Title: Social networks of the greater horseshoe bat (*Rhinolophus ferrumequinum*) during the hibernation season: a landscape-scale case-study.

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Abstract

Bats are highly social animals, and the interactions between groups and individuals are likely to be important to their ecology and conservation. Social structures are affected by the physical environment (spatial factors), as well as varying over time and seasons (temporal factors). Compared with many other taxa, individual bats are capable of moving large distances (so experience a range of spatial locations), have long lifespans (providing opportunities to interact with others over a long period), and are often highly gregarious. Using a long-term dataset, we examined the social behaviour, along with spatial and temporal influences, of greater horseshoe bats (*Rhinolophus ferrumequinum*) in the hibernation season using social network approaches. Across 17 years, 2808 individuals were monitored, yielding a total of 5952 records at 21 roost locations. We investigated how individuals' life history traits (sex, age and breeding status of females) and the frequency of observation affected social associations, and identified factors that influenced the movement of individuals between locations. Older and male animals were significantly associated more central in the social network, and adult males may act as a link between socially-separate individuals within the society. We also show the social network holds high non-random dyadic structuring; with assortment by age stronger in female bats compared to males, and that this is likely to be influenced by spatiotemporal factors. Finally, we demonstrate that captured movements between hibernacula were only associated with the frequency of observation rather than any life history trait. We describe the movement patterns between hibernacula, and show the significant effect that both age and sex have on the social network of hibernating *R. ferrumequinum*. These results illustrate the interconnectivity of across sites, stressing the need for appropriate cross-jurisdiction species management plans to be created for species that utilise and move between multiple sites within the landscape.

Introduction

Social networks within populations are dynamic structures that are strongly influenced by the physical environment and the spatial distribution of the interacting individuals (Croft, James, & Krause, 2008; Firth & Sheldon, 2016; He, Maldonado-Chaparro, & Farine, 2019). For social species, interaction between individuals (actively or passively), and the resultant creation and maintenance of beneficial relationships or competitive advantages for individuals, (Lewanzik, Sundaramurthy, & Goerlitz, 2019), is fundamental to a myriad of behaviours. These include mate selection, inter-species relationships, roost selection, identification of new foraging locations, to the avoidance of predation (Aplin, Farine, Morand-Ferron, & Sheldon, 2012; Doligez, Danchin, & Clobert, 2002; Farine & Milburn, 2013; Firth & Sheldon, 2016; Ioannou, Rocque, Herbert-Read, Duffield, & Firth, 2019; Krause, James, Franks, & Croft, 2015; Wilkinson, 1992). In turn, these behaviours can shape the population dynamics of a species, making social network analysis a useful tool for understanding, predicting and, potentially, manipulating population structures e.g. for disease management (Gil, Hein, Spiegel, Baskett, & Sih, 2018; Snijders, Blumstein, Stanley, & Franks, 2017). However, few studies monitor long-term changes in social structures of the same populations. Understanding such temporal relationships and social structures can allow for the identification of areas of conservation importance leading to properly targeted conservation interventions (Chaverri, 2010; Wilkinson et al., 2019). However, the outcomes of social network analyses can vary, depending on the scale at which the target species is studied, with many projects only focussing on individual sites at a local scale rather than taking a landscape-scale approach (e.g. August, Nunn, Fensome, Linton, & Mathews, 2014; Cox, Inger, Hancock, Anderson, & Gaston, 2016). Despite the opportunity for detailed data collection in highly focused studies, the inferences that can be drawn from them are constrained in species that have interactions at large spatial scales,

Bats provide an interesting opportunity to examine social relationships because they are widespread throughout the world (making up approximately one third of all mammal species), are long-lived, move between multiple roosting sites distributed across the landscape, and most are social for at least part of the year. Previous social network studies have shown that bats usually form fission-fusion societies, however there is high species-specific variation in social structures (e.g. August et al., 2014). For example, tree-dwelling species move frequently — in some cases daily — between roosting locations. The generation of communal knowledge about the locations of alternative roosting and foraging sites, through intra-specific transfer of information, is likely to be important for species survival (Carter et al., 2019; Kerth & Reckardt, 2003; Russo, Cistrone, & Jones, 2005). However, Kerth, Ebert, and Schmidtke (2006) suggest that while group decisions about roost selection occurs by a majority decision, individuals can use their own knowledge and the behaviour of others to decide where to roost, allowing individuals to ignore majority decisions that are unfavourable to them. For instance, in populations of *Nyctalus lasiopterus*, Popa-Lisseanu, Bontadina, Mora, and IbÁñez (2008) found that while the group composition changed with every movement between roosts, the social cohesion and structure of the overall population remained the same.

