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Bat community and roost site selection of tree-dwelling bats in a well-preserved European lowland forest

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Worldwide species density of bats is highest in forests ecosystems. European primeval forests are now reduced to a few small and isolated patches because almost all forests are subject to management. Therefore, knowledge about bats in ancient and near-natural forests in Europe is scarce. In the well-preserved forest stands of the Belovezhskaya Pushcha National Park in Belarus we studied the bat community (1), the presence of maternity colonies and their preference in tree roost selection (2) and parameters of roosts used by forest dwelling bats (3). By mist-netting surveys, we identified 13 bat species and acoustic data suggested the presence of another three species. We detected 15 maternity colonies of seven bat species by radio-tracking reproductive females and 40 tree roosts within the forest. Roosts of *Barbastella barbastellus*, *Pipistrellus pygmaeus* and *Plecotus auritus* were almost exclusively behind the loose tree bark of decaying trees, or within narrow crevices. *Myotis nattereri* and *Nyctalus leisleri* showed a preference towards hollows (e.g., woodpecker-made cavities) within oak trees (*Quercus robur*). Our study shows that all tree-dwelling bat species are highly dependent on natural processes within forests that allow the formation of roost sites. Therefore, we strongly support that the natural aging process of trees, as well as the consequences of natural disturbance (e.g. through weather), should be permitted. This should extend beyond the protected zones of National Parks. In contrast, sanitary cuttings decrease the habitat's suitability for forest-dwelling bats. Finally, our results indicate that the forest complex of Belovezhskaya Pushcha and Białowieża is one of the most important bat areas in Europe.

Key words: tree-dwelling bats, primeval forests, dead wood, radio tracking, Belovezhskaya Pushcha, conservation

Introduction

Bats represent a species rich mammalian order comprising more than 1,300 species worldwide. As diverse as the group of bats are, its members´ habitat requirements, roosting sites, foraging techniques and demographic parameters equally differ (Simmons and Conway, 2003). Globally, forests support the highest species density of bats (Russo *et al.*, 2016). In Europe, all bat species more or less spend at least part of their life cycle within forest stands as these provide important foraging habitats as well as roost sites (Law *et al.*, 2016).

Bat populations are influenced by several environmental factors, with the availability of suitable roosting sites being crucial to demographic parameters such as survival and reproductive success (Kühnert *et al.*, 2016). While some species adapted to roost in anthropogenic structures, many rely on natural roosts, e.g. rock crevices, caves and tree cavities. Tree-dwelling bats are highly dependent on the presence of large, old, dying or dead trees, as these provide potential roosts like woodpecker holes, fissures, peeling tree bark or decay holes (Racey and Entwistle, 2003).

The density, structure and quality of tree roosts affect thermoregulation, safety from predators and parasites, and the social behaviour (Kerth and König, 1999; Kerth *et al.,* 2001; Russo *et al.,* 2005; Dietz and Hörig, 2011; Kühnert *et al.,* 2016). Species-specific differences in roost choice have been reported, as well as the selection of different tree roosts depending on sex and reproductive cycle (Hörig and Dietz, 2013; Russo *et al.*, 2016). Therefore, the density and diversity of potential roosts affects the abundance, the diversity and the spatial distribution of bat communities.

Humans have shaped the distribution, composition and structure of forests (see Kahl and Bauhus, 2014; Kirby and Watkins, 2015). Due to commercial exploitation of forests and expansion of settlements, the overall forest area declined. Today, forest fragments cover a third (32.2%) of the European continent when excluding the Russian Federation (FAO, 2010). Yet, forests without logging activity are rare, with less than 3% (and declining) of European forests are classified as primeval (Kirby and Watkins, 2015) and less than 5% can grow without forest management.

Habitat diversity and carrying capacity for tree-dwelling bats often conflict with the interests of forest management (Ruczyński *et al*., 2010; Dietz and Pir, 2011). Timber is harvested before trees, considering age and size, become valuable as potential day-roosts (Ranius *et al*., 2009). Moreover, trees with fissures or large hollows and trees infected by diseases or pests are generally removed from the stand, as they produce wood of low quality or are considered a threat to the whole stand . Furthermore, forest managers reduce fire risk (removal of dry dead wood) and provide road security (removal of standing dead trees and dead branches). Hence, trees which are of high value for roosting bats are commonly kept to a minimum number in managed forests (Russo *et al.*, 2016). Therefore, roosting sites can be identified as the limiting factor for bats in managed forests (Racey and Entwistle, 2003).

