

Social network characteristics and predicted pathogen transmission in summer colonies of female big brown bats (*Eptesicus fuscus*)

Quinn M. R. Webber¹ · R. Mark Brigham² · Andrew D. Park¹ · Erin H. Gillam³ · Thomas J. O'Shea⁴ · Craig K. R. Willis¹

Received: 21 September 2015 / Revised: 21 February 2016 / Accepted: 23 February 2016
© Springer-Verlag Berlin Heidelberg 2016

Abstract

Host behavior can affect host-pathogen dynamics, and sociality is predicted to increase risk of pathogen exposure. Many species minimize costs of parasitism by only aggregating seasonally, such as during reproductive periods, but colonial species may still be limited in their potential to evade pathogens. Bats are among the most gregarious mammals and females of many temperate species form maternity colonies in summer where they communally raise pups in both natural and anthropogenic roost structures. Social network structure may differ between natural and anthropogenic roosts in ways that affect pathogen dynamics. We used social network analysis to quantify interactions of big brown bats (*Eptesicus fuscus*) in a tree-roosting colony, where the colony is divided among multiple trees each day, and a building colony, where most of the colony roosts together each day. We simulated transmission of a pathogen throughout both sets of networks. We tested three

hypotheses: (1) network metrics differ between pregnancy and lactation; (2) changing network structure between reproductive stages influences predicted pathogen dynamics; and (3) network metrics and predicted pathogen dynamics differ between colonies of bats in trees versus buildings. Network structure was weaker for bats roosting in trees during pregnancy and lactation compared to bats roosting in a building, and our models showed that a hypothetical pathogen would spread more rapidly for bats in the building colony. Our results are important for understanding variation in social tendencies and pathogen transmission among colonies of bats and have implications for conservation and public health.

Significance statement

Host behavior, particularly social behavior, can affect dynamics of wildlife pathogens. Bats are highly social mammals and females of temperate species form colonies in spring and early summer in tree or building roosts. Thermal characteristics of trees and buildings appear to differ in ways that affect roosting behavior and social interactions. We used social network analyses to quantify interactions of big brown bats in tree and building roosts and simulated consequences for pathogen dynamics. Network structure was weaker for bats roosting in trees with more frequent roost switching and relatively diffuse contacts across the network. Our models showed that a hypothetical pathogen could spread up to four times faster in a building colony compared to a colony of bats roosting in trees. Our results are important for understanding how sociality can influence pathogen dynamics in bats and have implications for conservation and public health.

Keywords Coloniality · Fission-fusion · Network analysis · Susceptible-infected model · Seasonal aggregation

Communicated by G. S. Wilkinson

Electronic supplementary material The online version of this article (doi:10.1007/s00265-016-2093-3) contains supplementary material, which is available to authorized users.

✉ Quinn M. R. Webber
webber.quinn@gmail.com

¹ Department of Biology and Centre for Forest Interdisciplinary Research (C-FIR), University of Winnipeg, Winnipeg, MB, Canada

² Department of Biology, University of Regina, Regina, SK, Canada

³ Department of Biological Sciences, North Dakota State University, Fargo, ND, USA

⁴ US Geological Survey (retired), P.O. Box 65, Glen Haven, CO 80532, USA

Introduction

Pathogen transmission can be influenced by host social behavior (Altizer et al. 2003; Hawley et al. 2011; Rifkin et al. 2012). At the group level, large and densely aggregated social groups of hosts are predicted to harbor higher prevalence, intensity, and diversity of parasites, all of which could negatively impact host fitness (Côté and Poulin 1995; Patterson and Ruckstuhl 2013). Although pathogens and parasites can be costly, sociality also results in potential benefits, such as improved predator vigilance (Townsend et al. 2011) or social thermoregulation (Blumstein et al. 2004), both of which can potentially increase fitness. For many species, social dynamics will be driven by the balance of these costs and benefits, in combination with the availability of habitat that provides opportunities for social interaction.

Many species minimize costs associated with parasitism by only aggregating seasonally, such as during reproduction (Altizer et al. 2006). Breeding sites can be reservoirs for both macroparasites (i.e., multicellular organisms with low reproductive output) and microparasites (i.e., microorganisms with high reproductive rate and short generation times; Anderson and May 1979), and increased transmission rates can occur at such sites (Ezenwa 2004). For example, seasonal aggregation by house finches (*Carpodacus mexicanus*) during breeding resulted in increased prevalence of *Mycoplasma* parasites (Hosseini et al. 2004) and aggregation by gregarious European rabbits (*Oryctolagus cuniculus*) during autumn breeding coincided with higher infection intensity by intestinal nematodes (Cattadori et al. 2005). Temporal and spatial heterogeneity in social interactions have potential to strongly influence host-pathogen dynamics (Altizer et al. 2003).

Temperate bats provide a unique opportunity to examine links between sociality and pathogen exposure and transmission. Many temperate bat species segregate in spring upon emergence from hibernation with females forming maternity colonies to rear pups (Kunz and Lumsden 2003). Particularly for species roosting in tree hollows, these colonies often exhibit fission-fusion sociality during summer, characterized by frequent splitting and reestablishment of subgroups (Kerth and König 1999). Females change roosts every few days, but not all members of each subgroup move together, resulting in variable group size and composition (e.g., Patriquin et al. 2010). Despite frequent splitting (fission) and merging (fusion) of groups, individuals maintain long-term relationships with preferred conspecifics within and between years (Willis and Brigham 2004; Rhodes 2007; Popa-Lisseanu et al. 2008; Patriquin et al. 2010; Kerth et al. 2011).

Bat maternity colonies are often associated with heightened ectoparasite prevalence (e.g., Zahn and Rupp 2004), and colonies can act as reservoirs for infected hosts or the ectoparasites themselves. Despite this cost of colonial roosting, there are pronounced thermoregulatory benefits to social roosting

for adult females (e.g., Willis and Brigham 2007). Low ambient temperature (T_a) can induce torpor in reproductive females which delays juvenile development (e.g., Racey and Swift 1981) and presumably survival (McAllan and Geiser 2014). Communal roosting in warm environments could benefit individuals and help maintain colonies, but the role of social thermoregulation may change as energy requirements change from pregnancy to lactation. T_a is typically lower when females are pregnant in spring and pregnant females tend to use torpor regularly. Social thermoregulation could, therefore, be beneficial to help individuals avoid torpor and/or share energetic costs of rewarming when torpor is used (e.g., Chruszcz and Barclay 2002; Solick and Barclay 2006), and social thermoregulation could lead to high levels of fusion within colonies during pregnancy. Meanwhile, during lactation, females will benefit from warmer conditions and greater prey availability while also preferentially seeking out the warmest roosts for their pups. This could allow them to remain more active and avoid torpor (e.g., Chruszcz and Barclay 2002) leading to higher levels of fission as individuals switch from roost to roost.

Thermal characteristics of roosts and roost quality can also vary widely. Some colonial bat species roost in both natural structures (e.g., trees, rock crevices) and buildings (e.g., Lausen and Barclay 2006; Rintoul and Brigham 2014). Building roosts tend to be warmer, promoting more rapid juvenile growth and improved fitness (Lausen and Barclay 2006). For example, duration and depth of torpor bouts were lower for reproductive big brown bats (*Eptesicus fuscus*) in buildings compared to conspecifics in trees (Rintoul and Brigham 2014). Numbers of bats roosting in buildings tend to be higher than those in natural structures (Lausen and Barclay 2006), and building colonies tend to be more stable with less frequent roost switching (Brigham and Fenton 1986; Lausen and Barclay 2002). Higher roost fidelity and more consistent interactions among individuals could increase the potential for pathogen transmission among colony members. This, in turn, could increase the rate at which pathogen prevalence and intensity increase in a colony during an active season.

