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Long-term roosting data reveal a unimodular social network in large fission-fusion society of the colony-living Natterer's bat (*Myotis nattereri*)

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Abstract

In many social animals, groups recurrently split into subgroups that regularly re-merge. Such fission-fusion behavior allows individuals to better balance the cost and benefits of group living. However, maintaining a large number of close social links in groups with fission-fusion dynamics may be difficult. It has been suggested that this is the reason why in several species, large groups show more subunits (higher modularity) than do small ones. Many bat species exhibit fission-fusion dynamics in their colonies. This makes them well suited to investigate the proposed link between group size, stability of social links, and group modularity. We studied the daily roosting associations of a Natterer's bat colony (*Myotis nattereri*), where up to 80 members carried individual RFID-tags. Based on more than 10,000 individual recordings, we analyzed the influence of relatedness, age, sex, and breeding status on the colony's social network structure during three breeding seasons. We found an almost fully connected social network with very low modularity and generally weak pairwise associations. Nevertheless, the relative strengths of associations between individuals remained stable across years. Sex, age, and breeding status significantly influenced the strength of an individual's associations and determined the influence of individuals in the network. In general, associations between bats that were similar in all abovementioned traits were stronger than those between dissimilar individuals. Our results show that despite high fission-fusion dynamics, large colony sizes, and low modularity of their social network, Natterer's bats were able to maintain stable long-term associations.

Significance statement

For a variety of social and ecological reasons, large social groups often consist of several communities with stronger individual bonds within and weaker individual bonds between such social subunits. Unlike that predicted for its relatively large size, the studied Natterer's bat colony that consisted of up to 80 individually marked bats was not subdivided into communities. Despite the fully connected network, the individual associations were not random. Instead, their strength was mainly driven by relatedness and similarity in age and breeding status of the colony members. Moreover, we found stable long-term pairwise relationships between individuals across several years. Our study shows that despite the strong fission-fusion behavior and large size of their colony, Natterer's bats formed a fully connected, unimodal social network.

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Introduction

In social animals, the strength of individual associations between group members often show a non-random pattern (Krause and Ruxton 2002; Krause et al. 2007). In general, animals may be passively associated with each other in space and time, for example because they share strategies for use of habitat and resources (Mitani et al. 1991; Chaverri et al. 2007; Aplin et al. 2013). Alternatively, they may be actively attracted to—or repelled by—certain other individuals. In this

case, their associations reflect individual preferences for each other (Gompper et al. 1997; Krützen et al. 2003; Archie et al. 2006; Mitani 2009). The strengths of individual associations are often influenced by individual preferences or demands that arise from differences in individual traits such as age, kinship, breeding status, or sex (Kerth and König 1999; Wolf et al. 2005; Mitani 2009; Patriquin et al. 2010; Wey and Blumstein 2010). Consequently, such traits often also determine the position and connectivity of individuals in the social network of a group, which reflects individual associations among group members (Wittemyer et al. 2005; Ramos-Fernández et al. 2009; Kerth et al. 2011). In many social networks, individuals show assortative mixing and form subunits with individuals that are similar to themselves with regard to traits such as those mentioned above (Newman 2003).

In order to balance individual needs and group preferences, groups can temporarily split into subgroups that later fuse again, a phenomenon called "fission-fusion" behavior (Aureli et al. 2008). In recent years, various studies investigated the fission-fusion dynamics of social groups in animals (e.g., Lehmann and Boesch 2004; Archie et al. 2006; Popa-Lisseanu et al. 2008; Ramos-Fernández et al. 2009; Kerth et al. 2011). Several of these studies show that despite the high fission-fusion dynamics of their groups, at least some individuals are able to maintain long-term associations (Archie et al. 2006; Patriquin et al. 2010; Kerth et al. 2011). Furthermore, in species with fission-fusion behavior, group size seems to predict group modularity as social links between individuals become more differentiated with increasing numbers of group members (Kudo and Dunbar 2001; Lehmann and Boesch 2004; Kerth et al. 2011; Baigger et al. 2013). It has been discussed that a limited number of close social relationships arising from the modular structure of groups might be a strategy to reduce disadvantages of large groups such as intragroup competition, vulnerability to diseases, or infanticide risk (Smith et al. 2008; Kashima et al. 2013). Alternatively, it could be a consequence of time constraints (Dunbar 1991, 1992a; Lehmann et al. 2007) or cognitive constraints (Dunbar 1992b; Kudo and Dunbar 2001; Wilkinson 2003; Lehmann et al. 2007; Kerth et al. 2011) that limit the number of close relationships that can be maintained in the long term.

Fission-fusion behavior is widespread among bats, but only a minority of species have been studied in enough detail to characterize their colony structure (see reviews by (Kerth 2008; Johnson et al. 2013). For Bechstein's bats, a strong link between the size and the modularity of colonies has been found and it has been suggested that individuals can maintain long-term relationships with only a limited number (≤ 20) of colony members (Kerth et al. 2011; Baigger et al. 2013). In the present study, we investigated the colony structure of Natterer's bats (*Myotis nattereri*), a species which is widespread throughout Europe and beyond (Dietz and Kiefer 2014). During summer, Natterer's

bats typically roost in tree cavities or bat boxes in forests, although occasionally, buildings are occupied as well (Smith and Racey 2005). Both sexes are highly philopatric (Rivers et al. 2005, 2006; Halczok et al. 2017). Females typically return to their natal colony, where they give birth and raise their young during the maternity season in summer. While some males can be found in these colonies, males have also reported to roost solitary or in all-male groups in the vicinity of their natal colony (Červený and Horáček 1981; Park et al. 1998; Rivers et al. 2006). During autumn, maternity colonies dissolve and the bats migrate to hibernation sites, which are often dozens of kilometers away from the summer habitat (Rivers et al. 2005; Dietz et al. 2007).

