THE USE OF EXPONENTIAL RANDOM GRAPH MODELS TO EXPLORE SOCIAL FORAGING DYNAMICS OF INTERSPECIFIC SONGBIRD ASSEMBLAGES

BY

JASON D. FISCHER

DISSERTATION

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy in Ecology, Evolution, and Conservation Biology
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2015

Urbana, Illinois

Doctoral Committee:

Associate Professor James R. Miller, Chair, Director of Research
Professor Emeritus Paul A. Garber
Professor Jeffrey D. Brawn
Assistant Professor Michael P. Ward

ABSTRACT

Network analysis has been applied in many ecological and behavioral contexts to investigate systems of complex interactions. Its broad applicability is due in part to the generality of what constitutes a network—a set of objects (referred to as nodes) that are linked by some sort of connection (termed edges). Until recently, however, network analyses were largely descriptive in nature, which limited their utility. Statistical advances now allow networks to be modeled, which has expanded the capabilities of network analysis for hypothesis testing. One such advance is exponential random graph models (ERGMs). Developed for the social sciences, ERGMs analyze how network structures (i.e., configurations of edges) and attributes of nodes and edges affect the formation of edges. This allows practitioners to explore how different mechanisms shape networks of interest. In this dissertation, we introduce ERGMs to ecologists and animal behaviorists, highlight their advantages and applications, and demonstrate some of their uses in a series of case studies of social foraging dynamics in a community of songbirds. Using radio frequency identification technology, we monitored behavior at bird feeders in east-central Illinois over a two-year period to develop a unique dataset of foraging activity and social interactions. Data were then used to build networks that were analyzed using ERGMs in the following chapters.

In chapter 2, we explored how urbanization affects species interactions within social foraging networks at bird feeders. Anthropogenic change reduces species richness and size of mixed-species foraging flocks, so we expected urbanization would reduce the number of species at feeders and simplify social foraging network structure. Though species richness declined with urbanization, complexity of social foraging networks did not. Interspecific foraging declined as

species that facilitate the formation of mixed-species foraging flocks were extirpated by urbanization, but reductions in interspecific foraging were compensated for by increases in intraspecific foraging among introduced species. This is the first study to demonstrate how urbanization shapes interactions in mixed-species foraging assemblages.

In chapter 3, we examined the role of interspecific interactions in shaping daily patterns of foraging activity of small birds in temperate winters. Theoretical investigations of this system are a classic case of modeling tradeoffs—in this instance between the risks of starvation and predation. However, these models do not account for interspecific variation in predator behavior or prey responses, though interactions among prey and between predators and prey are known to affect foraging behavior. We did not observe any influence of interspecific social foraging on temporal feeding patterns, but species varied in terms of daily foraging activity. We hypothesized that differences in vulnerability to predation due to variation in species-specific predator/prey relationships produced these patterns.

In chapter 4, we investigated how social dynamics can be modified by disease and how these changes can in turn affect disease transmission. We compared foraging behaviors of house finches (*Haemorhous mexicanus*) captured with and without a bacterial disease (mycoplasmal conjunctivitis) to determine if infected birds differed in foraging activity, patterns of association with heterospecifics and conspecifics, and sociality (i.e., number of foraging partners). Infected house finches were more likely to visit feeders and forage with other birds. These behavioral changes were likely the result of the disease but also increased the risk of disease transmission to healthy birds, particularly because of the possibility of indirect transmission at contaminated bird feeders.

We have demonstrated that ERGMs are a useful tool for studying mechanisms underlying

complex biological networks and hope our work stimulates future use of ERGMs in ecological and behavioral contexts.

ACKNOWLEDGEMENTS

This project was only possible because of the generous efforts of a small army of volunteers. Study-site owners purchased sunflower seed for the project and kept bird feeders filled throughout the study. Over fifty people (particularly Nancy Snellen) assisted with capturing and banding birds from late spring to early fall. Droll Yankees, Inc., donated the bird feeders used for the project and funding was provided by the Illinois Ornithological Society, the Champaign County Audubon Society, the Binky Foundation, and the National Science Foundation Graduate Research Fellowship Program. Special thanks go to David Bonter, Eli Bridge, Joseph Casto, and Ben Kamen for providing invaluable assistance on the construction and use of radio frequency identification readers, and Bethany Cutts assisted with ERGM analysis. Thanks are also due to collaborator Kevin Wolz, who conducted the Gaussian mixture modeling referenced in the following chapters. Christine Parker, Jaime Coone, Samniqueka Halsey, Scott Nelson, Henry Pollock, Brett DeGregorio and Matt Louder provided useful comments on drafts. My doctoral committee provided much needed guidance throughout this study and my advisor, Jim Miller, has overseen my development as a researcher, teacher, and writer, for which I will always be in his debt. Most importantly, I thank my wife, Sara Fischer, for her continual support and encouragement throughout the project.

TABLE OF CONTENTS

CHAPTER 1. Introducing exponential random graph models: the application of a network modeling approach to the study of ecology and animal behavior

Co-author: James R. Miller

INTRODUCTION

Network analysis has been widely applied in ecology and animal behavior to understand systems composed of complex interactions. Our knowledge of processes that shape intraspecific societies and mixed-species communities has been deepened through network studies of social interactions (Croft et al. 2008, Pinter-Wollman et al. 2013), and these insights have been applied in an epidemiological context to explain dynamics of disease transmission (Godfrey 2013). Ecological networks have been used to describe food webs, mutualisms (e.g., pollination networks), and host-parasitoid systems (Bascompte and Stouffer 2009, Ings et al. 2009), offering insight into factors affecting energy flow and network stability. Networks of habitat patches have also been used to study connectivity and dispersal (Cumming et al. 2010, Gonzalez et al. 2011). Across these varied contexts, network analyses are applicable because of the simplicity of the network definition and the ability of networks to describe complex systems.

A network is a set of objects (called nodes) and connections between them (called edges; see Table 1 for an overview of network terminology; Harris 2014). The biological meaning of nodes and edges can be tailored to any system, such as disease transmission among individuals, trophic linkages between species, or dispersal among habitat patches. Network analyses are then used to identify components of the network to reveal patterns that might not otherwise be apparent (Harris 2014). Such patterns can be made of simple network structures such as triads of

interconnected nodes (which indicate the presence of clusters of connected nodes) or more complex associations such as larger groups of nodes that are more connected to one another than to nodes in other groups (e.g., social groups within a larger society; Croft et al. 2008). Permutation tests of randomly generated networks determine whether observed network structures occur more or less frequently than expected by chance (Croft et al. 2011). This approach has been useful for deconstructing complex patterns of interconnection and testing hypotheses that predict nonrandom frequencies of different network structures (Croft et al. 2008). However, such methods cannot explain why particular nonrandom patterns are present or infer what conditions are likely to produce them (Lusher et al. 2013). In order to study the underlying mechanisms producing observed networks, an inferential modeling framework is needed for network analyses (Pinter-Wollman et al. 2013, Harris 2014).

Until recently, the primary barrier to creating an inferential modeling framework for networks has been an inherent assumption in the traditional generalized linear model framework (Croft et al. 2011, Harris 2014). The assumption of independence requires that measurements of dependent variables be independent of each other for each experimental unit in a study (Lusher et al. 2013). However, in networks where the experimental unit is a pair of nodes (called a dyad) and the dependent variable is the presence or absence of an edge, this assumption cannot be met (Harris 2014). The presence of one edge must be independent of the presence or absence of others in the network, but such dyadic independence is rare in real world networks. Instead, dependencies among dyads are responsible for many observed network structures (e.g., three edges must be simultaneously present in a triad of nodes to create a triangle; Harris 2014). To circumvent this issue, past studies of networks have randomly selected edges to remove dependencies among the analyzed subset of experimental units and then used generalized linear

models (Harris 2014). The problem with this approach is that it separates edges from the framework of network connections in which they occur (Lusher et al. 2013). To use a social science analogy, this is like trying to study family dynamics by only investigating the behavior of one person per family. The alternative to this approach is an analytical framework that explicitly models dyadic dependence rather than circumventing it (Harris 2014).

One such framework is the exponential random graph (or p*) model (ERGM; Hunter et al. 2008). Developed in the social sciences, ERGMs test hypotheses about processes that shape networks by modeling how edge formation is affected by specified variables (Harris 2014). These variables can be attributes of nodes and dyads or different kinds of network structures (Table 1; Figure 1). Different variables represent hypothetical mechanisms that could influence the likelihood of edges occurring in a network (Lusher et al. 2013). Thus, by comparing models made up of different combinations of structures and attributes, researchers can identify the set of mechanisms that best explain observed networks (Harris 2014). Mechanisms can then be interpreted in a framework similar to logistic regression (Harris 2014). Here, we review these features of ERGMs in greater detail as a means of introducing ecologists and animal behaviorists to the utility of this analytical framework.

ERGM OVERVIEW

ERGMs model edge formation using a logit function similar to that used in logistic regression (Harris 2014). Model parameters determine the probability of a binary outcome, which for ERGMs is the presence or absence of an edge for each dyad in the network (Hunter et al. 2008, Harris 2014):

$$\text{logit}\left(P\left(Y_{ij} = 1 \middle| n \text{ nodes}, Y_{ij}^{c}\right)\right) = \sum_{k=1}^{K} \theta_k \delta_{Z_k(y)}$$

Unlike logistic regression, the probability (P) that an edge forms for a given dyad ($Y_{ij} = 1$) is contingent on all other dyads in the network (Y_{ij}^{c}) made up of n nodes. As a result, model probabilities are conditional on the rest of the network and ERGM results are interpreted relative to the other parameters in the model (see Harris 2014 for details on probability calculation). A second difference between logistic models and ERGMs is that the k parameters (θ_k) in the model are multiplied by a change statistic $\delta_{Z_k(y)}$ for each dyad rather than values of an independent variable (Hunter et al. 2008). This is because many variables used in ERGMs (see below) are not inputted in a format that can be used to test their effect on the probability of edge formation; change statistics transform these variables to make the analyses possible (see Morris et al. 2008 for more detail).

The most basic ERGM parameters are node and dyad attributes, which are referred to as main effect variables (Morris et al. 2008). Node attributes can be categorical or continuous while dyad attributes (either for all dyads or only those with edges) are continuous. Continuous variables measure whether edges are more or less likely to form as the value of the variable increases (Harris 2014). For example, the likelihood of dispersal between habitat patches could be modeled as a function of patch size (continuous node attribute) or distance between patches (continuous dyad attribute). Categorical variables measure whether edges are more or less likely to form with nodes of a particular category compared to nodes of a baseline category (Harris 2014). Such a modeling approach could be used to compare the likelihood of attracting a mate between younger and older adults.

In addition to main effects, interaction effects can be modeled for dyads based on differences in nodal attributes (Morris et al. 2008). For continuous attributes, such as the mass of animals in a network of aggressive confrontations, one type of interaction effect could be the

effect of the mass differential between pairs on the likelihood of confrontations occurring (as opposed to a main effect of mass, which would test whether larger animals were more likely to engage in confrontations). For categorical node attributes, interaction affects are measured by assortment and attribute mixing. Assortment measures the degree to which nodes with similar or different categorical attributes are connected (Farine 2014). For example, in a food web in which nodes are species, a categorical variable for trophic level could be used in conjunction with assortment to assess the relative importance of intraguild predation versus predation between trophic levels. Assortment differentiates between nodes with the same or different attributes, but not unique combinations of different attributes. Attribute mixing, on the other hand, models the likelihood that each combination of attributes will form more or fewer edges than a specified baseline.

Both interaction and main effects are dyad independent, as no assumptions are made about how one edge affects the presence or absence of others (Morris et al. 2008). More complex network structures involving more than a single edge can also be incorporated into ERGMs (Hunter et al. 2008, Morris et al. 2008). Because multiple edges must be present to form these network structures, they are dyad dependent and can model a wide diversity of processes by indicating whether a particular network structure increases or decreases the likelihood of edges forming (Table 1, Harris 2014). For example, groups of three nodes can model dominance in networks of aggressive interactions (Shizuka and McDonald 2012). In this example, edges are directed, which means that the meaning of a connection in a dyad is different for each node. In our example, one individual wins an aggressive interaction and the other loses. In triads of nodes with two edges, an individual can win both interactions (i.e., two-outstar; Table 1) or lose both (i.e., two-instar; Table 1); the number of two-outstars and two-instars for each individual in the

network is a measure of its relative dominance. In triads of nodes with three edges, each individual wins once and loses once (i.e., cyclic triple), or one individual wins twice, one individual wins one and loses one, and one individual loses twice (i.e., transitive triple). Modeling cyclic and transitive triples in an ERGM can show whether dominance relationships are organized linearly or not. If transitive triples are more likely to occur than expected and cyclic triples are not, then dominance relationships among individuals are organized linearly (i.e., individual A beats all other individuals, B beats everyone but A, C beats everyone but A and B, etc.). Otherwise, particular individuals are not consistently dominant over others.

Variables selected for analysis can be combined into different models to determine which set of mechanisms best explains an observed network (Harris 2014). Model sets typically include a null, main effects models, interaction effects models, and dyad-dependence models. The null in ERGMs has a single model term, analogous to an intercept-only model in generalized linear models (Morris et al. 2008). This parameter corresponds to the density of the network (i.e., the proportion of dyads with edges) and models the hypothesis that edges are randomly distributed in the network (Harris 2014). Main effect and interaction models are parameterized using maximum likelihood estimation (Hunter et al. 2008), but such an approach is computationally prohibitive for models that incorporate dyad-dependent terms (Harris 2014). Instead, a Markov chain Monte Carlo algorithm calculates parameter estimates by iteratively sampling possible networks to identify the one with properties most similar to the observed network given the model parameters (Snijders 2002). Once models have been parameterized, they can be compared using an information theoretic approach or goodness-of-fit diagnostics (Goodreau et al. 2009). However, an information theoretic approach is less appropriate for comparisons with dyad-dependent models because they are based on calculations that assume dyadic independence

(Harris 2014). Despite this, when model comparisons show large differences in AIC values, the information theoretic and goodness-of-fit approaches produce lead to similar conclusions even with dyad-dependent models.

In addition to the network modeling described above, ERGMs have been adapted to model a broader range of network types applicable to the study of ecology and animal behavior (Figure 1; Lusher et al. 2013, Harris 2014). Here we introduce some of these network types, but in-depth coverage is beyond the scope of this overview. Bipartite networks involve two node types rather than just one (Morris et al. 2008), allowing attributes of both node types and the structures associated with each to be modeled. In connectivity studies, one node type could be habitat patches, another could be individuals that utilize those patches, and connections would be instances in which individuals use (or disperse to) a patch. Weighted networks reflect the strength of connections between node pairs (i.e., the number of times a connection occurs) rather than just the presence or absence of edges (Desmarais and Cranmer 2012, Krivitsky 2012). Modeling these weights can provide insights that would be lost using a binary approach, as weak and strong connections can have very different effects on network properties such as stability in food webs (Ings et al. 2009). Finally, dynamic ERGMs can model changes in network structure through time. This is accomplished by modeling processes that form and remove edges separately (Bender-deMol et al. 2008). From an epidemiological perspective, such an approach would be important for modeling how social dynamics and the development of resistance affect disease transmission during an outbreak.

CASE STUDIES

To our knowledge, ERGMs have yet to be applied in ecological and animal behavior contexts.

Here, we highlight some of the uses to which ERGMs can be put using a series of case studies involving social foraging behavior of songbirds at bird feeders.

In Chapter 2, we explored how changes in species-specific patterns of social foraging affected network structure along a gradient of urbanization. Networks were composed of individual birds connected by instances in which pairs foraged together. We constructed ERGMs that tested whether a node attribute (species) and assortment affected the likelihood of social foraging occurring and explained more complex network structuring. Species varied in their propensity to forage socially and the influence of interspecific foraging on network structure waned as urbanization increased.

In Chapter 3 we examined how interspecific interactions shaped daily patterns of foraging activity. Bipartite networks were used for this analysis. One node type was individual birds and the other was foraging bouts in which birds visited feeders together. We analyzed how attributes of each node type (species and time at which a foraging bout occurred) affected the likelihood that foraging occurred. While temporal foraging patterns were not strongly influenced by foraging associations among species, daily foraging patterns varied widely among species, which we attributed to differences in species-specific vulnerability to predation.

In Chapter 4, we investigated how social interactions and feeder use varied between house finches (*Haemorhous mexicanus*) with and without a bacterial disease. We used both unipartite and bipartite networks for this analysis and found that infected birds were more social and more likely to visit feeders. These behavioral changes were likely the result of the disease, but also increased the risk of infection for healthy house finches visiting feeders.

These studies demonstrate that ERGMs are a useful tool for studying the mechanisms underlying complex biological networks, though we only utilized a small portion of the potential

analyses available through the ERGM framework. We hope our work raises awareness of the potential applications of ERGMs and stimulates their incorporation into the fields of ecology and animal behavior.

LITERATURE CITED

Bascompte, J., and D. B. Stouffer. 2009. The assembly and disassembly of ecological networks. Philosophical Transactions of the Royal Society B: Biological Sciences **364**:1781-1787.

Bender-deMol, S., M. Morris, and J. Moody. 2008. Prototype Packages for Managing and Animating Longitudinal Network Data: dynamicnetwork and rSoNIA. Journal of Statistical Software **24**.

Croft, D. P., R. James, and J. Krause. 2008. Exploring animal social networks. Princeton University Press, Princeton, New Jersey.

Croft, D. P., J. R. Madden, D. W. Franks, and R. James. 2011. Hypothesis testing in animal social networks. Trends in Ecology & Evolution **26**:502-507.

Cumming, G. S., Ö. Bodin, H. Ernstson, and T. Elmqvist. 2010. Network analysis in conservation biogeography: challenges and opportunities. Diversity and Distributions **16**:414-425.

Desmarais, B. A., and S. J. Cranmer. 2012. Statistical inference for valued-edge networks: the generalized exponential random graph model. PLoS One **7**:12.

Farine, D. R. 2014. Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges. Animal Behaviour **89**:141-153.

Godfrey, S. S. 2013. Networks and the ecology of parasite transmission: A framework for wildlife parasitology. International Journal for Parasitology: Parasites and Wildlife **2**:235-245.

Gonzalez, A., B. Rayfield, and Z. Lindo. 2011. The disentangled bank: how loss of habitat fragments and disassembles ecological networks. American Journal of Botany **98**:503-516.

Goodreau, S., J. Kitts, and M. Morris. 2009. Birds of a feather, or friend of a friend? Using exponential random graph models to investigate adolescent social networks. Demography **46**:103-125.

Harris, J. K. 2014. An introduction to exponential random graph modeling. Sage Publications, Inc., Thousand Oaks, California.

Hunter, D. R., M. S. Handcock, C. T. Butts, S. M. Goodreau, and M. Morris. 2008. ergm: A package to fit, simulate and diagnose exponential-family models for networks. Journal of Statistical Software **24**.

Ings, T. C., J. M. Montoya, J. Bascompte, N. Blüthgen, L. Brown, C. F. Dormann, F. Edwards, D. Figueroa, U. Jacob, J. I. Jones, R. B. Lauridsen, M. E. Ledger, H. M. Lewis, J. M. Olesen, F. J. F. Van Veen, P. H. Warren, and G. Woodward. 2009. Review: ecological networks – beyond food webs. Journal of Animal Ecology **78**:253-269.

Krivitsky, P. N. 2012. Exponential-family random graph models for valued networks. Electronic Journal of Statistics **6**:1100-1128.

Lusher, D., J. Koskinen, and G. Robins. 2013. Exponential random graph models for social networks: theory, methods, and applications. Cambridge University Press, New York.

Morris, M., M. S. Handcock, and D. R. Hunter. 2008. Specification of exponential-family random graph models: terms and computational aspects. Journal of Statistical Software **24**.