One of the largest ancient near-natural forests in Europe spreads over the Polish-Belarusian border. The larger part of it is situated in Belarus (Belovezhskaya Pushcha together with adjoining forests) and the smaller part in Poland (Białowieża forest) (Kravchuk and Kravchuk, 2016). The vast forest area of Białowieża and Belovezhskaya Pushcha contains remnants of primeval forest as well as large areas of natural mixed forest well-preserved within natural heritage sites (Latałowa *et al*., 2015). The near-natural forest within the strictly protected zone is characterized by natural dynamics in an amount that is found only in very few European forests (Ruczyński, 2004; Krzyściak-Kosińska *et al*., 2014). This is reflected in high numbers and diversities of tree cavities resulting from dying and breaking trees as well as the activity of ten species of woodpeckers (e.g., Walankiewicz *et al.*, 2014). We hypothesize that natural dynamics and the lack of forest management in large parts of the forest provide high habitat suitability for forest-dwelling bats. Furthermore, considering the habitat continuity over centuries and the large area covered by near-natural forests, we assume that the forest complex of Belovezhskaya Pushcha and Białowieża is one of the most important bat areas in Europe.

Bat research in both parts of the forest has been conducted for decades [Belovezhskaya Pushcha — in 1955–1980's Kurskov (1958, 1981*a*, 1981*b*) and later in 1990–2010's Demianchik and Demianchuk (2006) and Demianchik (2013)] but with different results. For the Polish part of the forest 15 bat species were identified (I. Ruczyński, personal communication) but roost site selection was studied in detail only for *Nyctalus noctula* and *N. leisleri* (Ruczyński and Bogdanowicz, 2005). Both species are common and form maternity colonies in Białowieża but *N. leisleri* is barely known in Belarus and Belovezhskaya Pushcha (Demianchik and Demianchuk, 2006).

Our goal was to improve the knowledge of tree-dwelling bats for this unique forest and we intended to gain species-specific information on the type of roosts occupied by bats in this ancient and well preserved forest. In detail we intend to 1) analyse species composition of bats in the Belarusian part of the large forest, 2) localise maternity colonies and their preference in tree roost selection and 3) gain parameters of roosts used by forest dwelling bats.

Materials and Methods

Study Site

Our study was carried out on the territory of the "Belovezhskaya Pushcha" National Park in South-western Belarus (Fig. 1). It is part of a large and coherent forest complex spanning about 200,000 ha across the border to Poland. The forest is special because it appears to have never been substantially cleared for farming as have many other landscapes in Europe (Latałowa *et al*., 2015). It is one of the last remnants of European lowland forests. In total 141.890 ha of the forest are listed as UNESCO natural heritage site (IUCN). The Belarusian National Park stretches over an area of 152,900 ha of which 57,000 ha are strictly protected containing 8,000 ha of primeval forest (Nikiforov and Bambiza, 2008). Long-time protection measures and extensive anthropogenic forest use of main parts of the forest maintained a rather natural character (Krzyściak-Kosińska *et al*., 2014; Latałowa *et al*., 2015). Its location, between the Eurasian pine forest and the European broad-leaved forest region, provides the National Park with a transition forest type of the two regions. Dominating tree species are *Pinus sylvestris* and *Picea abies*. Broad-leaved forests are to the largest extent alder bogs with *Alnus glutinosa* as the main tree species, followed by broad-leaved and mixed-broad-leaved forest vegetation types dominated mainly by *Quercus robur*, *Tilia cordata*, *Fraxinus excelsior* and *Carpinus betulus*. Tree stands are of considerably old age with an average forest age of 97 years but in some areas 250–350 years. Individual trees may reach an age of 600 years (Nikiforov and Bambiza, 2008). Belovezhskaya

