



Seasonal changes and the influence of tree species and ambient temperature on the fission-fusion dynamics of tree-roosting bats

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Abstract

Many species of bats live in dynamic associations in which individuals aggregate or split into smaller or larger groups, moving between roost sites, but factors influencing group size and roost switching decisions in bats living in fission-fusion societies are poorly understood. To test the extent to which fission-fusion dynamics are species-specific and shaped by environmental factors, we radio-tracked two closely related species: noctule bats *Nyctalus noctula* and Leisler's bats *N. leisleri* in well-preserved, old-growth stands of the Białowieża Forest, where roost availability and diversity is high and bats can potentially freely exhibit fission-fusion behaviour. We estimated the number of bats per roost and noted the tree species selected as roost sites. We evaluated the influence of ambient temperature and roost tree species on bat group size and the process of roost switching, and their seasonal component. Our results revealed that bat group size showed species-specific differences in seasonal variation, relationship to ambient temperature and tree species. The number of noctule bats emerging from a roost was relatively stable with a weak tendency to decrease during the breeding season while the number of Leisler's bats emerging from a roost increased when the juveniles started to be volant. Group size of noctule bats increased with ambient temperature. Leisler's bats formed smaller colonies in oaks and ashes than in other tree species. Roost switching rate was associated with ambient temperature and tree species selected by the bats. The bats changed roosts more frequently when the minimum ambient temperature increased, and less often in ashes than in oaks and other tree species. Our results show that bat group size and roost switching behaviour are shaped by both environmental factors and the stage of reproduction.

Significance statement

Environmental factors may affect group size and roost switching behaviour of bats forming fission-fusion associations, but this is expected to vary depending on body size, environmental conditions, as well as seasonally. Few studies have explored this behaviour in tree-dwelling bats and examined how it differs between species. Here, we studied the group size dynamics and the process of roost switching in closely related bat species living in well-preserved, European old-growth forests, for which the knowledge of these patterns is particularly poor. We demonstrate for the first time that bat group size and roost switching rate relates to roost tree species selected by bats, the ambient temperature and varies seasonally, and that these effects are species-specific. The results point out the importance of the availability of suitable roost trees providing a range of microclimatic conditions for maintaining efficient fission-fusion dynamics throughout the reproductive period.

Keywords Roosts · Reproduction · Pregnancy · Lactation · Post-lactation · Social warming

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Introduction

Many mammals, such as primates, elephants, cetaceans, bats, carnivores or rodents live in social groups (Dunbar and Shultz 2007; Silk 2007). The groups may vary from highly cohesive with stable membership to highly fluid (Aureli et al. 2008). An example of the latter are temperate forest-dwelling bats, forming dynamic associations called fission-fusion societies (Kerth and König 1999; Kerth 2008, 2010; Popa-Lisseanu et al. 2008), in which individuals fuse or split into groups of

different sizes maintaining relatively stable social bonds. The factors shaping changes of group size in fission-fusion associations have been debated (Kerth and König 1999; Kerth 2010), but it is generally accepted that the group size is a result of a trade-off between the benefits and costs of association (Silk 2007).

Social warming has been suggested as a key factor in determining group size in bats (Willis and Brigham 2007), with the group size explaining the thermoregulatory patterns better than environmental factors (Willis and Brigham 2007; Russo et al. 2017). However, bats may also control energetic expenditure by selecting different roost types, e.g. boxes or trees and different tree species (Kerth et al. 2001; Ruczyński 2006; Ruczyński and Bogdanowicz 2008), or by an active use of torpor, which could also be a response to environmental conditions and food availability (Rambaldini and Brigham 2008; Czenze et al. 2017).