Pinter-Wollman, N., E. A. Hobson, J. E. Smith, A. J. Edelman, D. Shizuka, S. de Silva, J. S. Waters, S. D. Prager, T. Sasaki, G. Wittemyer, J. Fewell, and D. B. McDonald. 2013. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. Behavioral Ecology.

Shizuka, D., and D. B. McDonald. 2012. A social network perspective on measurements of dominance hierarchies. Animal Behaviour **83**:925-934.

Snijders, T. A. B. 2002. Markov chain Monte Carlo estimation of exponential random graph models. Journal of Social Structure **3**.

TABLES AND FIGURES

Table 1.1. Overview of network structures and terminology.

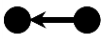
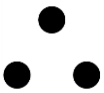
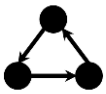
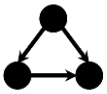
Network structure	Name	Description
	Node	objects that connect together to form a network (also vertices, individuals, members, actors)
	Dyad	node pair which may or may not be connected
	Edge	connection between a node pair (also links, lines, relationships, ties)
	Degree	number of edges connected to a node (e.g., degree 3)
	K-star	k is a specified number of edges connected to a node. Stars are nested so a node with degree of 3 has one three-star and three two-stars.
	Asymmetry	in a directed network, the connection between a node pair is unidirectional (this edge type is also called an arc)
	Mutuality	in a directed network, the connection between a node pair is directional in both ways (also reciprocity)
	Triad	group of three nodes that may or may not be connected
	Two-outstar	two asymmetric edges originating from a node
	Two-instar	two asymmetric edges received by a node
	Cyclic triple	three nodes connected by assymetric edges in which node A connects to node B connects to node C connects to node A

Table 1.1. Continued.

Network structure	Name	Description
	Transitive triple	three nodes connected by assymetric edges in which node A connects to node B and C and node B connects to node C
	Shared partners	number of nodes connected to both nodes of a dyad (dotted line); example shows 2 shared partners; the dyad can be unconnected (nonedgewise shared partners), connected (edgewise shared partners), or either (dyadwise shared partners)

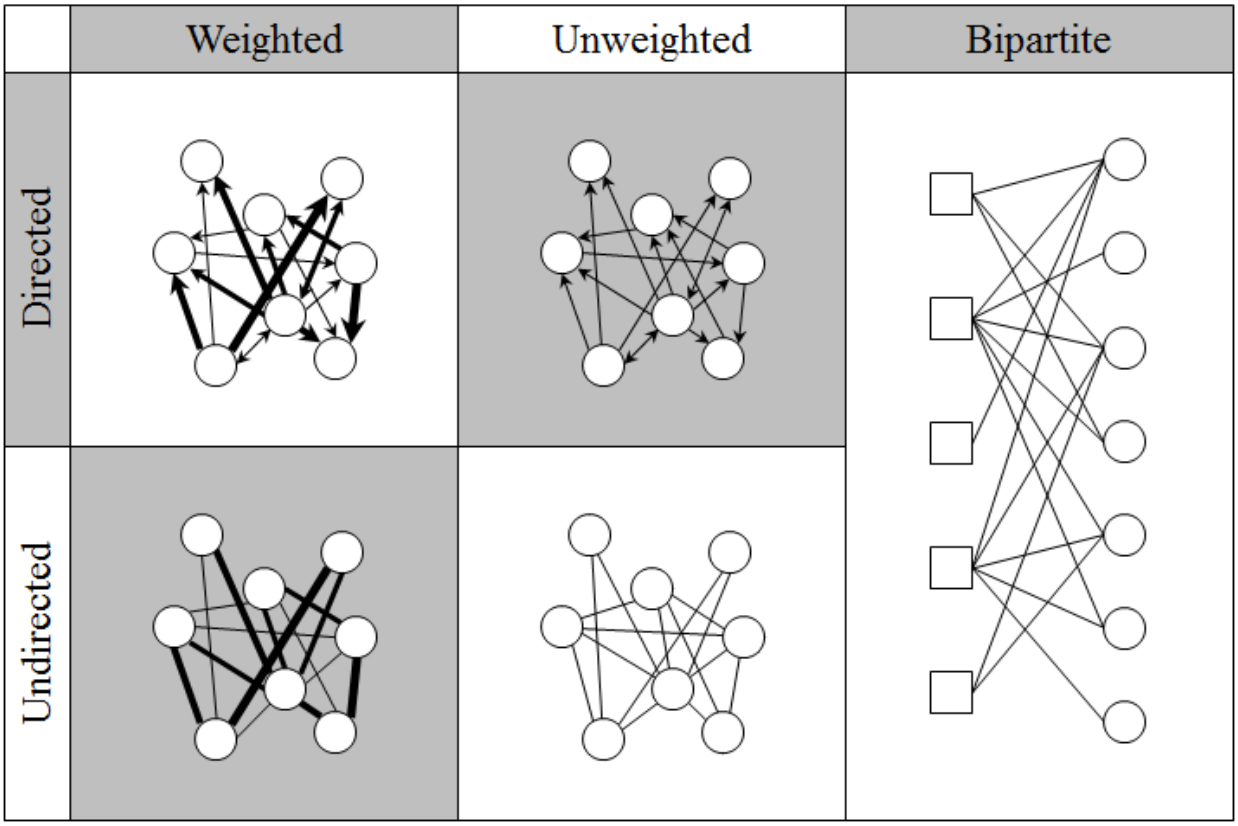


Figure 1.1. Common networks modeled by ERGMs. Networks are directed if edges have a different meaning for each of the nodes they join. Direction is indicated graphically by arrows. Networks can also be weighted if connections have values that indicate the strength of the connection or unweighted if connections are binary (i.e., present/absent). Weighting is depicted through line thickness. Most network types are comprised of one type of node (circles) but bipartite networks consist of two node types (circles and squares) that connect between node types (circle to square) but not within node types (e.g., square to square).

CHAPTER 2. Urbanization mediates interspecific interactions in mixed-species foraging assemblages of songbirds

Co-authors: Kevin J. Wolz and James R. Miller

INTRODUCTION

Urbanization profoundly alters wildlife communities and the species interactions within them (Shochat et al. 2006). Competition may increase with the introduction of invasive species (Shochat et al. 2010), predation pressure can be reduced because of abundant anthropogenic food (Fischer et al. 2012), and disease and parasite transmission rates may be greater because of artificially high host densities (Bradley and Altizer 2007). Urbanization can also affect facilitation—positive species interactions in which at least one species benefits and neither is harmed (Stachowicz 2001). Most studies of urbanization and facilitation have focused on plant-animal interactions, such pollination or seed dispersal (Reichard et al. 2001, Geslin et al. 2013), with other forms of facilitation among animals being largely overlooked.

Mixed-species foraging groups are an example of facilitation among animals that could be affected by urbanization. Such groups are common among birds, particularly in the non-breeding season (Harrison and Whitehouse 2011), and typically form around nuclear species that reduce predation risk and increase foraging efficiency for the species that forage with them (Cody 1971, Pulliam 1973, Sullivan 1985, Hutto 1994). Species vary in the degree to which they participate in and depend on mixed-species foraging flocks, with some species being obligates that are absent from habitats where their associated nuclear species are not found (Harrison and Whitehouse 2011). Anthropogenic changes can have a pronounced impact on mixed-species

foraging flocks by extirpating species sensitive to habitat degradation and reducing flock size (Maldonado-Coelho and Marini 2000, Sridhar and Sankar 2008, Knowlton and Graham 2011). These negative impacts can be particularly pronounced if nuclear species are lost, because they no longer facilitate the formation of mixed flocks (Maldonado-Coelho and Marini 2004). Consequently, both species richness and interactions could be negatively affected by landscape modification like urbanization (Lee et al. 2005).

A useful framework for describing the social interactions in mixed-species foraging flocks is network analysis (Farine et al. 2012, Aplin et al. 2013, Farine and Milburn 2013, Aplin et al. 2014, Farine 2014, Farine et al. 2014). This framework has been used extensively to investigate social dynamics (Croft et al. 2008, Pinter-Wollman et al. 2013), though only once in the context of mixed-species foraging groups and landscape change (Mokross et al. 2014). Mokross et al. (2014) found that social foraging networks become less connected (fewer species forage together) and less clustered (i.e., species are less likely to forage in groups) as species become more rare or are extirpated due to fragmentation and habitat degradation. In that study, network changes were not caused by the extirpation of nuclear species, but rather by the loss of species sensitive to habitat and landscape change (Mokross et al. 2014).

To assess how urbanization affects species interactions in interspecific foraging assemblages of birds, we used radio-frequency identification technology to track visitations to bird feeders along a gradient of urbanization in the Midwestern United States during the nonbreeding season. In deciduous forests of the Eastern United States, mixed-species foraging flocks form around nuclear species from the family Paridae following the breeding season (Morse 1970). The tufted titmouse (*Baeolophus bicolor*) is the primary nuclear species, though the black-capped chickadee (*Poecile atricapillus*) and Carolina chickadee (*Poecile carolinensis*)

act as nuclear species if titmice are absent (Morse 1970, Rodewald and Brittingham 2002). Parids are aggressive, quick to mob predators, and give alarm calls that convey information on the threat-level posed by predators (Templeton et al. 2005, Contreras and Sieving 2011, Hetrick and Sieving 2011). As such, titmice and chickadees reduce predation risk for species that commonly forage with them (Dolby and Grubb 1998), such as downy woodpeckers (*Picoides pubescens*), red-bellied woodpeckers (*Melanerpes carolinus*), and white-breasted nuthatches (*Sitta carolinensis*; Dolby and Grubb 1998, Dolby and Grubb 1999, Farley et al. 2008). These species regularly visit bird feeders (Horn et al. 2014, Johansen et al. 2014), which means temporal patterns of visitation can be used to infer social foraging relationships among individuals (Psorakis et al. 2012). Other species also regularly visit feeders in the Midwestern United States, including American goldfinches (*Spinus tristis*), northern cardinals (*Cardinalis cardinalis*), house finches (*Haemorhous mexicanus*), and house sparrows (*Passer domesticus*), though these species do not regularly participate in mixed-species foraging flocks with parids (Farley et al. 2008, Morris et al. 2008).

Previous research in our region has shown that tufted titmice respond negatively to urbanization (Schneider et al. 2014). As a result, we expected titmice would be absent or rare at our most urban sites, social foraging would be reduced as a result, and networks would become less clustered. We used a type of network analysis called exponential random graph modeling (ERGM) to characterize species-specific patterns of social foraging and determine how these patterns affected the structure of social foraging networks along a gradient of urbanization. This analytical framework is unique in that it models how simple network features such as species-specific social foraging affect the formation of more complex network structures like clustering (Harris 2014). This analysis has enabled us to investigate the effects of urbanization on species

interactions in mixed-species foraging assemblages for the first time.

METHODS

We quantified songbird visitations to bird feeders at seven study sites in east-central Illinois. Sites were private residences (n=5) or nature education centers (n=2) that represented three points along a gradient of urbanization: rural sites adjacent to deciduous forest fragments (n=3), residential neighborhoods adjacent to forest fragments (n=2), and residential neighborhoods surrounded by other forms of urban development (n=2; Table 1). Rural sites were surrounded by corn and soybean agriculture and forest fragments were dominated by oak (*Quercus* spp.), maple (*Acer* spp.), hickory (*Carya* spp.), and ash (*Fraxinus* spp.). Each site was equipped with a tube feeder (B-7F; Droll Yankees, Inc., Plainfield, CT) suspended from a 2.1-m shepherd's hook. The hook was placed within a 10-cm-diameter polyvinyl-chloride pipe at least 2 m from trees and buildings to prevent squirrels from accessing the feeders. Feeders were filled with black oil sunflower seed.

We captured birds at each site and marked them with radio frequency identification (RFID) tags to monitor foraging behavior. Sites were visited once per month from April-November in 2011 and May-October in 2012. We set up two mist nets at sunrise and monitored them for three hours on mornings with no precipitation. We placed color bands on the legs of all species captured and attached a 2x12mm RFID tag (CYNTAG, Inc., Cynthiana, Kentucky, USA) to the bands using all-weather electrical tape (Bridge and Bonter 2011) before releasing the birds.

Beginning in 2012, the sunflower feeder at each site was equipped with an RFID reader following the design of Bridge and Bonter (2011). The reader was housed in a waterproof

container attached to the bottom of the feeder with the RFID antenna affixed to the perch of the lowest feeding port. All other ports were blocked. The readers recorded the date, time, and RFID number for every second that a tagged bird was perched on the RFID antenna. Data were downloaded one to two times per week. In January of 2013, all readers were replaced by a revised design with a larger memory capacity, allowing downloads to be carried out once or twice per month. Because this study focused on social foraging in the nonbreeding season, only results from September 2012 to February 2013 were used in the analyses.

Statistical Analysis

To investigate the effect of species-specific foraging patterns on network structure, we constructed social foraging networks based on foraging bouts. Each bout was a cluster of visits to a feeder by one or more birds, and birds that visited a feeder during the same bout were considered to be foraging together (Psorakis et al. 2012). To identify bouts, we first condensed RFID data to one record per visit per individual (i.e., arrival time). Consecutive visits by the same individual were considered separate if the time between departure and arrival was >5 s. This threshold accounted for any instances in which a tagged bird was present on a feeder but not recorded for a particular second. We then constructed Gaussian mixture models for each day at each site using MATLAB R2013b (The MathWorks, Inc., Natick, Massachusetts, USA) to identify feeding bouts and the individuals that participated in them (Psorakis et al. 2012). This approach detected clusters based on the temporal structure of data (groups of visitations and the gaps between them) as opposed to the traditional method of grouping individuals based on co-occurrence within a specified time window (Psorakis et al. 2012). The latter approach is problematic because typically there is no biological justification for the length of the time

window used (Psorakis et al. 2012).

Foraging bouts were then used to construct social foraging networks (Psorakis et al. 2012). These networks were made up of interconnected objects, wherein objects were individual birds and connections were instances of social foraging that occurred between individuals that foraged together (i.e., in the same bout) more than five times. Separate networks were made for each site because the set of interacting birds differed among locations. To compare network structure among sites, we calculated the density and clustering coefficient for each site (Mokross et al. 2014). Density was the proportion of observed connections in a network relative to all possible connections and represented the extent to which birds foraged together at a site (Morris et al. 2008). The clustering coefficient measured the degree to which birds interacted in groups and was calculated as the number of triangles (i.e., three connected birds) divided by the number of triangles plus groups of three birds connected only twice (Handcock et al. 2008).

To determine whether social foraging varied by species and whether that variation affected network structure, we constructed networks in the 'statnet' package and analyzed them using exponential random graph models (Handcock et al. 2008). This analytical framework models how variables of interest affect the formation of connections in networks (Harris 2014), which for our study meant we modeled how variables affected the likelihood that social foraging occurred. We included three kinds of variables. The first variable was species of bird. One parameter was added to the model for each species (except one), and the resulting parameter estimates were interpreted as species-specific likelihoods of foraging with other birds relative to a baseline species (Morris et al. 2008, Harris 2014), which we specified as house finches because they were present in all study networks. The second variable was species assortment, which measured the likelihood that birds foraged with their own species compared to other species

(Morris et al. 2008, Farine 2014). One parameter was added for each species. Positive estimates indicated a species was more likely to forage with conspecifics and negative estimates meant foraging with heterospecifics was more likely. The third variable was a measure of clustering in the network called the geometrically weighted edgewise shared partner distribution (Hunter and Handcock 2006, Hunter 2007, Harris 2014). In essence, this variable measures the likelihood that triangles are likely to form with a connected pair in the network. One parameter is added to the model, and positive estimates indicate that clustering is occurring in a network, which would suggest individuals are foraging in groups in our study. A decay constant must also be specified with this variable, which controls for the reduction in likelihood of additional triangles forming given that others are already present; for this study we specified a decay constant of 1.

Because we created separate ERGMs for each study site, to summarize results across sites we conducted a multivariate meta-analysis using the 'metafor' package in R (Viechtbauer 2010). A multivariate approach was used because parameter estimates were not independent within sites. The resulting covariance was incorporated into the meta-analysis using a block-covariance matrix (Berkey et al. 1998, Gleser and Olkin 2009) in which between-site covariances were zero and within-site covariances form a block of nonzero values. Model inputs included ERGM parameter estimates as the dependent variable; the block-covariance matrix; a fixed species variable for social foraging and assortment estimates; and a random site variable. The intercept was left out of the model so meta-analysis parameters represented average social foraging and assortment estimates.

RESULTS

Social foraging networks of birds at feeders varied among sites in size (number of birds), density

(observed social connections relative to all possible connections), clustering (extent to which groups of individuals foraged together), and species composition (Table 2). Network size averaged 22.9±6.3 birds, though one unusually large rural network was composed of 35 birds. Average density was 0.44±0.11 and the average clustering coefficient was 0.43±0.14. No systematic differences in network size, density, or clustering coefficients were evident among urbanization categories (Size ANOVA, F_2=0.0669, P=0.9363; Density ANOVA, F_2=0.0451, P=0.9564; Clustering ANOVA, F_2=0.0362, P=0.9648). Species composition did change with urbanization, with nonforested urban sites having fewer species compared with forested urban and rural sites (Species ANOVA, F_2=20.4000, P=0.0080). In particular, parids, woodpeckers, and nuthatches were absent from nonforested urban networks.

To assess the role that different species played in structuring these networks, we constructed ERGMs that quantified social foraging, assortment, and clustering. The multivariate meta-analysis that summarized results of site-specific ERGMs indicated that species differed in social foraging (i.e., likelihood of foraging with other birds; Figure 1). House sparrows, northern cardinals, and house finches exhibited similar levels of social foraging (i.e., confidence intervals of average social foraging estimates overlapped zero). Tufted titmice, Carolina chickadees, white-breasted nuthatches, and downy woodpeckers were more likely to forage with other birds, though parids (i.e., titmice and chickadees) were the most social species as indicated by their larger social foraging estimates compared to other species. American goldfinches were least likely to forage with other species. Average assortment estimates (i.e., the likelihood of foraging with conspecifics or heterospecifics) could only be calculated for house sparrows and house finches in the meta-analysis because of the small number of individuals of other species in any single network. House sparrows and house finches were more likely to forage with conspecifics

(as indicated by positive average assortment estimates; house finches 1.20±0.32; house sparrows 1.77±0.50).

In order to assess how network structure was affected by social foraging patterns, we modeled social foraging and assortment with clustering in ERGMs to generate adjusted clustering estimates. These estimates reflected the amount of clustering not accounted for by interspecific foraging. Clustering estimates for both nonforested urban sites were positive (i.e., confidence intervals did not overlap zero), which suggested that interspecific foraging was not solely responsible for clustering in these networks. One forested urban site and one rural site also had positive clustering estimates (Figure 2). Networks without positive clustering estimates contained tufted titmice while networks with a positive clustering estimate did not (with one exception), which suggested that interspecific foraging with tufted titmice may account for much of the clustering in networks with this species. At the site with a positive clustering value and titmice, species that commonly participate in mixed species flocks (downy woodpecker, white-breasted nuthatch) were absent or present in low numbers. This was the only network in which the site-specific social foraging estimate for tufted titmice was not positive, which suggests that social foraging of titmice and its effect on network clustering depends on the other species in the network.

DISCUSSION

As expected, urbanization altered social foraging networks at bird feeders by affecting the species composition of networks, in particular by extirpating tufted titmice. This species was highly social with heterospecifics, to the point that network structure (as measured by clustering) was explained by interspecific foraging in networks with titmice (with one exception), but not in

networks without them. This suggests that tufted titmice were a primary driver of social foraging dynamics at bird feeders in our study. Given that titmice are a known nuclear species in mixed-species foraging flocks (Morse 1970, Dolby and Grubb 1998, Dolby and Grubb 1999, Rodewald and Brittingham 2002), the importance of their social role was unsurprising. However, the effect of their loss on social foraging dynamics at unforested urban sites highlights for the first time how urbanization degrades interspecific interactions as well as community diversity.