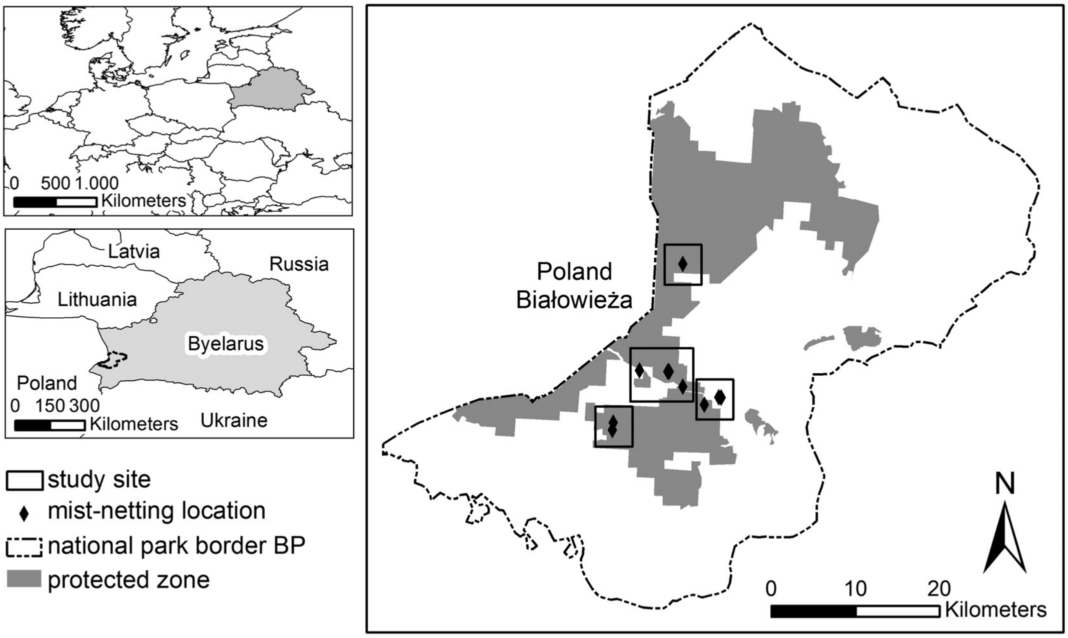

FIG. 1. Location of Belovezhskaya Pushcha (BP) National Park in Belarus with research areas in 2014–2016

Pushcha is situated in the temperate zone but with strong influence of continental climate. The average annual temperature is 6.6°C and spans between more than 30°C in summer and -26°C in winter time. The average precipitation is 648 mm per year with 420 mm during summer period from April to October. This is the lowest value in Belarus (Nikiforov and Bambiza, 2008). Prior to our study, 15 bat species had been proven within the territory of the 'Belovezhskaya Pushcha' National Park but knowledge about maternity-colonies, abundance and distribution of forest dwelling species was limited (Demianchik, 2013).

Species Detection

To identify day-roosts of tree-dwelling bats we used a combination of mist-netting and radio-tracking. Simultaneous acoustic monitoring allowed for additional species detection.

Mist-netting locations were set up at four different sites representing old forest types (e.g., Tilio-Carpinetum, Querco-Piceetum and Pino-Quercetum) within the strictly protected zone of the National Park and forests in the managed zone. Considering its dimensions, mist-netting surveys only covered a very small part of the total forest area (Fig. 1). At each mist-netting location, nets with a total length of at least 70–90 m were set up. Mist-netting took place during 22 nights in June 2014–2016 and each session lasted from sunset until sunrise. During a session nets were checked every 10–15 minutes and captured bats were immediately examined and released. Each individual was identified by species, sex and reproductive state following Racey (2009). Acoustic surveys were conducted at the mist-netting sites using a Pettersson D1000 bat detector. Additional automated acoustic surveys were conducted within the framework of another study on bat communities in different forest types (unpublished data). The surveys were performed within the area of the National Park using 'batcorder' (ecoObs GmbH, Nuremberg) ultrasonic recording devices. All bat calls were analysed using the software BatSound (Pettersson, Sweden) or bcAnalyze (ecoObs GmbH, Nuremberg).

Roost Identification

To gain information on roost occupation, female individuals captured during the 22 mist-netting sessions were fitted with small radio transmitters. Radio transmitters (Holohil, Canada, mass: 0.4 g) weigh less than 5% of one individual's body mass and therefore do not restrain activity (Aldridge and Brigham, 1988). The transmitters were attached with medical glue to the fur between the shoulder blades in order not to disturb flight movement. The tagged females were tracked during subsequent days to identify day-roosts according to the homing-in on the animal method (White and Garrott, 1990). We used a Yaesu receiver (Wagener, Cologne) with a two element Yagi antenna (HB 9CV).

In total 23 reproductive females of nine species were fitted with radio transmitters and tracked to their roosts (*Myotis daubentonii*, *M. nattereri, M. brandtii, Barbastella barbastellus, Plecotus auritus, Pipistrellus pygmaeus, P. nathusii, Nyctalus leisleri, Eptesicus nilssonii*). Parameters of roost trees (species, age, diameter at breast height (DBH) and vitality), of the cavities (height from ground, exposition and type) and of the habitat type (forest age, ground cover and tree species composition) were noted. Emergence counts were conducted in the evening. The coordinates of roost trees were taken using a GPS device (Garmin Etrex 20x).

RESULTS

Species Composition

In total, we identified 13 bat species and the collected acoustic data suggested the presence of another three species within Belovezhskaya Pushcha National Park (Table 1), representing almost all species known for the territory of Belarus. Twelve species were caught by mist-netting. Acoustic surveys provided distinct records of *Pipistrellus pipistrellus*. Furthermore, calls identified as *Myotis dasycneme*, *M. alcathoe* and *Nyctalus lasiopterus* appeared on our records, but will require mist-netting evidence.