The physical environment can play a significant role in roost selection and the social structures of bats. Rhodes, Wardell-Johnson, Rhodes, and Raymond (2006) illustrated that the removal of a single tree that acts as a communal hub for the white-striped free-tailed bat (*Tadarida australis*) could cause a breakdown in connectivity within the wider landscape, as well as affecting group stability and viability. This highlights how using social structures can help predict how anthropogenic impacts could cause fragmentation and a reduction of encounter rates within populations (Snijders et al., 2017). Social structures may also exist even within continuous, and apparently similar, habitat. For example, August et al. (2014) showed that within the same woodland some species form separate social groups which rarely interacted with one another, illustrating that there can be social divides, potentially important for conservation management, even within continuous habitat.

Greater horseshoe bats (*Rhinolophus ferrumequinum*) are a gregarious species, forming social groups during both the maternity and hibernation periods. In Western Europe, maternity colonies are typically found in buildings and classically contain predominantly female bats and their offspring; males are found throughout the landscape in smaller roost locations. During the hibernation period, both sexes and all ages can be found together in cooler, underground sites (caves and mines; Dietz & Kiefer, 2016; Hutson & Mickleburgh, 2001). There appear to be three different types of hibernacula for *R. ferrumequinum*; these are differentiated by the age and sex of individuals, as well as the potential mating activity which occurs within them (R. Ransome, 1968; R. D. Ransome & Hutson, 2000). The species arouses regularly from hibernation and recapture (ringing records) show that individuals often move between multiple hibernation sites each year. Generally the hibernation sites are within 50km of maternity roosts, though occasional movements of >60 km are recorded (Dietz & Kiefer, 2016; R. D. Ransome & Hutson, 2000). To date, there has been no systematic study on hibernacula use by hibernating *R. ferrumequinum* that takes into account the unique identity of each individual.

Using a large geographic area and individual underground hibernacula as nodes, our 17-year study assesses, how life history traits (sex, age and female breeding status) of hibernating *R. ferrumequinum* are linked with the social associations between individuals. We hypothesised that the sex of individuals would play an important role in the overall social structure and their assortment within the hibernacula. We aimed to use individuals' life history traits to investigate the movements of individuals between hibernation sites each year, and suggest how the social structures can help identify important areas for conservation.

Methods

Data collection

This long-term study took place over 17 years (2002- 2019) at 21 hibernacula in south-west England (Figure 1), with data being collected by members of the Wiltshire Bat Group. All the hibernacula fell within an area with a radius of approximately 30km and were grouped into 'core' and 'non-core' sites (Figure 1). Core sites were defined by having substantial numbers of bats recorded within them (>100), accounting for 97% of all *R. ferrumequinum* records in this study, while non-core sites accounted for only 3% of all the records and were geographically less central. During each survey, unique identification metal rings were placed on bats (Natural England licence 2019-41471-SCI-SCI-3 and previous associated licences) that had not previously been ringed; and the unique ring numbers were recorded for those bats that had been ringed previously. Only bats identified during these hibernation survey were used in the analysis. The age (subadult and adult), sex and breeding condition (females only) were also recorded during these surveys. Females were recorded as either parous or non-parous based on the size and presence of the nipples and false-nipples (defined as breeding status hereon). Individuals were recorded as having bred if they were found to be parous in any year of the study. The age of the bats were determined based on fur colouration and density (adults have brown dorsal pelage with dense under-fur whilst subadults have greyer sparser fur), the state of the wing membrane (shiny membrane that is slightly sticky and lacks extensive scarring in young animals), and the size of the metacarpal joints (which become progressively larger with age; Dietz & Kiefer, 2016).

A maximum of two visits (January and February) occurred at each location per year to minimise the risk of adverse effects from undue disturbance. Consequently, interactions were not directly observed (e.g. Vonhof, Whitehead, & Fenton, 2004) but bats were considered to be associating if they occurred within the same hibernation location at the same time. Given that R. ferrumequinum are known to fly extensively within hibernacula, this assumption is reasonable. These sorts of associations have been termed the 'gambit of the group' and are used when individuals are known to interact at a spatial scale of the group, with the interactions occurring at similar rates among individuals when in a group (Farine & Whitehead, 2015; Whitehead & Dufault, 1999). Individuals were excluded from the network analysis if they were only recorded once (e.g. Zeus, Reusch, & Kerth, 2018), or if they were recorded multiple times but were always solitary individuals (i.e. no social associations). This allowed for more precise estimation of associations to be identified and excludes transient individuals. Although clustering of individuals into tightly-packed groups of up to several hundred individuals sometimes occurs in this species, this phenomenon was largely restricted to two of our study sites and was therefore not explored further in our analyses.