Group size also affects the efficiency of searching for food and roosts (Ruczyński et al. 2007; Dechmann et al. 2010; Ruczyński and Bartoń 2012), which in turn may promote the stabilization of the group size (Sueur et al. 2011). Larger groups, however, may suffer from increased risk of infestation, disease transmission and food competition (Reckardt and Kerth 2007; Postawa and Szubert-Kruszyńska 2014). Therefore, bat group size in fission-fusion dynamics is a result of a trade-off between factors promoting smaller or larger groups, which change in time and space. These factors are still poorly understood in forest-dwelling bats. In fission-fusion dynamics, roost switching is a mechanism allowing for changing group size and the selection of new roosts offering a more favourable microclimate, placement, lower infestation level, etc. Patriquin et al. (2016) showed that roost switching occurred in response to changes in ambient conditions, suggesting that bats sought more suitable roosting conditions. Ecophysiological differences among bat species determine their preferences for roosting sites characterised by different microclimatic conditions (Bartonička and Řehák 2007; Boyles 2007; Webber and Willis 2018). It may generate a species-specific reaction to environmental conditions and fission-fusion dynamics. However, so far little is known as to which factors play a role in shaping group size and roost switching dynamics, what kind of impact they have and whether this process is species-specific.

We hypothesise that the number of bats gathering in a tree cavity differs between these species, depending on the bat energetic demands and environmental conditions. Conditions contributing to the temperature inside the roosting places include the ambient temperature, T_a , and the species of the tree. Higher number of bats in a roost should be observed when T_a is low and when the animals need to maintain high body temperature during intensive juvenile growth and milk production, i.e. gestation and lactation. Forearm length (FA) of pups at their first flight usually is at 95% of adult FA length

and the growth is almost finished; however, pups' body mass is clearly smaller than adult body mass (Barclay 1994; Kunz and Robson 1995; Hoying and Kunz 1998). Keeping a high body temperature seems to be less important for adults and juveniles when juveniles become volant because they need to invest more energy in storing fat reserves, so low body temperature as well as smaller groups should be preferred (Willis and Brigham 2007). This process should be even more intensive during the post-lactation period when females no longer need to maintain high body temperatures necessary for producing milk, juveniles are hunting independently and juvenile growth is almost finished (Pretzlaff et al. 2010; Nad'o et al. 2017). We therefore expect the frequency of roost switching to be higher during the stage when juveniles are more mobile, and particularly during warm weather, when the benefits from social warming are smaller.

For this study, we have chosen two closely related noctule species: the noctule bat *Nyctalus noctula* and Leisler's bat *N. leisleri*. The noctule bat is larger than Leisler's bat (respectively 15–40 and 11–20 g, Dietz et al. 2009). In smaller animals, maintaining a high body temperature and metabolic rate can be energetically more demanding (Porter and Kearney 2009); therefore, Leisler's bats are expected to form larger groups.

The aim of this study was to (1) estimate the number of bats in tree cavities and how it changes during the breeding season in two closely related bat species; (2) evaluate the influence of ambient temperature and roost type (tree species) on bats' group size; and (3) evaluate the seasonal changes, the effect of ambient temperature, and roost type on the process of roost switching.

Methods

Study area

The study was conducted in the Białowieża Forest, eastern Poland. The study area (100 km²) covered well-preserved stands of the Białowieża National Park (BNP), as well as parts of the managed forest with old-growth remnants (over 100 years old). This is a mosaic forest dominated by deciduous, mixed deciduous, black alder bog, streamside alder-ash, mixed coniferous and coniferous stands (Faliński 1986). The study site is described in more detail in Ruczyński et al. (2017).

Capture and radio tracking

We captured bats with mist nets by small forest rivers (Łutownia, Narewka, Hwoźna and Złota) and a small pond at the edge of the forest (BNP), from 1998 to 2002. We identified the species, sex, age and reproductive status of the bats.

The details are described in Ruczyński and Bogdanowicz (2008) and Ruczyński et al. (2017).