As they form colonies of up to 80 individuals, which show a strong fission-fusion behavior (Zeus et al. 2017), Natterer's bats are well suited for a study that aims to assess the social network structure in large and highly dynamic social groups. So far, however, very little is known about the fine scale social structure of Natterer's bats. To our knowledge, previously only two ringing studies addressed this issue (Park et al. 1998; August et al. 2014). The available data suggest that, unlike in many other European bat species, mixed sex groups may be common, with females having a higher number of associates (degree centrality; August et al. 2014). There is also some evidence for the existence of long-lasting but weak individual roosting associations between colony members (Park et al. 1998; August et al. 2014). The caveat of ringing studies is that they depend on capturing the bats from their roosts, and thus do not allow for monitoring roosting associations without disturbing the colony. In an effort to minimize stress on the animals, intervals between data collection in these studies were very long, resulting in very low numbers of recaptures per individual and year (August et al. 2014). Consequently, these studies did not allow for a detailed analysis of the daily fission-fusion behavior of the bats, group modularity, and the stability of social links within colonies over different time periods. Moreover, to our knowledge, no studies on Natterer's bats investigated the influence of kinship, age, and breeding status on the strength of roosting associations among colony members and on their position in the colony's social network.

During three consecutive years, between May and September, we daily monitored 134 bat boxes that were regularly used by one large colony of Natterer's bats as day roosts. In this colony, up to 80 colony members carried individual radio-frequency identification (RFID)-tags. Using automatic RFID-loggers attached to the bats' communal day roosts (bat boxes), we were able to quantify the individual roosting associations without disturbing the bats (Zeus et al. 2017). Based on these individual roost association data, we created social networks and assessed the influence of age, sex,

and individual relatedness on the strength of the roosting associations between colony members.

Due to the large size of the colony, we hypothesized that its social network shows a high modularity and comprises several communities, as has been reported for Bechstein's bats that use the same type of roosts (Kerth et al. 2011). We also expected membership within communities to be stable over time with colony members maintaining long-term individual associations (Kerth et al. 2011; Baigger et al. 2013; August et al. 2014). We further assumed that individual traits, namely sex, age class, relatedness, and breeding status, influence the summed strength of an individual's associations (node strength in the colony's network). Finally, we expected assortative mixing between individuals that share the same individual traits and are, therefore, likely to have similar preferences and demands.

Methods

Data collection

The study took place each May to September in the years 2013 to 2015 in a forest near the city of Würzburg, Germany. The area is home to one large colony of Natterer's bats (*Myotis nattereri* sensu stricto; Puechmaille et al. 2012). Every year before the 20th of May, when the females became visibly pregnant, and after the fledging of the offspring in late July and August, all bats were captured from their day roosts by hand (about two to three times per year). All unmarked individuals, adults and juveniles, were marked with RFID-tags that were inserted via subcutaneous injection, and DNA samples from the wing membrane were taken for subsequent analysis of relatedness (Kerth et al. 2002).

At the same capture events, we assessed the sex, age, and breeding status of the bats: As the colony members were first marked in 2011, it was not possible to determine the exact age of individuals that had already been adult in 2011. Therefore, we defined three distinct age classes: "juvenile" (born in the respective year of capture), "yearlings" (adult bats that had been captured as juveniles in the previous year) and "older bats" (adult bats that are two or more years old). We distinguished between juveniles (only present in July to September) and adult bats (yearlings and older bats) by examining the epiphyseal gap of the fourth metacarpal (Anthony 1988). Juveniles were not included in subsequent analyses because we expected them to still depend strongly on the presence of their lactating mother and thus not to be able to independently choose their day roosts. If bats were specified as adult in the year of their first capture, these individuals were labeled with age "unknown" for that year, as it was not possible to discriminate between yearlings and older without knowing the year of birth. In the following year, such bats were labeled as older

because then they had been at least 2 years old. Adult females were regarded as "breeding" if the bats showed worn patches around the nipples (Racey 1988) or "non-breeding" in the absence of such patches. We classified the breeding status of adult females as "unknown" if they were not captured during that time period or only so late in summer that signs of lactation were no longer explicit. All males that were present in the maternity colonies were classified as non-breeding as males of temperate bat species do not participate in the rearing of the young (Kunz and Hood 2000).

In previous years, 134 bat boxes (type 2FN, Schwegler, Germany) had been installed in the study area (Zeus et al. 2017). These boxes have been regularly used as communal day roosts by the colony during the study period. Each year, data recording started after the last marking event mid of May and stopped in September, when the colony started to dissolve. Roost associations were recorded for a total of 341 days (117 days in 2013, 114 days in 2014, and 110 days in 2015) with a radio-frequency identification (RFID) system that is well established for the automatic monitoring of bats in our study site (Kerth and König 1999; Kerth et al. 2011; Zeus et al. 2017). Every day, all boxes were checked visually without opening them, using an established monitoring protocol (Kerth and Reckardt 2003; Kerth et al. 2011). Occupied boxes were equipped with automatic RFID-tag readers (reader type "LID 650" by EURO I.D.) to monitor the individual group composition in the day roosts. The logger antennae were placed in the boxes' entrances in a way that bats that passed the entrance were recorded by their RFID-tag numbers together with the respective date and time. This set-up has proved to be very reliable in a study by Kerth and Reckardt (2003), where 97% of the bats passing the antenna had been recorded. Bats that were recorded during the emergence from the bat box in the evening were assigned as having spent the day associated with each other in the respective box (Kerth and Reckardt 2003; Kerth et al. 2011). As all association data were recorded automatically, there was little need for blinded methods. The rate of logger malfunctions due to technical problems such as battery failure or antennae damage was very low (3.7% of all monitored day roosts) and the respective days were excluded from the dataset.