Understanding links between sociality and pathogen transmission in bats has become increasingly important as the role of bats as reservoir hosts of zoonotic pathogens becomes more widely appreciated (e.g., Luis et al. 2013; Brook and Dobson 2015). One aspect of zoonotic spillover that could be important is the potential shift in social dynamics between natural structures and buildings. For both temperate (Brigham 1991; O'Shea et al. 2011a; Berkova et al. 2014) and tropical (Brosset et al. 1996) bat populations, loss or absence of natural roosts can lead to colonization of structures that house domestic animals or people. Thus, replacement of forest habitat with anthropogenic roosting sites could favor aggregation by bats and increased likelihood of zoonotic spillover (Halpin et al. 2007;

Lebarbenchon et al. 2008). This risk could be higher not just because of increased contacts between bats and humans, but because social dynamics in building roosts could favor more rapid increases in pathogen prevalence and intensity in the host. Social dynamics of some tropical bats, which may be more likely than temperate species to harbor zoonotic pathogens (Luis et al. 2013), are similar to those of temperate bats with fission-fusion dynamics (e.g., *Desmodus rotundus*, Wilkinson 1985). Therefore, understanding relationships between social behavior and pathogen dynamics in temperate zone bats could provide a good starting point for evaluating the links between social behavior and pathogen dynamics for all bats living in fission-fusion systems.

We used network analysis to quantify interactions among female big brown bats and explore relationships between sociality, roost sharing, and pathogen dynamics in maternity colonies. We used association data from two published datasets; one from a forest colony (Willis and Brigham 2004) and the other from a building colony (Gillam et al. 2011; O'Shea et al. 2011b). First, we tested the hypothesis that differences in social thermoregulation and individual association between pregnancy and lactation affect network structure across reproductive stages. We predicted that network connections would be stronger during pregnancy than lactation because of a greater need for social thermoregulation during pregnancy when T_a is colder, and because the combination of active associations between individuals and passive aggregation at relatively few warm roost trees during lactation would reduce novel roosting associations (Willis and Brigham 2004; Patriquin et al. 2010). Second, we used a susceptible-infected epidemiological model to test the hypothesis that differences in network structure between pregnancy and lactation influence pathogen dynamics. We predicted that the number of bats in the colony infected with a hypothetical pathogen (i.e., predicted pathogen prevalence) would increase more rapidly for pregnant compared to lactating bats because of greater social aggregation during pregnancy. Third, we tested the hypothesis that differences in network structure for bats roosting in different roost types also influence pathogen dynamics. We predicted that modeled values of pathogen prevalence would increase more quickly in an aggregated network of bats roosting in a building compared to the more diffuse networks of bats roosting in trees where the colony is subdivided each day among multiple tree hollows.

Methods

Study site and subjects

We used data from two well-studied big brown bat colonies from the Cypress Hills, Saskatchewan, Canada (49° 34' N,

109° 53' W), and Fort Collins, CO, USA (40° 33' N, 105° 4' W). Full details of the Cypress Hills study site and capture procedures are found in Willis and Brigham (2004). Female big brown bats at this site roosted exclusively in cavities of trembling aspen trees (*Populus tremuloides*) which were distributed among three discrete patches of forest within a 10-km² study area (Willis et al. 2003, 2006a). Female bats were caught at maternity roosts upon emergence at dusk and marked with numbered, plastic forearm bands (National Band and Tag Company, Newport, KY, USA), outfitted with radiotransmitters (0.7 g—less than 5 % of body mass, BD-2B, Holohil Systems Ltd, Carp, Ontario, Canada) and tracked to roost trees on as many days as possible (i.e., until a bat groomed off its transmitter or the transmitter battery failed) using handheld telemetry receivers (R-1000, Communication Specialists Inc., CA, USA). No adult males were captured at any roost trees. Our sample comprised roosting associations of 31 individual bats ($n = 16$ pregnant, 15 lactating) from one roosting area, representing 50–60 % of the total identified colony of big brown bats within that roosting area (Willis et al. 2006a). Our sample size was similar to that for previous social network studies in bats (e.g., Fortuna et al. 2009).

Detailed descriptions of the Fort Collins study site and capture procedures are outlined by Ellison et al. (2007), Gillam et al. (2011), and O'Shea et al. (2011a, b). As part of a long-term field study, bats were captured in the summer emerging from building roosts (Gillam et al. 2011) and permanently marked via subcutaneous injection of a passive transponder (PIT tag, AVID, Inc., Norco, CA) on the dorsum before being released (Wimsatt et al. 2005). Hoop-style PIT-tag antennas (Wimsatt et al. 2005) were deployed over roost openings to monitor entrance/exit of individual bats from roosts (see Gillam et al. 2011 for details). The Fort Collins study system included 16 colonies spread throughout the city (Gillam et al. 2011). We selected a colony with an emergence count prior to volancy of young ($n = 76$) that was most comparable to the tree-roosting colony from the Cypress Hills ($n = 50–60$). To ensure the sample size of bats used to estimate network characteristics in the building colony was comparable to that for tree-roosting bats during each reproductive period, we used a random subsample of bats from the building ($n = 16$) and we confirmed that our subsample was representative of the whole colony by using a randomization approach (see statistics below). In building roosts in Fort Collins, roost switching was infrequent compared to roost switching by bats in trees (O'Shea et al. 2011b). Although our data from each system were collected using different methods (i.e., radio-telemetry versus PIT-tags), we are confident in our comparisons because we studied colonies that were similar in size and we ensured approximately equal samples sizes of bats from each group of bats we compared (Table 1; see results).

Table 1 Summary of descriptive statistics and network metrics from four big brown bat (*Eptesicus fuscus*) roosting scenarios

	Tree roosting pregnant		Tree roosting lactation		Building roosting pregnant		Building roosting lactation	
	Observed	Random	Observed	Random	Observed	Random	Observed	Random
<i>N</i>	16	16	15	15	16	16	15	15
Edges	58	–	25	–	120	–	105	–
Roosts per bat	4.5 ± 1.8	–	4.3 ± 2.7	–	1	–	1	–
Tracking nights per bat	6.8 ± 3.0	–	8.1 ± 4.7	–	19.8 ± 2.9	–	20.5 ± 6.9	–
Bats detected per night	4.6 ± 2.1	–	4.20 ± 1.6	–	10.9 ± 5.4	–	10.2 ± 3.6	–
Half-weight index	0.18 ± 0.26	0.15 ± 0.005	0.08 ± 0.19	0.06 ± 0.005	0.67 ± 0.19	0.64 ± 0.007	0.54 ± 0.26	0.51 ± 0.008
Strength	2.85 ± 1.09	2.46 ± 0.08	1.22 ± 0.62	0.95 ± 0.07	10.7 ± 0.59	10.3 ± 0.12	8.07 ± 2.02	7.67 ± 0.11

Roosting scenarios include fission-fusion tree roosting bats during pregnancy and lactation and aggregated building roosting bats during pregnancy and lactation. Edges are the number of connections between bats, and numbers for half-weight index and strength are group means ± standard deviation

Data coding and statistical analyses

For tree and building roosting bats, we only included individuals in our analysis for which we obtained at least three tracking (tree-roosting) or detection (building-roosting) days of data (Table 1). For tree-roosting bats, we recorded the date and roost of initial capture for each individual, subsequent roosts identified during radio-tracking, and the number of radio-tagged bats found roosting together on any given day. For building roosting bats, we recorded the date and identification code of each individual entering the roost each morning.

We corrected for variation in roost sharing and sampling effort among bats by calculating the half-weight index (*HWI*; Whitehead 2008):

$$HWI = \frac{x}{x + y_{ab} + \frac{1}{2}(y_a + y_b)}$$

where x is the number of times individuals a and b were detected in the same roost on the same night, y_{ab} is the number of times a and b were detected on the same night, but not in the same roost, and $y_a + y_b$ is the sum of times where one of a or b were detected, while the other was not (Whitehead 2008). Values of *HWI* range from 0 to 1, where 0 represents a dyad that was never observed associating and 1 represents a dyad that was always observed associating. For all networks, we used the *asnipe* package (Farine 2013) in R (R Development Team 2012) to quantify *HWI* and construct undirected (i.e., with reciprocal interactions), weighted association matrices with nodes representing individual bats and edges representing associations between bats.