We caught 96 bats during 22 mist-netting sessions, most of them at small ponds in forest gaps and across small forest paths. The comparably high number of tree-dwelling *M. daubentonii* (*n* = 31) reflects the mist-netting location near waterbodies. *Plecotus auritus* (*n* = 19) and *M. nattereri* (*n* = 8) represent examples of species flying in cluttered habitat close to vegetation. Near-edge foragers are *B. barbastellus* (*n* = 10), *M. brandtii* (*n* = 1), *P. pygmaeus* (*n* = 5) and *P. nathusii* (*n* = 6). Open space foragers are represented by *N. leisleri, N. noctula*, *E. nilssonii, E. serotinus* and *Vespertilio murinus.* Nearly three-fourths (76%) of the captured bats were female and 24% male. For *E. serotinus* and *V. murinus*, only male bats were captured. The presence of *E. nilssonii*, *N. leisleri*, *N. noctula*, *P. nathusii* and *P. pygmaeus* was verified by female individuals only. All bats were adults. 49% of female bats were gravid and 33% lactating at the time of capture.

Maternity Roosts and Colony Size

Radio-tracking 23 females of nine species we identified 15 maternity colonies of *P. pygmaeus* (4), *P. auritus* (3), *B. barbastellus* (2), *M. nattereri* (2), *N. leisleri* (2), *E. nilssonii* and *P. nathusii* (one each). A distance of several kilometres between roosts of one species and simultaneous recordings allowed us to clearly distinguish different colonies. The size of the colonies differed widely between species but little within. Colonies of *P. pygmaeus* reached up to 200 adult individuals and colonies of *P. nathusii* up to 75 adults. Roosts of *N. leisleri, B. barbastellus, M. nattereri* and *P. auritus* never contained more than 24 adult females. During the life-span of the transmitters, radio-tracked females showed 41 maternity roosts (Fig. 2) of which 40 were natural tree roosts and only one was located in a farm house close to the forest (*P. pygmaeus*).

The identified eight tree roosts of *B. barbastellus* were all decaying and mainly coniferous trees, most of them dry spruce (*Picea abies*). Maternity colonies occupied crevices behind loose bark. For the narrow-space foragers *M. nattereri* and *P. auritus* eight and seven roosts were localized respectively. *M. nattereri* roosted in tree holes caused by woodpeckers (29%) or broken off branches (57%), whereas *P. auritus* were mainly located in crevices (40%) or behind loose tree bark (40%). *N. leisleri* showed eight roosts, all of them in more than 200-year-old, large oak (*Quercus robur*) and pine (*Pinus sylvestris*) trees (lightning-crevices, woodpecker made cavities). Maternity roosts of *P. pygmaeus*

TABLE 1. Bat community in the large forest complex of Belovezhskaya Pushcha and Białowieża. Recent study means own results from 2014–2016. Abbreviations explain the form of identification described in literature: summer roost in **T**ree cavity or **B**uilding, **br**eeding, **h**ibernation, **o**ther; numbers refer to citation

No.	Species	Recent study			Literature
		Mist-netting	Acoustic	Maternity roost	
1	*Barbastella barbastellus*	x	x	x	T, h: 1; 2; 4
2	*Myotis alcathoe*		x		o: 11
3	*M. brandtii*	x			T, o: 1; 13
4	*M. daubentonii*	x	x	x	H, br: 1; 2; 4; 6
5	*M. dasycneme*		x		o, br: 9
6	*M. nattereri*	x		x	h: 1
7	*Plecotus auritus*	x		x	B, h: 1; 2; 3;
8	*P. austriacus*				o: 12
9	*Nyctalus leisleri*	x	x	x	T, br: 4; 8; 10
10	*N. lasiopterus*		x		o: 11
11	*N. noctula*	x	x	x	T, br: 2; 4; 8;
12	*Eptesicus nilssonii*	x	x	x	o: 2; 4;
13	*E. serotinus*	x	x	x	B, br: 2; 3; 5
14	*Vespertilio murinus*	x	x	x	B, br; 2; 3; 4; 5;
15	*Pipistrellus nathusii*	x	x	x	B, br: 2; 3; 4
16	*P. pygmaeus*	x	x	x	B, br: 5;
17	*P. pipistrellus*		x	x	B, o: 2; 3; 4; 7

Daleszczyk, 2000[1]; Demianchik and Demianchuk, 2006[2]; Hermanns *et al*., 2001[3]; Kurskov, 1958, 1981[4]; Mazurska and Ruczyński, 2008[5]; Rachwald *et al*., 2001[6]; Rachwald and Ruczyński, 2015[7]; Ruczyński and Bogdanowicz, 2005[8]; Ruczyński and Ruczyńska, 2008[9]; Ruczyński and Ruczyńska, 2000[10]; I. Ruczyński, personal communication[11]; Ruprecht, 2004[12]; Sachanowicz and Ruczyński, 2001[13].