Like tufted titmice, chickadees can act as nuclear species in foraging flocks in North America (Morse 1970, Rodewald and Brittingham 2002). Consequently, Carolina and black-capped chickadees may have contributed to the interspecific foraging that explained clustering in networks with titmice. However, in the urban forested network where tufted titmice were absent and Carolina chickadees were present, and in rural network where tufted titmice were present but were less social than in other networks, clustering was not fully explained by interspecific interactions despite the fact that Carolina chickadees were present. This suggests that though Carolina chickadees are a highly social forager, they do not facilitate interspecific foraging to the same degree as tufted titmice (Farley et al. 2008).

In the absence of parids, networks were dominated by house finches and house sparrows. Contrary to our expectations, clustering coefficients were not lower in these networks, which suggested that a mechanism other than interspecific foraging with parids produced clustering. House finches and house sparrows did not replace parids in their role as nuclear species, as network clustering was not fully explained by interspecific interactions without parids. Instead, intraspecific dynamics were more important in house finch and house sparrow networks, as evidenced by the positive assortment documented for both species. House finches and house sparrows are known for their conspecific flocking behavior during the nonbreeding season

(Anderson 2006, Oh and Badyaev 2010), and while they do forage with heterospecifics, such affiliations are transitory. Neither species is native to Eastern North America; so house sparrows and house finches have not evolved with other species in the region to participate in mixed-species flocks (Farine et al. 2014).

Our study is part of a growing body of literature that shows how anthropogenic change alters communities and modifies species interactions (Mokross et al. 2014). The loss of nuclear species can reduce the incidence of flock formation and even lead to local extirpation of species that flock with them (Maldonado-Coelho and Marini 2003). In our study, tufted titmice were only absent from one network in which other flocking species were still present, but interspecific foraging was not as important in structuring this network. This suggests that flocking may be less common in the absence of tufted titmice, which has also been shown experimentally by Dolby and Grubb (1999). The loss of titmice could even have contributed to the absence of other flocking species from urban nonforested networks, as experimental removal of titmice has shown predation risk increases and nutritional condition declines for other species without titmice (Dolby and Grubb 1998).

These findings emphasize the importance of modifying human activities to retain nuclear species where possible. For example, in our study, it was not residential development per se that produced drastic change in species composition, but rather the loss of forest fragments adjacent to neighborhoods. By designing new developments to retain habitat remnants, urban planners may be able to retain both interspecific social dynamics and species diversity in avian communities in the Midwestern United States.

ACKNOWLEDGEMENTS

We would like to thank site owners who allowed access to their properties and maintained study feeders throughout the project, as well as the volunteers (particularly Nancy Snellen) who helped with capturing birds. Droll Yankees, Inc., donated the bird feeders used for the project, and funding was provided by the Illinois Ornithological Society, the Champaign County Audubon Society, the Binky Foundation, and the National Science Foundation Graduate Research Fellowship Program. David Bonter, Eli Bridge, Joseph Casto, and Ben Kamen provided much-appreciated assistance with the construction and maintenance of RFID readers, and Bethany Cutts provided guidance on ERGM analyses. Christine Parker, Jaime Coone, Samniqueka Halsey, and Scott Nelson provided useful comments on the manuscript.

LITERATURE CITED

Anderson, T. R. 2006. Biology of the ubiquitous house sparrow: from genes to populations. Oxford University Press, New York.

Aplin, L. M., D. R. Farine, R. P. Mann, and B. C. Sheldon. 2014. Individual-level personality influences social foraging and collective behaviour in wild birds. Proceedings of the Royal Society B: Biological Sciences **281**.

Aplin, L. M., D. R. Farine, J. Morand-Ferron, E. F. Cole, A. Cockburn, and B. C. Sheldon. 2013. Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). Ecology Letters **16**:1365-1372.

Berkey, C. S., D. C. Hoaglin, A. Antczak-Bouckoms, F. Mosteller, and G. A. Colditz. 1998. Meta-analysis of multiple outcomes by regression with random effects. Statitics in Medicine **17**:2537-2550.

Bradley, C. A., and S. Altizer. 2007. Urbanization and the ecology of wildlife diseases. Trends in Ecology & Evolution **22**:95-102.

Bridge, E. S., and D. N. Bonter. 2011. A low-cost radio frequency identification device for ornithological research. Journal of Field Ornithology **82**:52-59.

Cody, M. L. 1971. Finch flocks in the Mohave Desert. Theoretical Population Biology **2**:142-158.

Contreras, T. A., and K. E. Sieving. 2011. Leadership of winter mixed-species flocks by tufted titmice (*Baeolophus bicolor*): are titmice passive nuclear species? International Journal of Zoology **2011**:11.

Croft, D. P., R. James, and J. Krause. 2008. Exploring animal social networks. Princeton University Press, Princeton, New Jersey.

Dolby, A. S., and T. C. Grubb. 1998. Benefits to satellite members in mixed-species foraging groups: an experimental analysis. Animal Behaviour **56**:501-509.

Dolby, A. S., and T. C. Grubb, Jr. 1999. Functional roles in mixed-species foraging flocks: a field manipulation. The Auk **116**:557-559.

Farine, D., and P. Milburn. 2013. Social organisation of thornbill-dominated mixed-species flocks using social network analysis. Behavioral Ecology and Sociobiology **67**:321-330.

Farine, D. R. 2014. Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges. Animal Behaviour **89**:141-153.

Farine, D. R., L. M. Aplin, C. J. Garroway, R. P. Mann, and B. C. Sheldon. 2014. Collective decision making and social interaction rules in mixed-species flocks of songbirds. Animal Behaviour **95**:173-182.

Farine, D. R., C. J. Garroway, and B. C. Sheldon. 2012. Social network analysis of mixed-species flocks: exploring the structure and evolution of interspecific social behaviour. Animal Behaviour **84**:1271-1277.

Farley, E., K. Sieving, and T. Contreras. 2008. Characterizing complex mixed-species bird flocks using an objective method for determining species participation. Journal of Ornithology **149**:451-468.

Fischer, J. D., S. H. Cleeton, T. P. Lyons, and J. R. Miller. 2012. Urbanization and the predation paradox: the role of trophic dynamics in structuring vertebrate communities. BioScience **62**:809-818.

Geslin, B., B. Gauzens, E. Thebault, and I. Dajoz. 2013. Plant pollinator networks along a gradient of urbanisation. PLoS One **8**:13.

Gleser, L. J., and I. Olkin. 2009. Stochastically dependent effect sizes.*in* H. Cooper, L. V. Hedges, and J. C. Valentine, editors. The handbook of research synthesis and meta-analysis. Russell Sage Foundation, New York.

Handcock, M. S., D. R. Hunter, C. T. Butts, S. M. Goodreau, and M. Morris. 2008. statnet: software tools for the representation, visualization, analysis and simulation of network data. Journal of Statistical Software **24**.

Harris, J. K. 2014. An introduction to exponential random graph modeling. Sage Publications, Inc., Thousand Oaks, California.

Harrison, N. M., and M. J. Whitehouse. 2011. Mixed-species flocks: an example of niche construction? Animal Behaviour **81**:675-682.

Hetrick, S. A., and K. E. Sieving. 2011. Antipredator calls of tufted titmice and interspecific transfer of encoded threat information. Behavioral Ecology **23**:83-92.

Horn, D. J., S. M. Johansen, and T. E. Wilcoxen. 2014. Seed and feeder use by birds in the United States and Canada. Wildlife Society Bulletin **38**:18-25.

Hunter, D. R. 2007. Curved exponential family models for social networks. Social Networks **29**:216-230.

Hunter, D. R., and M. S. Handcock. 2006. Inference in curved exponential family models for networks. Journal of Computational and Graphical Statistics **15**:565-583.

Hutto, R. L. 1994. The composition and social organization of mixed-species flocks in a tropical deciduous forest in Western Mexico. Condor **96**:105-118.

Johansen, S. M., D. J. Horn, and T. E. Wilcoxen. 2014. Factors influencing seed species selection by wild birds at feeders. The Wilson Journal of Ornithology **126**:374-381.

Knowlton, J. L., and C. H. Graham. 2011. Species interactions are disrupted by habitat degradation in the highly threatened Tumbesian region of Ecuador. Ecological Applications **21**:2974-2986.

Lee, T. M., M. C. K. Soh, N. Sodhi, L. P. Koh, and S. L. H. Lim. 2005. Effects of habitat disturbance on mixed species bird flocks in a tropical sub-montane rainforest. Biological Conservation **122**:193-204.

Maldonado-Coelho, M., and M. A. Marini. 2000. Effects of forest fragment size and successional stage on mixed-species bird flocks in southeastern Brazil. Condor **102**:585-594.

Maldonado-Coelho, M., and M. A. Marini. 2004. Mixed-species bird flocks from Brazilian Atlantic forest: the effects of forest fragmentation and seasonality on their size, richness and stability. Biological Conservation **116**:19-26.

Mokross, K., T. B. Ryder, M. C. Cortes, J. D. Wolfe, and P. C. Stouffer. 2014. Decay of interspecific avian flock networks along a disturbance gradient in Amazonia. Proceedings of the Royal Society B-Biological Sciences **281**.

Morris, M., M. S. Handcock, and D. R. Hunter. 2008. Specification of exponential-family random graph models: terms and computational aspects. Journal of Statistical Software **24**.

Morse, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. Ecological Monographs **40**:119-168.

Oh, K. P., and A. V. Badyaev. 2010. Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. The American Naturalist **176**:E80-E89.

Pinter-Wollman, N., E. A. Hobson, J. E. Smith, A. J. Edelman, D. Shizuka, S. de Silva, J. S. Waters, S. D. Prager, T. Sasaki, G. Wittemyer, J. Fewell, and D. B. McDonald. 2013. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. Behavioral Ecology.

Psorakis, I., S. J. Roberts, I. Rezek, and B. C. Sheldon. 2012. Inferring social network structure in ecological systems from spatio-temporal data streams. Journal of The Royal Society Interface.

Pulliam, H. R. 1973. On the advantages of flocking. J Theor Biol **38**:419-422.

Reichard, S. H., L. Chalker-Scott, and S. Buchanan. 2001. Interactions among non-native plants and birds. Pages 179-223 *in* J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Boston, MA.

Rodewald, P. G., and M. C. Brittingham. 2002. Habitat use and behavior of mixed species landbird flocks during fall migration. The Wilson Bulletin **114**:87-98.

Schneider, S., J. Fischer, and J. Miller. 2014. Two-sided edge responses of avian communities in an urban landscape. Urban Ecosystems:1-13.

Shochat, E., S. B. Lerman, J. M. Anderies, P. S. Warren, S. H. Faeth, and C. H. Nilon. 2010. Invasion, competition, and biodiversity loss in urban ecosystems. BioScience **60**:199-208.

Shochat, E., P. S. Warren, S. H. Faeth, N. E. McIntyre, and D. Hope. 2006. From patterns to emerging processes in mechanistic urban ecology. Trends in Ecology & Evolution **21**:186-191.

Sridhar, H., and K. Sankar. 2008. Effects of habitat degradation on mixed-species bird flocks in Indian rain forests. Journal of Tropical Ecology **24**:135-147.

Stachowicz, J. J. 2001. Mutualism, facilitation, and the structure of ecological communities. BioScience **51**:235-246.

Sullivan, K. 1985. Selective alarm calling by downy woodpeckers in mixed-species flocks. The Auk **102**:184-187.

Templeton, C. N., E. Greene, and K. Davis. 2005. Allometry of alarm calls: black-capped chickadees encode information about predator size. Science **308**:1934-1937.

Viechtbauer, W. 2010. Conducting meta-analyses in R with the metafor package. Journal of Statistical Software **36**:1-48.

TABLES AND FIGURES

Table 2.1. Study site categories based on proximity to residential neighborhoods and forest fragments. Housing density was calculated as the number of single family residences within a 0.25-km radius of a site.

Site category	**Housing density**	**Distance from forest (km)**
Rural forested		
Site A	1	0.00
Site B	1	0.13
Site C	2	0.11
Urban forested		
Site A	90	0.10
Site B	95	0.05
Urban nonforested		
Site A	380	3.90
Site B	608	3.46

Table 2.2. Characteristics of site-specific social foraging networks

	Rural			Urban forested		Urban nonforested	
Site	**A**	**B**	**C**	**A**	**B**	**A**	**B**
Density	0.56	0.29	0.48	0.30	0.55	0.51	0.42
Clustering Coefficient	0.58	0.24	0.52	0.26	0.58	0.41	0.40
Species	7	8	6	7	8	3	3
American goldfinch	5	1	1	2	4		
Black-capped chickadee					6		
Carolina chickadee	8	1	3	2			
Downy woodpecker	4	2		1	5		
House finch	8	3	9	7	2	6	5
House sparrow		4	1	3	1	12	15
Northern cardinal				1	1	3	2
Red-bellied woodpecker	1	2					
Tufted titmouse	6	1	6		4		
White-breasted nuthatch	3	2	1	2	4		
Total birds	35	16	21	18	27	21	22

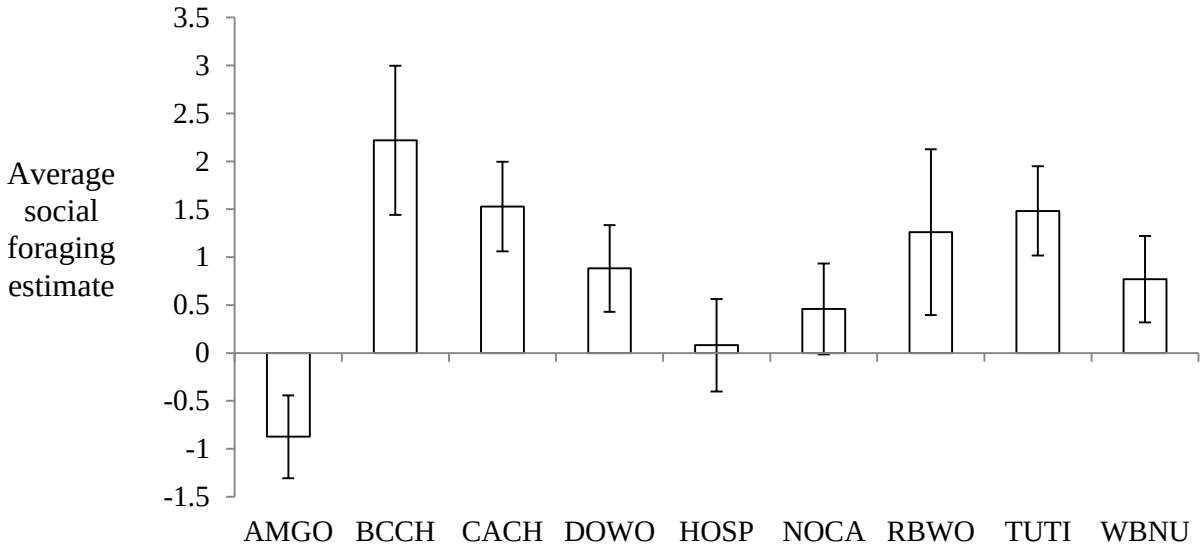


Figure 2.1. Species-specific social foraging estimates from a multivariate meta-analysis of site-specific ERGM parameters. Bars are 95% confidence intervals. Estimates are interpreted as the likelihood of foraging with other birds compared to social foraging of house finches, so confidence intervals overlapping zero indicate a similar level of social foraging compared to house finches. Species codes are as follows: AMGO=American goldfinch, BCCH=Black-capped chickadee, CACH=Carolina chickadee, DOWO=Downy woodpecker, HOFI=House finch, HOSP=House sparrow, NOCA=Northern cardinal, RBWO=Red-bellied woodpecker, TUTI=Tufted titmouse, WBNU=White breasted nuthatch.

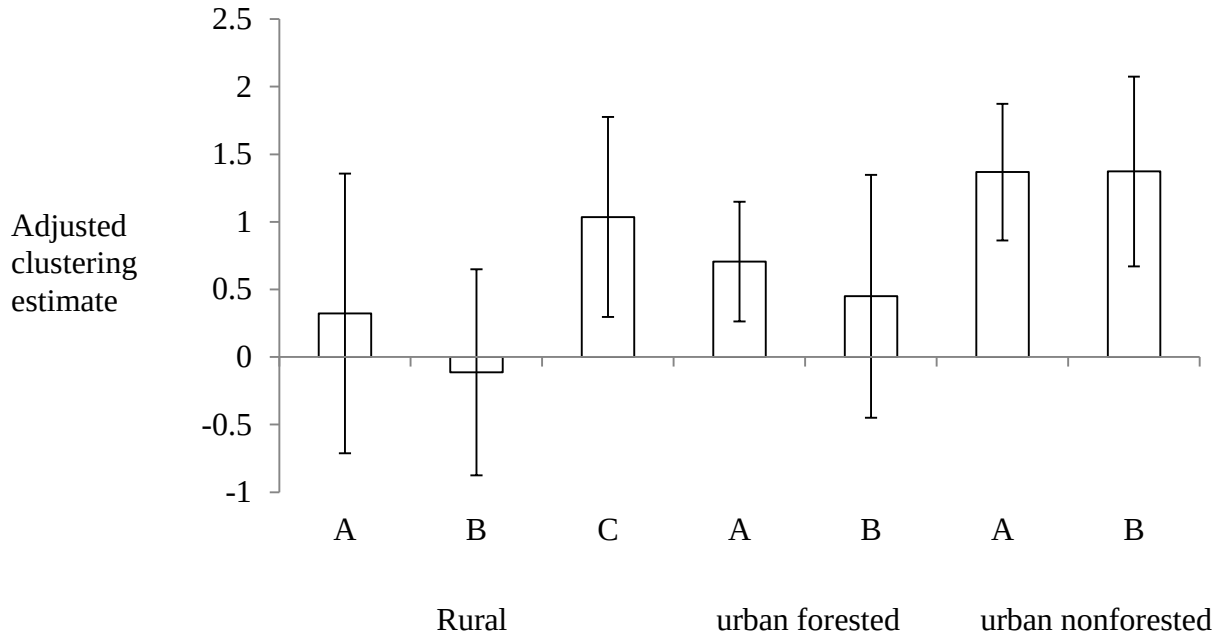


Figure 2.2. Network clustering estimates adjusted for species interactions. Confidence intervals that do not overlap 0 indicate that species interactions do not fully explain network structure as measured by clustering.

CHAPTER 3. Species-specific differences in daily foraging patterns of temperate songbirds challenge models of predation-starvation trade-offs

Co-authors: Kevin J. Wolz and James R. Miller

INTRODUCTION

Daily foraging activity of small birds in temperate winters is shaped by a trade-off between the risks of starvation and predation (Polo and Bautista 2006, Brodin 2007). Birds must consume enough food during short winter days to build sufficient energy reserves to survive long winter nights (Koivula et al. 2002). However, excessive energy stores in the form of body fat reduce flight maneuverability and increase the risk of depredation (i.e., mass-dependent mortality; Lima 1986, Witter et al. 1994). Mathematical models of the predation-starvation trade-off predict that under most environmental conditions, birds should forage early in the morning to replenish energy stores depleted overnight, reduce activity during the middle of the day to avoid being depredated, then increase foraging near dusk to build energy reserves for the coming night (McNamara et al. 1994, Brodin 2007). This bimodal foraging distribution allows birds to maintain minimal body fat reserves for as much of the day as possible, thereby minimizing mass-dependent mortality. Empirical tests of bimodal foraging have yielded mixed support, with some species showing a single peak in daily feeding. Such unimodal foraging patterns are typically explained by variation in predation or starvation risk. Greater predation pressure leads to less morning foraging to minimize mass-dependent mortality, and less predictable food results in more morning feeding to reduce the risk of not finding enough food later (Polo and Bautista 2006).