Social Network Analysis

Social Network Construction

Owing to the length of this study, there were large temporal overlaps between individuals with observations of each individual potentially covering multiple ages (adult or sub-adult) which could have changed over the 17 year period, consequently the age-class of each bat was calculated by the proportion of time it was recorded as a sub-adult and an adult (defined as age-score hereon). If the bat was always recorded as an adult its age score would have a value of 1 and if it was always recorded as a sub-adult it would have an age score of 0. We calculated a corrected version of a weighted non-directional association network using a “Simple Ratio Index” (SRI; Cairns & Schwager, 1987) for differing time observations outlined in Firth and Sheldon (2016); with the amount of time each individual was under observation considered within the SRI calculation for dyadic scores. The SRI index calculates the proportion of occurrences that two individuals (or nodes) are recorded together, where the weighted associations (or edges) between individuals range from zero (never found roosting together) to one (always found roosting together). Weighted SRI, compared to other association indices, has been shown to be better at describing true association patterns, making less assumption or biases with the data (Ginsberg & Young, 1992), particularly when the associations are determined by individuals of the same group (Whitehead & Dufault, 1999). This reduces the limitations that occur when using the ‘gambit of the group’ approach (Franks, Ruxton, & James, 2010). All analyses were performed in R version 3.5.0 (R Core Team, 2018).

Individual Traits and Network Position

To test for associations between individual bats and their life history traits (sex, age score and breeding status), we computed two descriptive metrics, weighted degree and betweenness centrality. Weighted degree is a simple measure of network centrality, calculating the sum of weighted connections between an individual (or node) and others in the network (Croft et al., 2008). Individual bats with high degrees are more central in the network. Weighted betweenness centrality counts the number of times an individual occurs on the shortest path between two other nodes in the network, and therefore measures an individual's propensity to bridge the network. This metric was calculated using the 'sna' package (Butts, 2010). High scores indicate that the individuals are more likely to connect largely independent communities (Farine & Whitehead, 2015) and that they are more vital for connecting different individuals within a network.

We created a single linear model for each response variable (weighted degree and betweenness centrality) to test the relationship between these node centrality metrics and our predictor variables (sex, age score, breeding status, the number of observation of an individual over the course of the study (frequency of observation) and the interaction between age score and sex). The best fit model for each response variable was identified as having the lowest Akaike Information Criterion (AIC) value (Burnham & Anderson, 2002). Since the individuals in networks are not independent of each other, for each estimate in the model we also calculated a p-value based on comparison with the same models carried out on randomised data using permutation tests (Farine & Whitehead, 2015). The randomised data used to assess these linear models was created using 1000 node permutations of the observed network, and the p-value was determined from where the observed linear model estimates lay in the distribution of the same linear model estimates generated from the using the permuted dataset i.e. a p-value of <0.05 would mean that the observed linear model estimate falls outside of the 95% range of the estimates generated from using the 1000 node permuted datasets, and therefore is significantly different from expected. We report these p-values a $P_{\text{null-Node}}$ (Whitehead & Dufault, 1999).

Individual Traits and Dyadic Associations

Assortment within social networks can typically be measured by considering the social associations between phenotypically similar or dissimilar individuals e.g. similar/dissimilar in a life history traits. An assortment value can be calculated using standard methods (Farine, 2014), ranging from '1' to '-1', whereby a value of '1' means that individuals are only associated with the same phenotype as themselves, while a value of '-1' means individuals are only associated with those of the opposite phenotype of themselves, and a value of '0' means that there is no assortment by the considered phenotype. We considered assortment by sex, and age score, and used the R package 'assortnet' (Farine, 2014). This was first done for assortment by sex on its own, then by comparing age score assortment separately within individual networks created using only female or male bats. We report the standard error around the estimates of assortment (calculated using bootstrapping – Farine, 2014) and the significance of the assortativity estimate was also tested by comparing the assortativity coefficients of the observed data with assortativity coefficients generated from datasteam permutations i.e. by permuting the group-by individual (gbi) and recalculating the social networks (as described in Farine & Whitehead, 2015). An initial permuted group-by-individual matrix was created using 100,000 permutations with a single random swap per permutation, while controlling for both spatial (hibernacula) and temporal factors (time in years). For every 100 swaps, a new randomised group-by-individual matrix was extracted, and the association matrix was re-calculated and stored, resulting in 1,000 permuted networks. We then calculated p-values by comparing the observed assortativity coefficient to the 1000 assortativity coefficients generated by these spatio-temporal controlled datastream permutations, and we report this p-value as $P_{\text{nullSTGBI}}$. We also repeated this permutation procedure without controlling for spatio-temporal factors, and we term this p-value P_{nullGBI}.