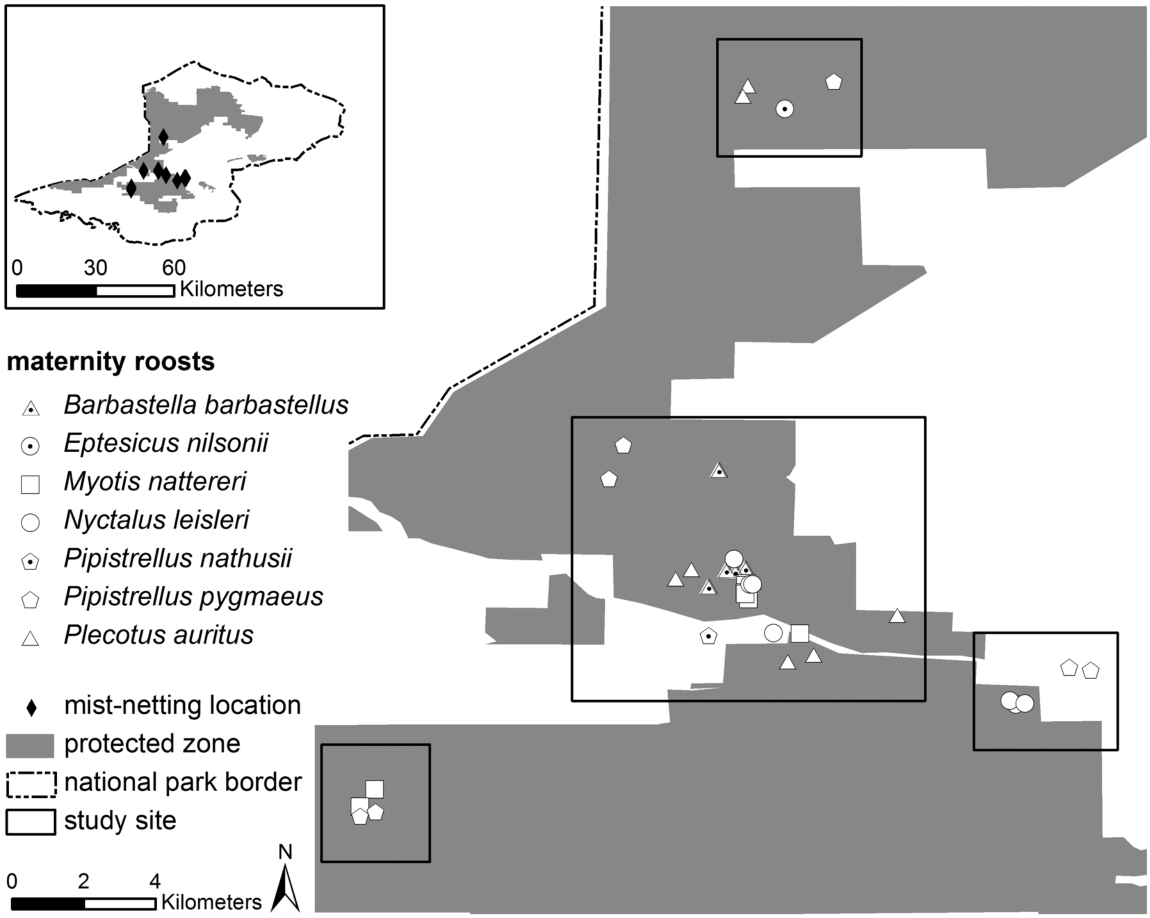

FIG. 2. Location of roost trees from maternity colonies localized in Belovezhskaya Pushcha National Park

settled behind bark or in crevices in broad-leaved trees, some of them decaying. The cavity of one day-roost was caused by lightning stroke and nearly 200 individuals emerged from branches in the canopy of a large old oak and a second colony was found at the top of an old maple tree (*Acer platanoides*), with 191 females flying out of a narrow crevice (Fig. 3). The two roosts discovered for *P. nathusii* were both in old (> 200 years) dying pine trees. One roost was located behind loose tree bark and the other in a crevice.

In summary, nearly 40% of all maternity roosts were in standing dead trees. More than 80% of the occupied roost-types were a consequence of natural aging processes like loose tree bark, fissures and crevices after lightning stroke or breaking-off of branches. The remaining 20% of the roosts were made by woodpecker species (e.g. *Dendrocopos major, Leiopicus medius*). Trees measured between 40 and more than 120 cm DBH and roost entrances were found between 6.5 and > 30 m height above ground (Fig. 4).

DISCUSSION

The study revealed the diversity of day-roosts for tree-dwelling bats in old-growth forests of Belovezhskaya Pushcha National Park in Belarus. The use of radio tags, which was implemented for the first time within the Belarusian part of the forest, allowed to collect new data on roosting sites of forest dwelling species, as historically data on bat roosting was mainly limited to roosts located in buildings and accidental records of roosts in trees (Kurskov, 1981*a* and 1981*b*, Demianchik and Demianchuk, 2006). According to the EUROBATS (2014) National Report, 19 bat species have been verified for Belarus; *M. dasycneme* is noted as rare, *M. alcathoe* is yet to be proven within the country and *N. lasiopterus* was recently rediscovered (Dombrovsky *et al.*, 2016). Beside the restricted *Myotis myotis* (last registration for Belarus in 1970) and *Pipistrellus kuhlii* as a new species identified in 2013 (Demianchik, 2013), we found all species in the Belovezhskaya Pushcha National Park.