Genetic analysis

Following the approach of Halczok et al. (2017), we used 15 nuclear microsatellite markers to assess relatedness between individuals (see supplement for more information). Markers were tested for Hardy-Weinberg equilibrium with Genepop version 4.5.1 (Raymond and Rousset 1995) and for the presence of Null-Alleles with Micro-Checker version 2.2.3 (van Oosterhout et al. 2004) with 10,000 iterations and a 95% confidence interval. In order to confirm natal philopatry in the colony, we identified mother-offspring pairs with Cervus

version 3.0.7 (Kalinowski et al. 2007). The relative related-ness between pairs of individuals was calculated with TrioML (Wang 2007) using Coancestry version 1.0.1.5 (Wang 2011).

Network analysis

In social network analyses, animals with fewer than a certain number of observations are often excluded because they may cause misinterpretations of the social structure (Whitehead 2008; Farine and Whitehead 2015). The determination of a threshold of minimum number of observations, however, has been handled in various ways in different studies. Many studies have excluded all data below a more or less arbitrarily selected number of observations. In our study, we followed the approach of Aplin et al. (2013) and tested for a relation-ship between the number of observations and the number of observed association partners. We analyzed each year sep-arately and plotted the number of observations against the number of different association partners (binary degree), which resulted in a saturation curve. We excluded all individuals that did not reach the plateau of the curve. This resulted in the omission of all individuals below 12 observations in 2013 (3 individuals; 5.8% of all analyzed bats in that year), all individ-uals below 10 observations in 2014 (9 individuals; 11.0%), and all individuals below 20 observations in 2015 (6 individuals; 7.0%). We do not expect any bias in the properties of the network by excluding such a limited number of bats with few observations, as according to Silk et al. (2015), as little as 30% of individuals can be enough to produce a conclusive network.

All network analyses were performed in "R" version 3.3.1 (R Core Team 2016). From our observed roosting data, we generated a weighted, undirected association network by using the R package "asnipe" (Farine 2016a) with values ranging between 0 (never found roosting together) and 1 (al-ways found roosting together). There is a wide variety of different association indices to compute associations between individuals, most of which correct for potential observation biases in the obtained data by giving certain observations a higher or lower weight (Whitehead 2008). However, such weightings are often somewhat arbitrary, generally do not re-sult in a better performance, and can even impede the inter-pretability of results (Hoppitt and Farine 2017). Therefore, we decided to use the "Simple Ratio Index" (SRI) (Cairns and Schwager 1987; Ginsberg and Young 1992) that needs no such corrections.

Due to the high reliability of the automatic RFID-monitor-ing, we are highly confident concerning the collected data on the presence or absence of individuals in our monitored boxes at any given day. Nevertheless, we only recorded on average 47% of all colony members per day (minimum 1%, maximum 98%). This can be mainly attributed to two factors: The pres-ence of unmonitored, natural roosting opportunities (tree cavities) at the study site and the departure of individuals at the end of summer. For both reasons, the probability of failing to record two individuals when they are together is the same as failing to record them when they are apart and in such a case, the SRI is unbiased (Hoppitt and Farine 2017).

In order to assess whether the observed network consisted of several subunits (communities), we used the "infomap" algorithm (Rosvall and Bergstrom 2008) as, according to Fortunato and Lancichinetti (2009), it is the best performing algorithm for undirected, weighted networks. Based on this output, we then calculated the modularity of the network. We used the R package "igraph" (Csardi and Nepusz 2006) for both the community detection via "infomap" and the subse-quent computation of modularity.

To test whether the pairwise associations in the observed network are non-random, we conducted 100,000 data stream permutations with one random swap per permutation (Farine and Whitehead 2015), as implemented in the "asnipe" pack-age. Subsequently, we computed a new association matrix after every 100 swaps, which resulted in 1000 permuted ran-dom networks. In the following, we calculated the proportion of times the coefficients of variation (CVs) of the 1000 per-muted random networks were larger than the CV of the ob-served network (Farine and Whitehead 2015). When 95% of the CVs from the random data were smaller than the CV of the observed data, the test was declared significant at the 5% level. This method was also used for all other analyses that required permutation tests as mentioned below.

In order to test whether the parameters sex, age class, and breeding status influence an individual's node strength, we conducted models of both the observed data and the random networks (Farine and Whitehead 2015). We applied restricted maximum likelihood linear-mixed effect models (LMMs) with normal errors to assess differences in node strength be-tween reproductive classes and between age classes. Since individuals were repeatedly sampled across the years, we in-cluded the individual ID as a random intercept in our model as individual association behavior might not be independent be-tween years (see our analyses on temporal stability of associ-ations) despite the complete disintegration of the colony dur-ing hibernation. We used a linear model (LM) for the influ-ence of sex on node strength, as this analysis was only possi-ble for 2013 due to the absence of males in the other 2 years. The influence of breeding status and age class was also tested for each year separately via LM and the results thereof can be found in Table S1 in the supplement. For each individual, we calculated the weighted degree to measure node strength which was used as the response variable in the linear models. The attributes sex, age class, and breeding status that were determined during the captures were set as the predictors in our model. P values were computed from the regression co-efficients of the observed and random networks and corrected via Holm's Sequential Bonferroni Procedure (Holm 1979;

Bretz et al. 2016) in order to avoid Alpha errors due to multiple comparisons. We also conducted the same analysis with eigenvector centrality—a measure of influence (Borgatti 2005)—as the response variable. However, as both network parameters were highly correlated for each year (Kendall rank correlation coefficient (Kendall 1938) 2013: 0.961; 2014: 0.972; 2015: 0.979), the results concerning eigenvector centrality can be found in the supplement (Tables S2 and S3).