Based on the *HWI*, we calculated social network strength, a metric thought to reflect the potential of an individual to transmit information or spread a pathogen within a network (Croft et al. 2008; Rushmore et al. 2013). Strength represents the weighted sum of all connections to an individual node (Croft et al. 2008), while high values of strength indicate a greater

number and frequency of contacts with conspecifics (Csardi and Nepusz 2006; Wey et al. 2008).

We separated the dataset into pregnancy and lactation periods for both tree and building roosting bats. The start of pregnancy for tree-roosting bats in Cypress Hills was delineated by the first capture of at least one pregnant bat (mid-June) and the start of lactation was delineated based on the first capture of lactating bats (mid-July; Willis and Brigham 2004). There were no instances when both pregnant and lactating bats were caught in the same roost. For building roosting bats in Fort Collins, we delineated pregnancy from lactation based on the median date of parturition (defined by Kunz 1974), as the start of the lactation period in 2005 (i.e., 16 June). Therefore, the majority of bats were pregnant before 16 June and the majority of bats were lactating after 16 June.

To ensure that the network based on our subsample of 16 bats was representative of the entire colony of 76 individuals, we compared characteristics of the data for our subsampled bats ($n=16$) to all bats from the colony using t tests. There were no differences in tracking nights per bat during pregnancy ($t_{25,6} = -1.5$, $p=0.16$) or lactation ($t_{45,4} = 0.8$, $p=0.42$), which means the subsample of data used for the observed networks was reflective of the data for the entire colony. Therefore, we used our initial network of 16 bats for all subsequent comparisons.

We quantified network metrics under four roosting conditions: (1) tree-roosting with observed fission-fusion dynamics during pregnancy; (2) tree-roosting with observed fission-fusion dynamics during lactation; (3) building roosting with high roost fidelity and colony aggregation during pregnancy; and (4) building roosting with high roost fidelity and colony aggregation during lactation. To determine whether observed network metrics differed from random we generated 1000 equivalent weighted networks based on the data stream (i.e., raw PIT-tag or radio-tracking data) rather than the association matrix (Farine 2013). Each permutation of the data stream had the same number of individuals and associations among

individuals as the observed data, and we randomly reassigned connections among dyads (e.g., Lusseau 2003), recalculating the *HWI* after each permutation (Farine 2013). To test whether the observed network structure (i.e., *HWI*) and metrics (i.e., strength) differed from random, we compared observed *HWI* and strength values to the distribution of 1000 randomly generated networks. We considered observed values of *HWI* and strength nonrandom if the mean observed value fell outside the 95 % confidence interval of the random distribution (Croft et al. 2011). These comparisons allowed us to assess whether our observed networks reflected biologically meaningful social structure or, alternatively, whether they were the outcome of random combinations of individual connections.

Comparisons among networks generated using different sampling methods can be problematic and must be interpreted cautiously (Perkins et al. 2009). Nevertheless, for illustrative purposes, we conducted quantitative comparisons of social network strength and *HWI* between all roosting conditions. We compared the test statistic (i.e., *t*-value) from a two-tailed *t* test (comparing observed strength or *HWI* values from different roosting conditions) to the distribution of *t*-values derived from comparing strength and *HWI* values from randomized data for each roosting condition (Farine and Whitehead 2015). For each combination of roosting conditions, we performed 1000 *t* tests comparing *HWI* and strength values, each using the same permutation procedure described above (i.e., randomization of the data stream as opposed to the association matrix before subsequently recalculating *HWI* or strength at each iteration). Significance was calculated by counting the number of randomized *t*-values that had a greater (when the *t*-value was positive) or lower (when the *t*-value was negative) values than the observed *t*-value and dividing this number by 1000 (Farine and Whitehead 2015). We used Fisher's combined probability test to account for multiple comparisons. We used the *igraph* package (version 0.7.0, Csardi and Nepusz 2006) to quantify network metrics and visualize network graphics in R.

Simulations

We inferred infectious disease dynamics by applying susceptible-infected (SI) epidemiological models to our empirically derived social networks (Perkins et al. 2009). We were interested in the influence of network dynamics on the increase in the proportion of individual hosts infected during a simulated epidemic over the course of one reproductive season. We assumed that the pathogen did not cause mortality in the host and that once an individual became infected it remained infected for the rest of the summer (e.g., Fortuna et al. 2009). Although little is known about host recovery rates and post-recovery resistance for bat pathogens, our assumptions are consistent with observed patterns (i.e., lack of

significant disease) for known viruses of bats (e.g., Misra et al. 2009; Luis et al. 2013).

We used a network epidemic simulation model (function "netsim" from the "EpiModel" package in R: version 1.1.4; Jenness et al. 2015) to model epidemic dynamics. The parameters for each series of models were optimized using metrics from each of our roosting conditions. Each simulation began with the introduction of a single infected bat into a colony of 15 or 16 susceptible bats, the number of bats in our empirically derived networks during lactation and pregnancy, respectively. We coded the average contact rate (*c*) in our SI models from empirical networks where *c* is the mean square of the degree distribution (*k*; i.e., the distribution of observed values for degree) divided by the mean of the degree distribution:

$$c = \frac{k^2}{k}$$

Thus, individuals with more contacts were more likely to become infected and were also more likely to transmit infections (May 2006; Wey et al. 2008).

Our models assumed that the pathogen was introduced once at the beginning of pregnancy or lactation and spread for 30 days throughout each network (i.e., the duration of data collection and observed duration of each reproductive period in the Cypress Hills and Fort Collins). To compare aggregated building and diffuse forest networks, we modeled infection rates across a 60-day period to represent the entire reproductive season with the pathogen being introduced at the beginning of pregnancy and continuing to spread for another 30 days throughout the lactation. We used a constant contact rate for the aggregated building network because the colony we studied was fully saturated (i.e., all bats connected with all other bats) during both pregnant and lactating periods, while for diffuse forest networks, we used separate contact rates for pregnancy and lactation (see equation above). We assumed that changes in pathogen prevalence were additive, and we modeled pregnancy and lactation for two distinct 30-day time periods, each of which was based on associations from empirical networks. Our analysis assumed that individuals sharing a tree hollow or a building on the same night interacted within the same roost during the day. This could overestimate contact rates if bats within a given structure did not always interact. However, this should not invalidate the comparison between roost types, because (1) colony sizes used to estimate network parameters were similar, (2) sample sizes used to estimate network parameters were virtually identical ($n=15-16$), and (3) models for both tree and building roosting bats were built using the same assumptions.

We modeled reproductive and roosting conditions using three rates of transmission based on β (i.e., the proportion of contacts that result in transmission). We selected values of β that reflected low, moderate, and high transmission rates seen

for other infectious pathogens of wildlife ($\beta = 1, 10, 25\%$, Begon et al. 1999; Hampson et al. 2009; George et al. 2011). Previously published β values for rabies in big brown bats were approximately 13% (George et al. 2011), but β values are not known for other pathogens of bats. Thus, our final analysis yielded 12 SI-models, consisting of three transmission scenarios applied to four reproductive-roosting conditions (i.e., tree and building roosting bats during pregnancy and lactation), and three transmission scenarios for each roosting condition for the full reproductive season (i.e., tree and building roosting). We ran 1000 iterations of each SI model. For each value of β , output of the 1000 iterations for each reproductive or roosting condition were compared using Mann–Whitney U tests with Bonferroni adjusted p values for multiple comparisons and Cohen's d effect sizes for each comparison (Cohen 1988). Cohen's d values <0.2 were considered to reflect small effects, between 0.2 and 0.8 to reflect medium-sized effects, and >0.8 to reflect large effects (McGough and Faraone 2009). It was not possible to record data blindly because our study involved focal animals in the field.

