

CHAPTER 16

Perspectives on social network analyses of bird populations

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Introduction to social network analysis in birds

Studies of birds have played a particularly important role in the development of evolutionary and ecological theories and their subsequent empirical verification. For instance, Darwin's ornithological natural history notes from his travels on the *Beagle* coloured his evolutionary thinking and contributed to his development of the theory of natural selection (N. Barlow 1963). Niko Tinbergen, Konrad Lorenz, Julian Huxley, and Robert Hinde, studying bird behaviour, were among the first to recognize that behaviour is subject to selection, and their bottom-up, mechanistic, and comparative approaches to its study led to the development of ethology (Birkhead et al. 2014). Also working on avian models, Nick Davies, John Krebs, Amotz Zahavi, and others became interested in the evolutionary basis and adaptive nature of behaviour and helped formalize the discipline of behavioural ecology (Birkhead et al. 2014). Finally, the broad evolutionary and ecological approaches of Robert MacArthur, David Lack, and Ernst Mayr were developed, or inspired, while studying avian populations and helped focus ecology on rigorous quantitative hypothesis testing and questions about how individual behaviours can influence population level processes (Birkhead et al. 2014). An important thread connecting many parts of this pioneering work was the recognition of a central role of social interactions. Whether they be competitive, cooperative, exploitative, or related to mating, social interactions can structure populations and influence the process of evolution.

Consequently, understanding the ecological and evolutionary processes that cause variation in social behaviour, and the emergence of social structure, is a major research theme in evolutionary ecology and its various subdisciplines (W. Hamilton 1964a,b; Maynard Smith and Szathmáry 1995; Krause and Ruxton 2002; Whitehead 2008a; Bourke 2011).

The important contributions of the above-mentioned pioneers and many others significantly advanced our knowledge of the form, function, and evolution of many aspects of avian social behaviours. For instance, we now have a firm understanding of the adaptive significance of the extensive variation in mating systems in birds, and we are able to quantify many of the ecological life-history trade-offs underlying individual behaviours. However, relative to this vast literature, there has been little research emphasis on understanding the social structure of birds in terms of the pattern, nature, and quality of social relationships within populations. Many bird species are social, and the extent and duration of social behaviours vary tremendously both across species and over the course of life cycles. Understanding both individual and across-species variation in the tendency to be social is key to understanding how and why different degrees of sociality evolve and the extent to which individual phenotypes relate to their bearers' participation in social behaviour. It is also important to understand how social structures emerge, because these structures determine the extent to which social behaviour might mediate selection on both social and other phenotypic characters.

The lack of work on bird social structure that builds from the level of individual associations has not been due to a lack of interest or effort. Quantitatively rigorous examinations of vertebrate social structures at this level require detailed data on interactions among identifiable individuals (Hinde 1976; Croft et al. 2008; Whitehead 2008a,b), and such interactions have been very difficult to collect for birds. Largely due to the generally high vagility of many avian species, it has been logistically difficult to monitor interactions among a sufficient number of marked individuals over time-scales appropriate for delineating social structure. Then, having marked and identified individuals, defining individuals as associated or not in a meaningful manner is also often not straightforward. Many methods for following individual birds require extremely intensive field work (e.g. 9288 hours spent watching colour-ringed manakins (D. McDonald 2007)) to follow what is sometimes, statistically speaking (Whitehead 2008b), few individuals. Thus, questions of flock social structures have most often been addressed with presentations of measures of mean group size and demography.

Hinde (1976) proposed a conceptual framework for the study of primate social systems that has been adopted for use while studying animal social systems in general (Whitehead 2008a). His approach is bottom-up and considers dyadic interactions to be the fundamental unit of social analysis. Relationships are defined by the content (what a pair are doing), quality (how they do it), and patterning of successive interactions. A social structure can then be inferred from the nature, quality, and patterning of social relationships. At each level we can abstract social properties not apparent at the level below; relationships emerge from the pattern of interactions, and social structure from the pattern of relationships (Figure 16.1). Almost four decades since its publication, Hinde's framework continues to be influential, having led to rich and novel insights into the ecology and evolution of complex and sometimes cryptic animal societies (Goodall 1986; Cheney 1987; Dunbar 1988; Whitehead 1997; Whitehead 2008a).