To test for a relationship between the association indices and pairwise relatedness, we used the multiple regression quadratic assignment procedure (MRQAP) that is implemented in the "asnipe" package. More specifically, we used the MRQAP with custom permutation networks from the data stream permutations. The association rate was set as the dependent variable and pairwise relatedness as the independent variable.

Moreover, we used the R package "assortnet" (Farine 2016b) to test for assortative mixing of the colony, a weighted measure to assess the extent to which individuals are associated with others that are similar to themselves. Thereby, sex, age, and breeding status were taken into account. The weighted assortativity coefficients of the observed data and the permuted networks were used to compute the p value. Moreover, the output allowed deeper insights into the distribution of association values (edge weights). As there might be a bias for classes that contain proportionally more individuals, we tested via permutation tests if the edge weights between and within classes were higher or lower than expected by chance.

Temporal analysis

To assess the temporal stability of the observed pairwise associations during the course of one maternity season, we calculated the lagged association rates (LARs) (Whitehead 2008), which is the probability of re-association after a certain period of time. To do so, we used the "asnipe" package and set the step length to 1 day. For this analysis, we used all non-juvenile individuals of the colony, including those that were previously excluded for the network analysis because of their low number of observations in some years. This was done in order to avoid positively biasing the LARs by only restricting the dataset to frequently observed individuals (Baird and Whitehead 2000; Whitehead 2008). To facilitate the interpretation of the LARs, we further determined the lagged rate of association null, which represents animals associated randomly. This rate was calculated by the mean group size experienced by an individual divided by the mean number of total associates of each individual (mean binary degree) (Farine 2013). We also calculated the lagged identification rate (LIR) which estimates the probability of re-identification after a certain time lag (Whitehead 2001). This measure provides information on demographic effects such as survival or emigration (Whitehead 2001) which might have influenced the

LARs. The standard errors of the LARs and LIRs were computed via jackknifing.

Finally, in order to test whether associations between individuals remain stable across years, we recalculated the association matrices from the observed data by only including individuals that were present in both years. These matrices were then compared to each other. To do so, we ran a MRQAP analyses by setting the association network in the later year as the dependent variable, generating 1000 permutation networks thereof via data stream permutation as described above, and using the network of the earlier year as the independent variable. Thereby, we were able to test if pairwise associations between years are interdependent and remain stable.

Data availability statement The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Results

Network structure

During the 341 days of the study, we recorded a total of 10,557 individual roosting associations (3028 in 2013, 3307 in 2014, 4221 in 2015). On average, each individual used between 30 and 32 different roost boxes per year (for yearly average with range see Table 1). Thereby, boxes were switched almost daily (see "mean number of consecutive days/box," Table 1). A plot for each year with the number of different roosts against the number of days a bat was present can be found in the supplement (Fig. S1). Regarding the roost use of two associated individuals, a pair of individuals spent on average between 14 and 20 days together per year (for yearly average with range, see Table 1). Thereby, a pair spent on average 1.4 consecutive days in their most frequented roost (Table 1). Thus, the most preferred roost accounted for roughly 20% of a pair's shared roost use (Table 1). A plot for each year with this proportion against the number of days spent together can be found in the supplement (Fig. S2).

In all 3 years, the colony showed high fission-fusion dynamics as can been seen by the percentage of days on which the colony occupied more than one box (2013: 80.3%; 2014: 61.4%; 2015: 77.2%; Zeus et al. 2017). Nevertheless, in each year, the network—that was based on the individual roosting associations (SRI values)—was almost fully connected (see "Network density," Table 2) with very low modularity and thus consisted of only one community (see Fig. 1 for the year 2015). However, associations were non-random (CV_{2013}: 62.756, mean random CVs_{2013}: 52.189, $p_{2013} < 0.001$; CV_{2014}: 59.627, mean random CVs_{2014}: 52.896, $p_{2014} < 0.001$; CV_{2015}: 44.584, mean random CVs_{2015}: 33.327, p_{2015}

Table 1 Average roost use of individual bats and associated pairs per year. The range is given in parentheses

Year	2013	2014	2015
Mean number of different boxes per individual	32.2 (5.0–46.0)	27.5 (7.0–45.0)	29.6 (11.0–43.0)
Mean number of consecutive days per box	1.4 (1.1–1.9)	1.4 (1.0–1.8)	1.4 (1.2–1.7)
Mean number of days a pair spent together	20.1 (1.0–62.0)	14.3 (1.0–54.0)	17.1 (1.0–53.0)
Mean number of days spent together in most frequented roost	1.4 (1.0–12.0)	1.3 (1.0–9.0)	1.3 (1.0–7.0)
% of days spent together in most frequented roost	20.7 (5.6–100.0)	22.2 (4.8–100.0)	17.2 (5.6–100.0)

< 0.001). SRI values indicated that in each year, pairs of individuals shared the same roost only about 20% of the monitoring days on average (see "mean SRI values" Table 2; Figs. 1, S3, and S4 in the Supplementary). Furthermore, individuals only associated with a relatively small proportion of colony members each day (mean per year 32–34%, compare "number of marked individuals" and "mean group size," Table 2).

Temporal stability of associations

Within each year, the LARs started at a value of around 0.5 and further decreased, albeit very gradually, with time. This suggests that in all 3 years, only half of the individual associations persisted after 1 day but remained relatively stable across an extended period of time. In 2015, this time frame is roughly limited to 25 days after which the LAR dropped below the lagged rate of association null, indicating that after this time lag, the probability of re-associations was less likely than expected by random associations. For 2013 and 2014, this was only the case at the end of the respective seasons when the LARs became increasingly unstable. In the same timeframe, the slopes of the LIRs alternate between increasing and decreasing which can be an indication that the bats used the monitored bat boxes less consistently.