Results

The tree-roosting bats we tracked in the Cypress Hills formed 58 dyads during pregnancy and 25 dyads during lactation in June and July 2002 (Fig. 1; Table 1). During pregnancy, the network was highly connected but subdivided into two distinct groups connected by a single individual (Fig. 1). The lactation network was relatively sparse compared to pregnancy with few connections among subgroups and two solitary individuals (Fig. 1). There was no difference between observed values of HWI and strength during pregnancy compared to lactation for tree-roosting bats (Fig. 2), while observed values for HWI and strength were significantly different from random during both reproductive periods (Fig. S1).

The building roosting bats from Fort Collins formed 120 dyads during pregnancy and 105 dyads during lactation in May, June, and July 2005 (Table 1). For both building networks, connections were widely distributed among all individuals with homogenous connections relative to the tree-roosting networks (Fig. 1). There were no differences in network HWI or strength for building roosting bats during pregnancy and lactation (Fig. 2), while observed values for HWI and strength were significantly different from random during both reproductive periods (Fig. S1).

We observed differences in network metrics across roosting conditions (Fig. 2). Observed HWI and strength values were highest for building roosting bats compared to tree-roosting bats (Fig. 2). Based on randomization tests, HWI differed significantly for tree-roosting bats during pregnancy and lactation compared to building roosting bats during pregnancy and lactation (Fig. 2;

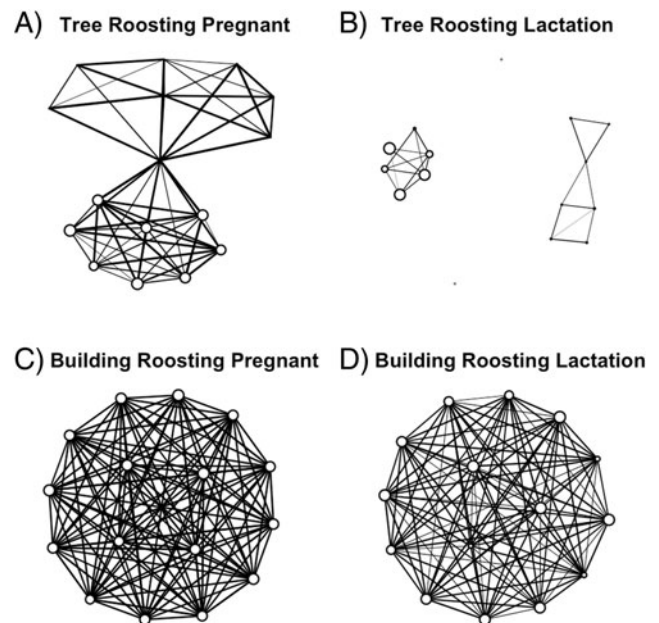


Fig. 1 Social network associations of observed fission-fusion tree and building roosting big brown bats during pregnancy and lactation. Node size is proportional to values of strength for each individual and line thickness is proportional to the strength of each dyadic connection. Note the larger node sizes for individual bats during pregnancy compared to lactation for tree-roosting bats, but not building roosting bats

Fig. S2). Meanwhile, strength only differed significantly between tree-roosting bats during pregnancy and building roosting bats during pregnancy and lactation (Fig. 2; Fig. S3). There was no difference in strength between tree-roosting bats during lactation and building roosting bats during pregnancy or lactation (Fig. 2; Fig. S3). When accounting for multiple comparisons between roosting conditions there were significant differences for both HWI ($X^2 = 5.8$, $p < 0.001$) and strength ($X^2 = 3.9$, $p = 0.0004$) (Fig. S2; Fig. S3).

For identical values of β , our models estimated a faster increase in predicted pathogen prevalence for pregnant tree-roosting bats compared to lactating tree-roosting bats (Fig. 3). For these models, there were large effect sizes for all β values (Table 2; Fig. 3). For identical values of β , our models estimated no difference in predicted pathogen prevalence for pregnant versus lactating bats in the building roost (Fig. 3). For these models, there were small effect sizes for high (25%) and moderate (10%) values of β and large effect size for low (1%) values of β (Table 2). Consistent with our prediction, when we compared results across roosting conditions, predicted pathogen prevalence was higher for building roosting bats during pregnancy and lactation compared to tree-roosting bats during pregnancy and lactation (Fig. S4). Effect sizes for these comparisons were large for all three β values (Table 2).

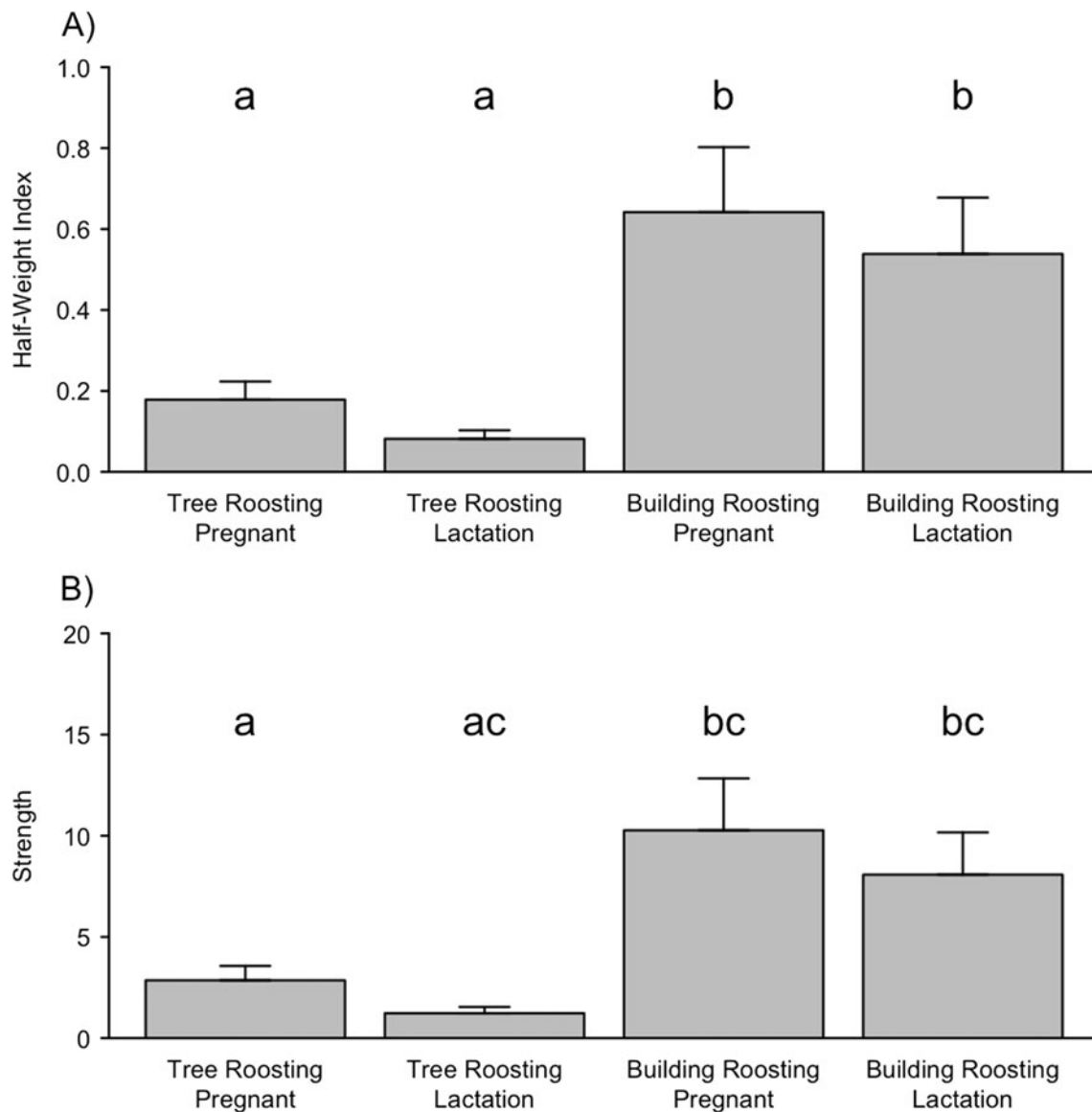


Fig. 2 **a** Comparison of half-weight index between tree and building roosting bats during pregnancy and lactation; **b** comparison of strength during all. Bar plots represent mean \pm standard error, and bars sharing the

same letter are not significantly different from each other (see Fig. S2 and S3 for full presentation of comparisons)

Discussion

Our results suggest that changes in social networks across reproductive periods and between habitats can affect rates of pathogen accumulation within populations of social hosts. Greater network aggregation during pregnancy, compared to lactation, led to a faster increase in predicted pathogen prevalence during pregnancy for tree-roosting bats. Similarly, greater social aggregation of bats in a building roosting colony led to a more rapid increase in predicted pathogen prevalence compared to colonies in natural forest habitat where the colony was divided among multiple tree hollows on any given day. Taken together, our results provide insight into how social

behavior can mediate pathogen dynamics throughout the reproductive season and in different habitats.