We localised the roosts with the use of radiotelemetry. The captured bats were fitted with radio-transmitters (0.5–0.7 g) and were tracked to roosts the next day (for details on tracking, see Ruczyński and Bogdanowicz 2005, 2008; Ruczyński et al. 2017). It was not possible to record data blind because our study involved focal animals in the field. The mass of a transmitter never exceeded 5% of the bat's body mass (Aldridge and Brigham 1988). The numbers of bats in tree cavities were estimated on the basis of visual observations carried out during the evening emergence of bats. The recorded bat group sizes are associated with the tracked individuals. Usually, only one tracked bat was present in a single roost. Most of the tree cavities were situated high above ground; therefore, the numbers of bats may have been underestimated. The recorded group size did not include young while they stayed in the tree cavities. Offspring were first counted when they became volant, 4–5 weeks after parturition.

Statistical analyses

We estimated the effects of roost tree species and ambient temperature on bat group size and the probability of roost switching and their seasonal component. For the ambient temperature, T_a , we used minimum daily temperatures (Pretzlaff et al. 2010) measured at the meteorological station in Białowieża on the night preceding the observation day. Tree species other than oak and ash (i.e. alder, lime, hornbeam, maple and pine) were pooled together as 'other', since each of these species constituted individually less than 7.4% of all records (oak 65%, ash 21%, other species 14% of all records). In the cases when two bats were present in one roost on the same day ($N = 10$), we excluded the record of the individual that was tracked for a shorter period.

For the modelling of roost switching and group size, we used generalized linear mixed models, including the random effect of individual and assuming by-individual, first-order autoregressive correlation structure to account for the longitudinal setting of the data (the details of model fitting are described in the Supplementary Material). The full model included the effects of T_a and its change (the difference between the current and the preceding day, dT_a), tree species, a nonlinear effect of the day of the year (as quadratic polynomial), as well as the interactions of these variables with a categorical variable representing the bat species. We performed model simplification by iteratively removing the least significant terms (up to a moderate p level of 0.1) from the full model (Hastie et al. 2009).

In the model of bat group size, we used a negative binomial error distribution with a logarithmic link to account for overdispersion in the count data. To model roost change probability, we used a binary response variable indicating whether the

group would switch roosts on the following day. In the latter analysis, we fitted models with binomial error distribution and a logit link function (chosen based on comparisons of model fit performance with alternative functions) to the subset of the data where individuals were tracked for at least two consecutive days ($N = 285$). Where tree species was included in the final model, we conducted post hoc tests with Tukey's HSD to compare differences among these groups, on per-species models to account for the species differences. All analyses were performed using R software, version 3.6.0 (R Core Team 2019), and packages 'mgcv' for model fitting (Wood 2017), 'effects' for effect plots (Fox 2003), and 'multcomp' for post hoc tests (Hothorn et al. 2008).

Results

We obtained data from 48 bats (24 noctule bats and 24 Leisler's bats), each of which visited from 1 to 5 cavities (mean 2.5 ± 1.05 SD). In total, 300 records were used, of which, 107 contained information on bat group size, and 285 on roost switching.