The colony members were able to maintain long-term associations across years, as the association networks were significantly positively correlated between successive years (MRQAP, 2013–2014: $n = 34$ individuals, regression coefficient = 0.423, $p < 0.001$; 2014–2015: $n = 57$ individuals, regression coefficient = 0.238, $p < 0.001$) as well as between 2013 and 2015 ($n = 28$ individuals, regression coefficient = 0.864, $p < 0.001$).

Influence of attributes on node strength

Assessing the influence of sex on node strength was only possible for 2013 due to the absence of males in the other 2 years. The LM *Strength~Sex* revealed that all six male individuals were significantly weaker associated with their association partners compared to the female individuals and their corresponding association partners (Table 3).

The LMM *Strength~Breeding status* across all 3 years further suggested that females that reproduced in a given year have higher node strength (Table 3) than non-breeding bats (in 2014 and 2015 only non-breeding females; in 2013: non-breeding females and males). Thus, they seem to have stronger links with their association partners. Conversely, according to the LMM *Strength~Age* across all 3 years,

Table 2 Attributes of individuals and network parameters in all 3 years. "Mean binary degree" is the average number of association partners within the respective year. "Mean group size" is the average number of colony members in a roost. "Network density" is the proportion of all possible links between individuals. "Mean SRI value ± CV" signifies the average association index between pairs of individuals and also stating the coefficients of variation in percent. "Modularity" expresses whether a network is divided into several sub-communities; the value of modularity can either be positive or negative with positive values hinting the presence of community structure

| Year	2013	2014	2015
Number of marked individuals	49	73	80
Sex: female/male	43/6	73/0	80/0
Age: older/yearling/n.a.	32/7/10	56/10/7	62/16/2
Breeding status: breeding/non-breeding/n.a.	25/7/17	51/7/15	47/12/21
Mean binary degree	47.6 (44–48)	70.7 (63–72)	79 (78–79)
Mean group size	16.432 (11.5–20.3)	23.267 (16.5–29.2)	27.074 (19.7–36.4)
Network density	99.150	98.136	99.968
Mean SRI value ± CV	0.224 ± 60.447	0.199 ± 58.048	0.243 ± 42.870
Modularity	−3.108624e−15	3.552714e−15	−4.884981e−15
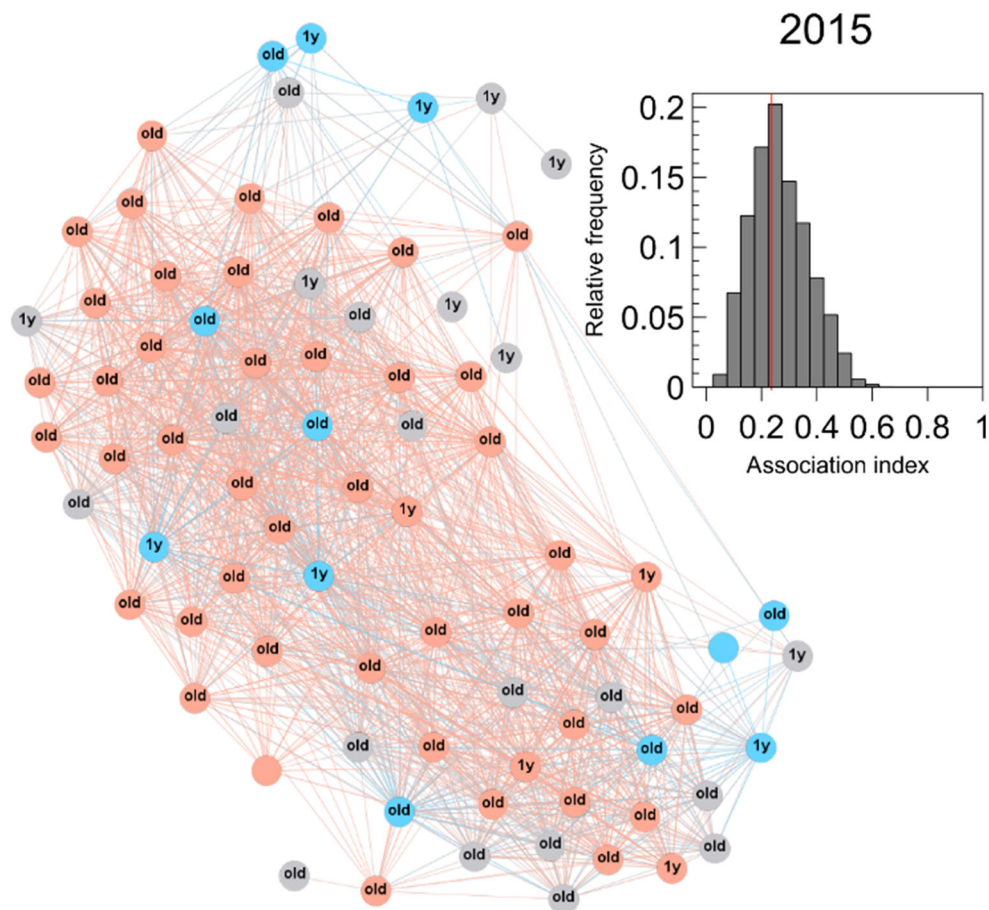
Fig. 1 The network structure and strength of pairwise associations in 2015, when 80 individuals had been analyzed: The right graph shows the frequency distribution of the strength of pairwise associations with the red vertical line indicating the mean association strength. The left graph presents the network structure that was produced with Gephi 0.9.2. (Bastian et al. 2009) using a force-directed algorithm where short edges between two nodes represent stronger associations between these two individuals. While the network is fully connected, for a better visualization, this graph only shows social links that are above average strength. The breeding status of the individuals is color coded (red = breeding, blue = non-breeding, gray = no information available) and the age of the individuals can be found in the node label ("1y" = yearlings, "old" = older bats). Respective figures for the years 2013 and 2014 can be found in the supplementary

yearlings had significantly weaker associations than older bats (Table 3).