Consistent with our first prediction and previous work (Willis and Brigham 2004; Patriquin et al. 2010), we found that the strength of associations within a tree-roosting colony was stronger during pregnancy than lactation. Bats may have greater need for social thermoregulation during pregnancy because T_a is colder (Willis and Brigham 2004). Meanwhile, during lactation the combination of passive aggregation at relatively few warm roost trees, combined with nonrandom preferences for some dyads to associate more often within the colony than others, may reduce novel roosting associations (Willis and Brigham 2004; Patriquin et al. 2010). During the pregnancy period, when

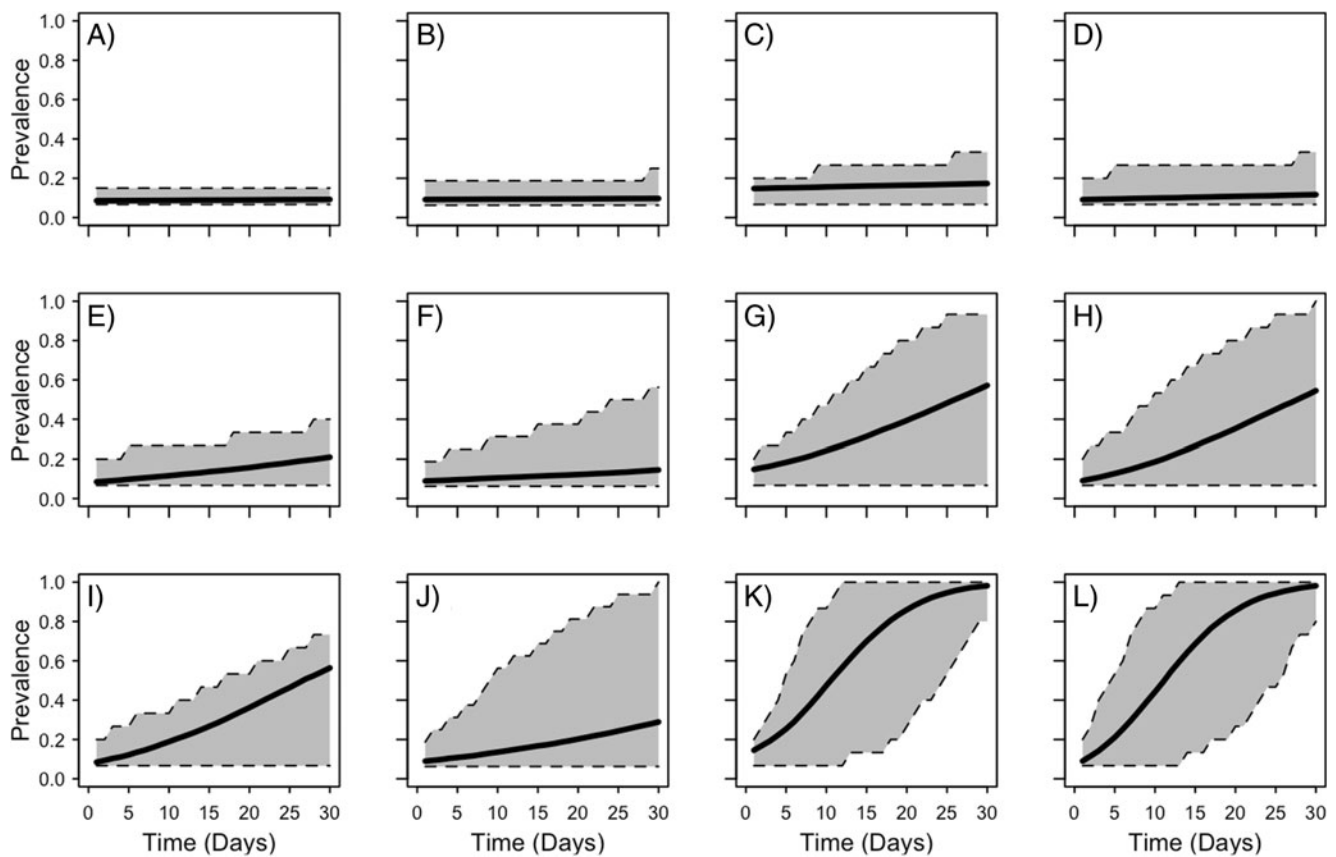


Fig. 3 Network epidemic simulations of a hypothetical pathogen in tree and building roosting colonies of big brown bats generated using an SI model with transmission rate (β) set to 1, 10, or 25 % over 30-day time periods. *Dark lines* represent mean proportion of bats infected across all models, and *gray shaded areas* are 95 % confidence intervals. Note: β

values are consistent across horizontal row of panels: **a–d** $\beta = 1$ %; **e–h** $\beta = 10$ %; and **i–l** $\beta = 25$ %, and roosting scenarios are consistent within each vertical column of panels: **a, e, i** tree-roosting pregnant; **b, f, j** tree-roosting lactation; **c, g, k** building-roosting pregnant; **d, h, l** building-roosting lactation

T_a is colder, pregnant females readily use torpor (Lausen and Barclay 2003; Solick and Barclay 2006; Wills et al. 2006b), but may also preferentially form larger aggregations that could be important for minimizing energetic costs during rewarming. Thus, differences in roosting energetics between pregnancy and lactation appear to influence social network dynamics.

Consistent with our second prediction, we found that differences in social dynamics between reproductive periods resulted in greater predicted pathogen prevalence during pregnancy than lactation for bats roosting in trees, but not buildings. In chimpanzees (*Pan troglodytes*), seasonal variation in social connectivity based on reproductive status influenced

Table 2 Summary of results for Mann–Whitney U tests comparing output of susceptible–infected models parameterized with three separate transmission rate (β) scenarios

Comparison		$\beta = 1$ %				$\beta = 10$ %				$\beta = 25$ %			
Model 1	Model 2	W	p value	d	Size	W	p value	d	Size	W	p value	d	Size
Tree roosting pregnant	Tree roosting lactation	5	<0.001	3.05	+++	629	0.13	0.89	+++	648	0.06	1.02	+++
Tree roosting pregnant	Building roosting pregnant	0	<0.001	12.7	+++	50	<0.001	1.99	+++	151	<0.001	1.52	+++
Tree roosting pregnant	Building roosting lactation	6	<0.001	2.64	+++	164	<0.001	1.42	+++	181	<0.001	1.37	+++
Building roosting pregnant	Tree roosting lactation	900	<0.001	11.8	+++	900	<0.001	2.33	+++	842	<0.001	2.23	+++
Building roosting pregnant	Building roosting lactation	900	<0.001	7.32	+++	537	0.99	0.32	+	471	0.99	0.06	+
Tree roosting lactation	Building roosting lactation	128	<0.001	1.67	+++	95	<0.001	1.71	+++	99	<0.001	2.02	+++

Model comparisons included all combinations of (1) tree-roosting pregnant bats; (2) tree-roosting lactating bats; (3) building-roosting pregnant bats; and (4) building-roosting lactating bats. Displayed p values in italics are significant ($\alpha = 0.05$) after post hoc Bonferroni correction

+ Small effect size, ++ medium effect size, +++ large effect size

predicted pathogen prevalence (Rushmore et al. 2013), while in European badgers (*Meles meles*), an increase in social contacts during winter also influenced disease dynamics (Böhm et al. 2008). Our results for tree-roosting bats contribute to the body of evidence from a range of species that links seasonal changes in social dynamics with the potential of pathogens to proliferate within host populations. An additional explanation for our observed diffusion of social structure during the lactation period could be our omission of juveniles. Inclusion of juveniles could potentially alter the social structure we observed, especially if juveniles associate with non-kin in the roost. Juveniles are often reservoirs for ectoparasites at maternity colonies (Christe et al. 2000) and, if juveniles come in close contact with many adult females, they could also be more susceptible to acquiring microparasites. We suggest that future studies incorporate juvenile bats into social network studies of bats at maternity colonies, while also quantifying variation in contact-rates among female and juvenile bats.