Social Community Structuring

Community structure was examined using the package ‘igraph’ to detect community modularity within the 21 hibernacula (Csardi & Nepusz, 2006; Rosvall & Bergstrom, 2008). The function ‘graph.adjacency’ was used to create a weighted undirected network, while ‘infomap.community’ was then used to create community structure within the network, listing individuals (members) of those communities together. Modularity can be derived from the proportion of edges (associations) that occur within a given community, by their listed members, minus the expected proportion that would be observed were they randomly distributed throughout the network. The values obtained can range from zero to one, with values above 0.5 often being regarded as indicating social structure within a network (Shizuka & Farine, 2016).

Movements

The movements of bats were examined within the network to identify the most important central hibernation locations and assess the bat characteristics that were linked with inter-site movements. To identify what influenced movement of individuals between hibernacula we used a quasi-binary GLM model (link = logit), using the package ‘lme4’ (Bates, Mächler, Bolker, & Walker, 2015). The response was the presence or absence of at least one movement within the study period. The predictor variables were age score, sex, breeding status, frequency of observation, and the interaction between age score and sex. A quasi-poisson GLM was also created using the same predictor variables as above but with the number of movements (count) of each individual as the response variable. AIC values were used to determine the best-fit model.

Figure 1: A map geographically representing the locations of all 21 hibernation roost surveyed. Core sites are shown in black, and non-core sites in white. Numbers in the centre of each circle are associated with the hibernation identities shown in Table 1.

Results

Over the 17 year monitoring period, 2,808 individual *R. ferrumequinum* were recorded in a total from 5,952 encounters, across the 21 hibernacula. The frequency with which these bats were caught ranged from 1 to 15 times (mean = 2.1; SD = 1.7; Supplementary Material Figure S1). The mean number of bats recorded each year was 351.4 (SD = 134.4), with a mean of 36.2 bats per year per hibernaculum (SD = 25.9; range 0-221). Figures S2 and S3 (Supplementary Material) also show the variations in *R. ferrumequinum* numbers recorded over the course of this study at each core and non-core hibernaculum.

From calculating the social network (Figure 2), the mean weighted degree was 36.2 per bat (SD = 25.9), the mean binary degree was 77.9 per bat (SD = 49.0), and the mean group size within the association matrix experienced by any one individual was 31.5 (SD = 18.6). Forty nine percent of individual bats recorded over the study period were female. While the majority of sites showed similar proportion of each sex, some had comparably more males or females recorded (e.g. hibernacula number three, five and six), as well as five of the non-core hibernacula which were either solely male or female sites (Table 1).