Assortative mixing

Even though the colony consisted of only one community, we found significant assortative mixing for all traits that were taken into account, namely sex (significant in all years; 2013 by permutation test, and in 2014 and 2015 by the absence of males), age (significant in 2013 and 2014), and breeding status (significant in 2013 and 2015, Table 4). This shows that associations were significantly stronger between individuals that were similar in the measured traits.

Having a closer look at the discrete attributes in years with significant assortative mixing (Table 4), data of 2013 revealed that, with a mean edge weight of 0.263 (95% CI = 0.254 to 0.271), associations between females accounted for 90% of the sum of all edge weights in the network. This effect was not

a byproduct of their large class size as the p value of the permutation test was significant ($p = 0.001$). This indicates that females did associate with each other stronger than expected by chance. In contrast, edge weights between males with a mean of 0.204 (95% CI = 0.161 to 0.248, proportion of all edge weights = 1.2%) were not significantly higher than expected by chance ($p = 0.137$), while those between sexes were significantly lower (proportion of all edge weights = 8.8%, $p = 0.001$) with an average value of 0.090 (95% CI = 0.083 to 0.097). This suggests that female individuals prefer the presence of their own sex, while males might even avoid females. This evidence for social sexual segregation is also supported by the low proportion of males in the colony in 2013 and their total absence in 2014 and 2015.

For the attributes of age and breeding status, we had to deal with a considerable proportion of individuals with unavailable data ("n.a." in Table 2) ranging between 4 and 24% concerning the age and between 27 and 57% concerning the
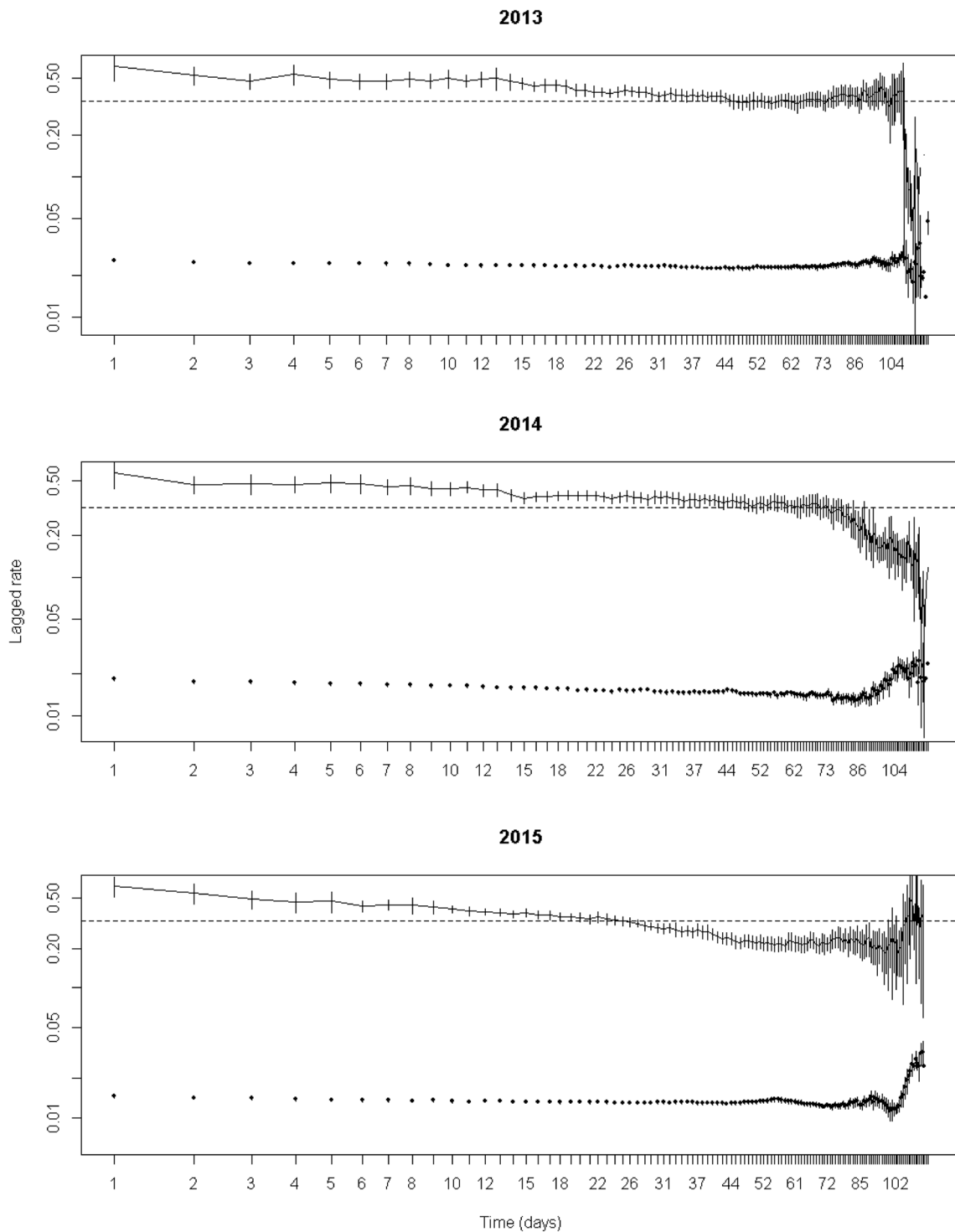
Fig. 2 Lagged rates: The solid line is the LAR, the dashed line is the lagged rate of association null, and the dotted line the LIR. Vertical lines signify the standard error

breeding status. Thus, for better comprehension, in the following paragraph, 100% reflects the number of individuals with known status only.