Despite differences in predicted pathogen prevalence between pregnant and lactating bats, social network characteristics had a greater influence on temporal/reproductive changes in predicted pathogen dynamics at moderate to high (i.e., 10 or 25 %) transmission rates. This is consistent with empirical data from prairie dogs (*Cynomys sp.*) which showed that higher transmission rates associated within large colonies led to more rapid outbreaks of Sylvatic plague (Cully and Williams 2001). Similarly, variation in frequency of host-host and host-substrate contact rates for three frog species (*Litoria nannotis*, *L. lesueuri*, *L. genimaculata*) influenced transmission rate for chytridiomycosis and, ultimately, caused greater overall infection (Rowley and Alford 2007). The results of our simulations highlight the potential importance of variation in transmission rates for predicting epidemic outcomes.

Consistent with our third prediction, changes in predicted pathogen prevalence were greater for bats in buildings compared to trees because of greater aggregation of the social network in the building colony. An increase in the number and size of bat colonies aggregating in developed habitats could increase pathogen prevalence and intensity in these colonies (Plowright et al. 2015). This has both conservation and public health implications in light of the potential importance of bats as hosts of zoonotic pathogens (e.g., Luis et al. 2013). If species that are reservoirs for zoonotic pathogens (likely tropical species) exhibit similar fission-fusion dynamics (e.g., Wilkinson 1985; Rhodes 2007; Toth et al. 2015) to the big brown bats we studied, destruction of natural roosts followed by aggregation in human dwellings or barns could increase the likelihood of outbreaks within host colonies and zoonotic spillover. Not only could loss of natural roosting habitat increase rates of contact between humans or livestock and bats (e.g., as for Nipah and Hendra viruses:

Daszak et al. 2006), it could increase the risk that these contacts will involve infected bats. Livestock agriculture in Malaysia increased the number of flying foxes (*Pteropus vampyrus* and *P. hypomelanus*) roosting in close proximity to pigs, which likely contributed to the emergence and persistence of Nipah virus (Pulliam et al. 2011). Similarly, an increase in the number and size of urban flying fox (*P. poliocephalus* and *P. alecto*) colonies in Australia likely increased the likelihood of Hendra virus spillover events from bats to horses (Plowright et al. 2011). In both cases, spillover from bats to livestock resulted in human deaths (Daszak et al. 2006). Taken together, these results suggest the importance of preserving and potentially enhancing natural roosting habitat for bats, and designing structures in ways that prevent bats from roosting in large, highly aggregated colonies with high rates of contact among bats, as well as with humans or livestock. If artificial roosts are to be provided in places where natural roosting habitat has been lost, it could be beneficial to provide smaller or multiple-compartment structures to help maintain natural roosting dynamics and avoid the large, highly aggregated colonies that are less likely to occur in natural habitats.

A potential limitation of our analysis is that data were collected using different methods and even small differences in data collection can drive potential differences in observed social structure which can affect interpretation (for details, see Perkins et al. 2009; Farine and Whitehead 2015). However, because of the stark differences in roosting behavior between tree and building roosting big brown bats (Lausen and Barclay 2006), we are confident our results reflect biologically meaningful differences in social structure. Tree-roosting big brown bats have pronounced fission-fusion dynamics, with individuals switching roosts every 1–2 days on average and rarely returning to the same tree within a given year (Willis and Brigham 2004). Moreover, the colony is divided among multiple tree-hollows each day, while the whole colony rarely roosts in the same tree on the same day. By contrast, building roosting big brown bats typically roost in a single (with perhaps a few less used satellite roosts), often large, roost structure for weeks at a time. Thus, these biological effects seem likely to overwhelm differences in observed social structure that might arise because of differences in data collection methods.

The patterns we observed could also differ for parasites with different modes of transmission. Our models are most likely to approximate transmission dynamics for microparasites and some ectoparasites that require direct contact between hosts for transmission (e.g., *Basilia nana*: Reckardt and Kerth 2007). However, they may not capture dynamics of macroparasites with alternative transmission strategies (e.g., mobile ectoparasites with a winged adult stage). Thus, we suggest that future studies use empirical data on individual host (e.g., social behaviors and/or personality: Webber et al. 2015a, b) and parasite (e.g., contact-mediated or mobile parasites) behavior and heterogeneity in susceptibility of individual hosts

(e.g., immune capacity) to assess potential differences in patterns of transmission and prevalence. In the absence of data on transmission rates for the vast majority of bat pathogens, we assumed transmission rate values for our models. Transmission rate is a function of the host-parasite system (Fenton et al. 2002) and variation in transmission can be influenced by intrinsic characteristics of the host, like mating strategy or dispersal ability (Whiteman and Parker 2004) both of which can be linked to sociality. To our knowledge, no comprehensive review exists linking host social behavior of bats (i.e., group size, mating system or any index of sociality) to any measurement of parasitism, including diversity, abundance, or rate of transmission, although such studies exist for rodents (e.g., Bordes et al. 2007), primates (e.g., Nunn et al. 2003), and ungulates (e.g., Ezenwa 2004). Thus, we also recommend that future studies identify ecological, behavioral, and epidemiological predictors of host-pathogen dynamics in bats.

Conclusion

We quantified social network metrics of female big brown bats during pregnancy versus lactation and in natural versus anthropogenic roost structures. Bats in buildings had greater connectivity compared to bats roosting in trees during both pregnancy and lactation, and our models suggested that this could increase pathogen proliferation within colonies during the active season. We suggest that future studies empirically test for relationships predicted by our models between social dynamics and parasite prevalence during pregnancy and lactation and for bats roosting in both trees and buildings. The changes in pathogen dynamics predicted by our models were, in part, proportional to the transmission rates we used, so we also recommend that future studies empirically quantify transmission rates for natural pathogens of bats. In general, our results suggest that habitat alteration can influence pathogen dynamics in bats via changes in social dynamics associated with habitat composition. This has implications for conservation and human public health and highlights the importance of protecting and potentially enhancing natural roosting environments for bats.

Acknowledgments We are grateful to Julie Adams, Ryan Fisher, Quinn Fletcher, Amanda Karst, Kristen Kolar, Seb Martinez, Melissa Ranalli, Christine Voss, and Michael Yaremko for helping with fieldwork in the Cypress Hills. We thank all staff and volunteers who collected data in Fort Collins. We also thank Alex Silvis for help with social network analysis, Quinn Fletcher, Gerald Wilkinson, and two anonymous reviewers for outstanding suggestions on earlier versions of this manuscript. Funding was provided by a Discovery Grant to CKRW from the Natural Sciences and Engineering Research Council (NSERC, Canada), a Manitoba Graduate Scholarship to QMRW, a Discovery Grant to RMB from NSERC, and field portions of the Fort Collins study were funded by a grant from the National Science Foundation Ecology of Infectious Diseases Program (#0094959).