The problem with many of these explanations and theoretical models is that they do not account for the community context in which foraging occurs (Roth et al. 2006). Interactions among prey species determine the social environment in which organisms forage and can dramatically alter feeding behavior (Farine et al. 2012). Likewise, interactions between predator and prey vary depending on the species involved, leading to species-specific variation in predation risk that could affect foraging patterns. Consequently, interspecific interactions may be responsible for some of the variation in foraging patterns observed in empirical studies.

Interspecific foraging among prey species could influence daily foraging patterns through positive and negative foraging associations among species (Harrison and Whitehouse 2011, Farine et al. 2012). Positive associations form when species forage more together than separately as a result of increased feeding efficiency or reduced predation risk (Farine et al. 2012). Such associations should synchronize temporal foraging patterns between species. Negative associations are the result of resource competition, in which subordinate birds avoid feeding near dominant individuals because of foraging interference (Farine et al. 2012). This interference can cause subordinates and dominants to feed at different times of day (Polo and Bautista 2006).

Daily foraging patterns may also differ among prey species because of variation in predator-prey interactions (Roth et al. 2006). Theoretical models of daily feeding activity treat predation risk as a constant or a function of prey mass (Brodin 2007), but predator hunting behavior strongly affects prey behavior and is not uniform throughout the day. For example, the Cooper's hawk (*Accipiter cooperi*), one of the primary predators of small birds in temperate North America (Dunn and Tessaglia 1994, Roth and Lima 2007), hunts most in the early morning and late afternoon (Roth and Lima 2007). If prey species respond to predator foraging patterns, they may reduce foraging efforts when predators are most active (Van Der Veen 2000,

Roth et al. 2006). The impact of predators on prey behavior also may vary depending on dietary preferences of predators. Cooper's hawks preferentially depredate certain species (e.g., house sparrows, *Passer domesticus*) but rarely kill others (e.g., tufted titmouse, *Baeolophus bicolor*; Roth and Lima 2006, Roth et al. 2006). Such preferences may generate variation in vulnerability to predation that could mediate the extent to which prey avoid foraging when predators are more active.

To investigate the effect of interspecific interactions on avian foraging patterns in temperate winters, we studied foraging behavior of songbirds at bird feeders in the Midwestern United States and evaluated the following hypotheses. H1) The uniform foraging hypothesis is based on theoretical models that assume species interactions have a minimal effect on foraging patterns; we predicted that all species would exhibit a bimodal distribution of foraging activity throughout the day (Brodin 2007). H2) The species-specific foraging hypothesis proposes that variation in predator-prey interactions results in different foraging patterns of prey species (Roth et al. 2006). We predicted that preferred prey of different predator species would avoid feeding during periods of peak predator activity and feeding patterns of other prey would be less affected by predator behavior. H3) The social foraging hypothesis suggests that foraging associations among prey species influence daily patterns of feeding activity (Polo and Bautista 2006). We predicted that positive associations would lead to similar foraging patterns among species and negative associations would produce divergent patterns. This hypothesis assumes that social relationships are consistent throughout the day (e.g., species that forage together in the morning also forage together in the afternoon). H4) The variable social foraging hypothesis relaxes the assumption of static social relationships and posits that the strength of foraging associations changes through the day depending on variation in predation and starvation risk. In our study

system, we assumed there was little variation in starvation risk because food was continuously available at bird feeders. Predation risk, on the other hand, is likely to vary because predators are more active at dawn and dusk in our region (Roth and Lima 2003, Roth and Lima 2006, Roth et al. 2006, Roth and Lima 2007, Horn et al. 2011). Consequently, we predicted that social foraging would be more beneficial at times of day when predation risk is greater, leading to stronger foraging associations at these times.

To test these hypotheses, we used radio frequency identification (RFID) technology. This enabled us to track individual foraging behavior of seven species at bird feeders over a two-year period, thus obtaining an unprecedented level of data on social foraging activity at multiple study sites across a landscape. We analyzed these data using a network analysis framework that has not been previously applied to studies of animal behavior (exponential random graph models; Pinter-Wollman et al. 2013). This allowed us to assess the effect of species interactions on daily foraging patterns for the first time.

METHODS

We examined patterns of avian foraging activity at bird feeders at seven sites in east-central Illinois, USA. Sites included private residences (n=5) and nature education centers (n=2), which were located in either a rural setting (n=3) surrounded by corn and soybean agriculture and deciduous forest fragments (outside of the village of Homer), or residential housing in the cities of Monticello, Champaign, and Urbana (n=4). Two urban locations were adjacent to forest fragments and two were not. Study sites were at least 2 km apart. Sites were visited monthly from April-November in 2011 and May-October in 2012 to capture birds at feeders using mist nets and mark them with RFID tags. Tags were attached to color bands and placed on the left leg

of each bird (Bridge and Bonter 2011). From January 2012 to February 2013, a tube feeder filled with black oil sunflower seed and equipped with an RFID reader was maintained at each site. Food was continuously available but only one bird could feed at a time. The reader was programmed to record the identification number, date, and time for each second that a bird with an RFID tag was perched at the feeding port. Data from January 2012-February 2012 and November 2012-February 2013 were used for this study and were pooled across years because data were only available for one winter at two sites.

We used RFID data to identify bouts of foraging activity at bird feeders (Psorakis et al. (2012). These bouts consisted of temporal clusters of visits to feeders by one or more birds and were used as the basis for analysis because they were a measure of both foraging activity of individuals (i.e., frequency of visits to a feeder) and social foraging (i.e., co-occurrence at the feeder with other individuals; Psorakis et al. 2012). RFID data were condensed from second-by-second records to a time-of-arrival record for each visit. Consecutive visits by the same bird were considered separate when the time gap between RFID records was >5 s, which accounted for instances in which a marked bird was present on the feeder but not recorded for a particular second. Any days with fewer than 30 seconds of data were removed from the analysis, as we assumed that the reader malfunctioned or the feeder had been emptied.

We constructed Gaussian mixture models in MATLAB R2013b (The MathWorks, Inc., Natick, MA) for each day at each site to identify clusters of feeder visitations that were considered unique foraging bouts (Psorakis et al. 2012). This method is an improvement over traditional means of identifying bouts because it does not rely on an a priori assumption of how far apart two visitations can be while still belonging to the same bout. Instead, clusters are identified based on the structure of the data (i.e., groupings of visitations and the size and

frequency of gaps between them). Individuals that rarely visited a feeder (<5 feeding bouts) were not included in further analyses because they were unlikely to provide sufficient data on temporal foraging patterns or social interactions to be relevant.

Foraging bouts were analyzed using exponential random graph models (ERGMs; Harris 2014)—a type of network analysis originally developed in the social sciences. Like other network analyses, ERGMs characterize configurations of connections among a set of objects (Figure 1; Handcock et al. 2003), with different configurations of connections providing information about the way objects associate with one another. For this study we constructed bipartite networks, which are composed of two types of objects. One object type was individual birds and the other was foraging bouts; connections between objects were instances in which a particular bird participated in a particular bout (Figure 1; Psorakis et al. 2012). Using traditional network analyses, a study of our bipartite networks would have been limited to describing different configurations of connections and whether they were more or less likely to occur than expected by chance. ERGMs, on the other hand, are inferential models that test hypotheses about how variables (such as attributes of objects) affect the formation of network connections. In our study, we used ERGMs to analyze how an attribute of individual birds (species) and an attribute of foraging bouts (time of day) affected the likelihood of connections occurring between birds and foraging bouts (i.e., a proximate measure of foraging activity). In other words, we tested whether foraging activity varied by time of day and whether foraging patterns differed among species.

In addition to testing how object attributes affect the presence or absence of network connections, ERGMs can be used to test how those attributes affect the formation of different configurations of connections (Morris et al. 2008, Harris 2014). In our study, we used a simple

configuration of two connections between a pair of individual birds and a particular foraging bout as a measure of social foraging (Figure 1). We analyzed how an attribute of individual birds (species) and an attribute of foraging bouts (time of day) affected the occurrence of social foraging. In other words, we tested whether different species were more or less likely to forage together as a measure of positive and negative foraging associations, as well as whether these associations varied throughout the day. Because day length changed throughout the study period from 9.3–11.3 hr, we divided each day into 7 time blocks of equal duration and assigned foraging bouts to these blocks based on when they began. Since the temporal comparisons of interest were made within days (among time blocks) rather than between days, the variation in length of time blocks on different days did not affect our analyses. All networks and ERGMs were constructed using the 'statnet' package (Handcock et al. 2003) in R 3.0 (R Core Team 2012), and sites were modeled separately because each was associated with a unique network of interacting birds.

To determine which of the four hypotheses best explained patterns of foraging activity, we constructed five ERGMs—one for each hypothesis plus a null model. The null model contained a single term that is analogous to an intercept in general linear models. For the uniform model (H1), we added terms to the null that quantified changes in the likelihood of foraging among time blocks but did not allow foraging patterns to vary by species. In the species-specific model (H2), we allowed foraging patterns to vary by species. For the social model (H3), we added terms for foraging associations among species to the species-specific model. In the variable social model (H4), we allowed the strength of associations to vary among time blocks. Model terms associated with the likelihood of foraging in time blocks included a parameter estimate for each block except for one that served as a baseline for comparison. We selected the

middle of the day (fourth time block) as the baseline because changes in foraging through the morning and afternoon were of primary interest in this study. Consequently, parameter estimates indicated whether foraging was more or less likely to occur in in a particular time block compared to the middle of the day. Model terms for foraging associations included one parameter estimate for each pair of species. Positive or negative estimates indicated whether two species were more or less likely to forage together. We visualized these associations by constructing a unipartite network for each association type (positive, negative, neutral). Unipartite networks are composed of one type of interconnected object compared to two types in bipartite networks. The objects in our association networks were species and the connections were the presence or absence of an association between a species pair.

ERGMs were compared using an information theoretic approach, in which relative support for models was determined using Akaike's Information Criterion (Burnham and Anderson 1998, Goodreau et al. 2009). These comparisons determined what combination of species identity, time of day, and foraging associations best explained networks of foraging activity and were sufficient to differential all hypotheses except the species-specific (H2) and social (H3) hypotheses. This was because a well-supported social model (H3) including time and foraging associations would not necessarily mean that daily foraging patterns were affected by social foraging—rather it would indicate that both were important factors influencing networks of foraging activity. To assess the effect of foraging associations on temporal patterns of feeding activity, parameter estimates for time of day were compared from models with and without foraging associations. Including associations adjusted temporal parameter estimates for the effect of social foraging, so changes in temporal parameter estimates between models assessed how social foraging affected daily foraging patterns.

To quantify temporal foraging patterns across study sites and compare them between models with and without foraging associations, we summarized results of site-specific ERGMs for a given model type (e.g., species-specific model) using multivariate meta-analyses to account for covariance of parameter estimates from the same model ('metafor package'; Lubbers and Snijders 2007, Viechtbauer 2010). To facilitate comparisons among models, parameter estimates were standardized within sites by subtracting the estimate for the first time block from the others. Covariance among the parameter estimates was incorporated into the meta-analyses using a block-covariance matrix in which between-site covariances were zero and within-site covariances were taken from the site-specific ERGMs (Berkey et al. 1998, Gleser and Olkin 2009). Fixed effects in the models were interactions between a continuous time variable and a categorical species variable. Both linear and quadratic terms were included for each species to model whether daily foraging activity patterns were bimodal, unimodal, or linear. Random variation in species at each time block among sites was modeled using a compound symmetric covariance structure. For each site, species with data from only one individual were not included in the meta-analyses, nor were species with data from only one site.

The analyses comparing temporal parameter estimates from models with and without foraging associations assume that all individuals of a given species exhibit similar foraging associations with heterospecifics. If this assumption is violated (e.g., because of individual variation in behavior or inadequate sampling for some individuals), then the effect of foraging associations on temporal foraging patterns could be underestimated. To assess this assumption, we repeated the analyses above using a subset of the total bipartite networks that only included foraging bouts among birds that preferentially foraged together. Preferred foraging was determined using a network permutation test that determined whether each pair of birds foraged

together more than expected by chance (Psorakis et al. 2012).

RESULTS

Gaussian mixture modeling yielded 8712 winter foraging bouts involving 172 individuals of 10 species, though three species were not included in all analyses because of small sample sizes (Table 1). Species composition varied among sites, particularly between forested locations where all study species were recorded and nonforested urban sites where only northern cardinals, house finches, and house sparrows were documented by RFID readers (see Table 1 for scientific names).

Comparisons of ERGMs at each site showed that species identity and foraging associations affected winter foraging activity of small birds at feeders (Table 2). Uniform models were poorly supported relative to other models at all sites, indicating that daily foraging patterns varied among species. Social models were consistently 'best', which suggested that foraging associations among species were occurring at all sites but were not simply a result of the same species visiting feeders during the same time blocks (which would have been indicated by similar or better support for species-specific models). However, support for the social models over the species-specific models did not necessarily reject the species-specific foraging hypothesis (see below). The lack of support for variable social models suggested that foraging associations were consistent through time rather than varying throughout the day. Collectively, these comparisons rejected the uniform foraging hypothesis (H1) and the variable social foraging hypothesis (H4).

To determine whether the species-specific (H2) or social (H3) foraging hypothesis best explained our data, we compared species-specific daily foraging estimates from species-specific

models with estimates that were adjusted for the effect of foraging associations from social models (Figure 2). Daily foraging patterns changed little between species-specific and social models, which suggested that temporal foraging was not strongly affected by interspecific foraging interactions. In other words, birds foraged with heterospecifics enough to produce non-random patterns of foraging association at the species level, but individuals did not feed with heterospecifics consistently enough for foraging associations to determine daily foraging patterns. It was possible that the effect of foraging associations on daily foraging patterns was being masked by individual variation in social foraging, so we reran out analyses using only those individuals that regularly foraged with heterospecifics. Again, species-specific daily foraging patterns were similar from the species-specific and social models, which provided further evidence that social foraging had a minimal effect on daily foraging patterns.

The meta-analysis of social and species-specific models showed striking differences in daily foraging patterns among species (Table 3, Figure 2). Northern cardinals, Carolina chickadees, and downy woodpeckers exhibited a bimodal foraging distribution in which the likelihood of foraging was higher in the morning and late afternoon compared to midday, as indicated by the positive quadratic terms for these species. House finches and house sparrows, on the other hand, showed a unimodal foraging pattern that peaked in the middle of the day as evidenced by negative quadratic terms. Tufted titmouse foraging activity declined through the day, and the likelihood of foraging for white-breasted nuthatches was unaffected by time of day.

Social models showed that foraging associations differed among species (Figure 2). There were few instances of positive associations (i.e., species foraging together more than expected; Figure 2a), and northern cardinals and house sparrows had none. Neutral associations (i.e., foraging association estimates with confidence intervals that overlapped 0) were more

common than positive ones, particularly with house sparrows (Figure 2c), but negative associations (i.e., species foraging together less than expected; Figure 2b) predominated for the majority of species. Most species also associated negatively with conspecifics, with the exception of positive associations for tufted titmice and Carolina chickadees.

DISCUSSION

Contrary to foraging theory models and the uniform foraging hypothesis (H1), daily patterns of foraging activity varied among species in winter. These species exhibited foraging associations that were consistent through time in accordance with the social foraging hypothesis (H3) as opposed to the variable social foraging hypothesis (H4). However, these associations did not strongly affect daily foraging patterns as predicted by the social foraging hypothesis (H3). Consequently, species-specific foraging hypothesis (H4) was best supported by out data.

The species-specific hypothesis proposes that variation in predation pressure experienced by different prey species shapes patterns of temporal foraging. While we did not directly measure predation risk, the winter ecology of predators of small birds in our region (Cooper's hawk, sharp-shinned hawk [*Accipiter striatus*], domestic cat; Dunn and Tessaglia 1994) is well known (Roth and Lima 2003, Roth and Lima 2006, Roth et al. 2006, Roth and Lima 2007, Horn et al. 2011). Collectively, these predators are most active in the morning and evening, which could cause prey to avoid feeding at these times—particularly species that are preferred prey. *Accipiter* hawks preferentially consume house sparrows and house finches (i.e., their proportion in *Accipiter* diets is higher than their proportion in the avian community) compared to other study species (Roth and Lima 2006, Roth et al. 2006), and cats also eat large numbers of house sparrows (Loss et al. 2013). These prey exhibit daily foraging patterns that are the inverse of

predator hunting activity, with most feeding occurring midday. Other researchers have also suggested that small birds avoid foraging when their predators are most active. Yellowhammers in Sweden feed less at the end of the day, presumably because sparrowhawks (*Accipiter nisus*) and great grey shrikes (*Lanius excubitor*) forage more at this time (Van der Veen 2008). In addition, three of four species studied at bird feeders in New York reduced foraging at dusk when owls began to hunt (Bonter et al. 2013).

Foraging patterns of species less vulnerable to predation may be less affected by peaks in predator activity and more influenced by factors typically included in theoretical foraging models (i.e., starvation risk and mass-dependent mortality). Northern cardinals and Carolina chickadees, for instance, are not preferred prey for *Accipiter* hawks despite being vocal and conspicuous birds (Roth and Lima 2006, Roth et al. 2006). Their foraging patterns exhibited the bimodal distribution predicted by foraging theory, which suggests that an early morning peak in foraging replenished energy stores that were depleted overnight and foraging decreased through the day until late afternoon to avoid mass-dependent mortality. For species that are particularly unlikely to be depredated by *Accipiter* hawks, such as tufted titmice (Roth and Lima 2006, Roth et al. 2006), the risk of mass-dependent mortality may be reduced to the point that midday foraging and the associated weight gain are no longer disadvantageous. As a result, foraging should be greatest in the morning to compensate for energy metabolized overnight and lowest at the end of the day once birds are satiated—a temporal pattern that corresponded to the foraging behavior of tufted titmice in our study.

Surprisingly, these species-specific foraging patterns were not strongly influenced by social dynamics. We had expected negative associations and divergent foraging patterns among species that regularly displaced each other at feeders. For example, other studies have found that

northern cardinals are dominant over house sparrows, which in turn supplant house finches at feeders (Nice 1927, Anderson 2006). We observed an inverse foraging pattern for northern cardinals compared to house finches and house sparrows. However, foraging associations with northern cardinals were not consistently negative and the pronounced negative association between house sparrows and house finches did not lead to different foraging patterns for these species. Therefore, daily foraging patterns and foraging associations were not tightly coupled in our study because individual positive and negative associations with heterospecifics were not so constant that they produced particular temporal patterns of foraging.

We had also expected positive foraging associations would lead to similar foraging patterns between species in the family *Paridae* (tufted titmouse, black-capped chickadee, Carolina chickadee) and other study species. Mixed-species foraging flocks form in winter in association with parids (Dolby and Grubb 1998, Dolby and Grubb 1999) because they reduce predation risk by detecting predators and conveying information about the threat to conspecifics and heterospecifics (Morse 1970, Contreras and Sieving 2011). Despite these benefits, we found no consistent positive associations between parids and other species. This may have been due to a reduced benefit of flocking at bird feeders because of the consistently available food. Alternatively, our methods may have failed to detect positive associations that were present, though we do not believe this to be the case. We did observe positive associations among conspecifics for some species, and previous studies have successfully used methods similar to ours to study heterospecific flock dynamics in winter (Farine et al. 2012, Aplin et al. 2014, Farine et al. 2014).