In 2013 and in 2014, the years with significant assortative mixing concerning age class, associations between older bats were significantly stronger than expected from random (2013: mean edge weight = 0.284, 95% CI = 0.272 to 0.296, proportion of all edge weights = 70.2%, $p < 0.001$; 2014: mean edge weight = 0.218, 95% CI = 0.212 to 0.223, proportion of all edge weights = 77.1%, $p = 0.021$). Even though, only small proportions of the total edge weights occurred between yearlings (2013: 3.5%; 2014: 1.3%), these were significantly

Table 3 Results of the LM (*Strength~Sex*, 2013 only) and the LMMs (across all 3 years) assessing relationships between node strength and attribute sex (basic level: female), breeding status (basic level: non-breeding), and age (basic level: older bats). The estimate (coef$_{observed}$) is given with standard error, degrees of freedom, and *t* value, as well as the mean estimate of the permuted networks (mean coef$_{random}$), and the computed *p* value from the observed and permuted data (corrected via Holm's sequential Bonferroni procedure). Significant *p* values are shown in italics

Model	coef$_{observed}$	SE	df	*t*	mean coef$_{random}$	*p*
Node strength~Sex	− 6.684	1.189	47	− 5.623	− 6.175	*0.001*
Node strength~Breeding status	4.075	1.008	53	4.042	3.157	*< 0.001*
Node strength~Age	− 2.635	0.922	81	− 2.858	− 1.557	*< 0.001*

stronger than expected by chance in 2013 (mean edge weight = 0.335, 95% CI = 0.294 to 0.367, $p < 0.001$). In contrast, individuals of different age classes were significantly weaker associated than expected from the permuted data in both years (2013: mean edge weight = 0.235, 95% CI = 0.220 to 0.251, proportion of all edge weights = 26.3%, $p < 0.001$; 2014: mean edge weight = 0.160, 95% CI = 0.151 to 0.170, proportion of all edge weights = 20.6%, $p < 0.001$).

Concerning the breeding status, the largest proportions of the total edge weights were found between breeding females (2013: 81.4%, mean edge weight = 0.307, 95% CI = 0.294 to 0.320; 2015: 68.0%, mean edge weight = 0.281, 95% CI = 0.276 to 0.287). These associations were significantly stronger than expected by chance in both 2013 ($p < 0.001$) and 2015 ($p < 0.001$). Edge weights were significantly lower than expected from random between bats that did not breed in 2015 (mean edge weight = 0.212, 95% CI = 0.190 to 0.235, proportion of all edge weights = 3.1%, $p = 0.009$). Breeding and non-breeding bats also associated significantly weaker than expected from the permutated data in 2013 and 2015 (2013: mean edge weight = 0.099, 95% CI = 0.085 to 0.112, proportion of all edge weights = 15.2%, $p < 0.001$; 2015: mean edge weight = 0.228, 95% CI = 0.220 to 0.237, proportion of all edge weights = 28.8%, $p < 0.001$).

Influence of relatedness on pairwise associations

Pairwise relatedness was significantly positively correlated with the strength of pairwise association between individuals in all 3 years (pairwise relatedness: regression coefficient$_{2013}$ = 0.129, p value$_{2013} < 0.001$; regression coefficient$_{2014}$ = 0.041, p value$_{2014}$ = 0.001; regression coefficient$_{2015}$ = 0.074, p value$_{2015} < 0.001$).

Discussion

In large social groups, individuals often maintain a few strong individual associations and many weak associations to other members of their group which typically results in a modular network with several communities. Such modular social groups have been described for instance in primates (Lehmann and Boesch 2004) and in bat species such as the Bechstein's bat (Kerth et al. 2011; Baigger et al. 2013). The modularity of large animal groups has been interpreted as a strategy to reduce disadvantages of living in large groups such as increased intra-group competition, infanticide risk, or vulnerability to diseases (Smith et al. 2008; Kashima et al. 2013). Alternatively, it might be a result of time and/or cognitive constrains that may prevent individuals from keeping close bonds with many individuals (Dunbar 1991, 1992a; Kudo and Dunbar 2001; Wilkinson 2003; Lehmann et al. 2007; Kerth et al. 2011) or simply a byproduct of how individuals use space and resources. Interestingly, such group modularity did not occur in the large colony of Natterer's bats (up to 80 adult colony members) during this study, although its roost-switching and fission-fusion behavior was similar to that of Bechstein's bat colonies (Zeus et al. 2017). For comparison, strong modularity occurred in Bechstein's bat colonies that compromised between 30 and 40 individuals while it was absent in small colonies of less than 20 bats (Kerth et al. 2011; Baigger et al. 2013).

One notable factor that determined the strength of an individual's associations to other colony members was their relative relatedness with stronger associations between closely related individuals. Besides in our study species, which is known to show high natal philopatry (Rivers et al. 2005, 2006; Halczok et al. 2017), such a positive influence of kinship on association strength has been described in several other species with fission-fusion behavior, e.g., African elephant (Archie et al. 2006), white-nosed coati (Gompper et al. 1997), common vampire bat (Wilkinson 1984), and Bechstein's bat (Kerth et al. 2003, 2011). In all of the aforementioned species, including Natterer's bats (Rivers et al. 2005), mating takes place outside the natal group. With such a breeding strategy, closely related individuals do not run the risk of inbreeding (Godfrey et al. 2014).