Of the studies that have assessed pair-wise associations among individually identifiable birds, and thus implicitly or explicitly followed Hinde (1976),

social structure has been best studied among temperate non-migratory passerines (e.g. Nilsson and Smith 1985; Ekman 1989; Elena et al. 1999; Brotons 2000; Kraaijeveld and Dickinson 2001; Drent 2003; Griesser et al. 2009; Liker et al. 2009; Michler et al. 2011). The typical life history for this group consists of (1) a breeding season, during which pairs, sometimes together with helpers, defend territories and rear offspring; followed by (2) a brief period of continued offspring dependence post-fledging and a breakdown of breeding territoriality; and finally (3) winter flock formation. The social structures described for these species are broadly similar, at least superficially, to many other fission–fusion social systems in that fluid associations occur among pairs either within largely closed social units or across unbounded socially fluid populations. A third category of social structure, multi-tiered hierarchical associations among social groups at multiple levels (e.g. African elephants (Wittemyer et al. 2005)), has to our knowledge not been identified for birds. Within closed-unit fission–fusion systems, social flocks typically comprise of fewer than ten individuals who occupy exclusive ranges and are most often characterized by linear dominance hierarchies among group members (Ekman 1989). In unbounded fission–fusion systems, individuals form loose flocks that mingle and thus exchange individuals with other flocks in non-exclusive home ranges. Within these groups, dominance is typically site related (e.g. Krebs 1982; Brawn and Samson 1983; Yasukawa and Bick 1983; S. Smith 1984).

There has also been some focus on understanding the structure and consequences of sociality during breeding (e.g. Davies and Lundberg 1984; Davies and Hartley 1996; Double et al. 2005; D. McDonald 2009; Grabowska-Zhang et al. 2012; Hatchwell et al. 2013). For instance Grabowska-Zhang et al. (2012) used a 41-year dataset to show that great tits that had previously bred on adjacent territories and were thus familiar with their neighbours had greater breeding success. This suggests that social relationships on breeding territories can also be important.

Much of this previous work does not explicitly consider temporal aspects of social relationships, a key component of Hinde's framework. One of the first studies to do so in any taxa was a study

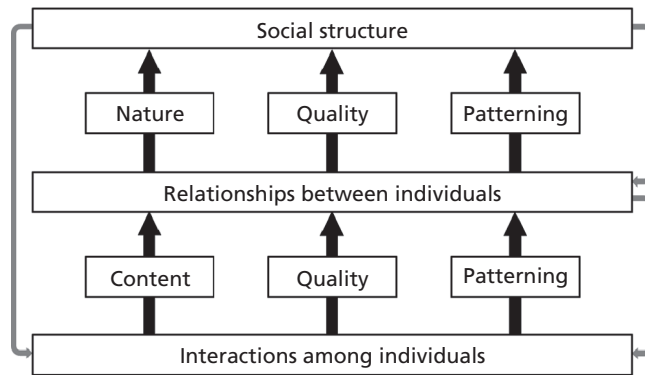


Figure 16.1 A summary of Hinde's (1976) framework for the analysis of animal social structures, after Figure 1.3 in Whitehead 2008a. Black arrows indicate characteristics of the lower level that are used to define the higher-level organization. Grey arrows indicate potential feedback mechanisms.

of the social structure of sanderlings (*Calidris alba*) in California (Myers 1983); incidentally, this work is also perhaps the first to formally compare association patterns to a null expectation of random associations, a practice that is now standard (Croft, Madden, et al. 2011). The research findings in this regard, however, were summed up well in the title which tells us that 'sanderlings have no friends'. Thus, while it is clear that mated pairs can remain associated across years, we still know very little about the persistence of other types of social relationships over time for most avian species. Incorporating time directly into network analyses is not straightforward, but progress is being made to identify appropriate techniques (Blonder et al. 2012; Hobson et al. 2013).

The general dearth of research into bird social structures, together with recent technological and analytical advances that allow for high-resolution data collection, presents researchers with an exciting opportunity to address consequential and broad questions about social evolution. In the rest of this brief overview of avian social network analysis, we highlight network building techniques and discuss recent work. In addition, we outline new research directions which illustrate that avian social network analyses are well placed to expand our understanding of social evolution and ecology.

Building avian social networks

Recent technological and analytical advances have alleviated some of the difficulties associated with monitoring sufficient numbers of individuals for

detailed analyses of social structure and now allow for large-scale quantitative social analyses of wild bird populations. However, more low-tech approaches are still valuable for many questions and can have advantages over other approaches in some instances. In this section, we discuss the primary approaches used to build avian social networks and briefly highlight advantages and disadvantages of each (Table 16.1).

Ringling and observation in avian social networks

Constructing social networks based upon colour ringling is straightforward; unique colour combinations of rings on birds allow individuals to be visually identified by an observer (e.g. D. McDonald 2007; Farine and Milburn 2013) (Figure 16.2a). A major advantage of this method is that interactions can be directly observed rather than inferred from associations, as is often the case with the automated methods described below. However, there is still scope for subjectivity, and particular types of interactions may often be unobservable. Observing direct interactions can provide an important context for social network construction and analyses. For example, directionality can be introduced into the network structure, and agonistic interactions can be differentiated from non-aggressive interactions for more rich descriptions of social networks.

One drawback of this approach is that it is difficult to observe many highly vagile species in the wild. It is also difficult to identify a great number of individuals at one time. Finally, the quantity and

Table 16.1 Comparison of the pros and cons of different methods for building avian social networks.