FIG. 3. Examples of maternity roost trees discovered by radio telemetry in Belovezhskaya Pushcha. Top left: dying coniferous trees with peeling bark, maternity roosts of *B. barbastellus*; Top centre: fissure and loose bark of a pine tree, maternity roost of *B. barbastellus*; Top right: loose tree bark of an oak tree, maternity roost of *B. barbastellus*; Middle left: woodpecker hole in an oak tree, maternity roost of *N. leisleri*; Centre: large old oak with a lightning crevice as maternity tree of *N. leisleri*; Middle right: branch break-off in a birch tree, maternity roost of *M. nattereri*; Bottom left: dying spruce stands with maternity roost of *P. auritus*: Bottom centre: fissure in an aspen tree, maternity roost of *P. pygmaeus*; Bottom right: maternity roost of *P. pygmaeus* behind bark in the canopy of an old oak destroyed by lightning

The study confirms the efficient approach for localizing maternity roosts in trees by radio-tracking reproducing females. We identified four maternity colonies of *P. pygmaeus* in trees, whereas one colony changed between different trees and an old farm house. Further we found maternity colonies of the endangered *B. barbastellus*, *M. nattereri* and *N. leisleri* and a reproductive female of *M. brandtii*, assumed as one of the rarest species of the Belarusian bat fauna (Shpak, 2010). Although searching for several days we could not identify the maternity colony of this species because we lost the signal of the tag, perhaps caused by a technical defect. Mainly female bats were captured, which highlights the importance of the Belovezhskaya Pushcha forest area for maternity roosts and hence for the reproductive success of these species. This is in accordance to Ruczyński and Bogdanowicz (2005) who stated that a rich community of vertebrates uses tree holes as breeding sites in Białowieża Forest on the Polish site.

The tagged females showed high frequency in roost switching; it occurred every (other) day for several consecutive days. This behaviour avoids

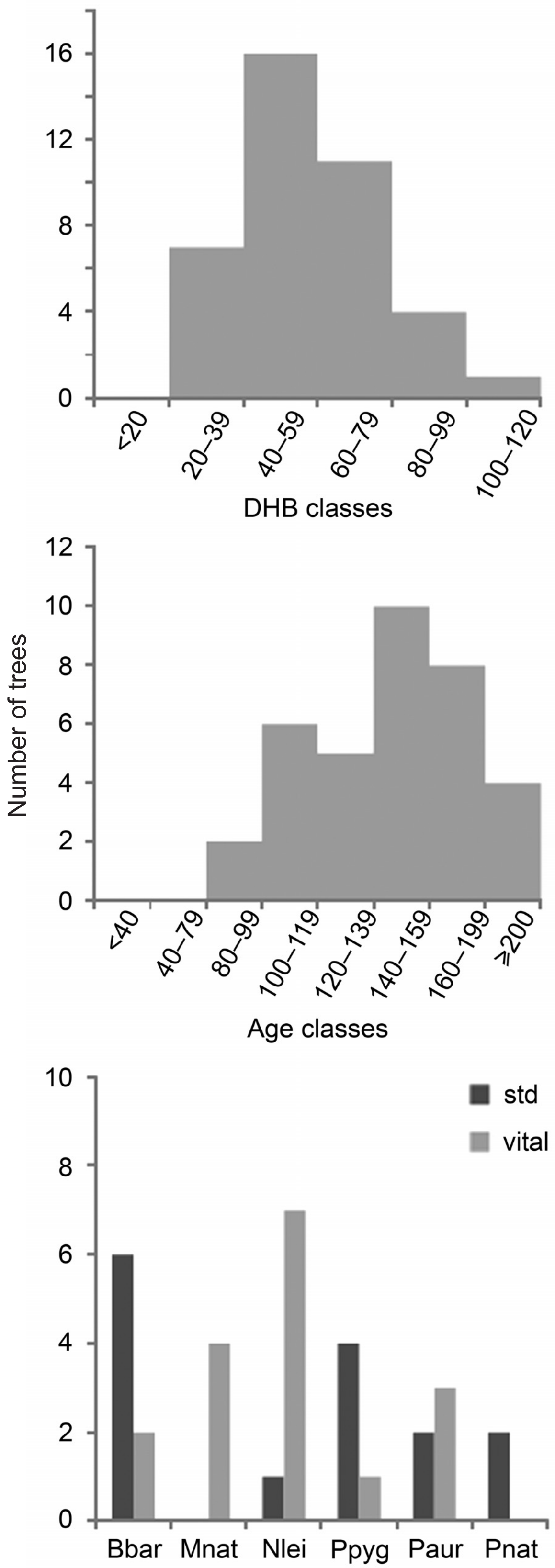

FIG. 4. Characteristics of maternity trees in Belovezhskaya Pushcha (top: diameter breath height: DBH; middle: age class; bottom: vitality; sdt: standing dead tree) (Bbar = *B. barbastellus*; Mnat = *M. nattereri*; Nlei = *N. leisleri*; Ppyg = *P. pygmaeus*; Paur = *P. auritus*; Pnat = *P. nathusii*)