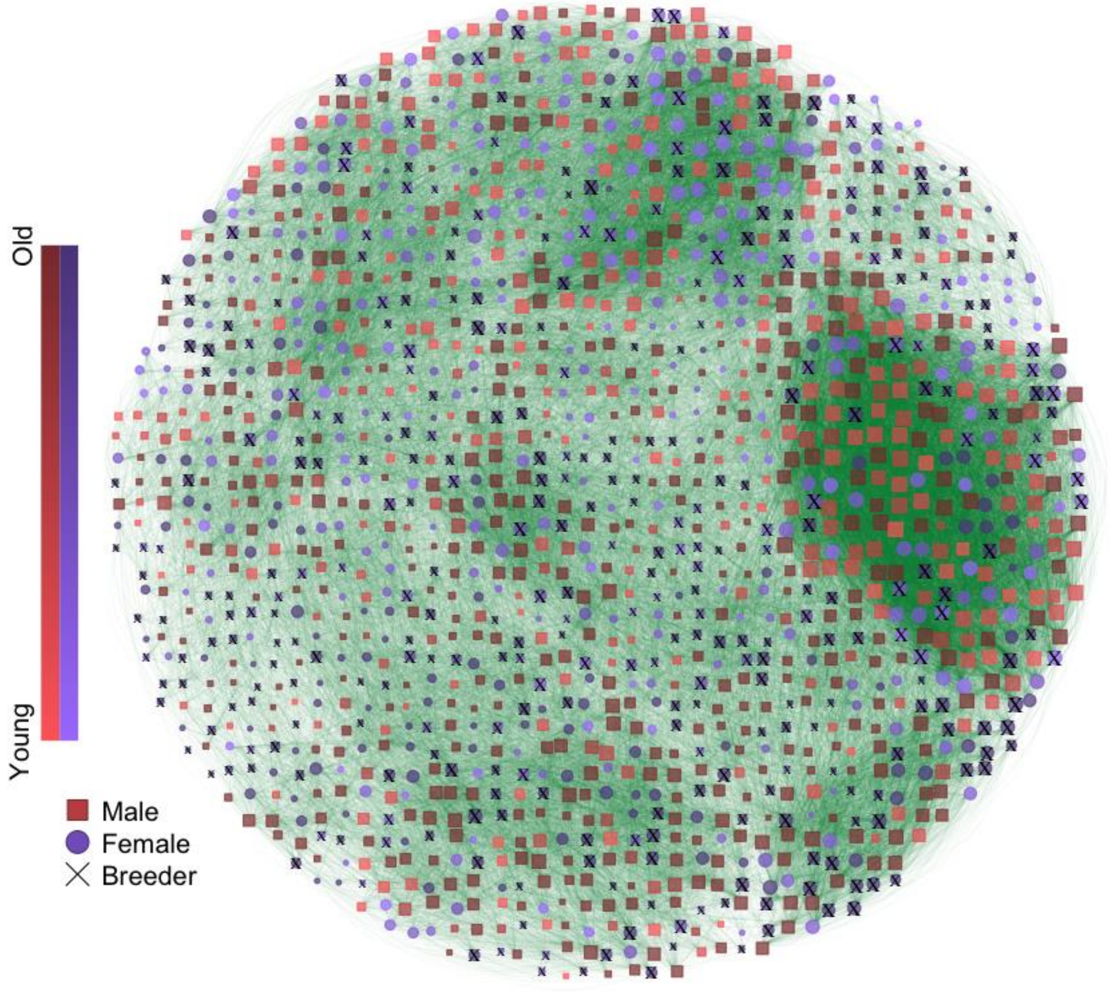

Figure 2: Illustration of the social network over all individuals recorded more than once during the study period. The points show individuals, with males as red squares and females as purple circles, and breeding females marked with an 'X'. The size of the point indicates the ranked weighted network degree of the individual. The darkness of the colouring of the points shows the age score of the individuals (lightest=only sub-adult, darkness=only adult). The green lines between individuals show the social associations, with the thickness of the lines denoting the weight of the social association. The figure does not illustrate the spatial distribution of individuals.

Table 1: Table showing total number of *Rhinolophus ferrumequinum* (GHS) recorded, median roost size, mean weighted degree centrality/betweenness values, proportion of bat movements, and proportion of each sex in each core and non-core hibernacula.

ID	Core or Non-core	Total No. of GHS recorded	Median hibernacula size	Mean weighted degree centrality	Mean weightyed betweenness centrality	Proportion of movement from:to hibernacula	Proportion of movements compared to total number of GHS (%)	Sex ratio – Female:Male
1	Core	1475	91	39	4006	49:51	16	49:51
2	Core	1407	72	34	3838	34:66	16	46:54
3	Core	965	112	76	2528	47:53	6	42:58
4	Core	763	53	32	3885	51:49	18	49:51
5	Core	385	23	17	2955	51:49	15	67:33
6	Core	361	23	28	2645	59:41	16	65:35
7	Core	309	30	28	2670	70:30	21	45:55
8	Core	113	7	27	3258	56:44	42	54:46
9	Non-core	62	23	28	2033	95:5	35	31:69
10	Non-core	47	4	21	1559	74:26	24	79:21
11	Non-core	11	2	20	6452	50:50	45	18:82
12	Non-core	11	1	18	1618	70:30	45	18:82
13	Non-core	11	1	17	1743	67:33	55	36:64
14	Non-core	11	6	9	523	75:25	18	9:91
15	Non-core	8	1	22	4114	50:50	50	63:37
16	Non-core	3	2	22	1185	50:50	67	100:0
17	Non-core	3	1	16	1150	25:75	67	33:67
18	Non-core	2	1	16	0	100:0	25	0:100
19	Non-core	2	2	9	74	100:0	50	0:100
20	Non-core	2	2	9	78	NA*	NA*	100:0
21	Non-core	1	1	24	1058	100:0	50	0:100

*No bats were recorded moving to or from this location.

Individual Traits, Sociality and Community Structure

The results from Table 2 show that the age score of individual *R. ferrumequinum* had a significant negative effect on weighted degree centrality ($\text{Coef}_{\text{observed}}$ = -7.24, SE = 2.19, t-value = -2.76, *p-value* = 0.006, $P_{\text{null-node}} < 0.001$), but the frequency of observations ($\text{Coef}_{\text{observed}}$ = 2.25, SE = 0.39, t-value = 5.75, *p-value* < 0.001, $P_{\text{null-node}} < 0.001$) plus the interaction between age score and sex ($\text{Coef}_{\text{observed}}$ = 9.71, SE = 3.73, t-value = 2.60, *p-value* = 0.009, $P_{\text{null-node}} < 0.001$) had positive associations within the network. However, age score had a significantly positive association with weighted betweenness centrality ($\text{Coef}_{\text{observed}}$ = 432.80, SE = 175.60, t-value = 2.47, *p-value* =0.014, $P_{\text{null-node}} < 0.001$); in addition to frequency of observation ($\text{Coef}_{\text{observed}}$ = 1567.00, SE = 51.30, t-value = 30.55, *p-value* < 0.001, $P_{\text{null-node}} < 0.001$).