		Colour ring observations	Capture and recapture	Passive integrated transponder tags	VHF telemetry	Satellite and GPS telemetry	Encounternternet
Data characteristics	Distinguish directionality and/or type of interaction	Yes	No	No	No	No	No
	Gambit-of-the-group assumption	No	Yes	Yes	Yes	Yes	Yes
	Sample size (no. individuals)	Small	Medium	Large	Small	Small	Small/medium
	Temporal resolution	Low	Low	Medium	Medium/high	Medium/high	High
Costs	Labour intensity	High	High	Low	High/low ¹	Low	Low
	Costs of marks/tags	Low	Low	Low	Medium	High	Medium
	Costs of observation method	Low	Low	Medium	Low/high ¹	Medium/high	Medium
Longevity	Lifetime of marks/tags	Long	Long	Long	Short	Short/medium	Short
Biases	Risk of observer bias	Yes	Low	No	No	No	No
	Observation method affects distribution of individuals	Possibly	Possibly	Yes	No	No	No

¹ Triangulation with handheld antennae is labour intensive, but antennae are relatively cheap. In contrast, using antennae towers is less labour intensive but much more expensive.

quality of the data strongly depends on the skills of the observers, and the ambiguous nature of interactions might result in variations between observers. Overall, colour ringing and subsequent visual identification of associations is a useful strategy to address questions that require detailed information on a subset of individuals that occur together (e.g. constructing social networks to describe mating

systems; D. McDonald 2007). It is generally less suited to address questions about social networks at the population level due to limits of observations and sample size. Observations based on captures of birds with standard numbered rings (Figure 16.2) can also be used to construct social networks. Here, individuals trapped within the same timeframe are considered



Figure 16.2 (a) A wild New Caledonian crow fitted with a harness-mounted miniature proximity logger ('Encounternternet') as well as colour rings and a standard numbered metal ring (photo by Dr James St Clair; reproduced with permission from Rutz et al. 2012, *Current Biology*). (b) A wild great tit with an integrated passive integrated transponder tag in a plastic split ring on its left leg, and a standard numbered metal ring on its right leg (photo by Nicole Milligan).

to be a part of the same flock. Relative to some of the automated methods, it is difficult to obtain large sample sizes with this approach; however, often more individuals can be sampled than via colour ringing and observation. Therefore, this method can begin to address population level questions about social structure (Oh and Badyaev 2010).

This approach begins by making a number of assumptions common to many types of studies of social structure in order to construct the network. For example, because we do not directly observe interactions among individuals, we assume individuals that are associated in 'flocks' (i.e. are caught together) interact to the same degree with every other individual in the flock. This assumption is termed the 'gambit-of-the-group' (Whitehead and Dufault 1999) and can be useful when sample sizes are appropriately large and weighted network measures are used for analyses (Franks et al. 2010).

There is also a degree of arbitrariness associated with assumptions made here about the time window within which individuals are grouped that needs to be considered. We know a priori that the choice of a fixed time window within which to define individuals as grouped will not be ideal. For example, environmental conditions vary across days and seasons, and individuals mature; both of these factors are likely to lead to variation in social tendencies. Nevertheless, for many species, biologically informed, fixed time windows may serve purposes well.

Passive integrated transponder tags in the study of avian social networks

Passive integrated transponder tag (sometimes 'passive inductive transponder tag'; PIT tag, Gibbons and Andrews 2004) monitoring systems are increasingly being used for the automated study of animal social structure (e.g. bats (Patriquin et al. 2010), flying squirrels (Garroway et al. 2012), and birds (Aplin et al. 2012)). PIT tags are microchips that are activated when they pass through the electromagnetic field of a logger antenna, whereupon the unique chip ID is sent from the tag to the logger and recorded, together with the date and time. Typically, PIT tags are encased in 'bio-compatible' glass and so can be implanted subcutaneously

(Nicolaus et al. 2008; Schroeder et al. 2011). Implantation is straightforward, and detailed instructions for implantation can be found elsewhere (Gibbons and Andrews 2004; Nicolaus et al. 2008). Glass-encased PIT tags have also been glued to colour rings with no ill effects (as reported for house sparrows (Schroeder et al. 2011)), although potential detrimental effects likely vary among species.

PIT tags have also recently been incorporated into plastic split rings (e.g. IB Technology, UK, and Dorset ID, the Netherlands) (Figure 16.2b) that are suitable for some bird species. A benefit of using rings with encased PIT tags is that only one worker is required to mark an individual, whereas implantation is usually a two-person job. In addition, ringing is generally favoured from an ethical point of view, because it is regarded as being less invasive than implantation. The use of PIT tags incorporated into standard plastic split rings can usually be covered by an amendment to standard bird ringing licences.