predation and parasitism and requires a high abundance of suitable roosts. With respect to the small research areas within this large forest (see Fig. 1), and the very limited investigation periods with a couple of days in June 2014–2016, the results are remarkable and indicate a high habitat quality. The forest provides refuge to species dependent on natural forests, which are probably highly abundant in Belovezhskaya Pushcha. The large forest has never been significantly cleared for agricultural land use, but a variety of anthropogenic interventions of different intensity occurred . Mainly in the strictly protected zone the forest is characterized by natural dynamics which is found in very few European forests (Ruczyński, 2004; Krzyściak-Kosińska *et al.*, 2014). The natural aging process leads to a rather old stand age with accumulations of dead wood and gaps caused by falling trees (Ranius *et al.*, 2009). Weather events such as storms and lightnings entail not only the creation of small gaps but also of fissures due to broken off branches or lightning strokes.

For the Polish part of the forest, data about roost choices for bats is rare but very well investigated for noctules (Ruczyński and Ruczyńska, 2000; Ruczyński, 2004). Ruczyński and Bogdanowicz (2005) compared roost cavity selection of *N. noctula* and *N. leisleri*. They found that *N. leisleri* used crevices and cavities caused by branches breaking off more often (90%) than woodpecker cavities (10%), whereas *N. noctula* showed the opposite tendency and mainly occupied woodpecker-made cavities. The authors assume that the ratio of woodpecker-excavated cavities to natural ones in Białowieża forest is smaller than that recorded in forests in Western Europe, suggesting a possible preference by bats in Western Europe for woodpecker-made cavities. In the managed forests of Western Europe, woodpeckers are a key species for several tree-dwelling bat species by providing suitable day-roosts (Dietz and Hörig, 2011; Dietz and Pir, 2011). Besides this, studies on bat assemblages in Central and Western Europe show that roost choice is species dependent. Roosts created by natural processes are essential for a diverse bat community in forests (Dietz, 2010; Krannich and Dietz, 2013; Bouvet *et al.*, 2016) and for the occurrence of specialised species. Russo *et al.* (2010) found dead and dying trees as favoured roost sites for *B. barbastellus* six times more in unmanaged than in managed European beech (*Fagus sylvatica*) forests in central Italy. From the seven maternity roosts in Belovezhskaya Pushcha and 45 tree-roosts that we found in Germany and Luxemburg (Pir and Dietz, 2014), more than 75% were situated behind loose tree bark and decaying trees older than 80 years. An important driver of suitable roost sites is dryness and the colonisation of large spruce (*Picea abies*) by European spruce bark beetle (*Ips typographus*). A recent study of Kortmann *et al.* (2017) revealed that outbreaks of bark beetles result in forest structural attributes that are suitable habitat for *B. barbastellus*. The study, in the Bavarian National Park in Germany, recorded maternity colonies of *B. barbastellus* exclusively in trees that died after bark beetle settlements. The assumption is that salvage logging, i.e., the removal of beetle-affected trees, generally deteriorates the positive effects of bark beetle outbreaks on the foraging and roosting habitat of *B. barbastellus*.

For *P. pygmaeus,* seven roosts were identified in Belovezhskaya Pushcha, of which only one was in a farm building. All the tree roosts were behind loose tree bark or in crevices. Most of them were located in decaying broadleaved trees of DBH 60–120 cm. From a cavity in the canopy of an old oak caused by a lightning strike, more than 200 individuals emerged. Recently, only a few tree roosts of the Soprano pipistrelle are known in Europe. Therefore, the information we could collect is invaluable for conservation measures. In Germany, most maternity roosts known from this species are located in buildings (Dietz *et al.,* 2009). Natural roosts from this species are found in standing dead wood of huge diameter (Bouvet *et al.,* 2016). Compared to *B. barbastellus*, maternity colonies of *P. pygmaeus* were nearly ten times larger in Belovezhskaya Pushcha. Therefore, they may require larger crevices, which in Central and Western Europe are partly substituted by roosts in buildings.

Conservation Implication

Our results confirm that the forest complex of Belovezhskaya Pushcha and Białowieża is one of the most important bat areas in Europe. This is in accordance with previous studies on bats (e.g., Kurskov, 1981*a*, 1981*b*; Demianchuk and Demianchik 2006, Ruczyński and Bogdanowicz, 2005, 2008; Ruczyński *et al*., 2010; Polakowski *et al*., 2014), and also on birds (e.g., 10 species of woodpeckers which comprises nearly the entire European fauna in the family Picidae — Wesołowski *et al*., 2006).