Compliance with ethical standards All protocols applied in Cypress Hills were approved by the University of Regina President's Committee on Animal Care and were in accordance with the Guidelines of the Canadian Council on Animal Care. All procedures involving bats in Fort Collins were approved by the Animal Care and Use Committee of Colorado State University and the US Geological Survey.

References

- Altizer S, Nunn CL, Thrall PH et al (2003) Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annu Rev Ecol Evol Syst* 34:517–547
- Altizer S, Dobson A, Hosseini P, Hudson P, Pascual M, Rohani P (2006) Seasonality and the dynamics of infectious disease. *Ecol Lett* 9:467–484
- Anderson RM, May RM (1979) Population biology of infectious diseases: part I. *Nature* 280:361–367
- Begon M, Hazel SM, Baxby D, Bown K, Cavanagh R, Chantrey J, Jones T, Bennet M (1999) Transmission dynamics of a zoonotic pathogen within and between wildlife host species. *Proc R Soc Lond B* 266:1939–1945
- Berkova H, Pokorny M, Zukal J (2014) Selection of buildings as maternity roosts by greater mouse-eared bats (*Myotis myotis*). *J Mammal* 95:1011–1017
- Blumstein DT, Im S, Nicodemus A, Zugmeyer C (2004) Yellow-bellied marmots (*Marmota flaviventris*) hibernate socially. *J Mammal* 85:25–29
- Böhm M, Palphramand KL, Newton-Cross G, Hutchings MR, White PCL (2008) Dynamic interactions among badgers: implications for sociality and disease transmission. *J Anim Ecol* 77:735–745
- Bordes F, Blumstein DT, Morand S (2007) Rodent sociality and parasite diversity. *Biol Lett* 3:692–694
- Brigham RM (1991) Flexibility in foraging and roosting behaviour by the big brown bat (*Eptesicus fuscus*). *Can J Zool* 69:117–121
- Brigham RM, Fenton BM (1986) The influence of roost closure on the roosting and foraging behaviour of *Eptesicus fuscus* (Chiroptera: Vespertilionidae). *Can J Zool* 64:1128–1133
- Brook CE, Dobson AP (2015) Bats as 'special' reservoirs for emerging zoonotic pathogens. *Trends Microbiol* 23:172–180
- Brosset A, Charles-Dominique P, Cockle A, Cosson JF, Masson D (1996) Bat communities and deforestation in French Guinea. *Can J Zool* 74:1974–1982
- Cattadori IM, Boag B, Bjørnstad ON, Cornell SJ, Hudson PJ (2005) Peak shift and epidemiology in a seasonal host-nematode system. *Proc R Soc Lond B* 272:1163–1169
- Christe P, Arlettaz R, Vogel P (2000) Variation in intensity of a parasitic mite (*Spinturnix myoti*) in relation to the reproductive cycle and immunocompetence of its bat host (*Myotis myotis*). *Ecol Lett* 3:206–212
- Chruszcz BJ, Barclay RMR (2002) Thermoregulatory ecology of a solitary bat, *Myotis evotis*, roosting in rock crevices. *Funct Ecol* 16:18–26
- Cohen J (1988) Statistical power analysis for the behavioral sciences, 2nd edn. Lawrence Erlbaum Associates, Hillsdale
- Côté IM, Poulin R (1995) Parasitism and group size in social animals: a meta-analysis. *Behav Ecol* 6:159–165
- Croft DP, James R, Krause J (2008) Exploring animal social networks. Princeton University Press, Princeton
- Croft DP, Madden JR, Franks DW, James R (2011) Hypothesis testing in animal social networks. *Trends Ecol Evol* 26:502–507
- Csardi GT, Nepusz T (2006) The igraph software package for complex network research, <http://igraph.org>