Table 2: Best fit linear models for both weighted degree (Table 2a) and betweenness (Table 2b), showing coefficient ($\text{Coef}_{\text{observed}}$), standard error (SE), t-value, and *p-value* from the observed best fit linear model. In addition to the mean coefficient (Mean $\text{coef}_{\text{random}}$) and *p-value* from the random null model created by node permutation ($P_{\text{null-node}}$).

Table 2a: weighted degree model	$\text{Coef}_{\text{observed}}$	SE	t-value	Observed model *p-value*	Mean $\text{coef}_{\text{random}}$	$P_{\text{null-node}}$
Age score	-7.24	2.19	-2.76	0.006	4.83	< 0.001
Sex	2.43	2.95	0.82	0.410	0.36	< 0.001
Freqency of observation	2.25	0.39	5.75	< 0.001	14.56	< 0.001
Age score *sex	9.71	3.73	2.60	0.009	0.41	< 0.001

Table 2b: weighted betweenness model	$\text{Coef}_{\text{observed}}$	SE	t-value	Observed model *p-value*	Mean $\text{coef}_{\text{random}}$	$P_{\text{null-node}}$
Sex	432.80	175.60	2.47	0.014	8.04	< 0.001
Freqency of observation	1567.00	51.30	30.55	< 0.001	0.16	< 0.001

Within this network, strong assortment by sex (i.e. females roosting with females, and males roosting with males) was observed when compared with a null model (Observed Assortment = 0.033, SE = 0.003, Mean Null Assortment = -0.001, $P_{\text{nullGBI}} < 0.001$). However, further analysis revealed that there was no significant association when the model was compared with a null model that controlled for spatiotemporal factors (Observed Assortment = 0.033, SE = 0.003, Mean Null Assortment = 0.031, $P_{nullSTGBI}$= 0.306; Table 3). The results therefore indicate that that the assortment of *R. ferrumequinum* by sex is controlled by the location of individuals across the network of potential hibernacula and the year in which the individual was observed. Assortment by age score appeared to be higher in females compared to males (Table 3). Again, comparing these against a random null model which controlled for spatiotemporal factors demonstrated that female age-assortment were also more likely to be explained by space and time (Observed Assortment = 0.187, SE = 0.001, Mean Null Assortment = -0.001, $P_{nullGBI}$ < 0.001).

While there were high fission-fusion dynamics within the network over the length of this study, modularity was also high (0.59), demonstrating non-random community structure. This illustrates that individuals (members) of the same community are likely to be choosing to associate together over time.

Table 3: The assortativity of the network with respect to *Rhinolophus ferrumequinum* traits: sex and age score. The observed assortativity coefficient is given with standard error (SE), as well as the mean assortativity coefficient of the spatio-temporal controlled GBI permutations (mean Assort_{stGBI}) and the computed *p-value* between the observed and spatio-temporal controlled permuted null data ($P_{nullSTGBI}$).

Trait	Assortativity coefficient	SE	Mean Assort_{stGBI}.	$p_{nullSTGBI}$
Sex	0.033	0.003	0.031	0.306
Female ~ age score	0.187	0.001	0.191	0.165
Male ~ age score	0.126	0.002	0.040	<0.001

Movement between Hibernacula

Overall, the mean average number of bat movements between caves per individual was 0.6 (SD = 0.9) over the 17 years of this study. In total there were 940 records of *R. ferrumequinum* travelling between all hibernacula, 833 of which included movement to or from one of the eight core sites (Figure 3). Of those bats that did move, the mean number of movements recorded per individual was 1.5 (SD = 0.8); a maximum of seven movements between underground sites was recorded for one individual. Hibernaculum 2 two had the highest amount of movement both to and from it, with almost 50% more records of individual bats moving to the hibernaculum rather than from it (Table 1).

The average weighted degree centrality of *R. ferrumequinum* occurring in each of the 21 hibernacula ranged from 9.2 to 76.5, with seven out of eight core hibernacula being in the top eight uppermost ranking locations for higher centrality in *R. ferrumequinum*. The single other core hibernaculum, which is geographically quite central, was ranked 14th (Table 1). Similarly, the core hibernacula showed, on average, higher weighted betweenness centrality compared to non-core sites. However, the highest betweenness was observed at a non-core hibernaculum (hibernaculum 11; Table 1).

Only frequency of observation had a significant effect on the probability of detecting movement of an individual between hibernation sites; for both binary (moved/not moved; OR: 1.44, CI: 1.33 – 1.55, *p-value* < 0.001) and count models (number of movements; OR: 1.26, CI: 1.23 – 1.23, *p-value* < 0.001). We therefore found no evidence for a significant relationship between life-history traits and the probability of movement.