To our knowledge, our study is the first to assess the role of species interactions in shaping daily foraging patterns. Social dynamics affect many ecological patterns (e.g., disease

transmission, habitat use), but investigations into how individual interactions scale up to produce such patterns have been hampered by technological and statistical limitations (Farine et al. 2012). Automated animal-tracking technologies such as RFID are overcoming previous data limitations by providing detailed information on individual behavior (Krause et al. 2013), providing the raw material for network analyses to explore social dynamics (Farine et al. 2012). A useful tool in this burgeoning field will be ERGMs (Pinter-Wollman et al. 2013). Unlike other network analyses that are primarily descriptive (Croft et al. 2008), ERGMs are statistical models that test how social processes affect network structures (Harris 2014). The framework also allows multiple processes to be incorporated in the same model to determine the relative importance of each. As such, ERGMs are a more flexible tool than many other network analyses and hold great promise for the study of social dynamics.

We showed that daily patterns of foraging activity differ among species and are likely affected by variation in predation pressure experienced by prey. Theoretical foraging models of small birds in temperate winters have largely treated species as biologically identical (but see work on caching and noncaching species; Pravosudov and Lucas 2001), assuming that factors that shape foraging patterns apply to all species in the same way (Brodin 2007). Similarly, predation pressure is treated as constant rather than as temporally variable depending on the predator species (Roth et al. 2006, but see McNamara et al. 2005). Our findings suggest that these model assumptions are oversimplifications and that the behavior of different predators and prey need to be incorporated if foraging models are to more accurately approximate reality.

ACKNOWLEDGEMENTS

We would like to thank study site owners who purchased sunflower seed for this project and kept

bird feeders filled throughout the study, as well as numerous volunteers (particularly Nancy Snellen) who assisted with capturing birds and downloading RFID data. Droll Yankees, Inc., donated the bird feeders used for the project, and funding was provided by the Illinois Ornithological Society, the Champaign County Audubon Society, the Binky Foundation, and the National Science Foundation Graduate Research Fellowship Program. David Bonter, Eli Bridge, Joseph Casto, and Ben Kamen provided invaluable assistance on the construction and use of RFID readers, and Bethany Cutts assisted with ERGM analysis. Christine Parker, Jaime Coone, Samniqueka Halsey, and Scott Nelson provided useful comments on the manuscript.

LITERATURE CITED

Anderson, T. R. 2006. Biology of the ubiquitous house sparrow: from genes to populations. Oxford University Press, New York.

Aplin, L. M., D. R. Farine, R. P. Mann, and B. C. Sheldon. 2014. Individual-level personality influences social foraging and collective behaviour in wild birds. Proceedings of the Royal Society B: Biological Sciences **281**.

Berkey, C. S., D. C. Hoaglin, A. Antczak-Bouckoms, F. Mosteller, and G. A. Colditz. 1998. Meta-analysis of multiple outcomes by regression with random effects. Statitics in Medicine **17**:2537-2550.

Bonter, D. N., B. Zuckerberg, C. W. Sedgwick, and W. M. Hochachka. 2013. Daily foraging patterns in free-living birds: exploring the predation–starvation trade-off. Proceedings of the Royal Society B: Biological Sciences **280**.

Bridge, E. S., and D. N. Bonter. 2011. A low-cost radio frequency identification device for ornithological research. Journal of Field Ornithology **82**:52-59.

Brodin, A. 2007. Theoretical models of adaptive energy management in small wintering birds. Philosophical Transactions of the Royal Society B-Biological Sciences **362**:1857-1871.

Contreras, T. A., and K. E. Sieving. 2011. Leadership of winter mixed-species flocks by tufted titmice (*Baeolophus bicolor*): are titmice passive nuclear species? International Journal of Zoology **2011**:11.

Croft, D. P., R. James, and J. Krause. 2008. Exploring animal social networks. Princeton University Press, Princeton, New Jersey.

Dolby, A. S., and T. C. Grubb. 1998. Benefits to satellite members in mixed-species foraging groups: an experimental analysis. Animal Behaviour **56**:501-509.

Dolby, A. S., and T. C. Grubb, Jr. 1999. Functional roles in mixed-species foraging flocks: a field manipulation. The Auk **116**:557-559.

Dunn, E. H., and D. L. Tessaglia. 1994. Predation of birds at feeders in winter. Journal of Field Ornithology **65**:8-16.

Farine, D. R., L. M. Aplin, C. J. Garroway, R. P. Mann, and B. C. Sheldon. 2014. Collective decision making and social interaction rules in mixed-species flocks of songbirds. Animal Behaviour **95**:173-182.

Farine, D. R., C. J. Garroway, and B. C. Sheldon. 2012. Social network analysis of mixed-species flocks: exploring the structure and evolution of interspecific social behaviour. Animal Behaviour **84**:1271-1277.

Gleser, L. J., and I. Olkin. 2009. Stochastically dependent effect sizes.*in* H. Cooper, L. V. Hedges, and J. C. Valentine, editors. The handbook of research synthesis and meta-analysis. Russell Sage Foundation, New York.

Handcock, M. S., D. R. Hunter, C. T. Butts, S. M. Goodreau, and M. Morris. 2003. Statnet: software tools for the statistical modeling of network data.

Harris, J. K. 2014. An introduction to exponential random graph modeling. Sage Publications, Inc., Thousand Oaks, California.

Harrison, N. M., and M. J. Whitehouse. 2011. Mixed-species flocks: an example of niche construction? Animal Behaviour **81**:675-682.

Horn, J. A., N. Mateus-Pinilla, R. E. Warner, and E. J. Heske. 2011. Home range, habitat use, and activity patterns of free-roaming domestic cats. Journal of Wildlife Management **75**:1177-1185.

Koivula, K., M. Orell, and K. Lahti. 2002. Plastic daily fattening routines in willow tits. Journal of Animal Ecology **71**:816-823.

Krause, J., S. Krause, R. Arlinghaus, I. Psorakis, S. Roberts, and C. Rutz. 2013. Reality mining of animal social systems. Trends in Ecology & Evolution **28**:541-551.

Lima, S. L. 1986. Predation risk and unpredictable feeding conditions - determinants of body-mass in birds. Ecology **67**:377-385.

Loss, S. R., T. Will, and P. P. Marra. 2013. The impact of free-ranging domestic cats on wildlife of the United States. Nature Communications **4**:1396.

Lubbers, M. J., and T. A. B. Snijders. 2007. A comparison of various approaches to the exponential random graph model: A reanalysis of 102 student networks in school classes. Social Networks **29**:489-507.

McNamara, J. M., Z. Barta, A. I. Houston, and P. Race. 2005. A theoretical investigation of the effect of predators on foraging behaviour and energy reserves. Proceedings of the Royal Society B: Biological Sciences **272**:929-934.

McNamara, J. M., A. I. Houston, and S. L. Lima. 1994. Foraging routines of small birds in winter - a theoretical investigation. Journal of Avian Biology **25**:287-302.

Morris, M., M. S. Handcock, and D. R. Hunter. 2008. Specification of exponential-family random graph models: terms and computational aspects. Journal of Statistical Software **24**.

Morse, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. Ecological Monographs **40**:119-168.

Nice, M. M. 1927. Experiences with cardinals at a feeding station in Oklahoma. Condor **29**:101-103.

Pinter-Wollman, N., E. A. Hobson, J. E. Smith, A. J. Edelman, D. Shizuka, S. de Silva, J. S. Waters, S. D. Prager, T. Sasaki, G. Wittemyer, J. Fewell, and D. B. McDonald. 2013. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. Behavioral Ecology.

Polo, V., and L. M. Bautista. 2006. Daily routines of body mass gain in birds: 1. An exponential model. Animal Behaviour **72**:503-516.

Psorakis, I., S. J. Roberts, I. Rezek, and B. C. Sheldon. 2012. Inferring social network structure in ecological systems from spatio-temporal data streams. Journal of The Royal Society Interface.

R Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Roth, T. C., and S. L. Lima. 2003. Hunting behavior and diet of Cooper's hawks: an urban view of the small-bird-in-winter paradigm. The Condor **105**:474-483.

Roth, T. C., and S. L. Lima. 2006. Predatory behavior and diet of wintering male Cooper's Hawks in a rural habitat. Journal of Raptor Research **40**:287-290.

Roth, T. C., and S. L. Lima. 2007. The predatory behavior of wintering *Accipiter* hawks: temporal patterns in activity of predators and prey. Oecologia **152**:169-178.

Roth, T. C., S. L. Lima, and W. E. Vetter. 2006. Determinants of predation risk in small wintering birds: the hawk's perspective. Behavioral Ecology and Sociobiology **60**:195-204.

Van Der Veen, I. T. 2000. Daily routines and predator encounters in Yellowhammers *Emberiza citrinella* in the field during winter. Ibis **142**:413-420.

Viechtbauer, W. 2010. Conducting meta-analyses in R with the metafor package. Journal of Statistical Software **36**:1-48.

Witter, M. S., I. C. Cuthill, and R. H. C. Bonser. 1994. Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. Animal Behaviour **48**:201-222.

TABLES AND FIGURES

Table 3.1. Number of individuals by species visiting a bird feeder equipped with an RFID reader. Number of foraging bouts documented at each site are in parentheses. Data for American goldfinches, black-capped chickadees, and red-bellied woodpeckers were not included in the meta-analyses because of small sample sizes.

Species	Nonforest urban A	Nonforest urban B	Forest urban A	Forest urban B	Forest rural A	Forest rural B	Forest rural C	Total
American goldfinch *Spinus tristis*	0	0	0	0	2	1	0	3
Black-capped chickadee *Poecile atricapillus*	0	0	0	6	0	0	0	6
Carolina Chickadee *Poecile carolinensis*	0	0	2	0	9	3	1	15
Downy woodpecker *Picoides pubescens*	0	0	0	4	4	0	2	10
House finch *Haemorhous mexicanus*	15	3	6	2	9	14	4	53

Table 3.1. Continued

Species	Nonforest urban A	Nonforest urban B	Forest urban A	Forest urban B	Forest rural A	Forest rural B	Forest rural C	Total
House sparrow *Passer domesticus*	23	14	3	1	0	1	6	48
Northern cardinal *Cardinalis cardinalis*	4	2	1	1	0	0	0	8
Red-bellied woodpecker *Melanerpes carolinus*	0	0	0	0	2	0	2	4
Tufted titmouse *Baeolophus bicolor*	0	0	0	4	6	5	1	16
White-breasted nuthatch *Sitta carolinensis*	0	0	2	2	2	1	2	9
Total	42 (1504)	19 (469)	14 (303)	20 (517)	34 (3855)	25 (1663)	18 (398)	172 (8712)

Table 3.2. Model comparison of five ERGMs of songbird foraging networks.at bird feeders from three types of landscapes (nonforested urban, forested urban, forested rural).

Site *Model*	AIC	k	ΔAIC
Nonforest urban A			
null	26594.2	1	1157.8
uniform	26595.1	7	1158.7
species-specific	26004.8	19	568.4
social	25436.4	25	0.0
variable social	25814.2	48	377.8
Nonforest urban B			
null	7044.5	1	459.9
uniform	7022.9	7	438.3
species-specific	6703.8	19	119.2
social	6584.6	25	0.0
variable social	6596.9	50	12.3
Forest urban A			
null	6814.1	1	638.7
uniform	6824.1	7	648.7
species-specific	6477.4	26	302.0
social	6175.4	37	0.0
variable social	6248.6	98	73.2
Forest urban B			
null	8471.9	1	1311.2
uniform	8472.3	7	1311.6
species-specific	7550	39	389.3
social	7160.7	65	0.0
variable social	7380.3	143	219.6

Table 3.2. Continued

Site *Model*	AIC	k	ΔAIC
Forest rural A			
null	91551.5	1	8121.2
uniform	91458.1	7	8027.8
species-specific	85507.8	37	2077.5
social	83430.3	56	0.0
variable social	84047.5	150	617.2
Forest rural B			
null	23758.4	1	4243.7
uniform	23762.4	7	4247.7
species-specific	19903.9	30	389.2
social	19514.7	44	0.0
variable social	19693.7	88	179.0
Forest rural C			
null	4356.4	1	637.4
uniform	4366.66	7	647.7
species-specific	3833.6	41	114.6
social	3719	64	0.0
variable social	3842.0	129	123

Table 3.3. Species-specific parameter estimates (B) showing the relationship between time of day and likelihood of foraging. Linear (x) and quadratic (x^2) terms are given and were calculated using multivariate meta-analyses of species-specific and social ERGMs. Bold values are $p<0.05$ and italicized values are $0.10>p>0.05$.

		Species-specific			Social		
		B	SE	p	B	SE	p
Carolina Chickadee	x	**-0.5083**	**0.1432**	**0.0004**	**-0.299**	**0.1201**	**0.0128**
	x^2	**0.1045**	**0.0268**	**<.0001**	**0.0651**	**0.0222**	**0.0034**
Downy Woodpecker	x	-0.2061	0.1506	0.1711	**-0.2739**	**0.1328**	**0.0391**
	x^2	*0.0471*	*0.0285*	*0.0985*	**0.0551**	**0.0248**	**0.0264**
House Finch	x	**0.3694**	**0.1044**	**0.0004**	**0.3624**	**0.0932**	**0.0001**
	x^2	**-0.0811**	**0.0201**	**<.0001**	**-0.0774**	**0.0176**	**<.0001**
House Sparrow	x	**0.3198**	**0.1359**	**0.0186**	**0.272**	**0.1179**	**0.021**
	x^2	*-0.0445*	*0.0258*	*0.0851*	*-0.0421*	*0.0219*	*0.0542*
Northern Cardinal	x	**-0.5291**	**0.176**	**0.0026**	**-0.5234**	**0.1548**	**0.0007**
	x^2	**0.0791**	**0.0328**	**0.0159**	**0.0794**	**0.0284**	**0.0051**
Tufted Titmouse	x	**-0.5111**	**0.1502**	**0.0007**	**-0.2853**	**0.1251**	**0.0225**
	x^2	*0.0482*	*0.0283*	*0.0889*	0.0146	0.0234	0.5322
White-breasted	x	0.0781	0.1545	0.6134	0.0546	0.1407	0.698
nuthatch	x^2	-0.0044	0.0295	0.8828	-0.006	0.0262	0.8184

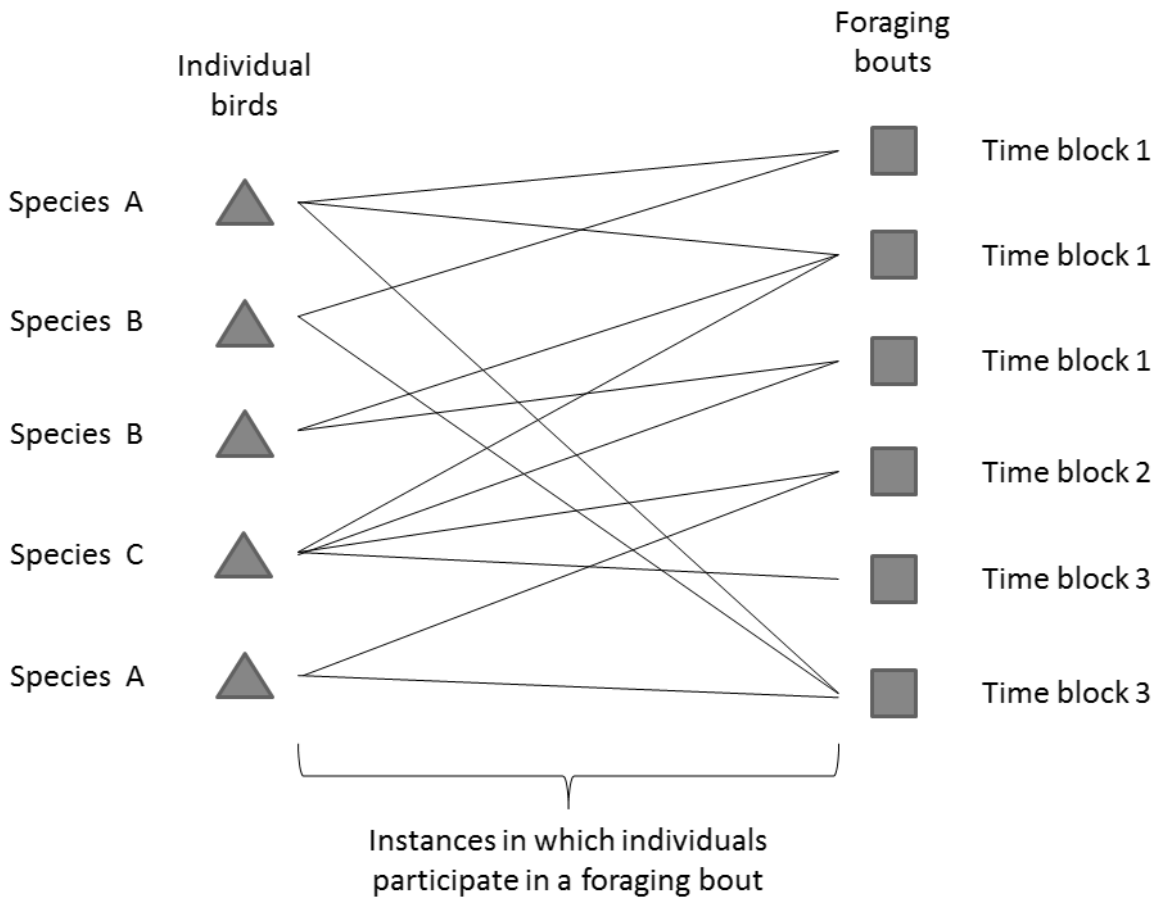


Figure 3.1. Hypothetical bipartite network of social foraging. Bipartite networks consist of two types of objects (birds and foraging bouts) in which connections occur between objects of a different type (an individual bird participates in a particular foraging bout) but not between objects of the same type (e.g., no connections between birds). Social foraging occurs when two or more birds participate in the same foraging bout. Attributes of birds (e.g., species) and foraging bouts (e.g., time block in which the bout occurred) can be incorporated into exponential random graph models to determine whether attributes affect the formation of connections between birds and bouts.