A major advantage of PIT tag logging systems is that PIT tags are not battery powered and so, barring defective tags, they are expected to last the lifetime of the bird. The logging systems do, however, need power. PIT tags are also relatively cheap; thus, many birds can be marked. Loggers can range from very inexpensive systems (Bridge and Bonter 2011) to quite expensive, custom-built systems (e.g. selective feeders, and problem-solving devices).

One potential drawback that should be considered is that, when loggers are affixed to feeders, they act as attractants; so, care is needed during study design to disentangle the effects of non-social association at a limiting resource from those of social association. Another potential drawback of feeders at fixed locations is that it can be difficult to separate social from spatial effects. Possible solutions for both issues involve scheduling logging sessions to minimize attraction, and randomly moving systems throughout an area to reduce their predictability and thus decouple social from spatial effects. However, a counter-argument is that the use of fixed points, under a controlled sampling regime, allows a degree of control over the type of observations collected, which might be of particular use when carrying out experimental analysis. We should also note, from personal experience,

that feeders also act as attractants for other animals which may cause expensive damage to systems (e.g. feral grey squirrels at our study site in the UK).

A number of companies will build bespoke PIT tag data-logging systems, and low-cost instructions have been published for those that wish to build loggers themselves (Bonter and Bridge 2011; Bridge and Bonter 2011). Thus, marked birds can be monitored via PIT tags in a variety of ways. Typically, social associations are inferred from joint visits to feeding stations (although they might also be extracted from records of individuals passing through fixed points on the landscape). This gives a temporal data stream of individuals visiting a feeder. However, it is not straightforward to extract social groups and infer associations from this type of data.

Making the 'gambit-of-the-group' assumption here again, in this case the assumption that individuals that are temporally associated interact socially, it may sometimes be biologically meaningful to simply set a time window within which one defines groups or associations. An advantage of fixed time windows is that they are easy to calculate. However, they rely on an arbitrary cut-off for defining associations, and this cut-off is assumed to be fixed in space and time, which again is unlikely. Psorakis et al. (2012) suggest that a more rigorous method for extracting social groups from temporal data is to search for and extract regions of dense bird activity from the data stream of feeder visits. They term these regions 'gathering events' and these can be used to define social groups. From these groups, association indices can be calculated, networks constructed, and the duration of gathering events inferred from the data. This method avoids choosing a time window, which tends to have a large effect on the network measures extracted from the data (Psorakis et al. 2014).

Telemetry tracking in the study of avian social networks

Telemetry tools for tracking individuals are well developed and in wide use across taxa. There are now four basic types of telemetry tracking systems: systems based on VHF radio-telemetry, systems that use satellite transmitters, systems that use GPS receivers, and the recently developed Encounternet

system, which is based upon digital radio-telemetry. All of these technologies can give information on the spatial locations of individuals.

In principle, these location data could be used to build social networks based upon measures of individual proximity in space. In practice, however, this is easier for some systems than others. The spatial location of individuals affixed with VHF radio-telemetry tags are calculated via triangulation, which can be labour intensive and requires more than one observer (more observers leads to greater accuracy). It will rarely be possible for a sufficient number of marked individuals to be tracked concurrently and for sufficient spatial resolution of positions to be calculated to construct social networks with this method.

Alternatively, a grid of antennae towers can be used to monitor individuals with VHF radio tags continuously. This approach has not to our knowledge been used for birds, and examples in other taxa are scarce (e.g. Crofoot et al. 2008; Lambert et al. 2009), probably due to the high cost of towers and limited spatial coverage. However, it is possible to follow focal individuals via VHF telemetry to their flocks, identify those colour-ringed individuals that are present, and then construct social networks from these data (e.g. Templeton et al. 2012). Satellite tracking uses a high-powered transmitter to transmit data to satellites that calculate the spatial location of individuals and send that information to researchers over the Internet (e.g. Scherr et al. 2010; Trierweiler et al. 2013). GPS tracking involves affixing GPS receivers to individuals, which either need to be retrieved to recover data (e.g. Weimerskirch et al. 2002; Guilford et al. 2008) or send data via radio transmission on prescheduled times to a receiver (e.g. Van Gils et al. 2007). For gathering social data on birds, both of these techniques suffer from constraints associated with the cost and size of these instruments as well as occasionally inaccurate location determination.

The current costs of these technologies are likely to be prohibitively high for most researchers wishing to monitor the social behaviour of a considerable number of marked individuals, although costs are falling and accuracy improving, driven by developments in technology areas such as the mobile phone industry. In addition, the power requirements of

these techniques require the use of large batteries that make the size and mass of the units too big for many species of birds. The current smallest commercially available GPS tracker for birds weighs 12.5 g, so it is suitable for use with birds that weigh >250 g (following the '5% rule of thumb'; but see Barron et al. 2010). These problems seem likely to dissipate in the future as technological advances decrease both the size and cost of equipment, making these technologies potentially more useful for social analyses.

