learn a foraging skill from unrelated adults, rather than their parents. Social learning strategies (Rendell *et al*., 2011) may therefore be plastic and investigating if this phenomenon occurs in the wild would be valuable. Learning is itself a form of plasticity (Snell-Rood, 2013) and examining the ability of individuals to learn to alter their position within their social network, or learning to socially learn (Mesoudi *et al*., 2016), would add an additional dimension to studies of the flexibility of social behaviour.

Evidence from studies of primate cooperation suggests that partner switching (i.e. ‘partner-choice’), rather than manipulation of the same partner over multiple interactions (‘partner-control’), is likely the key mechanism governing cooperative exchange (Schino & Aureli, 2017). Generally, partner switching has been found to be the more prevalent mechanism when both processes have been investigated (Schino & Aureli, 2017). Interestingly, as jackdaw queuing seems to be commonly embarked upon by kin or breeding pairs, ‘partner-control’ dynamics may be important for determining the dynamics of jackdaw queuing. Experimental determination contributions of the relative contributions of ‘partner-choice’ and ‘partner-control’ processes to maintenance of turn-taking could be achieved by experimentally manipulating the frequency or value of queuing interactions between social partners.

Similarly, theoretical work (i.e. ‘evolutionary graph theory’) has shown that social network structure is a key factor determining of the emergence of cooperation in social groups (e.g. Ohtsuki *et al*., 2006; Santos *et al*., 2008). Specifically, greater clustering enables the maintenance of cooperation, as it increases the probability of co-operators interacting with each other (Kurvers *et al*., 2014). The introduction of partner switching dynamics may establish cooperation in populations (Santos *et al*., 2006). Examination of the feedback between network structure and cooperation has been conducted for human social networks (Fehl *et al*., 2011; Rand *et al*., 2011; Wang *et al*., 2012), but has not been tested for animals. Experimentally altering the social structure of wild populations (e.g. Firth *et al*., 2015a) and observing the effect on patterns of cooperation could therefore enable tests of the predictions of certain ‘evolutionary graph theory’ models.

Conclusions

Jackdaws exhibit individual variation in both foraging behaviour and their position within networks derived from social associations occurring during foraging. Social network position is related to fitness and is also plastic, as it can be affected by developmental conditions. Jackdaw social network position is therefore potentially under selection, but can also be flexible. In recent years, the analysis of animal social networks has graduated from mere description of social structure to investigation of the ecological and evolutionary processes acting upon and being influenced by social networks. Therefore, jackdaw colonies may be ideal systems for the study of social evolution and social plasticity. Furthermore, I found that interesting patterns of cooperation and turn-taking occur when multiple jackdaws forage together. The study of cooperation and turn-taking has largely been confined to captive groups, but our wild jackdaw populations could be used for innovative tests of theories of cooperation.

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