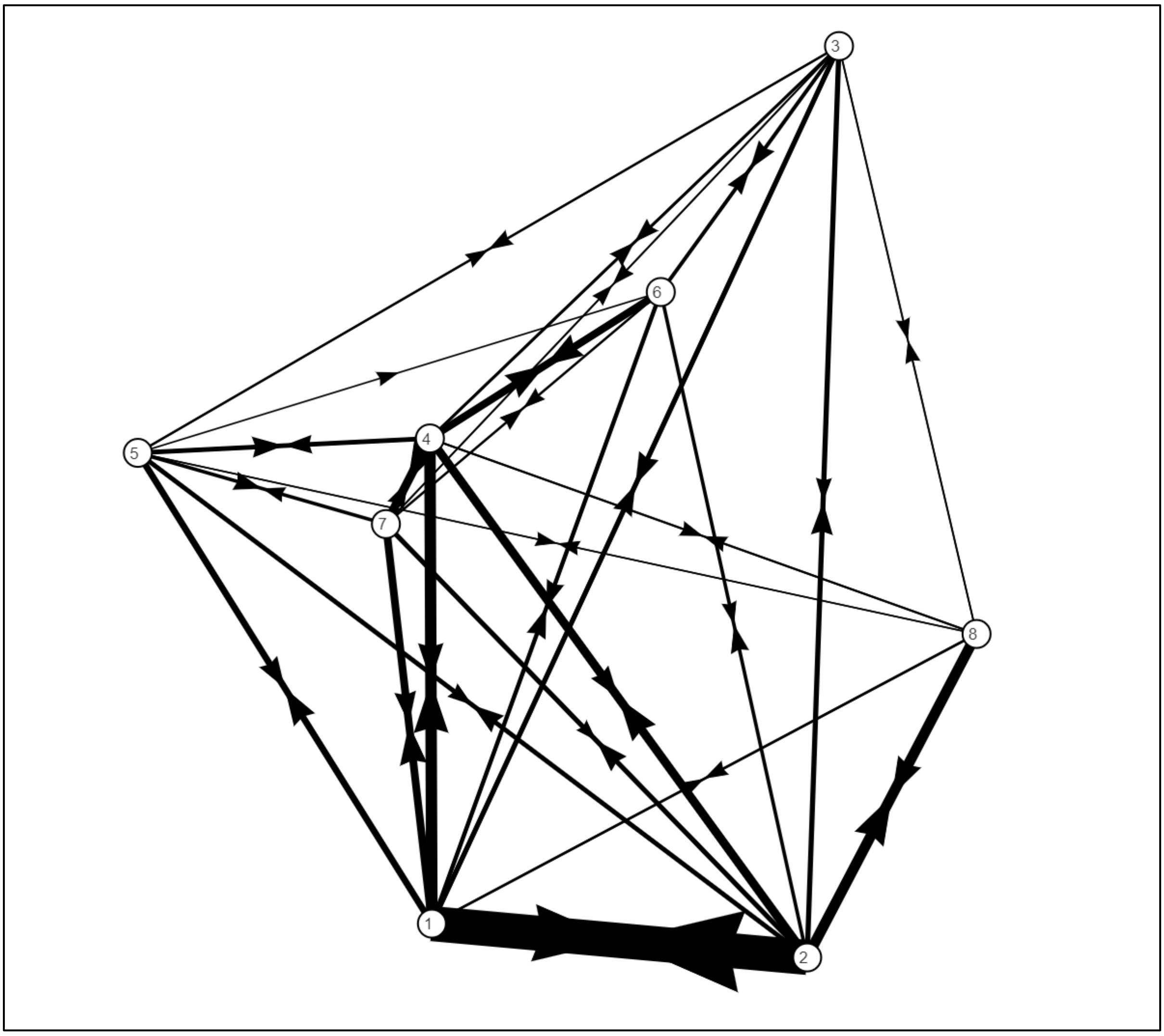

Figure 3: A depiction of the movement patterns of individual *Rhinolophus ferrumequinum* to and from core hibernacula. Thicker lines represent higher rates of movements between the hibernacula. Hibernacula are numbered according to the data in Table 1. The representation of the hibernacula on the diagram reflects their geographical positioning.