Encounternet is a recently developed digital radio-telemetry technology that holds great promise for providing detailed data that can be used to construct social networks (Mennill et al. 2012; Rutz et al. 2012; Krause et al. 2013). Encounternet tags (Figure 16.2a) transmit pulses that contain a unique identifier together with date and time stamps. Importantly, they also log pulses from other tags within range, and the received signal strength of pulses, which can be used to estimate the distance between individuals. Ultimately, the tags communicate these data to base stations from which researchers can remotely download and reprogram tags. Thus, detailed information about associations can be recorded on tags carried by the individuals (Rutz et al. 2012).

Similar to the challenge of defining individuals as associated or not in time with PIT tag data, it is necessary to choose distance thresholds to define social associations in space using Encounternet (Rutz et al. 2012). Appropriate distance thresholds will be species- and context-dependent, and indeed various distance thresholds are likely to be appropriate for different social processes within the same species. Mennill et al. (2012) have posted a useful video demonstrating the use of Encounternet for tracking individuals as a supplement to their recent paper introducing the technology (<<http://youtu.be/47XIZdXGOpU>>).

Choosing the best method for studying avian social networks

For most species, it is now possible to use automated monitoring systems for the collection of high-resolution data about social associations among individuals. Particularly, we feel that Encounternet

and PIT tag rings show great promise for adding insight into the social networks of birds in particular, by increasing the scale and resolution of data from which social networks are typically sampled. Which methodology will be best to use will of course depend on the scientific questions of interest.

PIT tags should last the lifetime of the bird and are cheap. However, in many cases, loggers require an attractant. Encounternet tags provide continuous data about social associations. However, Encounternet tags are more costly than some other marking methods, so often fewer birds can be marked. Encounternet tags are also larger than other kinds of tags (although still suitable for many small, passerine-sized birds) and are battery powered, so they have a limited lifespan. Finally, although the sample sizes obtained by direct observation will be smaller than those obtained by the automated systems, there will certainly be many instances when direct observation of interactions among individuals will be preferable to using the automated systems, as direct observation can provide contextual information that would be unavailable using the automated remote methods.

Exploring avian social networks

Using the methods described above, social network approaches are increasingly used to investigate avian sociality. However, the literature using a social network approach is still sparse. In this section, we present findings from a sample of this literature to illustrate the methodologies described in 'Building avian social networks' and present the scope of some questions being addressed by current research. The studies presented first investigate how the individual is affected by social structure, before taking a broader view to look at studies describing population level networks.

Two pioneering studies of avian social networks have suggested that social lability can potentially influence individual fitness (D. McDonald 2007; Oh and Badyaev 2010). In the first study, D. McDonald (2007) used a long-term dataset of colour-ringed long-tailed manakins (*Chiroxiphia linearis*) to show that early social lability, as measured by 'information centrality', predicted future reproductive success in this species. Long-tailed manakins have an

unusual lek-mating system, in which pairs of males cooperate at leks to perform dance and song courtship displays. Before forming this alliance, males spend up to 8 years interacting with many other males, thus forming dynamic social networks. During this time, males strive to rise in social status from a non-dancer, to a dancer, and finally to a beta or alpha male (the cooperative pair).

D. McDonald found that, for individual males, current social position was not related to social rise; however, the male's social position 5 years earlier was a strong predictor of social rise. It seems likely that young males seek to maximize their chance of rising in status to alpha male, and consequently achieving maximum copulatory success, by establishing relationships in leks where, relative to other males, they have the best chance of rising.

Similarly, Oh and Badyaev (2010) found that socially labile house finches (*Carpodacus mexicanus*), as determined by 'betweenness centrality', may also select their social environments to increase fitness. Male house finches display colourful breast plumage, ranging from pale yellow to deep red/purple, which is important for mate choice by females. During the non-breeding season, individuals interact in flocks within which mate selection, based upon plumage ornamentation, is thought to occur (Oh and Badyaev 2006). When Oh and Badyaev (2010) constructed a social network of associations during this non-breeding period, they found that less well-ornamented but socially labile males were able to increase their pairing success by choosing social groups according to the attractiveness of their ornamentation relative to that of others (see also Bateson and Healy 2005). Highly ornamented males increased their pairing success by having low lability, and less well-ornamented males did best to move between groups until they found a group within which their ornamentation compared favourably to that of the other male members. Together, these two studies provide evidence that animals can actively manipulate their social environments and thus the associated social selection pressures.

It is expected that individuals use social information to find food, and there have been several documented examples of this use (e.g. Lachlan et al. 1998). Aplin et al. (2012) recently showed that social information can be a benefit of social connectivity.

In their study of PIT-tagged, mixed-species tit flocks (family Paridae), they showed that not only do individuals use social information to exploit ephemeral food resources but that social network position predicted access to information. Specifically, network-based diffusion analysis (Franz and Nunn 2009) showed that social network position predicted the order of arrival at artificial food patches, suggesting that social tendencies influence access to information. Further, the order in which information is acquired can to some extent be predicted from the measured network.