The results underline the importance of natural dynamics in old-growth and partly unmanaged forests for tree dwelling bats. Minimal anthropogenic interference leads to old trees, a high volume of trees and increasing dead wood. All factors support the development of tree cavities and therefore roost sites for bats (see also Ranius *et al*., 2009). A comparison of managed and unmanaged forest areas in Białowieża forest revealed the highest density of cavities in the unmanaged national park (12.5/ha) and the lowest in managed forest plots (3.0/ha). Most cavities were found in dead trees (Walankiewicz *et al*., 2014).

The amount of tree holes is one key habitat requirement for bats in forests. Tree dwelling bats frequently switch roosts, either to maintain social relationships (Kerth *et al.*, 2011), to develop cognitive maps of alternative roost locations (Russo *et al.,* 2005) or to decrease parasite burden (Bartonička and Gaisler, 2007). Many bat species roost in trees, which provide a variety of cavity types offering a range of thermal conditions (Kunz and Lumsden, 2003; Dietz and Hörig, 2011). Continuous radiotracking studies showed that a maternity colony uses many tree roosts during a summer and recurrently over several years (Dietz and Pir, 2011). To preserve even a bat population of small size, large numbers of suitable trees are needed (Russo *et al*., 2016). Therefore, destruction of roosts through forest management is one of the main factors responsible for population declines (Racey and Enwistle, 2003; Hayes and Loeb, 2007).

In the Białowieża National Park, tree volume is more than twice as high as in the surrounding commercial managed forests and dead wood volume may reach 87–160 m^3/ha (Bobiec, 2002). Considering dead wood quantity in Belarusian forests declined between 2000 and 2010 from 2.1 to 1.2 m^3/ha the importance of natural forest patches with high quantity of dead wood increases obviously (Ranius *et al*., 2014; European Environment Agency, 2015).

In managed forest stands wood is regularly removed, which alters quantity but also quality of dead wood. Forest management goal is to use timber before reaching natural decay and death phases of trees to provide a sufficient amount of timber with a high grade. Moreover, it is common to remove deadwood in managed forests due to concerns over forest health and to avoid fires. Unfortunately, this can also take place in National Parks. For example, the Polish government started to conduct massive logging assumed to counter an outbreak of European spruce bark beetle (*Ips typographus*) disease in the Białowieża Forest (Chylarecki and Selva, 2016; Michalak, 2016). Our results in the Belarusian part of the large forest and equally results in the previously mentioned German study showed that many maternity roosts of the endangered barbastelles are still settling in these decaying stands of spruce and pine forests. Hence, the so called sanitary-cuttings are in contrast with the conservation targets of National Parks.

In managed forests the removal of trees before their terminal phase leads to very little dead wood originating from natural mortality processes. Dead wood, though, provides key ecosystem functions like C-storage, nutrient cycling and the provision of habitat for many species (Kahl and Bauhus, 2014). It is a key factor for biodiversity in most forest ecosystems and hence the most dramatic resource loss during transition from natural to managed forest (Kaila *et al*., 1997; Paillet *et al*., 2010; Bernes *et al*., 2016; Jonsson *et al*., 2016). Bouvet *et al*. (2016) found that the richness of especially gleaner bats is positively influenced by the density of standing dead wood. Standing dead wood may facilitate roosts of bats dependent on tree cavities. In fact, the presence of standing dead wood implies natural mortality processes, may they be caused by age, disease, catastrophic events or pests. Yet, lying dead wood may not provide roosts but support insect populations and structural diversity. Kirby and Watkins (2015) state that areas designated for biodiversity conservation have to increase in Europe as well as the amount of dead wood in forests (European Environment Agency, 2015). Yet, the quality of dead wood and its distribution across forest patches has not been addressed. It nonetheless plays a significant role in identifying consequences for bat conservation.

Further, foraging areas are a crucial part of suitable habitat. Flying is an energy demanding way of locomotion, hence the distance to and the quality of feeding grounds factor into habitat suitability. Forests with decaying and dead wood may support high insect populations, allowing for close foraging areas (Bernes *et al.,* 2016; Tillon *et al*., 2016). In general forests provide foraging areas for multiple species as diverse structures are available for different foraging styles: clearings, forest edges, forest ground, cluttered vegetation or the canopy (Fuentes-Montemayor *et al.*, 2013).

As a consequence forests need to provide great quantities of potential roosts in form of either old trees with narrow crevices, woodpecker-made cavities or decaying and dead trees with loose bark. Our results indicate that the natural aging processes and day roosts caused by catastrophic weather events, disease or pests need to be tolerated, in particular in the protected zones of National Parks. It is of major importance to support natural dynamics in European forests, provide a substantial amount of old, decaying and dead trees and to cut back on anthropogenic interference in order to provide habitats for forest dwelling bats and many other species.

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