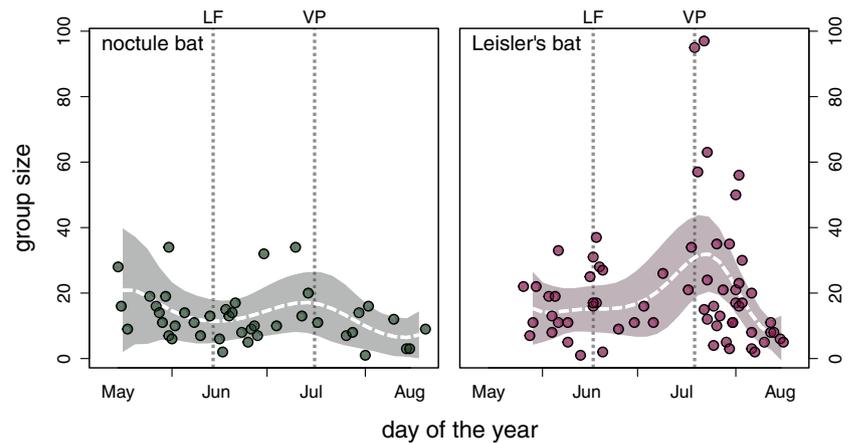
Bat group size

The bats were solitary or formed groups of up to 97 individuals (mean 17.53 ± 16.1 SD). Groups of noctule bats were smaller and less variable (15.75 ± 7.9 , up to 34 individuals) than those of Leisler's bats (mean 25.0 ± 19.1) (Fig. 1). Group size of Leisler's bats peaked when pups started to be volant, followed by a decrease at the end of the season. Noctule bats showed a slowly decreasing trend over the course of the year (although statistically not significant, Fig. 1). The final model for the group size included effects of bat species interacting with minimum ambient temperature, tree species and seasonal change (Table 1), and explained 17.1% of deviance. The model showed the differences between both species in the selection of tree species and to a lesser extent in the seasonal component. Specifically, the model confirmed a nonlinear seasonal change in Leisler's bats ($t = -2.28$, $p = 0.03$), and no trend in noctule bats ($t = -0.38$, $p = 0.71$) (Fig. 2, Table S1 in the Supplementary Material). In Leisler's bats, the groups were significantly smaller in ash ($z = 2.75$, $p = 0.02$) and oak ($z = 2.31$, $p = 0.05$) cavities compared to other tree species (Fig. 2, Table S2). There was no clear effect of tree species in noctule bats (Fig. 2, Table S2). The model also indicated a positive relationship of group size with the minimum ambient temperature in noctule bats (Fig. 2, Table S1).

Roost switching rate

The bats were observed in one roost for 1 to 12 days (mean 2.6 ± 2.0 SD days). Noctule bats stayed in a roost on average

Fig. 1 Group size in the two studied bat species during the reproductive season. Dashed line and the shaded area show the seasonal trend (mean \pm 95% confidence interval). Vertical, dashed lines denote the date of first observation of lactating females (LF) and volant pups (VP)



for 2.76 ± 2.4 and Leisler's bats for 2.50 ± 1.7 days. The daily roost switching rate was 0.23 ($N = 137$) and 0.31 ($N = 148$), respectively for noctule and Leisler's bats.

The final model included the effects of the ambient temperature change, as well as species-wise effects of roost tree species and seasonal component (Table 1), explaining 8.5% of deviance. The model showed that early in the year, the switching rate in noctule bats is lower than in Leisler's bats, and it starts to increase at the beginning of July, when pups are still flightless (Fig. 3). There was a significant difference to Leisler's bats (Table 1), where the switching rate did not show

fluctuations over the whole reproductive period (Fig. 3, Table S1).

The overall effect of roost tree species was not significant (Table 1). Also, the post hoc comparisons showed little differences between tree species (Table S2). In noctule bats, the switching rate was highest in the ash trees, and lowest in the tree species from the 'other' group. Conversely, in Leisler's bats, the switching rate was highest when they roosted in the 'other' tree species. In both bat species, roost switching rate rose with increasing change in ambient temperature (Fig. 3).

Table 1 Anova (type II) table of the final models for bat group size and roost switching. The columns give the model term's degree of freedom, the F test statistic and associated p value. 'Species' is a categorical variable representing the two bat species. ' T_a ' is the minimum ambient temperature and ' dT_a ' is its day-to-day change. 'Tree species' is a categorical variable with three levels. 'Day of the year' is represented as a second-order polynomial

Model term	df	F	p
Group size			
Species	1	2.01	0.16
T_a	1	4.21	<i>0.04</i>
Day of the year	2	1.05	0.35
Tree species	2	1.27	0.29
Species * T_a	1	2.36	0.13
Species * Tree species	2	3.37	<i>0.04</i>
Day of the year * Species	2	2.47	0.09
Roost switching			
Species	1	0.52	0.47
dT_a	1	6.46	0.01
Day of the year	2	2.79	0.06
Tree species	2	2.68	0.07
Day of the year * Species	2	2.13	0.12
Species * Tree species	2	4.00	<i>0.02</i>

Significant effects (within 95% CI) are denoted in italics

Discussion

Our results show that the size of bat groups and the rate at which they switch between roosting sites is affected by different factors in a species-specific manner. We found that largest groups of Leisler's bats emerged from roosts when the juveniles started to be volant, while noctule bats increased the frequency of roost switching during the reproductive period. In contrast to our hypothesis, the minimum ambient temperature, T_a had no negative influence on group size (conversely, our results suggest a positive effect in noctule bats). T_a also had no effect on the roost switching rate; however, the effect of the day-to-day change in T_a was positive. Our results confirm that bat group size and roost switching behaviour are related to the stage of reproduction and environmental factors.