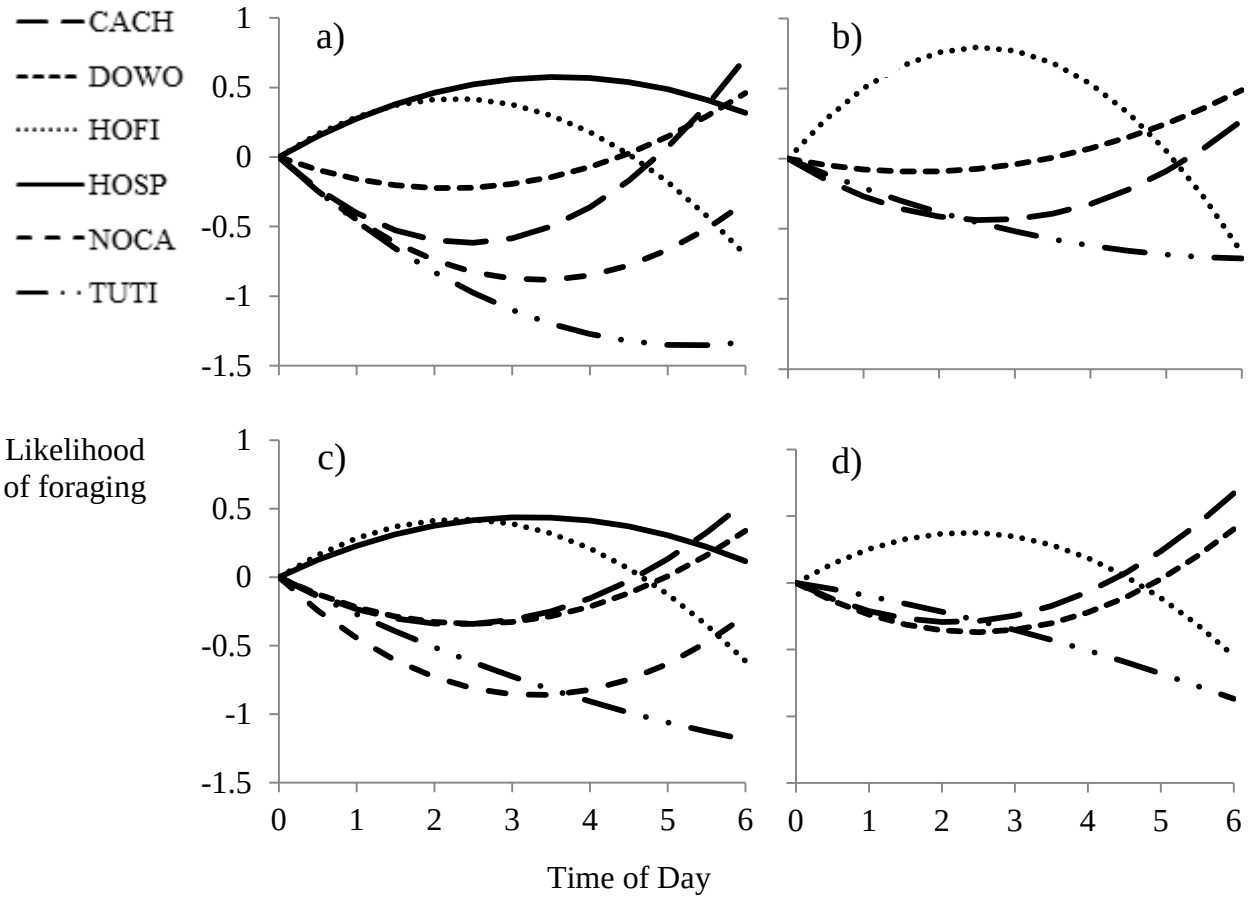


Figure 3.2. Species-specific daily foraging patterns at bird feeders from species-specific models (a and b) and social models (c and d). ERGMs were used to estimate species-specific foraging at each site then a multivariate meta-analysis was used to model how foraging parameters changed through time (a and c). These analyses were repeated using only individuals that regularly foraged together (b and d). Lines shown are predicted quadratic relationships for each species. Time of day was broken into seven time blocks (0–6) with the model intercept set to early morning (0). Species codes are for Carolina chickadee (CACH), downy woodpecker (DOWO), house finch (HOFI), house sparrow (HOSP), northern cardinal (NOCA), and tufted titmouse (TUTI). Data for white-breasted nuthatches were not included because their likelihood of foraging was unrelated to time of day, and northern cardinals and house sparrows were not modeled in c and d because of insufficient sample sizes.

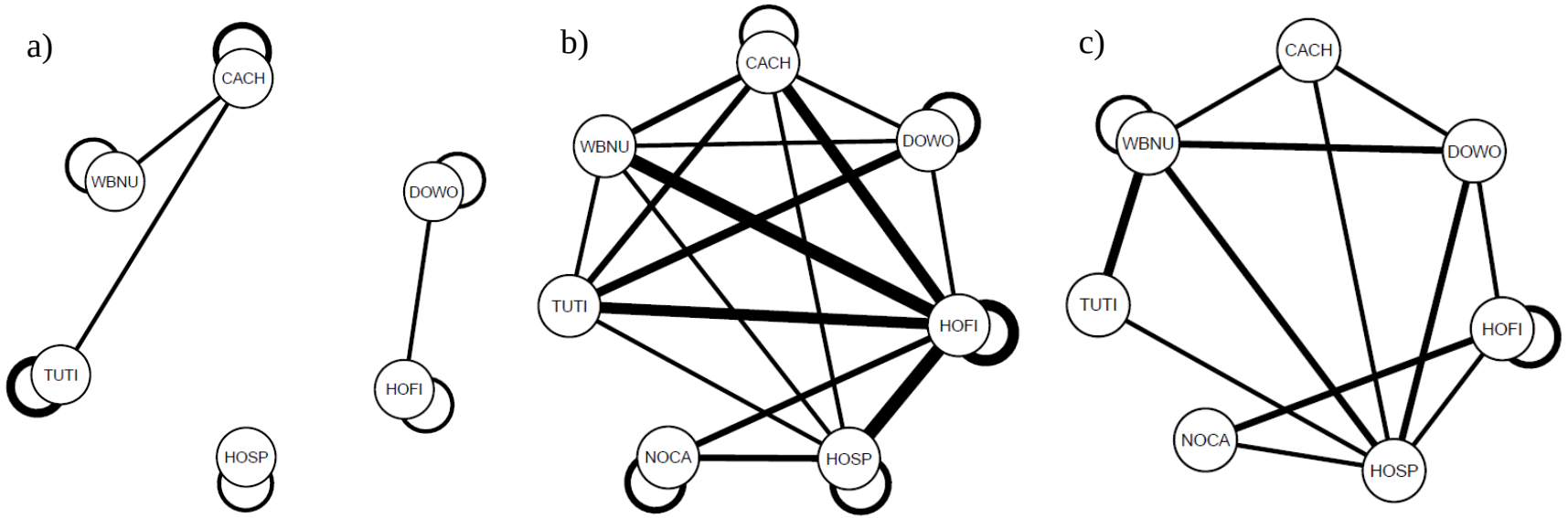


Figure 3.3. Foraging association networks among songbird species visiting bird feeders in winter based on site-specific social foraging ERGMs. Associations measure whether species were more (a; positive) or less (b; negative) likely to forage together than expected by chance, though associations may also be neutral (c). Positive and negative associations reflected ERGM association estimates whose 90% confidence intervals did not overlap 0. The thickness of lines indicates the number of sites at which a type of association was documented for a pair of species, and loops on circles indicate intraspecific associations. Codes are for Carolina chickadee (CACH), downy woodpecker (DOWO), house finch (HOFI), house sparrow (HOSP), northern cardinal (NOCA), tufted titmouse (TUTI), and white-breasted nuthatch (WBNU).

CHAPTER 4. Social foraging dynamics of a gregarious songbird and implications for disease transmission

Co-authors: Kevin J. Wolz and James R. Miller

INTRODUCTION

The recent integration of host social networks with studies of pathogen and parasite transmission has greatly enhanced scientific understanding of disease dynamics (Godfrey 2013). An individual's position in a social network is often a strong predictor of infection risk, with more social or connected animals being at greater risk of exposure (Corner et al. 2003, Christley et al. 2005, Godfrey et al. 2009, Leu et al. 2010, Bull et al. 2012). The frequency and strength of social interactions can vary based on individual traits such as sex and age or spatiotemporal patterns of habitat use (e.g., Perkins et al. 2008, Godfrey et al. 2010). Such traits can be incorporated into social networks to quantify how they affect patterns of social interaction and associated disease dynamics (Godfrey 2013). While such network analyses have improved our understanding of social systems and how diseases are transmitted within them, they have focused on networks of healthy individuals. Parasites and pathogens often alter social behavior of their hosts, which can in turn affect social interactions and the risk of disease transmission (Moore 1984, 2002). Here, we use a gregarious songbird and a bacterial disease as a case study to demonstrate how network analyses can be used to quantify social dynamics of healthy and infected individuals that could affect disease transmission.

In 1994, a novel disease called mycoplasmal conjunctivitis emerged in house finch (*Haemorhous mexicanus*) populations of the Eastern United States and spread rapidly, causing

local declines of up to 60% (Badyaev et al. 2012). The disease is caused by a bacterium (*Mycoplasma gallisepticum*) that produces swollen tissues around the eyes, ocular and nasal discharge, and in severe cases, impaired vision and death (Luttrell et al. 1998). Because the bacteria spreads through direct contact, social interactions among house finches may mediate disease transmission (Hosseini et al. 2006). Physical contact occurs through agonistic interactions over food resources, roost sites, and nests; courtship and breeding behaviors between mates; and within roosts (Badyaev et al. 2012). The strength of these social interactions is affected by mycoplasmal conjunctivitis, as infected birds tend to be less social than healthy house finches (Hotchkiss et al. 2005, Hawley et al. 2007). Reduced sociality could in turn feed back to affect disease dynamics through decreased direct contact and transmission rates.

Transmission could also be affected if social interactions are mediated by individual traits like age and sex. In social network studies, such trait-based variation is often quantified by social associations, which measure whether for individuals with similar or dissimilar attributes are more or less likely to interact than expected by chance (Godfrey 2013). For example, male and female yellow-necked mice (*Apodemus flavicollis*) associate more with the opposite sex than intrasexually (Perkins et al. 2008), which affects transmission dynamics of parasitic nematodes within and between the sexes. Social associations may play a critical function in many disease systems (Godfrey 2013), but to our knowledge these associations have yet to be investigated in the context of mycoplasmal conjunctivitis.

In addition to direct contact, mycoplasmal conjunctivitis can be transmitted indirectly via contaminated food or water (Dhondt et al. 2007). Given the proclivity for this species to forage at bird feeders in the Eastern United States, feeders may be transmission hotspots where mycoplasmal conjunctivitis is spread through direct contact between healthy and infected birds

and indirect contact via contamination (Hartup et al. 1998). Infected house finches spend more time foraging at feeders than healthy birds (Hotchkiss et al. 2005, Hawley et al. 2007), which increases the likelihood that feeders will be colonized by *M. gallisepticum*.

Finally, in addition to intraspecific transmission among house finches, mycoplasma conjunctivitis can be spread between songbird species. The disease has been documented in over 30 species to date, particularly house sparrows (*Passer domesticus*), northern cardinals (*Cardinalis cardinalis*), and American goldfinches (*Spinus tristis*; Hartup et al. 2001b, Dhondt et al. 2013). Though the bacteria does not cause widespread mortality for these species, it can be transmitted back to house finches from infected heterospecifics (Hartup et al. 2001b, States et al. 2009, Dhondt et al. 2013). As a result, interspecific associations with house finches could be relevant to disease transmission, particularly if social associations differ for healthy and infected finches.

Because bird feeders may be transmission hotspots in this disease system, we investigated social foraging networks of birds visiting feeders over a two-year period in east-central Illinois. Our objectives were to 1) document patterns of mycoplasma conjunctivitis prevalence by age and sex in our study system, 2) quantify variation in foraging activity at bird feeders by age, sex, and disease status, 3) compare sociality of house finches by age, sex, and disease status, 4) compare social foraging associations by species, age, and sex for house finches with and without the disease, and 5) discuss how patterns of foraging, sociality, and foraging associations pertain to transmission of mycoplasmal conjunctivitis among house finches. To meet these objectives, we tracked bird visitations to feeders using a radio-frequency identification (RFID) system and applied a form of network analysis that has shown great promise in studies of human epidemiology but has yet to be applied to studies of wildlife disease

(Valente 2010, Pinter-Wollman et al. 2013).

METHODS

From 2011-2013, we studied foraging dynamics at 16 sites with bird feeders in east-central Illinois in and around the villages of Homer and Mahomet and the cities of Champaign, Monticello, and Urbana. Sites were residential properties (n=14) or nature education centers (n=2) surrounded either by corn and soybean agriculture (n=5) or residential neighborhoods (n=9). Three of the agricultural sites and four residential sites were located near deciduous forest fragments ($\leq$0.1 km). Other sites were $\geq$0.5 km from forests. At each site we erected a tube feeder (B-7F; Droll Yankees, Inc., Plainfield, CT) that was continuously filled with black oil sunflower seed and hung from a 2.1-m shepherd's hook. The hook was surrounded by a 10-cm-diameter polyvinyl chloride pipe and placed 2 m from adjacent objects to prevent squirrels from accessing the feeder.

We visited sites once per month (March-November in 2011, May-October in 2012, May-August in 2013) to capture birds at bird feeders. Two mist nets were set up for three hours beginning at sunrise on days with no precipitation. All birds captured were aged, sexed, and identified to species (Pyle 1997). Any swelling of tissues around the eyes was recorded as evidence of mycoplasmal conjunctivitis. We placed color bands on the left leg of each bird and attached a 2x12mm RFID tag (CYNTAG, Inc., Cynthia, Kentucky, USA) to the bands using all-weather electrical tape (Bridge and Bonter 2011). Three residential sites were eliminated from the study after 2011 because too few birds were captured, and four sites (two residential and two farms) were added in May 2012.

In January 2012, we installed a RFID reader on the tube feeder at each study site to track

avian foraging activity (Bonter and Bridge 2011, Bridge and Bonter 2011). All but the bottommost feeding port was blocked and the reader was installed below it so the RFID antenna was part of the perch for the open port. The reader recorded the time, date, and RFID code for every second that a bird with a tag was perched at the feeding port. Data were downloaded once or twice per week. In January of 2013, all units were replaced with readers with a larger memory capacity, which allowed a download interval of 4–6 weeks. Downloads continued through November 2013. House finches captured with mycoplasma conjunctivitis when RFID readers were present were referred to as "infected", birds captured with symptoms in the year before RFID readers were installed were referred to as "recovered" since birds typically die or recover within 3–4 months (Kollias et al. 2004), and finches captured without symptoms were referred to as "asymptomatic".

Statistical analysis

We examined capture data to determine if numbers of infected and asymptomatic house finches varied by month, year, sex, and age. Comparisons were made using chi-square tests (Ott and Longnecker 2001). We also calculated a sex ratio for adults as the intercept from a general linear mixed model with site and year as random effects (SAS Enterprise Guide 4.3; SAS Institute, Cary, North Carolina, USA; Ott and Longnecker 2001). Only sites at which more than three house finches were captured in a given year were included in the analysis to exclude sex ratios that may have been biased because of small sample size.

Prior to network analyses, RFID data were condensed to the arrival times for each visit (i.e., one record per visit). Consecutive visits by the same bird were considered separate if there were >5 s between visits. This time gap accounted for instances in which a reader may have

briefly failed to record the presence of a marked bird. Days in which fewer than 30 s of data were recorded were excluded from the analysis to account for times when the readers malfunctioned or the feeders ran out of seed.

To investigate social foraging behavior we first identified bouts of foraging activity from RFID records (Psorakis et al. 2012). These bouts were produced by groups of visitations from one or more birds followed by periods of no activity at a feeder. Thus, participation in bouts was a measure of individual and social foraging activity To identify bouts, we constructed Gaussian mixture models in MATLAB R2013b (The MathWorks, Inc., Natick, Massachusetts, USA) for each day at each site to detect discrete clusters of visitations (Psorakis et al. 2012). This method is an improvement over the traditional approach, which defines bouts based on co-occurrence within a specified time frame (Whitehead 2008). The problem with the traditional method is that the time frame often does not have a biological basis. Gaussian mixture models, on the other hand, rely on the structure of visitation data (i.e., clusters of visits and gaps between them) to identify foraging bouts (Psorakis et al. 2012).

Foraging bouts were used to construct bipartite networks that were analyzed with exponential random graph models (ERGMs) in the 'statnet' package (Handcock et al. 2003) in R 3.0 (R Core Team 2012). Bipartite networks are composed of two types of objects, with connections occurring between objects of different types but not of the same type (Figure 1). In this study, one object type was individual birds and the other was foraging bouts. Each connection was an instance in which a bird participated in a bout, so the bipartite network reflected individual differences in foraging activity. ERGMs are used to test how variables affect the likelihood of connections forming in a network (Morris et al. 2008, Harris 2014, Chapter 3), so we tested whether attributes of individuals (e.g., species) and foraging bouts (e.g., season)

affected the likelihood of foraging at a feeder. We constructed a series of nested ERGMs to assess the effect of species (species model), house finch age and sex (i.e., hatch year, adult male, adult female; sex/age model), and house finch disease status (i.e., infected, recovered, asymptomatic; disease model) on foraging likelihood. All three models were run with and without seasonal variation to determine whether foraging likelihoods were constant throughout the year. The six models were compared using an information theoretic approach with Akaike's information criterion (AIC; Burnham and Anderson 1998). Separate networks and ERGMs were constructed for each study site because of the unique assemblages of interacting individuals at each site.

We also used ERGMs to test for different types of foraging associations that could affect disease transmission (Morris et al. 2008). In our bipartite networks, individuals that foraged together were represented by a pair of connections between two individuals and a foraging bout (Figure 1). By testing whether attributes of individuals and foraging bouts affect the likelihood of pairs occurring in a network, ERGMs measure whether individuals with particular combinations of attributes are more or less likely to forage together than expected by chance. For example, a sex ERGM would indicate whether male-male, female-female, or male-female foraging associations were more or less likely to occur in a network than expected. We constructed six ERGMs that incorporated associations: species, sex/age, and disease models with and without seasonal variation included. In all models, foraging activity was included to control for variation in visitation frequency to feeders, which could have affected the likelihood of associations forming (i.e., model terms from the seasonal disease foraging model were included in all association models). Models were compared using AIC.

Finally, we used ERGMs to model sociality (Morris et al. 2008). To do so, we converted

bipartite networks to unipartite networks (i.e., networks made up of only one node type; Figure 1) using the 'bipartite' package in R (Dormann et al. 2008). In our unipartite networks, individuals were directly connected via instances in which they foraged together rather than indirectly as in bipartite networks. This connection scheme allowed sociality to be modeled as the number of connections (i.e., foraging partners) for each bird in the network.

Because ERGMs were constructed separately per site, to summarize results across sites we used a multivariate meta-analysis framework in the 'metafor' package in R to account for covariance among parameter estimates in site-specific ERGMs (Viechtbauer 2010). Covariance was incorporated using a block-covariance matrix in which covariances between sites were zero while covariances within each site formed a block of nonzero values (Berkey et al. 1998, Gleser and Olkin 2009). Meta-analysis inputs included the parameter estimates from the ERGM models as a dependent variable, the block-covariance matrix, a fixed categorical variable whose levels varied depending on the ERGM (e.g., sex, species, individual), and a random site effect. The meta-analysis for foraging activity also included a compound symmetric covariance structure in the random effect to account for any differences between years.

In order to visualize the potential role of direct and indirect transmission at bird feeders, we created two networks for two of the infected bird networks. The first network was the network used to quantify sociality except only house finches were included. Network connections represented instances in which two birds foraged together and thicker lines represented birds that foraged together more often. We assumed that this frequency of social foraging reflected the probability of direct transmission. We truncated the data set down to the one month of data following the infected bird's capture to focus on a time interval in which the bird was likely to still have mycoplasmal conjunctivitis. In the second network, we added

connections that represented the increased probability of infection because of indirect transmission. *M. gallisepticum* is infectious on feeders for up to 12 hours (Dhondt et al. 2007) so we added a connection for every instance in which birds foraged at a study feeder after the infected bird for each day. We compared the indirect and direct transmission networks by reporting changes in the number of asymptomatic birds foraging with (i.e., connected to) infected birds in each network as well as the change in the overall number of connections to infected birds.

RESULTS

During the 3 years of the study we banded 473 house finches, most of which were captured from May to August (86%) due to greater sampling effort during these months (Table 1). We report numbers of males, females, and hatch years captured because relative abundance of these groups can affect disease transmission if social interactions vary by age or sex. More males were caught than females (sex ratio of 1.41:1; 95% CI: 1.09–1.73) and 55% of captures were hatch-year birds (Table 1). We caught 22 house finches exhibiting swollen tissue around the eyes, for an overall conjunctivitis prevalence of 4.7% (Table 1). Monthly prevalence ranged from 1.6–10.0% (Table 1) and varied among years from 3.9% in 2011 to nearly absent in 2012 (0.7%) to 9.8% in 2013. Though females were not statistically more likely to be infected than males (X^2=0.6728, P=0.1783), prevalence was 4.8% for males and 10.1% for females (Table 2). Hatch-year birds with conjunctivitis symptoms were rare outside of August (Table 1) and exhibited a lower prevalence than adults (3.2% vs 6.9%; Table 2; X^2=0.7681, P=0.0869).