In addition to identifying ways in which individuals stand to benefit from their position within their social network, network analysis has also given more general insight into how social structure interacts with population processes. Here, we describe four examples; in each case social network structure has provided insight into individual relationships. First, Templeton et al. (2012) used radio-telemetry to follow focal juvenile male song sparrows and subsequently identify their associates via colour rings, in order to build their social network. The authors found that the density of the network varied throughout the season and that seasonality was related to the individual's number of associates of different age and sex classes. Juvenile males formed stable relationships, often with other juvenile males, and these alliances had long-term consequences, because males were more likely to hold future territories near each other and acquire similar song types.

Second, D. McDonald (2009) used the long-tailed manakin dataset described earlier to investigate social, spatial, and genetic structures and determine commonalities between them. Although he found that genetic relatedness decreased with increasing social distance, there was no evidence for kin selection in his study, because all social distances were less than expected by chance. Such a comparison of social structure with genetic relatedness gives unique insight into population processes, as well as individual association strategies.

Third, Aplin et al. (2013) have recently shown that for great tits, individual variation in personality traits underlies some aspects of social structure. Finally, social networks have also been used to investigate between species interactions. Farine

and Milburn (2013) studied a mixed-species social network based upon associations within thornbill (*Acanthiza* spp.)-dominated flocks. The authors built their network via visual identification of colour-ringed individuals. They found a rich mixed-species structure similar to that found within species and identified a shift in foraging niche by thornbills depending upon flock composition. Beyond population level analysis, there is also scope for social network analyses of mixed-species flocks that would make important contributions to our understanding of the evolution of species interactions (Farine et al. 2012).

This section was not at all an exhaustive survey of avian social network research. While there are some emerging themes, such as social niche selection (D. McDonald 2007; Oh and Badyaev 2010), it is clear that social network analysis as a tool has broad scope to address many interesting questions. Additional topics within which network analysis has been used as a tool include disease transmission (MacGregor et al. 2011), the fitness consequences of within family social interactions (Royle et al. 2012), mating systems (Ryder et al. 2008; Ryder et al. 2011), mate choice (Henry et al. 2013), communication (Miller et al. 2008), and collective navigation (Bode, Franks, Wood, et al. 2012), among many others.

Social network analysis of avian societies

A small but growing body of literature has examined avian social networks, and recent technological advances will increasingly facilitate detailed studies. Thus, future avenues of avian social network research are exciting. Here, we discuss a few particular lines of research that we believe will be particularly fruitful for addressing questions about social evolution in birds in the near future.

Eco-evolutionary processes affected by the structure of avian societies

In general, across taxa, we have very little understanding of the importance of social interactions and social structure for ecological and evolutionary processes. In part, this is a result of difficulties associated with characterizing social behaviour at suitable scales in terms of sample sizes of individuals,

and numbers of generations (T. Clutton-Brock and Sheldon 2010). Relative to many other taxa, birds are particularly amenable to detailed multigenerational study of large, sometimes whole, populations (e.g. Kluijver 1951; Lack 1964). Long-term studies have typically focussed upon relatively easy-to-monitor species but have come from across diverse avian taxa including passerines (e.g. Kluijver 1951; Lack 1964; Grant 1999), seabirds (Dunnet et al. 1979), waders (Harris 1970), waterfowl (F. Cooke and Rockwell 1988), and raptors (Newton 1985). The number of individuals monitored annually in these studies ranges between hundreds to thousands of individuals, and, very often, detailed life-history data pertaining to reproductive effort, timing, and success, together with environmental data associated with breeding locations, individual survival, morphology, and other measures can be collected. These types of data also allow for the construction of detailed pedigrees.

Such long-term studies are certainly not unique to birds (e.g. Goodall 1968; Connor and Smolker 1985; Festa-Bianchet 1989). However, the life histories of many birds species make them particularly tractable for such detailed data collection on a very large number of individuals and the subsequent monitoring of social structure. With detailed multigenerational data on life histories and large sample sizes, studies of avian population wide social networks can be constructed. These studies could have important implications for our understanding of the life-history costs and benefits of sociality.

Social phenotypes and gene \times environment interactions in avian societies

An interesting question, although one that is difficult to address, is the degree to which genetics and environment interact to produce an individual's social phenotype. Teasing apart these processes is likely not possible without experimental manipulations. This is because parents, offspring, and siblings all share similar environments; such conditions lead to genotype \times environment correlations. The life history of many bird species also makes them particularly amenable to experiments in the wild. Cross-fostering experiments, where eggs or chicks are taken from their genetic parents

and reared by unrelated foster-parents according to an appropriate experimental design, are straightforward to conduct and widely used in wild avian populations. Cross-fostering experiments among parents and environments could be used to account for the effects of environmental and genetic sources of similarity between relatives (Kruuk and Hadfield 2007).