In line with our first hypothesis, we observed species-specific differences in the number of bats emerging from roosts, with groups of Leisler's bats tending to be larger than those of noctule bats. Keeping high body temperature during cold weather is energetically expensive for small mammals; therefore, to minimize energetic costs, bats should stay in the thermoneutral zone when they remain normothermic (Pretzlaff et al. 2010). Social warming seems to be the most effective method of elevating temperature and creating optimal thermal conditions in roosts, especially when T_a is low (Scantlebury et al. 2006; Willis and Brigham 2007; Pretzlaff

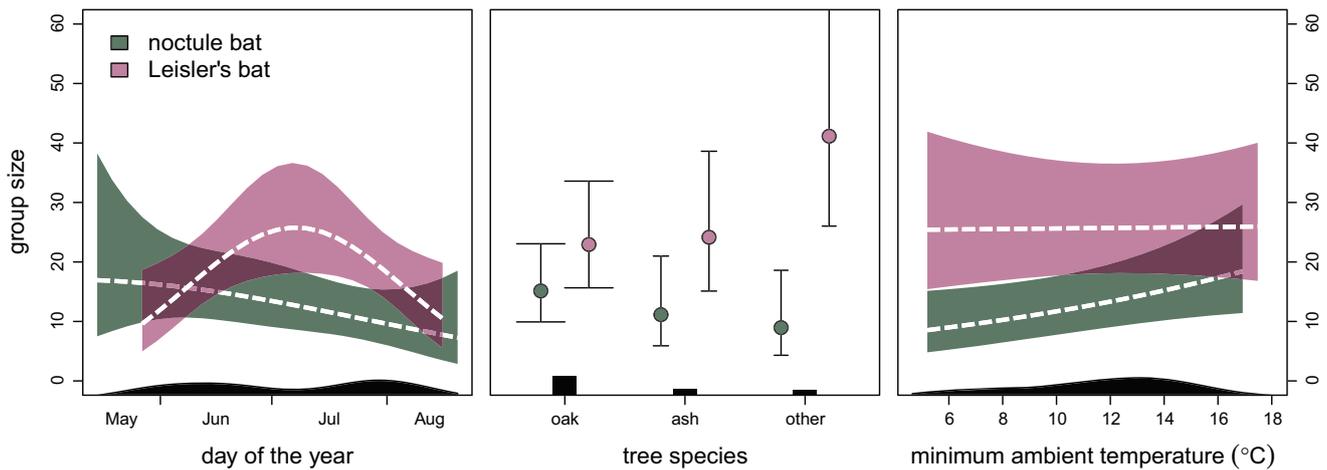


Fig. 2 Results of the final model for bat group size. The panels show predictions of the seasonal changes, in different roost tree species, and along the ambient temperature gradient, for the two studied bat species. The remaining explanatory variables were kept at their mean values or

most common factor levels. Bullets and white line show the mean, with whiskers or shading denoting 95% confidence intervals. The distribution of the original data is shown at the bottom axis as a kernel density plot or a histogram for categorical data

et al. 2010). Leisler's bats, smaller than noctule bats, potentially need larger groups for maintaining suitable microclimatic conditions in roosts, which may explain the difference in the group size dynamics when the juveniles start to be volant. The number of emerging Leisler's bats in some roosts increased until the end of July. These large groups suggest that juveniles stay with mothers in the same roosts or fuse with other individuals. The lack of such an increase in noctule bats indicates that in this species colonies split into smaller groups upon the emergence of young, even if the young stay with their mothers (Ripperger et al. 2019).