Of banded birds, 418 were marked with RFID tags (Table 2), including all 22 birds with conjunctivitis. We documented about half returning to RFID feeders (n=204), including 9 that

had exhibited symptoms at the time of capture. Asymptomatic males were as likely as females to be recorded by the RFID readers (X^2=0.8471, P=0.3574), but only one of six infected males returned to the RFID feeders compared to 6 of 8 females. Marked hatch years were much less likely to be recorded by RFID feeders than adults (X^2=0.8740, P=0.0251; Table 2), with only two of eight hatch years returning.

We focused subsequent analyses on the time interval over which infected birds were recorded at bird feeders (Table 3). This restricted the data set to 5 sites and 65 house finches because insufficient RFID data were collected for birds with mycoplasmal conjunctivitis at some sites. For each site, we constructed a social network including 1–2 infected house finches, 4–17 other house finches, and 2–7 additional species (Table 3). At one site, separate networks were constructed for two infected house finches because the data for each were from separate years and the two networks only shared five individual birds in common. Three networks reflected behavior of birds with mycoplasmal conjunctivitis symptoms (referred to as "infected") and the social context in which it occurred. Data collection on foraging behavior began immediately after capture and lasted 21–125 days, after which these birds died, emigrated, or lost their RFID tag (Table 3). The remaining three networks reflected behavior of birds that had recovered from mycoplasmal conjunctivitis (referred to as "recovered"). These birds had the disease when they were captured in July and August of 2011, but RFID monitoring did not begin until January of 2012. House finches typically recover or die from the disease within 10–14 weeks (Kollias et al. 2004), so recovered birds should have been asymptomatic by the time foraging behavior data were collected (though reinfections are possible).

To determine whether foraging activity of house finches varied by sex, season, or disease status, we compared a series of ERGMs for each network (Table 4, Figure 2). Models including

season, sex, and disease status were best supported for all networks but one. For this network, foraging varied by season and sex but not disease status. Using a multivariate meta-analysis to summarize results of the best-supported ERGM for each network, we found asymptomatic males and females exhibited similar foraging activity in the spring. Males and females were less likely to forage at feeders in the summer than in the spring, but the seasonal difference was much greater for females. Infected birds had similar foraging activity in the spring and summer and compared to asymptomatic males in both seasons and females in the summer. Infected birds were more likely to visit feeders in summer than asymptomatic females, which was particularly noteworthy given that all infected birds were female. Recovered house finches were more likely to forage at feeders than any other group in spring and less likely to visit feeders compared to infected birds and asymptomatic males in summer. Results focused on spring and summer because of insufficient data on infected birds in other seasons.

To determine whether foraging associations of house finches varied by season, sex, or disease status, we compared ERGMs for each network and found that sex and disease models were not well supported (Table 4). For all but one network, the species model was best supported, which indicated that species varied in the extent to which they foraged with or avoided conspecifics and heterospecifics. Because these patterns did not differ between male and female house finches or infected and asymptomatic birds, we did not report species-level association patterns here.

To determine whether sociality of house finches varied by sex and disease status, we estimated sociality for every bird using network specific ERGMs and summarized results across ERGMs using a multivariate meta-analysis. Networks were constructed from spring and summer data so findings were based on the same time interval as the foraging models. Recovered house

finches and asymptomatic males and females foraged with similar numbers of birds, but infected birds were more social (Figure 3). The difference in sociality between infected and recovered birds suggests that the observed increase in sociality during an active infection was temporary.

Finally, in order to visualize how direct and indirect transmission could affect risk of exposure to mycoplasmal conjunctivitis for house finches at bird feeders, we compared networks that represented the risk of direct transmission with ones that also incorporated the risk of indirect transmission (Figure 4). Infected birds foraged with (i.e., were connected to) all other birds in each direct transmission network (network A: n=8, network B: n=9), so indirect transmission networks did not increase the number of house finches exposed to an infected birds. Line thickness, on the other hand, was much greater in the indirect transmission networks. The sum of connections to the infected bird in each network (i.e., aggregated line thickness) was 2.1 to 3.3 times greater in the indirect compared to direct networks (network A: 129 vs 269; network B: 92 vs 308). This suggested that the potential for bacteria to contaminate bird feeders and indirectly infect healthy birds greatly increased the risk of exposure to mycoplasmal conjunctivitis.

DISCUSSION

Our network analyses revealed differences in foraging activity and sociality between infected and asymptomatic birds that had important implications for the transmission of mycoplasmal conjunctivitis. Infected house finches were more social at feeders than asymptomatic birds, which increased the risk of exposure to *M. gallisepticum* for healthy birds. Infected females were also more likely to forage at feeders than asymptomatic females in the summer, so transmission risk was greater than it would have been had infected birds behaved like healthy individuals.

These behavioral changes were likely the result of impaired vision and reduced activity levels caused by the disease (Luttrell et al. 1998). Mycoplasmal conjunctivitis symptoms make finding food and avoiding predators more difficult, but foraging at feeders with other birds may simultaneously reduce the risks of starvation and predation (Hartup et al. 1998). Consequently, changes in foraging behavior that were likely caused by the disease ultimately increased the risk of exposure for healthy finches at bird feeders.

The increase in sociality we observed for infected birds contrasts with previous studies that found infected individuals were less social. The difference may be due to seasonal dynamics of mycoplasmal conjunctivitis, as our comparison was made in spring and summer while other studies were conducted in fall or winter (Hotchkiss et al. 2005, Hawley et al. 2007). Alternatively, different definitions of "sociality" could account for the discrepancy. Hotchkiss et al. (2005) defined sociality as the number of house finches present on two adjacent feeders when a focal bird was eating, and Hawley et al. (2007) quantified the number of finches within 1 m of a feeder when a focal bird was feeding. Our metric counted the number of birds of any species marked with an RFID tag that came to a feeder within a foraging bout. Consequently, our measure was not as spatially or temporally restrictive as other studies, and probably included more birds in social foraging groups as a result. We used our method to identify the subset of individuals an infected bird was likely to interact with, which was the relevant social group from the perspective of disease transmission.

In addition to behavioral differences between infected and asymptomatic house finches, variation in foraging activity between males and females could have important implications for disease transmission. Infected females and asymptomatic adults of both sexes exhibited similar foraging activity in the summer and spring, except asymptomatic females visited feeders less in

the summer. These visitation patterns suggest that risk of exposure to *M. gallisepticum* at bird feeders was similar between spring and summer, but that females were less likely to contract the disease because fewer visits to feeders meant less direct contact with infected birds and contaminated bird seed. Previous work has shown infected birds and females sometimes spend more time at feeders during single visits (fall study, Hotchkiss et al. 2005; winter study, Hawley et al. 2007), but these projects did not quantify patterns of visitation. Davis (2008) reported similar visitation rates at feeders for adult male and female house finches and more visitations by birds with mycoplasmal conjunctivitis, but his findings were aggregated across a two-year study. To our knowledge, ours is the first study to report patterns of seasonal feeder visitation by sex or disease status for house finches.

Such seasonal complexities in social behavior are critical to understanding systems in which disease dynamics vary throughout the year, as they do for mycoplasmal conjunctivitis. Prevalence of symptomatic individuals is lowest in the spring and summer and increases to a peak in late fall due to increased gregariousness and presence of hatch years not previously exposed to the disease (Dhondt et al. 1998, Hartup et al. 2001a, Roberts et al. 2001, Altizer et al. 2004a, Altizer et al. 2004b, Hosseini et al. 2006). Consequently, social behavior of the small proportion of infected birds in summer could be a key determinant of transmission dynamics to naïve hatch year birds in late summer and fall. We did not observe variation in foraging associations by age or sex for house finches, particularly between infected and asymptomatic birds. Thus, particular age or sex classes do not appear to be more at risk of mycoplasma conjunctivitis infection based on social interactions among conspecifics.

One shortcoming of this study was the small number of birds with mycoplasmal conjunctivitis that returned to feeders. Our results must be interpreted cautiously, given that

small sample sizes are more likely to be biased. For example, the difference in foraging at feeders between summer and spring for recovered house finches was difficult to interpret given that recovered birds included one male, two females, and one bird of unknown sex. The return of only one male captured with mycoplasmal conjunctivitis was also puzzling given the male-bias of house finch populations in this and other studies (Badyaev et al. 2012). The dearth of males could have been an artifact of small sample size, but could also be an indication that infected females were more likely to return to feeders than infected males—a finding that could have important implications for disease transmission. Low return rates of diseased males were not the result of a general difference in feeder usage between the sexes, as a similar proportion of males and females marked with RFID tags returned to the RFID readers. The larger number of returning females was also not a result of male-biased disease mortality, which would have eliminated or reversed the male-bias in the sex ratio (Nolan et al. 1998). Interpretation challenges aside, the small sample size of infected birds in our study was balanced against the comprehensive foraging data collected for house finches over the two-year study at multiple sites. Despite its limitations, our dataset is the most detailed account of foraging behavior of infected and asymptomatic house finches published to date.

Our study was the first to conduct detailed tracking of foraging behavior for house finches with and without mycoplasmal conjunctivitis. We documented increased foraging and sociality at bird feeders that was likely caused by the disease and also increased the risk of transmission. Feeder use by infected birds was particularly important because of the possibility for indirect disease transmission, which, from a network perspective, increased the strength of connections among individuals and therefore infection risk as well. Our findings highlight the complexity of social interactions affecting disease dynamics, the importance of considering how

diseases mediate social interactions, and the utility of network analyses in studying such socially mediated processes.

ACKNOWLEDGEMENTS

We would like to thank site owners who allowed use to their properties as study sites and filled study feeders with sunflower seed throughout the project. We are also grateful to volunteers (particularly Nancy Snellen) who helped catch birds and Droll Yankees, Inc., which donated the bird feeders used for the project. We appreciate funding provided by the Illinois Ornithological Society, the Champaign County Audubon Society, the Binky Foundation, and the National Science Foundation Graduate Research Fellowship Program. David Bonter, Eli Bridge, Joseph Casto, and Ben Kamen helped with the construction and maintenance of RFID readers, and Bethany Cutts provided input on ERGM analyses and interpretation. Christine Parker, Jaime Coone, Samniqueka Halsey, and Scott Nelson provided useful comments on the manuscript.

LITERATURE CITED

Altizer, S., A. K. Davis, K. C. Cook, and J. J. Cherry. 2004a. Age, sex, and season affect the risk of mycoplasmal conjunctivitis in a southeastern house finch population. Canadian Journal of Zoology **82**:755-763.

Altizer, S., W. M. Hochachka, and A. A. Dhondt. 2004b. Seasonal dynamics of mycoplasmal conjunctivitis in eastern North American house finches. Journal of Animal Ecology **73**:309-322.

Badyaev, A. V., V. Belloni, and G. E. Hill. 2012. House Finch (*Haemorhous mexicanus*).*in* A. Poole, editor. The Birds of North America Online Cornell Lab of Ornithology, Ithaca, NY.

Berkey, C. S., D. C. Hoaglin, A. Antczak-Bouckoms, F. Mosteller, and G. A. Colditz. 1998. Meta-analysis of multiple outcomes by regression with random effects. Statitics in Medicine **17**:2537-2550.

Bonter, D. N., and E. S. Bridge. 2011. Applications of radio frequency identification (RFID) in ornithological research: a review. Journal of Field Ornithology **82**:1-10.

Bridge, E. S., and D. N. Bonter. 2011. A low-cost radio frequency identification device for ornithological research. Journal of Field Ornithology **82**:52-59.

Bull, C. M., S. S. Godfrey, and D. M. Gordon. 2012. Social networks and the spread of Salmonella in a sleepy lizard population. Molecular Ecology **21**:4386-4392.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag New York Inc., New York.

Christley, R. M., G. L. Pinchbeck, R. G. Bowers, D. Clancy, N. P. French, R. Bennett, and J. Turner. 2005. Infection in social networks: using network analysis to identify high-risk individuals. American Journal of Epidemiology **162**:1024-1031.

Corner, L. A. L., D. U. Pfeiffer, and R. S. Morris. 2003. Social-network analysis of *Mycobacterium bovis* transmission among captive brushtail possums (*Trichosurus vulpecula*). Preventive Veterinary Medicine **59**:147-167.

Dhondt, A. A., K. V. Dhondt, D. M. Hawley, and C. S. Jennelle. 2007. Experimental evidence for transmission of *Mycoplasma gallisepticum* in house finches by fomites. Avian Pathology **36**:205-208.

Dhondt, A. A., K. V. Dhondt, W. M. Hochachka, and K. A. Schat. 2013. Can American goldfinches function as reservoirs for *Mycoplasma gallisepticum*? Journal of Wildlife Diseases **49**:49-54.

Dhondt, A. A., D. L. Tessaglia, and R. L. Slothower. 1998. Epidemic mycoplasmal conjunctivitis in house finches from Eastern North America. Journal of Wildlife Diseases **34**:265-280.

Dormann, C. F., B. Gruber, and J. Fruend. 2008. Introducing the bipartite package: analysing ecological networks. R news **8**:8-11.

Gleser, L. J., and I. Olkin. 2009. Stochastically dependent effect sizes.*in* H. Cooper, L. V. Hedges, and J. C. Valentine, editors. The handbook of research synthesis and meta-analysis. Russell Sage Foundation, New York.

Godfrey, S., C. M. Bull, R. James, and K. Murray. 2009. Network structure and parasite transmission in a group living lizard, the gidgee skink, *Egernia stokesii*. Behavioral Ecology and Sociobiology **63**:1045-1056.

Godfrey, S. S. 2013. Networks and the ecology of parasite transmission: A framework for wildlife parasitology. International Journal for Parasitology: Parasites and Wildlife **2**:235-245.

Godfrey, S. S., J. A. Moore, N. J. Nelson, and C. M. Bull. 2010. Social network structure and parasite infection patterns in a territorial reptile, the tuatara (*Sphenodon punctatus*). International Journal for Parasitology **40**:1575-1585.

Handcock, M. S., D. R. Hunter, C. T. Butts, S. M. Goodreau, and M. Morris. 2003. Statnet: software tools for the statistical modeling of network data.

Harris, J. K. 2014. An introduction to exponential random graph modeling. Sage Publications, Inc., Thousand Oaks, California.

Hartup, B. K., J. M. Bickal, A. A. Dhondt, D. H. Ley, and G. V. Kollias. 2001a. Dynamics of conjunctivitis and *Mycoplasma gallisepticum* infections in house finches. The Auk **118**:327-333.

Hartup, B. K., A. A. Dhondt, K. V. Sydenstricker, W. M. Hochachka, and G. V. Kollias. 2001b. Host range and dynamics of mycoplasmal conjunctivitis among birds in North America. Journal of Wildlife Diseases **37**:72-81.

Hartup, B. K., H. O. Mohammed, G. V. Kollias, and A. A. Dhondt. 1998. Risk factors associated with mycoplasmal conjunctivitis in house finches. Journal of Wildlife Diseases **34**:281-288.

Hawley, D. M., A. K. Davis, and A. A. Dhondt. 2007. Transmission-relevant behaviours shift with pathogen infection in wild house finches (*Carpodacus mexicanus*). Canadian Journal of Zoology-Revue Canadienne De Zoologie **85**:752-757.

Hosseini, P. R., A. A. Dhondt, and A. P. Dobson. 2006. Spatial spread of an emerging infectious disease: conjunctivitis in house finches. Ecology **87**:3037-3046.

Hotchkiss, E. R., A. K. Davis, J. J. Cherry, and S. Altizer. 2005. Mycoplasmal conjunctivitis and the behavior of wild house finches (*Carpodacus mexicanus*) at bird feeders. Bird Behavior **17**:1-8.

Kollias, G. V., K. V. Sydenstricker, H. W. Kollias, D. H. Ley, P. R. Hosseini, V. Connolly, and A. A. Dhondt. 2004. Experimental infection of house finches with *Mycoplasma gallisepticum*. Journal of Wildlife Diseases **40**:79-86.

Leu, S., P. Kappeler, and C. M. Bull. 2010. Refuge sharing network predicts ectoparasite load in a lizard. Behavioral Ecology and Sociobiology **64**:1495-1503.

Luttrell, M. P., D. E. Stallknecht, J. R. Fischer, C. T. Sewell, and S. H. Kleven. 1998. Natural *Mycoplasma gallisepticum* infection in a captive flock of house finches. Journal of Wildlife Diseases **34**:289-296.

Moore, J. 1984. Parasites that change the behavior of their host. Scientific American **250**:108.

Moore, J. 2002. Parasites and the behavior of animals. Oxford University Press, Oxford, UK.

Morris, M., M. S. Handcock, and D. R. Hunter. 2008. Specification of exponential-family random graph models: terms and computational aspects. Journal of Statistical Software **24**.

Nolan, P. M., G. E. Hill, and A. M. Stoehr. 1998. Sex, size, and plumage redness predict house finch survival in an epidemic. Proceedings of the Royal Society B: Biological Sciences **265**:961-965.

Ott, R. L., and M. Longnecker. 2001. An introduction to statistical methods and data analysis. Wadsworth Group, Pacific Grove.

Perkins, S. E., M. F. Ferrari, and P. J. Hudson. 2008. The effects of social structure and sex-biased transmission on macroparasite infection. Parasitology **135**:1561-1569.

Pinter-Wollman, N., E. A. Hobson, J. E. Smith, A. J. Edelman, D. Shizuka, S. de Silva, J. S. Waters, S. D. Prager, T. Sasaki, G. Wittemyer, J. Fewell, and D. B. McDonald. 2013. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. Behavioral Ecology.

Psorakis, I., S. J. Roberts, I. Rezek, and B. C. Sheldon. 2012. Inferring social network structure in ecological systems from spatio-temporal data streams. Journal of The Royal Society Interface.

Pyle, P. 1997. Identification guide to North American birds. Slate Creek Press, Bolinas.

R Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Roberts, S. R., P. M. Nolan, L. H. Lauerman, L.-Q. Li, and G. E. Hill. 2001. Characterization of the mycoplasmal conjunctivitis epizootic in a house finch population in the Southeastern USA. Journal of Wildlife Diseases **37**:82-88.

States, S., W. Hochachka, and A. Dhondt. 2009. Spatial variation in an avian host community: implications for disease dynamics. EcoHealth **6**:540-545.

Valente, T. W. 2010. Social Networks and Health: Models, Methods and Applications. Oxford University Press, Inc., New York, USA.

Viechtbauer, W. 2010. Conducting meta-analyses in R with the metafor package. Journal of Statistical Software **36**:1-48.

Whitehead, H. 2008. Analyzing animal societies: quantitative methods for vertebrate social analysis. University of Chicago Press, Chicago, Illinois.

Table 4.1. Numbers of house finches captured per month pooled from 2011-2013. Cases of mycoplasmal conjunctivitis are given in parentheses.

	March	April	May	June	July	August	September	October	November	Total
Adult male	10 (1)	6	27 (2)	29	37 (3)	10	2	1	2	124 (6)
Adult female	7	4 (1)	13 (2)	10	30 (5)	12	1	0	2	79 (8)
Hatch year	0	0	0	22 (1)	92 (1)	104 (5)	16	8	6 (1)	248 (8)
Unknown age	0	0	0	1	1	6	4	10	0	22
Monthly total	17 (1)	10 (1)	40 (4)	61 (1)	159 (9)	126 (5)	19 (0)	9 (0)	10 (1)	473 (22)
Proportion adults	1.00	1.00	1.00	0.64	0.42	0.17	0.16	0.11	0.40	0.45
Disease prevalence	0.059	0.100	0.100	0.016	0.057	0.040	0.000	0.000	0.100	0.047

Table 4.2. Numbers of house finches captured, marked with radio frequency identification (RFID) tags, and subsequently recorded by bird feeders equipped with RFID readers.