- Cully JF Jr, Williams ES (2001) Interspecific comparisons of sylvatic plague in prairie dogs. *J Mammal* 82:894–905
- Daszak P, Plowright RK, Epstein JH et al (2006) The emergence of Nipah and Hendra virus: pathogen dynamics across a wildlife-livestock-human continuum. In: Collinge SK, Ray C (eds) *Disease ecology: community structure and pathogen dynamics*. Oxford, University Press, pp 186–201
- Ellison LE, O’Shea TJ, Neubaum DJ, Bowen RA (2007) Factors influencing movement probabilities of big brown bats (*Eptesicus fuscus*) in buildings. *Ecol Appl* 17:620–627
- Ezenwa VO (2004) Host social behavior and parasitic infection: a multi-factorial approach. *Behav Ecol* 15:446–454
- Farine DR (2013) Animal social network inference and permutations for ecologists in R using *asnipe*. *Methods Ecol Evol* 4:1187–1194
- Farine DR, Whitehead H (2015) Constructing, conducting and interpreting animal social network analysis. *J Anim Ecol* 84:1144–1163
- Fenton A, Fairbairn JP, Norman R, Hudson PJ (2002) Parasite transmission: reconciling theory and reality. *J Anim Ecol* 71:893–905
- Fortuna MA, Popa-Lisseanu AG, Ibanez C, Bascompte J (2009) The roosting spatial network of a bird-predator bat. *Ecology* 90:934–944
- George DB, Webb CT, Farnsworth ML, O’Shea TJ, Bowen RA, Smith DL, Stanley TR, Ellison LE, Rupprecht CE (2011) Host and viral ecology determine bat rabies seasonality and maintenance. *Proc Natl Acad Sci U S A* 108:10208–10213
- Gillam EH, O’Shea TJ, Brigham RM (2011) Nonrandom patterns of roost emergence in big brown bats, *Eptesicus fuscus*. *J Mammal* 92:1253–1260
- Halpin K, Hyatt AD, Plowright RK, Epstein JH, Daszak P, Field HE, Wang L, Daniels PW (2007) Emerging viruses: coming in on a wrinkled wing and a prayer. *Clin Infect Dis* 44:711–717
- Hampson K, Dushoff J, Cleaveland S, Haydon DT, Kaare M, Packer C, Dobson A (2009) Transmission dynamics and prospects for the elimination of canine rabies. *PLoS Biol* 7, e1000053
- Hawley DM, Etienne RS, Ezenwa VO, Jolles AE (2011) Does animal behavior underlie covariation between hosts’ exposure to infectious agents and susceptibility to infection? Implications for disease dynamics. *Integr Comp Biol* 51:528–539
- Hosseini PR, Dhondt AA, Dobson A (2004) Seasonality and wildlife disease: how seasonal birth, aggregation and variation in immunity affect the dynamics of *Mycoplasma gallisepticum* in house finches. *Proc R Soc Lond B* 271:2569–2577
- Jenness S, Goodreau SM, Wang L, Morris M (2015) EpiModel: mathematical modeling of infectious disease. R Package version 1.1.4, <http://epimodel.org/>
- Kerth G, König B (1999) Fission, fusion and nonrandom associations in female Bechstein’s bats (*Myotis bechsteinii*). *Behaviour* 136:1187–1202
- Kerth G, Perony N, Schweitzer F (2011) Bats are able to maintain long-term social relationships despite the high fission-fusion dynamics of their groups. *Proc R Soc Lond B* 278:2761–2767
- Kunz TH (1974) Reproduction, growth, and mortality of the Vespertilionid bat, *Eptesicus fuscus*, in Kansas. *J Mammal* 55:1–13
- Kunz TH, Lumsden LF (2003) Ecology of cavity and foliage roosting bats. In: Kunz TH, Fenton MB (eds) *Bat Ecology*, 3rd edn. University Chicago Press, Chicago, pp 3–89
- Lausen CL, Barclay RMR (2002) Roosting behaviour and roost selection of female big brown bats (*Eptesicus fuscus*) roosting in rock crevices in southeastern Alberta. *Can J Zool* 80:1069–1076
- Lausen CL, Barclay RMR (2003) Thermoregulation and roost selection by reproductive female big brown bats (*Eptesicus fuscus*) roosting in rock crevices. *J Zool* 260:235–244
- Lausen CL, Barclay RMR (2006) Benefits of living in a building: big brown bats (*Eptesicus fuscus*) in rocks versus buildings. *J Mammal* 87:362–370
- Lebarbenchon C, Brown SP, Poulin R, Gauthier-Clerc M, Thomas F (2008) Evolution of pathogens in a man-made world. *Mol Ecol* 17:475–484
- Luis AD, Hayman DTS, O’Shea TJ et al (2013) A comparison of bats and rodents as reservoirs of zoonotic viruses: are bats special? *Proc R Soc Lond B* 280:1–9
- Lusseau D (2003) Emergent properties of a dolphin social network. *Proc R Soc Lond B* 271:S477–S481
- May RM (2006) Network structures and the biology of populations. *Trends Ecol Evol* 21:394–399
- McAllan BM, Geiser F (2014) Torpor during reproduction in mammals and birds: dealing with an energetic conundrum. *Integr Comp Biol*. doi:10.1093/icb/ucu093
- McGough JJ, Faraone SV (2009) Estimating the size of treatment effects: moving beyond P values. *Psychiatry* 6:21–29
- Misra V, Dumonceaux T, Dubois J, Willis CKR, Nadin-Davis S, Severini A, Wandeler A, Lindsay R, Artsob H (2009) Detection of polyoma and corona viruses in bats of Canada. *J Gen Virol* 90:2015–2022
- Nunn CL, Altizer S, Jones KE, Sechrest W (2003) Comparative tests of parasite species richness in primates. *Am Nat* 162:597–614
- O’Shea TJ, Ellison LE, Stanley TR (2011a) Adult survival and population growth rate in Colorado big brown bats (*Eptesicus fuscus*). *J Mammal* 92:433–443
- O’Shea TJ, Neubaum DJ, Neubaum MA, Cryan PM, Ellison LE, Stanley TR, Rupprecht CE, Pape WJ, Bowen RA (2011b) Bat ecology and public health surveillance for rabies in an urbanizing region of Colorado. *Urban Ecosyst* 14:665–697
- Patriquin KJ, Leonard ML, Broders HG, Garraway CJ (2010) Do social networks of female northern long-eared bats vary with reproductive period and age? *Behav Ecol Sociobiol* 64:899–913
- Patterson JEH, Ruckstuhl KE (2013) Parasite infection and host group size: a meta-analytical review. *Parasitology* 140:803–813
- Perkins SE, Cagnacci F, Stradiotto A, Arnoldi D, Hudson PJ (2009) Comparison of social networks derived from ecological data: implications for inferring infectious disease dynamics. *J Anim Ecol* 78:1015–1022
- Plowright RK, Foley P, Field HE, Dobson AP, Foley JE, Eby P, Daszak P (2011) Urban habituation, ecological connectivity and epidemic dampening: the emergence of Hendra virus from flying foxes (*Pteropus* spp.). *Proc R Soc Lond B* 278:3703–3712
- Plowright RK, Eby P, Hudson PJ et al (2015) Ecological dynamics of emerging bat virus spillover. *Proc R Soc B* 282:20142124
- Popa-Lisseanu AG, Bontadina F, Mora O, Ibañez C (2008) Highly structured fission-fusion societies in an aerial-hawking carnivorous bat. *Anim Behav* 75:471–482
- Pulliam JRC, Epstein JH, Dushoff J, Rahman SA, Bunning M, Jamaluddin AA, Hyatt AD, Field HE, Dobson AP, Daszak P (2011) Agricultural intensification, priming for persistence and the emergence of Nipah virus: a lethal bat-borne zoonosis. *J R Soc Interface* 9:89–101
- R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, <https://www.r-project.org/>
- Racey PA, Swift SM (1981) Variations in gestation length in a colony of pipistrelle bats (*Pipistrellus pipistrellus*) from year to year. *J Reprod Fertil* 61:123–129
- Reckardt K, Kerth G (2007) Roost selection and roost switching of female Bechstein’s bats (*Myotis bechsteinii*) as a strategy of parasite avoidance. *Oecologia* 154:581–588
- Rhodes M (2007) Roost fidelity and fission-fusion dynamics of white-striped free-tailed bats (*Tadarida australis*). *J Mammal* 88:1252–1260
- Rifkin JL, Nunn CL, Garamszegi LZ (2012) Do animals living in larger groups experience greater parasitism? A meta-analysis. *Am Nat* 180:70–82

- Rintoul JLP, Brigham RM (2014) The influence of reproductive condition and concurrent environmental factors on torpor and foraging patterns in female big brown bats (*Eptesicus fuscus*). *J Comp Physiol B* 184:177–187
- Rowley JJJ, Alford RA (2007) Behaviour of Australian rainforest stream frogs may affect the transmission of chytridiomycosis. *Dis Aquat Org* 77:1–9
- Rushmore J, Caillaud D, Matamba L, Stumpf RM, Borgatti SP, Altizer S (2013) Social network analysis of wild chimpanzees provides insights for predicting infectious disease risk. *J Anim Ecol* 82:976–986
- Solick DI, Barclay RMR (2006) Thermoregulation and roosting behaviour of reproductive and non-reproductive female western long-eared bats (*Myotis evotis*) in the Rocky Mountains of Alberta. *Can J Zool* 84:589–599
- Toth CA, Cummings G, Dennis TE, Parsons S (2015) Adoption of alternative habitats by a threatened, “obligate” forest-dwelling bat in a fragmented landscape. *J Mammal* 96:927–937
- Townsend SW, Zottl M, Manser MB (2011) All clear? Meerkats attend to contextual information in close calls to coordinate vigilance. *Behav Ecol Sociobiol* 65:1927–1934
- Webber QMR, Czenze ZJ, Willis CKR (2015a) Host demographic predicts ectoparasite dynamics for a colonial host during pre-hibernation mating. *Parasitology* 142:1260–1269
- Webber QMR, McGuire LP, Smith SB, Willis CKR (2015b) Host behaviour, age and sex correlate with ectoparasite prevalence and intensity in a colonial mammal, the little brown bat. *Behaviour* 152:83–105
- Wey T, Blumstein DT, Shen W, Jordan F (2008) Social network analysis of animal behavior: a promising tool for the study of sociality. *Anim Behav* 75:333–344
- Whitehead H (2008) Analyzing animal societies: quantitative methods for vertebrate social analysis. The University of Chicago Press, Chicago
- Whiteman NK, Parker PG (2004) Effects of host sociality on ectoparasite population biology. *J Parasitol* 90:939–947
- Wilkinson GS (1985) The social organization of the common vampire bat: I. Patterns and causes of association. *Behav Ecol Sociobiol* 17: 111–121
- Willis CKR, Brigham RM (2004) Roost switching, roost sharing and social cohesion: forest-dwelling big brown bats, *Eptesicus fuscus*, conform to the fission-fusion model. *Anim Behav* 68:495–505
- Willis CKR, Brigham RM (2007) Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity-dwelling bat. *Behav Ecol Sociobiol* 62:97–108
- Willis CKR, Kolar KA, Karst AL, Kalcounis-Rueppell MC, Brigham RM (2003) Medium- and long-term reuse of trembling aspen cavities as roosts by big brown bats (*Eptesicus fuscus*). *Acta Chiropterologica* 5:85–90
- Willis CKR, Voss CM, Brigham RM (2006a) Roost selection by forest-living female big brown bats (*Eptesicus fuscus*). *J Mammal* 87:345–350
- Willis CKR, Brigham RM, Geiser F (2006b) Deep, prolonged torpor by pregnant, free-ranging bats. *Naturwissenschaften* 93:80–83
- Wimsatt J, O’Shea TJ, Ellison LE, Pearce RD, Price VR (2005) Anesthesia and blood sampling of wild big brown bats (*Eptesicus fuscus*) with an assessment of impacts on survival. *J Wildl Dis* 41: 87–95
- Zahn A, Rupp D (2004) Ectoparasite load in European vespertilionid bats. *J Zool* 262:383–391