Aside from kinship, we found several individual traits to also influence the strength of an individual's associations (node strength). Although we analyzed each parameter separately, some of them might not be independent of each other as for example breeding individuals in maternity colonies are always female (Kunz and Hood 2000; Rivers et al. 2005), and yearlings might have a lower breeding rate than older bats

Table 4 The assortativity of the network with respect to sex, age, and breeding status in all 3years. The observed assortativity coefficient is given with standard error, as well as the mean assortativity coefficient of the permutated networks (mean coef$_{random}$) and the computed p value from the observed and permuted data. Significant p values are shown in italics

	Year	Assortativity coefficient	SE	Mean coef$_{random}$	p
Sex	2013	0.163	0.034	0.123	*< 0.001*
Age	2013	0.245	0.012	0.219	*< 0.001*
	2014	0.247	0.008	0.238	*0.002*
	2015	0.072	0.011	0.067	0.077
Breeding status	2013	0.253	0.007	0.230	*< 0.001*
	2014	0.298	0.006	0.296	0.126
	2015	0.229	0.005	0.219	*< 0.001*

(Gaisler 1979). Given that in many bat species, including Natterer's bats, females form maternity colonies with the purpose to give birth and communally rear their young (McCracken and Wilkinson 2000), the observed closer bonds between breeding females may not be surprising. While in most bats of the temperate zone maternity colonies also comprise non-breeding females and—depending on the species—occasionally males, there are no reports that these individuals contribute actively in the rearing of the young (Kunz and Hood 2000). As a consequence, breeding and non-breeding colony members are not expected to share the same roosting requirements. For instance, while torpor (reduction of body temperature) is generally seen as beneficial for adult bats to optimize their energy budget at times of low food availability, it can slow down the development of the pups (Hoying and Kunz 1998; Kunz and Hood 2000) and interfere with lactation in breeding females (Wilde et al. 1999). Thus, stronger associations between individuals that have similar traits—the observed assortative mixing—might be due to similar needs and shared preferences for certain roost conditions. Yet, it is surprising and requires further studies to answer why the significant assortative mixing in the colony did not result in a modular network.

Despite the high fission-fusion dynamics in the colony, we found associations between individuals to be relatively stable up to a timeframe of around 80 days (see LARs), which equals roughly the duration of pregnancy and lactation period (Swift 2001). Afterwards, until the bats started to leave the study area in September, individuals were less present in the monitored boxes (data not shown) which can also be seen in the slopes of the LIRs. Bats might have used natural tree cavities more often at this time (compare (Kerth et al. 2001) or temporally may have left the study site for mating at so-called swarming sites (Rivers et al. 2005). Both behaviors could explain the observed breakdown of individual association in late summer.

We also found evidence that individual associations persist across several years. This could be explained with individual social bonds being revived after long periods of separation as the maternity colonies disintegrate in autumn and individuals spend the subsequent hibernation period, which lasts several months, mostly solitary (Beaucournu 1958; Hanák et al. 1962; Gaisler and Hanák 1969). However, most of the parameter that potentially influenced the strength of individual associations within each year, namely relatedness, sex, breeding status, and age class—once the individual is older than one year—did not differ (much) between years. For example, of those individuals with sufficient data, 43 individuals out of 53 (87%) did not differ in their breeding status in two successive years, and 8 out of 9 that were included in the analysis had the same breeding status in 2013 and 2015 (not shown in results). Thus, we cannot fully distinguish whether for Natterer's bats the observed long-term associations are the consequence of long-term individual social bonds—as (Kerth et al. 2011) suggested for Bechstein's bats, a species that also shows fission-fusion behavior (Zeus et al. 2017)—or also reflect assortativity due to shared roosting requirements that remain largely unchanged across several years. Nevertheless, as a pair's most frequented roost only accounted for one quarter of its shared roost use on average, it seems highly unlikely that shared roost preferences alone explain the observed individual roosting associations.

We are aware that the results presented in this paper reflect the social network of one single bat colony. As it has been shown for Bechstein's bats, the social network structure might differ between colonies of the same species (Kerth et al. 2011) or even change in the same colony over time (Baigger et al. 2013). However, in both mentioned studies, group size predicted modularity. Thus, our finding of a non-modular network in such a large colony of Natterer's bats shows that bat species with a very similar roosting and fission-fusion behavior can differ drastically in their network structure, as Bechstein's bats already showed modularity at much smaller colony sizes.

To conclude, while the ecologically similar bat species Bechstein's bat and Natterer's bat both form stable long-term associations with stronger links between closely related individuals (Kerth et al. 2003, 2011), they differ considerably in their network structure: Previous studies have shown—in

accordance with our findings—that extensive fission-fusion behavior, as present in our study species (Zeus et al. 2017), seems to come at the expense of close individual bonds that may be too costly to maintain with many individuals (Dunbar 1991, 1992b; Kudo and Dunbar 2001; Lehmann et al. 2007). A counter-measure that has been observed in many other species, including the Bechstein's bat, is the segregation of the group into communities with strong bonds within and weak bonds between these social units (Lehmann and Boesch 2004; Kerth et al. 2011). In contrast, Natterer's bats maintained full connectivity with overall weak associations. At the same time, pairwise associations were significantly stronger between individuals that were closely related or similar in age and breeding status (assortativity). It remains puzzling, why and how Natterer's bats were able to maintain stable long-term individual associations despite large colony sizes, high fission-fusion dynamics, and low modularity of their social network.

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Handling and tagging of the bats were conducted under the permits for species protection (55.1-8642.01-2/00) and animal welfare (55.2-2531.01-47/11 and 55.2-2532-2-20) that had been issued by the government of Lower Franconia.

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