During most of the lactation period, juveniles grow intensively (Kunz and Robson 1995; Hoying and Kunz 1998; Speakman 2008), and the prolonged torpor of adults and juveniles may slow down offspring development (Racey 1973; Racey and Swift 1981; but see Willis et al. 2006). Therefore, maintaining large groups during lactation is an energy-saving

strategy that avoids the use of torpor, due to the additive effect of juveniles and adults on the roost microclimate. However, large groups can suffer from increased risk of parasite infestation (Kaňuch et al. 2005).

When they start to be volant, juveniles have almost finished intensive growth and begin to hunt independently (Kunz and Robson 1995; Hoying and Kunz 1998), accumulating fat reserves for their first winter (Kunz et al. 1998). More frequent use of torpor can foster fat accumulation by decreasing the costs of body heating (Dietz and Kalko 2006; Pretzlaff et al. 2010; McGuire et al. 2014). The large colonies of Leisler's bats observed after emergence of young suggest that females still lactated at that time, and juveniles benefit from social warming (Willis and Brigham 2007). Information transfer and mother's guidance may also play a role in forming large colonies during that stage (Willis and Brigham 2007; Ripperger et al. 2019). This explanation is also supported by

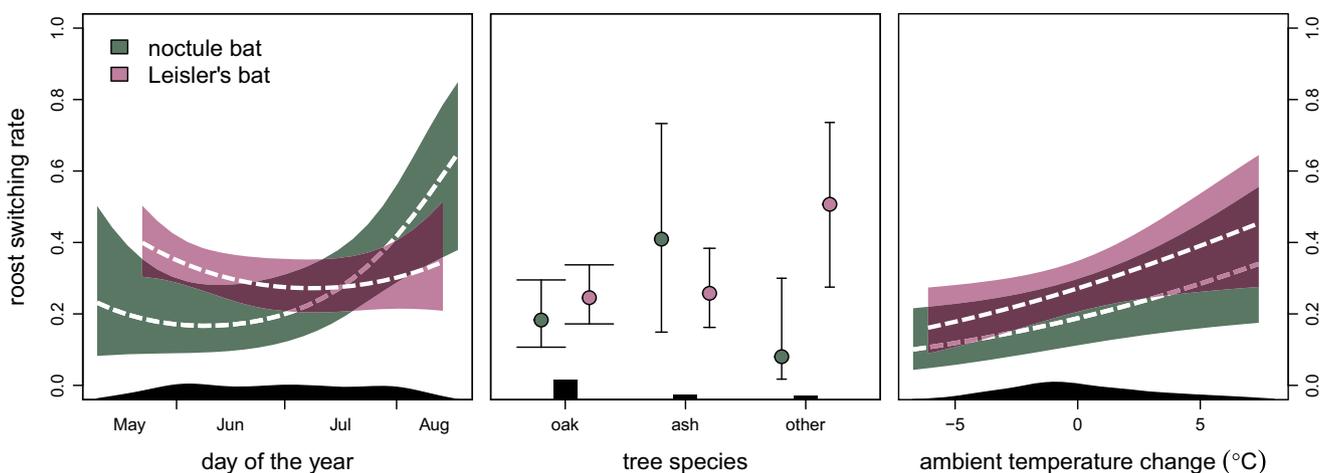


Fig. 3 Results of the final model for roost switching rate. The panels show predictions of the seasonal changes, in different roost tree species, and along the range of change in the ambient temperature. See the description for Fig. 2 for details

the observations of Leisler's and Bechstein's bats in which group size was relatively large during pregnancy and lactation, and decreased mostly during the post-lactation period (Pretzlaff et al. 2010; Nad'ó et al. 2017).