Another reason to perform cross-fostering experiments is that the expression of an individual bird's social phenotype is likely to depend on the social phenotypes of the birds it is interacting with. When offspring tend to stay close to their natal area, they are more likely to interact with relatives; thus, the genetic and shared environment effects on the social phenotype may be overestimated. This will be the case when the probability that an individual initiates an interaction correlates with the probability it responds to an interaction (e.g. individuals initiating aggression towards conspecifics are also more likely to respond with aggression towards aggressive encounters initiated by conspecifics). With experimental approaches such as cross-fostering, we can begin to address questions that are currently wide open regarding the heritability and strength of selection on social network position.

The social characteristics of individuals, and emergent network structure in avian societies

Recent advances in monitoring technology, and the development of PIT tag loggers in particular, enable direct experimentation on social networks. The automated detection of individuals with PIT tags can be used as the basis for applying experimental treatments at the individual level, in order to test how individual traits influence the structure of social networks. For instance, individuals might be selected to receive audio playback, or visual stimulus (such as predator presentation), to determine how individual variation in the perception of the environment feeds through to the emergent properties of the population. Alternatively, and more speculatively, linking detection to food delivery offers the possibility of targeting certain individuals with specific dietary supplements, hormones, or psychotropic drugs, and thus asking how changes in individual nutritional or physiological

state influences social structure. Finally, loggers can be designed so that they require birds to solve a complicated task (e.g. Morand-Ferron and Quinn 2011) in order to gain some reward, thus enabling researchers to monitor innovation and learning on social networks.

The role of social context in natural and sexual selection in avian societies

Studies of social processes will benefit from being able to put the individual into its broader social context (see Oh and Badyaev 2010; G. McDonald et al. 2013). It is generally unrealistic to assume that a focal individual is affected similarly by all other individuals in a population. It will therefore often be desirable to account for the importance of associations between specific other individuals within the context of the entire population.

For instance, with a network approach, studies of sexual selection no longer need to assume that each individual has a choice of all other individuals in the population but rather can assume, more realistically, that each individual has a choice of just those individuals that are within its social network (see Benton and Evans 1998; Kasumovic et al. 2008). An important paper by G. McDonald et. al (2013) highlights this, stressing the importance of considering the social network at a number of different levels. For example, the sexual network limits the population to the individuals a focal bird copulates with (these ideas are expanded upon in detail in Chapter 4) and thus is expected to be important for sperm competition, maternal investment, and sexually transmitted disease transfer. Similarly, the social network limits the population to the individuals a focal bird has contact with, revealing a realistic subset of the population under consideration for, for example, mate choice.

Underlying social structure and collective behaviour in avian societies

Another area in which bird social structure has been quantified is the context of collective behaviour. Collective behaviour is the study of how coordinated group-level patterns emerge from interactions

among individuals. The fields of animal social network analysis and collective behaviour are developing somewhat separately but are perhaps more closely aligned than is often considered (Krause and Ruxton 2010). Social networks and the data used to generate individual-based models of collective behaviour are often derived from similar sources and so, in some cases, social networks can be seen as static summary representations of collective social group behaviour (Krause and Ruxton 2010). Perhaps one of the most striking images of collective behaviour is that of European starling (*Sturnus vulgaris*) murmurations. Three-dimensional analyses of murmurations suggest that the impressive coordinated movement emerges from individuals monitoring the nearest seven or so birds (Ballerini et al. 2008).

Jolles et al. (2013) recently showed that heterogeneous social structure related to dominance hierarchies and mated pairs in mixed-species corvid flocks shaped collective flight behaviour. Nagy et al. (2013) recently incorporated hierarchical social networks into analyses of collective motion in domestic pigeons (*Columba livia*) to show that dominance and leadership hierarchies were independent of each other in this species. Taken together, these two studies suggest that there is information to be gained about collective processes by accounting for social relationships among individuals with social networks, rather than by assuming that individuals are interchangeable and all follow the same simple rule in the same manner.

Individual interactions and social structure in avian societies

Most studies of social networks in birds are based on gambit-of-the-group observations (i.e. it is assumed that individuals that are part of the same foraging flock directly interact with all other individuals); relatively few studies have used social network analyses to investigate interactions per se. An exception is the work on communication networks (Naguib et al. 2004; McGregor 2005; Matessi et al. 2008; also see Chapter 9). In communication networks, directionality is known, and the meanings of interactions are often known as well. The identities of the receivers are, however, not always

clear, as the travel distances of communications often vary with environmental conditions (Matessi et al. 2008).

One advantage of studying interactions is that they can more easily be translated into particular types of behaviour, such as competition for mates. Competition for mates is probably best studied by means of so-called sexual networks (G. McDonald et al. 2013). Other competition-based networks can be constructed as well; however, competitive interactions are generally harder to measure than co-operative ones (e.g. avoidance).