Discussion

Most research on bat social behaviour is conducted during the maternity period, with much less attention being paid to the hibernation season, despite the fact that finding suitable locations to hibernate is critical to their survival. At present, for example, we do not know how juvenile bats find hibernation sites during their first winter. R. ferrumequinum are known to arouse from torpor during the winter to forage and they will also move to new hibernacula, presumably to exploit more thermally-suitable conditions according to external temperatures and their body condition (Park, Jones, & Ransome, 2000). Our results show non-random social structures in hibernating *R. ferrumequinum*, with males potentially playing a key role in the social structure present in the hibernacula network. This demonstrates the importance of long-term studies in identifying social structures, and shows that an individual's life history traits can influence their social interactions. Using the metric of weighted degree centrality, adult males were significantly more central in the network, compared to any other trait at the geographic scale of this study. This contrasts with behaviour in the summer, where adult males are typically found on their own or in small groups of bats, with limited interactions with maternity colonies (R. Ransome, 1968, 1991). In the hibernation season, our results show that adult males may play a key role in social connectivity, having multiple contacts with other individuals and being more likely to be the link connecting individuals with otherwise low inter-connectivity, whereas while subadult bats of both sexes and adult females are more likely to be more independent.

Similar to weighted degree centrality, male bats also have higher weighted betweenness scores. Our results suggest that future work to uncover the nature of knowledge exchange between individuals, as well as issues such as disease transfer, should not overlook the importance of adult male bats in the social network.

The frequency with which individuals were observed in the 17 years of study was a significant predictor of weighted degree, betweenness centrality, and movement counts (in the latter case, it was the only significant predictor). This highlights the importance of accounting for this factor in studies utilising social network analysis, and the need to develop metrics that account for duration of observation when considering factors such as age class, which clearly change over time.

Most of the core sites had, on average, more central bats within them, but several of the smaller, geographically peripheral non-core roosts (satellite roosts) had more bats with high centrality scores than the core sites. The highest weighted betweenness centrality score (number of times an individual occurs on the shortest path) was also recorded in a non-core hibernaculum, suggesting that these sites, despite low numbers of bats being present, can act as locations to connect largely independent individuals as well as communities. These results stress the importance of these smaller sites to the movement and interaction of *R. ferrumequinum*, increasing connectivity and encounter rates at larger geographic scales. When considering how to facilitate the restoration of species across a landscape (or conversely how to prevent fragmentation of populations), such small sites may play a critical role (Schofield, 1996). Understanding which physical features in the landscape act as barriers to movements, or how alterations to the environment can influence social structures, can be vital for conservation (He et al., 2019). For example, the red-backed fairy-wren (*Malurus melanocephalus*) whose habitats are affected by wildfires were shown to have higher densities of network ties compared to those unaffected, due to habitat availability (Lantz & Karubian, 2017).

While most of the sites are used by both males and females, some have a higher proportion of one sex, and one location has only ever had females throughout the 17 years of the study. Detailed analysis shows that the assortment by sex is controlled by time and space. In other words, sexes have preferences for specific hibernaculum during certain periods of time; at a minimum during January and February of the hibernation period. There is also assortment by age, with this factor being stronger in females than males, and again being likely to be a product of the effects of time and space.

As in any colonial species, the transmission of infectious diseases harmful to either bats or humans is a concern, with there being considerable potential for rapid spread (Kruse, Kirkemo, & Handeland, 2004; Shi, 2013). Our results illustrate that during the hibernation period, adult male *R. ferrumequinum* could potentially spread diseases at a quicker rate due to their positioning in the social network compared to bats with other life history traits. Similar results were found for male Daubenton's bats (*Myotis daubentonii*) during the maternity season (August et al., 2014). Identifying how these patterns of annual social interactions can vary through time may have specific considerations when thinking about disease management, particularly when dealing with outbreaks that spread rapidly across populations and geographical areas, such as the white-nose syndrome in North America (Blehert, 2012).

Nevertheless, there are considerable benefits to communal roosting and group decision-making, with the increased likelihood of information transfer. In bats, this has been shown to aid group foraging and to act as places where individuals can exchange information about resources in the wider landscape, as well as to help members coordinate roosting behaviour (Cvikel et al., 2015; Kerth et al., 2006; Kerth & Reckardt, 2003; Wilkinson, 1992).

Understanding year-round patterns of species interactions, associations and movement is essential for developing realistic management plans. This is particularly true for elusive species that travel between multiple locations within a single year (e.g. Hays, Mortimer, Ierodiaconou, & Esteban, 2014), this includes cross-boundary jurisdictions, whether between countries, or between local authorities within a single country. The implementation of such management plans, and the collaboration of decision makers needs to be taken at a species level; which considers their entire annual ecology, not just during the breeding period, as is increasingly recognised for long-range migrants (e.g. Bonter, Gauthreaux Jr, & Donovan, 2009; Chevallier, Le Maho, Brossault, Baillon, & Massemin, 2011; Tack, Naugle, Carlson, & Fargey, 2012).

In conclusion, we demonstrate that both age score and sex significantly influence the centrality of individual *R. ferrumequinum* bats, with older males potentially playing a key role in the social network during January and February of the hibernation period. Females show more social assortment by age compared to male bats, but this appears to be driven by their spatio-temporal occurrence in space and time.

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