Contrary to our expectations, we found a positive relation between T_a and noctule bats' numbers in roosts, and no relation between group size and T_a in Leisler's bats. A positive or no relation between T_a and the number of bats in roosts in our studies is presumably a result of high flexibility in torpor use by bats and thermal conditions inside roosts, which we did not monitor in this study. Under laboratory conditions, Webber and Willis (2018) observed that bats tend to form larger groups when roost temperature, T_r , was low relative to T_a , and the difference between T_r and T_a was at its lowest (Webber and Willis 2018). Studies conducted in the field showed that Bechstein's bats remained mostly normothermic and group sizes were relatively large during pregnancy and lactation, presumably to benefit from social thermoregulation (Pretzlaff et al. 2010). In contrast, smaller groups were formed on days when bats used torpor, which occurred mostly during the post-lactation period (Pretzlaff et al. 2010). The positive relation between T_a and the numbers of noctule bats may also suggest that some noctule bats did not hunt during the night (thus, they were not counted) at low T_a .

The roosts vary in their thermal inertia, due to the height above ground, entrance size, wall thickness and canopy cover (Ruczyński and Bogdanowicz 2005; Ruczyński 2006). Therefore, T_r may differ from T_a in a wide range, and in this study, the tree species served as a crude proxy for roost microclimate conditions (Ruczyński and Bogdanowicz 2008). Noctule and Leisler's bats tend to prefer oaks when T_a is low, while they prefer ashes in high temperatures (Ruczyński and Bogdanowicz 2008) indicating that microclimate conditions, and indirectly the tree species, are actively selected by bats. Smaller groups of Leisler's bats in oak and ash (the most selected roost tree species) than in other trees may be linked to the stage of the reproductive period: the 'other' trees (mostly alder) were largely selected when group size increased after the pups start to be volant, while oaks and ashes are used over the whole reproductive period. Our observations are in line with the hypothesis that the number of bats in the roosts is not a simple response to the ambient conditions but also a result of roost quality. To our knowledge, this is the first field study demonstrating that the selection of tree species by bats is linked with the group size.

The rate of roost switching was similar in both bat species despite the differences in body size. The results did not confirm that the switching behaviour is connected to the ambient temperature as such; however, we found that both species were more likely to leave a roost as the temperature increased. A larger increase, or smaller decrease, of ambient temperature from 1 day to the next has a positive effect on the roost switching rate. The roost tree also may have an

effect—the studied Leisler's bats stayed longer in oaks and ashes than in other tree species, although the difference was not significant. Therefore, the roost switching rate may be explained by the necessity of selecting more suitable roosting conditions after changes in weather conditions but may also be shaped by roost parameters. The results of Patriquin et al. (2016) on northern long-eared bats, where roost switching rates increased at higher temperatures and depended on tree condition, further support that roost switching behaviour is a species-specific trait and is shaped by roost parameters.

Accounting for social mechanisms of maintaining group cohesion, which may play an important role in shaping group size and the process of roost switching (Chaverri et al. 2013; Nad'ó and Kaňuch 2015; Nad'ó et al. 2017), should greatly improve the models explaining the roosting behaviour of bats. Ecological similarities among bat species were observed in previous studies analysing roost site selection and activity patterns (Ruczyński and Ruczyńska 2000; Ruczyński and Bogdanowicz 2005, 2008; Ruczyński et al. 2017). That suggests the mechanisms of fission-fusion dynamics in closely related species of bats living in the same area are similar, but not exactly the same.

Our study demonstrated that tree species and temperature influence the fission-fusion dynamics of European forest-dwelling bats in terms of group size and roost switching rate, depending on the stage of the reproductive period. A lack of clear effects of T_a on group size points out the complexity of bats' behaviour, therefore monitoring of components such as social bonds, food availability, body temperature, T_a and T_r , and possibly the metabolic rate is recommended in future studies of the fission-fusion dynamics. Importantly for conservation and management, our results suggest that the presence of suitable trees providing different microclimates is important for maintaining efficient fission-fusion dynamics.

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Data availability The datasets used in the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval We obtained permission for the field research from the Ministry of Environment of Poland and Local Ethical Commission in Białystok nr 2001/52. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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