	Adult male	Adult female	Hatch Year	Unknown age	Total
Banded	124	79	248	22	473
Infected	6	8	8	0	22
Prevalence	0.048	0.101	0.032	0.000	0.047
RFID tag	118	69	216	15	418
RFID data	70	39	85	10	204
Proportion recorded	0.593	0.565	0.394	0.667	0.488

Table 4.3. House finches captured with mycoplasmal conjunctivitis whose foraging behavior was subsequently monitored at bird feeders equipped with radio frequency identification (RFID) technology. Data include the site where the individual was captured, the date it was marked with an RFID tag, the first and last dates the bird was recorded by an RFID reader, its sex and age when RFID data were collected, and the number of individuals of other species recorded by the RFID readers.

Individual	1	2	3	4	5	6	7	8	9	
Site	A	A	B	B	B	C	C	D	E	
Date	5/10/2012	5/9/2013	7/14/2011	7/14/2011	7/14/2011	8/21/2013	8/10/2011	7/22/2011	7/3/2013	
Data range	5/10/12-9/11/12	5/9/13-6/10/13	2/7/12-5/24/12	3/12/12-2/10/13	1/14/2012*	9/15/13-9/18/13*	4/12/12-3/14/13	1/19/12-6/5/12	7/6/13-7/26/13	
Days of data	125	33	108	336	1	4	337	139	21	
Sex	F	F	F	F	F	U	U	M	F	
Age	Adult	Adult	Adult	Adult	Adult	HY	Adult	Adult	Adult	
Species^										*Totals*
AMGO	2						12	1	7	22
CACH	3						9	3	2	17
DOWO		1					7	1	1	10
HOSP	2		15	19					3	29

Table 4.3. Continued

Individual	1	2	3	4	5	6	7	8	9	
NOCA	1		1	4				1		6
RBGR							3	1		4
RBWO							2		1	3
TUTI	1						7	1	4	13
WBNU		2					3		3	8
HOFI HY	5	3					3			8
HOFI F	3	2	1	3			1	4	1	12
HOFI M	8	2	8	6			7	1	2	28
HOFI U	1		2	2				4	1	8

^AMGO=American goldfinch (*Spinus tristis*), CACH= Carolina chickadee (*Poecile carolinensis*), DOWO=downy woodpecker (*Picoides pubescens*), HOFI=house finch (*Haemorhous mexicanus*), HOSP=house sparrow (*Passer domesticus*), NOCA=northern cardinal (*Cardinalis cardinalis*), RBWO=red-bellied woodpecker (*Melanerpes carolinus*), RBGR=rose-breasted grosbeak (*Pheucticus ludovicianus*), TUTI=tufted titmouse (*Baeolophus bicolor*), WBNU=white-breasted nuthatch (*Sitta carolinensis*), HY=hatch year, F=female adult, M=male adult, U=unknown sex

*Insufficient data for foraging behavior analysis

Table 4.4. Comparisons of foraging and association models for six networks. For each network, ERGMs were constructed for species-level patterns (Species), species patterns in addition to differences between the sexes for house finches (HOFI), and species patterns in addition to differences in sex and disease status for house finches (Disease). Models were run with and without seasonal variation for foraging activity and associations. Comparisons were made using Akaiki's information criterion (AIC) and are reported as number of parameters in a model, AIC value in parentheses, and ΔAIC relative to the model with the lowest AIC value (in bold).

	Network A (1)	Network B (2)	Network C (3,4)
Foraging Models			
No season			
Species	6 (12069.35) 1064.15	3 (4741.56) 84.17	3 (72453.76) 1293.95
HOFI	9 (11351.42) 346.22	5 (4674.43) 17.04	5 (72221.05) 1061.24
Disease	10 (11173.51) 168.31	6 (4673.36) 15.97	6 (72207.28) 1047.47
Season			
Species	11 (12224.08) 1218.88	4 (4756.88) 99.50	10 (71839.23) 679.42
HOFI	17 (11189.80) 184.60	8 (4661.28) 3.90	19 (71318.33) 158.52
Disease	**19 (11005.20) 0**	**10 (4657.39) 0**	**22 (71159.81) 0**
Association Models			
No season			
Species	**34 (10830.92) 0**	**14 (4529.34) 0**	28 (70709.50) 448.10
HOFI	47 (10870.33) 39.41	21 (4542.70) 13.35	36 (70555.88) 294.48
Disease	52 (10898.77) 67.85	25 (4540.41) 11.06	41 (70545.34) 283.94

Table 4.4 Continued.

	Network D (8)	Network E (9)*	Network F (7) ^
Season			
Species	40 (10887.82) 56.90	16 (4608.95) 79.60	**46 (70261.40) 0**
HOFI	56 (10867.66) 36.74	29 (4616.12) 86.78	71 (70307.68) 46.28
Disease	62 (10896.72) 65.80	37 (4621.89) 92.55	83 (70346.33) 84.93
Null	1 (33838.67) 22833.47	1 (7748.61) 3091.23	1 (251736.40) 180576.59
Foraging Models			
No season			
Species	7 (8368.17) 206.67	8 (3854.82) 59.15	8 (197613.80) 11633.70
HOFI	9 (8283.52) 122.02	10 (3827.83) 32.16	10 (195852.90) 9872.80
Disease	10 (8276.02) 114.52	**11 (3795.67) 0**	11 (195887.50) 9907.40
Season			
Species	13 (8381.01) 219.50	8 (3854.82) 59.15	30 (190397.10) 4417.00
HOFI	**21 (8161.50) 0**	10 (3827.83) 32.16	38 (186146.30) 166.20
Disease	21 (8184.95) 23.44	**11 (3795.67) 0**	**43 (185980.10) 0**
Association Models			
No season			
Species	33 (8029.65) 52.40	**45 (3777.41) 0**	NA
HOFI	**44 (7977.25) 0**	59 (3787.19) 9.78	NA
Disease	47 (7981.54) 4.29	61 (3789.08) 11.67	NA
Season			
Species	46 (8080.19) 102.94	**45 (3777.41) 0**	NA
HOFI	69 (8003.60) 26.35	59 (3787.19) 9.78	NA
Disease	74 (8015.20) 37.95	61 (3789.08) 11.67	NA
Null	1 (23233.52) 15072.02	1 (9085.00) 5289.33	1 (664640.00) 478659.90

*Network E was constructed from data from a single season, so models with and without season were identical.

^Association ERGMs would not converge for this site.

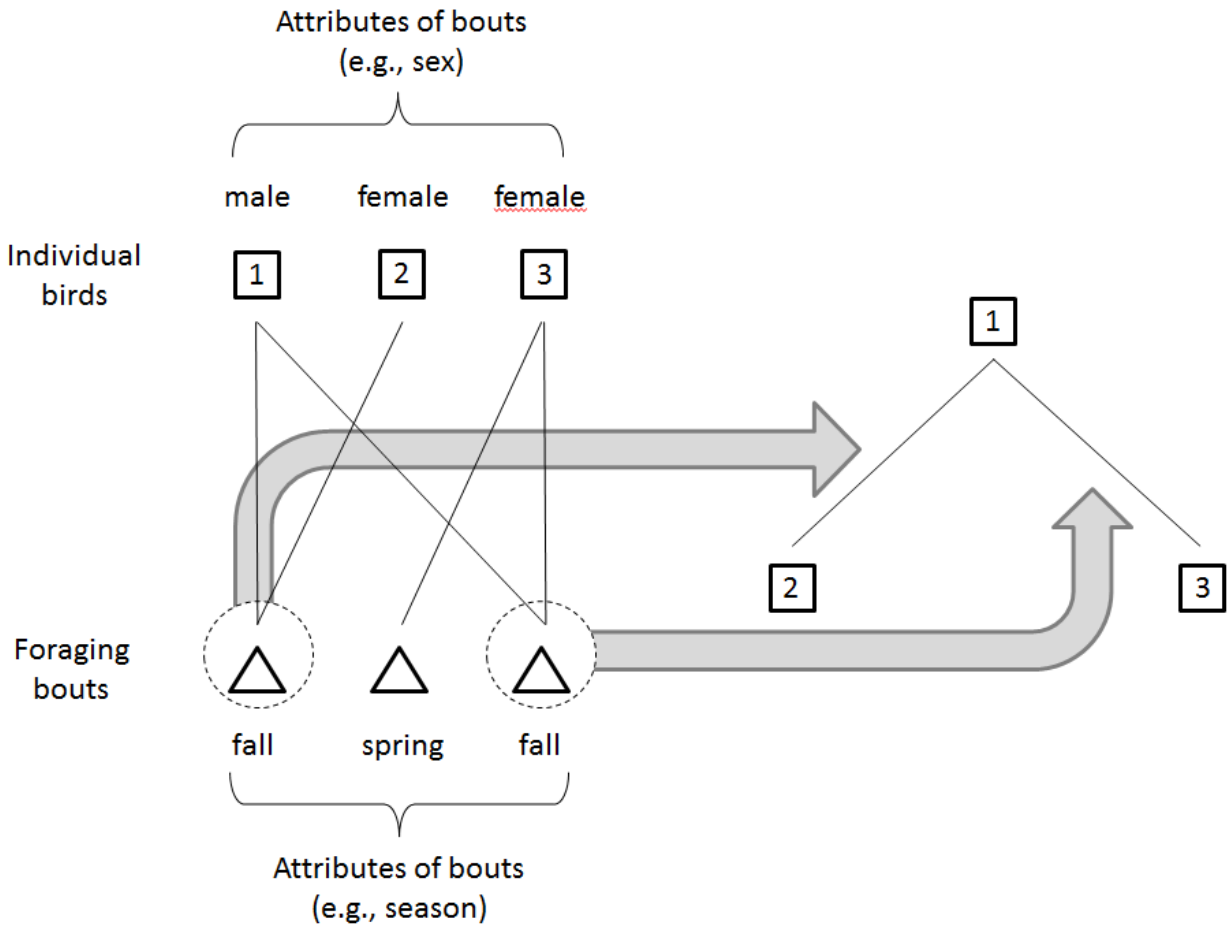


Figure 4.1. Hypothetical bipartite and social networks. Bipartite networks consist of two types of objects (e.g., individual birds and foraging bouts) that connect to each other (e.g., instances in which a bird participates in a foraging bout). In bipartite networks, connections only form between objects of different types (i.e., birds cannot connect directly). These networks can be used to analyze how attributes of each object type (e.g., sex of birds and seasons in which bouts occur) affect the likelihood of connections forming. Social networks can be derived from bipartite networks by converting pairs of bipartite connections (e.g., two birds participating in the same foraging bout) into single connections between objects of one type (e.g., connections between birds). These networks analyze how social connections are formed.

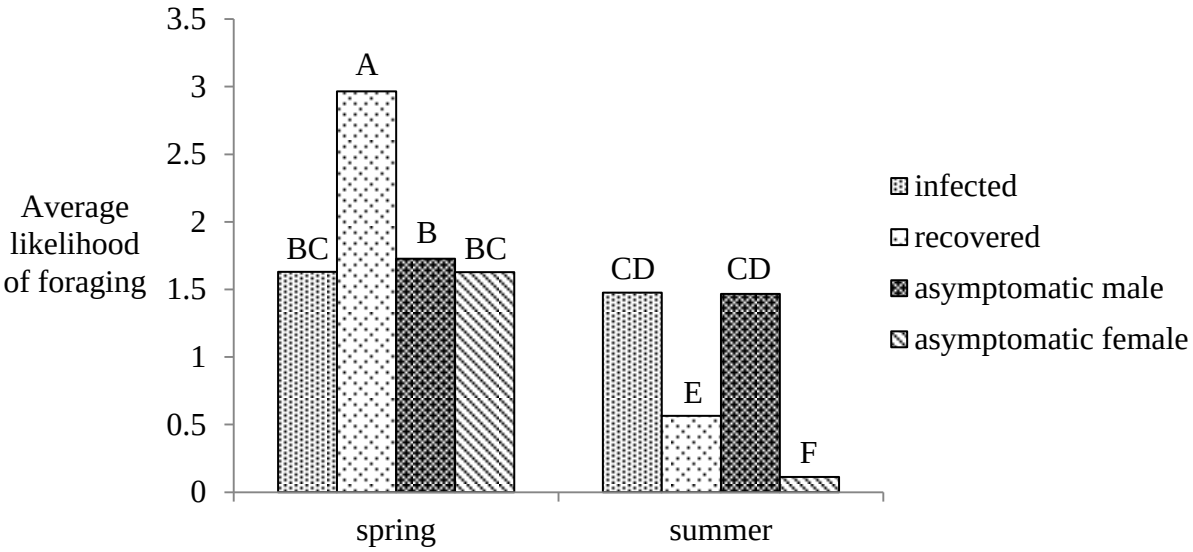


Figure 4.2. Foraging activity of house finches infected with mycoplasmal conjunctivitis, recovered from the disease, or asymptomatic at the time of capture. Average foraging likelihoods were from a multivariate meta-analysis of parameter estimates from foraging activity ERGMs. Letters represent significant differences ($p<0.05$). Foraging likelihoods in ERGMs are calculated relative to baseline, which in this case was foraging activity of hatch-year house finches or finches of unknown sex (i.e., a value of 0 indicates foraging was similar between the group of interest and hatch years).

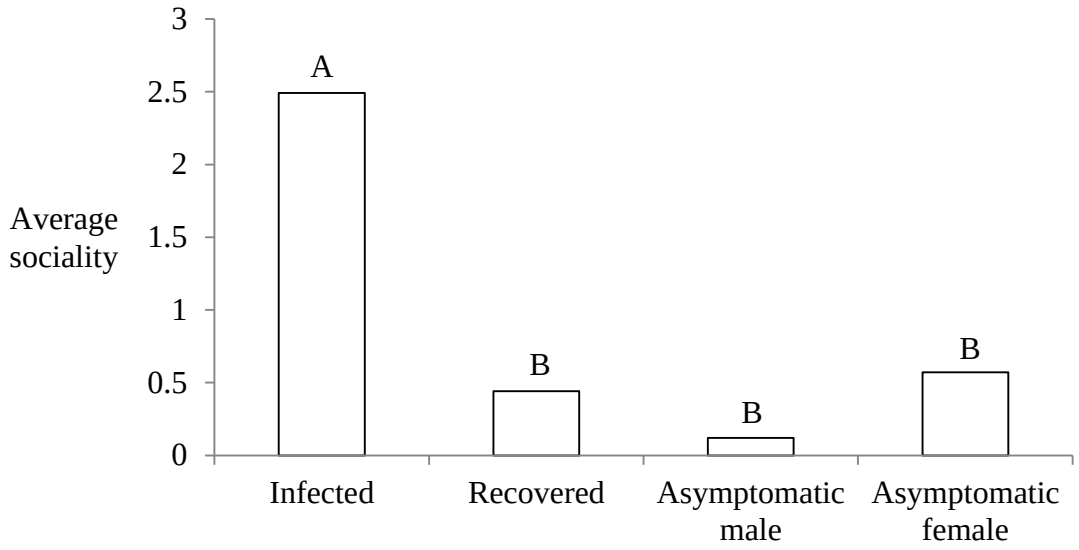


Figure 4.3. Sociality of house finches infected with mycoplasmal conjunctivitis, recovered from the disease, or asymptomatic at the time of capture. Average sociality was calculated from a multivariate meta-analysis of parameter estimates from sociality ERGMs of spring and summer data. Letters represent significant differences ($p<0.05$). Sociality in ERGMs is calculated relative to baseline, which in this case was sociality of hatch-year house finches or finches of unknown sex (i.e., a value of 0 indicates sociality was similar between the group of interest and hatch years).

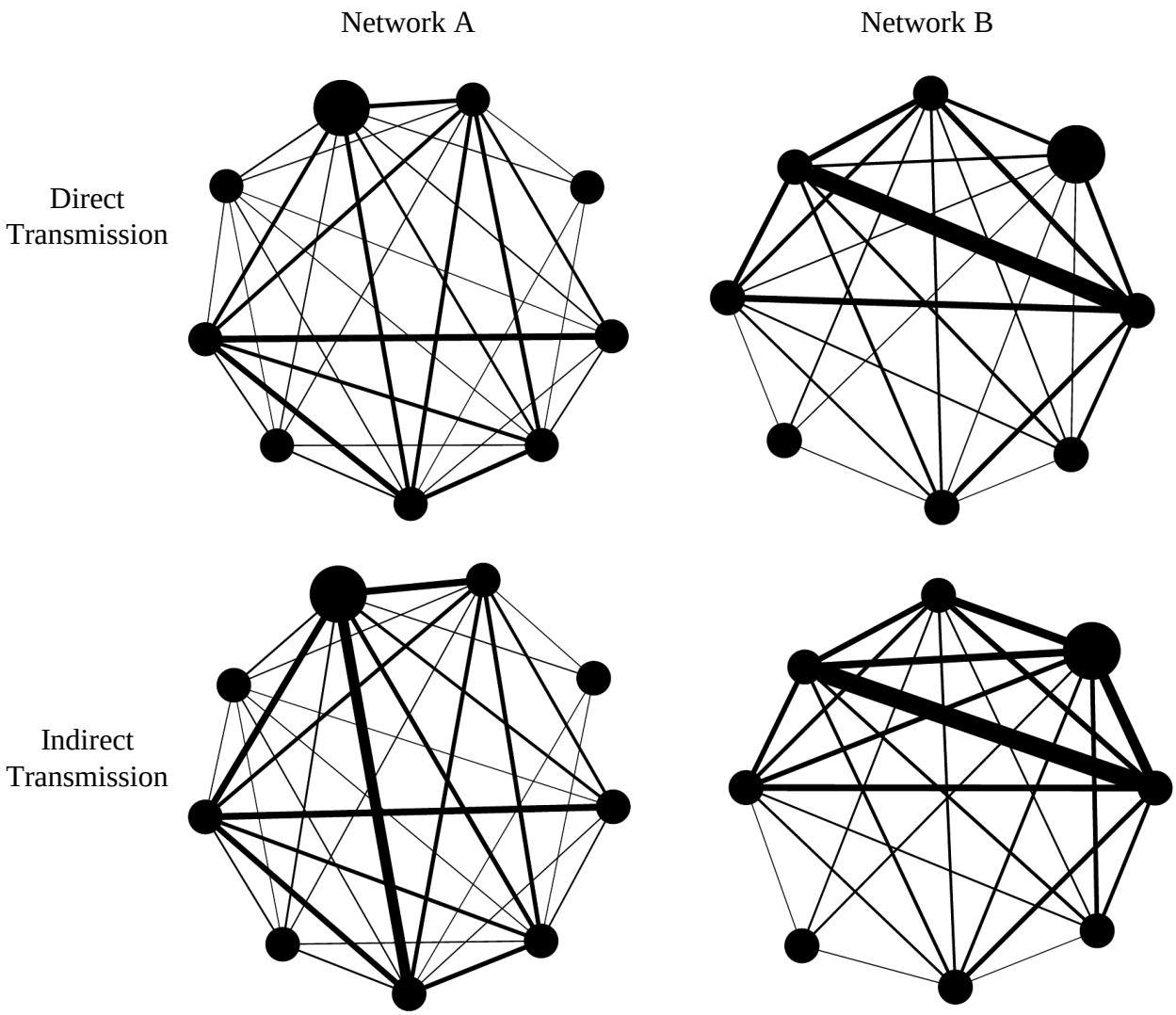


Figure 4.4. Direct and indirect transmission risk for study networks A and B. Networks were based on the month of data following the capture and release of a house finch with mycoplasmal conjunctivitis (large circle; smaller circles are other house finches). Connections in direct networks were instances in which two birds participated in the same foraging bout, with the line thickness indicating the frequency at which birds foraged together as a proxy for direct transmission risk. In indirect networks, additional connections were added for instances in which an asymptomatic bird foraged after an infected bird on a given day. The resulting increase in line thickness was taken as a proxy for indirect transmission risk.