For example, avian social networks can be constructed by measuring the exploration or exploitation of resources by different individuals so that the exploitation or exploration of the same resources is counted as an interaction. Visits to the same nest cavity can be monitored via PIT tags, and competition-based bipartite networks built based upon visits to potential nest sites. Alternatively, aggression between individuals can be measured. Indeed, there is a rich literature exploring dominance hierarchies, and a recent emphasis placed upon exploring dominance hierarchies within a network context (D. McDonald and Shizuka 2012; Shizuka and McDonald 2012; also see Chapter 7).

The conservation and management of social units in avian societies

Delineating management units is difficult, due to well-known problems associated with choosing the appropriate definition of a population. These problems are typically related to genetic structure, space use, and population size. Once a population is defined, management actions are often directed towards individuals as the constituents of the population. However, active association among individuals implies a benefit of being social. It seems likely that, for some social species, the appropriate target for conservation within populations should be social groups rather than individuals, if social relationships are important for survival and reproduction.

For instance, many passerine species flock during winter. Benefits of flocking are thought to be associated with predator avoidance and dilution as well as increased foraging efficiency (Sridhar et al.

2009). Targeting management at solely the individual level may ignore important features associated with maintaining flock cohesion, potentially inducing something akin to Allee effects (Allee 1938): a negative relationship between social group size and reproduction. Network analyses provide efficient methods for delineating complex social structure (Newman 2006) and so could be particularly important for understanding conservation needs relative to social structure.

Genetic determinants of variation in social phenotypes in avian societies

Although sociality can, like other phenotypic traits, affect fitness (Silk 2007) and therefore be under selection, very few studies have explored the relation between genetics and individual variation in the tendency to be social. Some avian studies have explored the heritability of socio-behavioural traits such as dispersal (e.g. McCleery et al. 2004; Charmantier et al. 2011; Doligez et al. 2012) and personality (e.g. Dingemanse et al. 2003) but, to our knowledge, only a few studies of mammals have explored the heritability of the tendency for individuals to occupy certain social positions within broader social structures (Fowler et al. 2009; Lea et al. 2010; Brent, Heilbronner, et al. 2013; Christakis and Fowler 2013). The next step is to link individual social tendencies and genetics to fitness but, again to our knowledge, this has only been done for humans (Christakis and Fowler 2013). Potential reasons for this are that (1) social traits can be more difficult to measure than morphological traits; (2) sociality is expected to be more prone to additional sources of variation than morphological traits; and (3) social traits are thought to be more plastic than morphological traits and are therefore more likely to respond flexibly rather than through evolutionary changes. Studies of the heritability of social positions have found wide variation ($h^2 = 0.10 - 0.84$) (Lea et al. 2010; Brent et al. 2013). The availability of long-term studies on birds with pedigrees (i.e. for quantitative genetics models and to assess fitness (Clutton-Brock and Sheldon 2010)), the rapid technical advances and reduction of costs of molecular genotyping of non-model

species (i.e. for marker-based genetic models (Ellegren 2008; Garvin et al. 2010)) and the advances in techniques for collecting social network data (as discussed extensively in this book) open up exciting new possibilities for understanding the genetic basis of sociality and for linking the ecological significance of sociality to its evolutionary dynamics.

The interaction of genetic and social structures in avian societies

In landscape and population genetics, the importance of social processes such as dispersal, kin structure, and social segregation are widely accepted and integrated into analyses (Sokal and Oden 1978; Fortin and Dale 2005; Fowler et al. 2009). Studies often tend to either correct for those effects or model them as spatial autocorrelation, which serves as a receptacle for many social and non-social biotic processes such as genetic drift and shared population histories (Diniz-Filho et al. 2012). In animal breeding, quantitative genetic models incorporating indirect genetic effects have recently been developed to take social structure into account. Until now, indirect genetic effects were based on either dyadic responses (Sartori and Mantovani 2013) or group or cage effects (i.e. multiple unweighted but fully saturated networks (Bijma et al. 2007)). There is scope for introducing social networks in quantitative genetics models, similar to the way indirect genetic effects are modelled by introducing weighted social networks as variance–covariance matrices in models resembling techniques for incorporating spatial structure (e.g. Stopher et al. 2012).

Another interesting approach for studying the interdependence of social and genetic structures is the use of eigenvector-based methods for canonical ordination of graphs. These methods can be used to model the effect of social structures on multivariate datasets (such as genetic markers), similar to the way those methods are currently used to model spatial structures (Legendre and Legendre 2012). Both social and spatial structures can be modelled simultaneously to separate spatial from social effects and thus are particularly useful for studies on wild populations (Radersma et al. 2014).

Social network analysis in birds: conclusions and future directions

The importance of social processes in evolution has long been recognized, and the study of avian social networks has the potential both to refine existing theory and to contribute new insights. New technology now allows for detailed social network construction based upon many more individuals than had previously been feasible. The types of opportunities for research discussed here are not uniquely avian; however, many will be particularly amenable to avian systems.

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