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RESEARCH PAPER

Maternity roosts of the giant noctule, *Nyctalus lasiopterus*, in preserved and disturbed forests of the Western Carpathians

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Abstract. The giant noctule is a rare European bat about which we have little ecological information, but it is a priority species for which we need to determine the best conservation measures. Acoustic monitoring followed by a radio-tracking survey resulted in the localisation of two maternity colonies in different forest areas in the Western Carpathians, one in protected mixed stands in a national park (Muránska planina Mts) and the other in disturbed secondary spruce forests (Balocké vrchy Mts). The 95% home-range polygon of the roosts was about 3.5 km^2 for both colonies. Eurasian aspen (*Populus tremula*) accounted for 100% of roosts (n = 18 trees) in mixed stands. However, even in the spruce monocultures, bats roosted in cavities of this tree whenever possible, although 76% of roosts (n = 21 trees) were still in Norway spruce (*Picea abies*). Regardless of forest type, the bats preferred to roost at the edges of the stands and on steep slopes that offered a free exit from the roost into open space. Small-scale salvage logging during bark beetle outbreaks can also create suitable open roosting habitats. Our observations indicate that structured stands with a higher proportion of aspen will positively affect tree-dwelling bats in mountain forests.

Key words: arboreal bats, greater noctule, forest management, nature conservation, temperate zone, tree hollows

Introduction

The European bat fauna comprises only a fraction (approx. 3%) of the worldwide species diversity of this group (Simmons & Cirranello 2024). Although bats in Europe or the Western Palaearctic region have been extensively studied, and we have relatively complete ecological knowledge of most species compared to the rest of the world, there are still some representatives for which we need more information. These species are usually scarce, and descriptions of their ecological requirements are often biased by the local environmental characteristics from which the data originate. One such species is the giant noctule (*Nyctalus lasiopterus*), the largest vespertilionid in the continent, which is listed as a priority species for autecological studies according to the current resolution of the Agreement on the

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Conservation of Populations of European Bats to identify the best conservation action (EUROBATS 2022). Research should focus primarily on roosts, habitat and spatial activity, among other aspects. This characteristic tree-dwelling species inhabits extensive forest formations with large and/or dead, cavity-rich trees, and its distribution area is highly fragmented and concentrated in the Mediterranean region and the Balkans. Breeding populations in the Western Carpathians (Slovakia, Hungary) and East European Plain (Ukraine, Belarus, Russia) occur at the northern limit of its range (Ibáñez & Juste 2023).

The best current information on the roosts and roost-switching behaviour of the species comes from Andalusia in southern Spain. Detailed studies of the large population (approx. 500 individuals), which occupies several dozen roosts in a small old city park, have shown that the maternity colonies of the giant noctule live in fission-fusion dynamics, with smaller groups reassembling daily. In this unique population, all roost trees are in close proximity to each other, and all bats can use each roost equally (Popa-Lisseanu et al. 2008, Fortuna et al. 2009, Santos et al. 2021). Much less information is available from other regions where tree roosts of nurseries (Hungary – Estók et al. 2007, France – Dubourg Savage et al. 2013, Belarus – Dombrovski et al. 2017, Slovakia – Naďo et al. 2019, Italy – Russo et al. 2023) or non-reproductive male colonies (Corsica – Beuneux et al. 2010, Catalonia – Camprodon & Guixé 2013) have been reported. Only roosts of a single maternity colony were identified in each area where breeding was confirmed. As these colonies roost in distinct bioclimatic regions, the differences in forest cover, roost trees, size and spatial arrangement of roosts are probably due to local environmental conditions (e.g. mean summer temperature) rather than preferences of the different populations. Therefore, to elucidate general patterns in habitat selection, data from contrasting forest habitats within the same region might be more appropriate (Fabianek et al. 2015). For example, a comparison between colonies in the urban park of Seville and in the forests of Doñana National Park, both in Andalusia, has shown that greater home ranges occur in areas where roosts are a scarce and widely dispersed resource (Popa-Lisseanu et al. 2009).

In this paper, we compare the habitat and spatial characteristics of the roosting territories of two breeding colonies of the giant noctule in the mountainous region of the Western Carpathians. These colonies roosted in distinct forest environments, one characterised by protected mixed stands in a national park and the other by disturbed spruce plantations. Along with new observations, we also re-analysed some data previously published by Naďo et al. (2019), aiming to contribute to the knowledge of the ecology of this rare species.

Material and Methods

Data collection

Data collection occurred in central Slovakia, around and between two localities, where the first three specimens of the giant noctule were mist-netted almost simultaneously in the summer of 2005 (Uhrin et al. 2006). Our sampling therefore focussed on the mountains of Poľana, Sihlianska planina, Balocké vrchy and Muránska planina. To find potential sites to focus survey efforts, we first employed acoustic monitoring and then radio-tracking of individuals to locate maternity colonies of this rare woodland bat (O'Malley et al. 2023). From May to September 2017-2020, we recorded bat activity with the automatic ultrasonic detectors Batlogger A and Batlogger C (Elekon, Switzerland) at 21 sites for 153 days (1-30 days per site). The devices were preferably installed on hilltops in open habitats or near larger water reservoirs, where we expected a higher probability of detecting foraging or drinking individuals. To equip the individuals with transmitters (standard VHF tags Pip Ag379 and PicoPip Ag376 or the GPS devices PinPoint 50 VHF Download with beacon radio signal; Lotek, UK), we caught them in mist nets that were set up over small bodies of water or stream fords. While the GPS tags (2.9 g) accounted for about 5% of the animal's body mass, the various radio tags (≤ 1.7 g) were far below the ethically acceptable package weight for this species. The efficiency of the mist-netting was increased by playing echolocation and social calls of conspecifics on a BatWav PCM384 (Peersonic, UK) bat lure. Roosting individuals were located during the day using a TRX-3S receiver (Wildlife Materials, USA) with a three-element directional Yagi antenna. We tracked nine individuals (four adult females, one juvenile female, and four juvenile males) in July and August 2017-2018 (10-30 days per individual) in the Muránska planina Mts and 11 adult females in July and August 2021-2022 (3-17 days per individual) in the Balocké vrchy Mts. For more details on equipment and radio-tracking, see also Naďo et al. (2019). Information on the structure of tree species in forest habitats was obtained from the online map resources of the National Forest Centre in Slovakia (https://gis.nlcsk.org/islhp/).

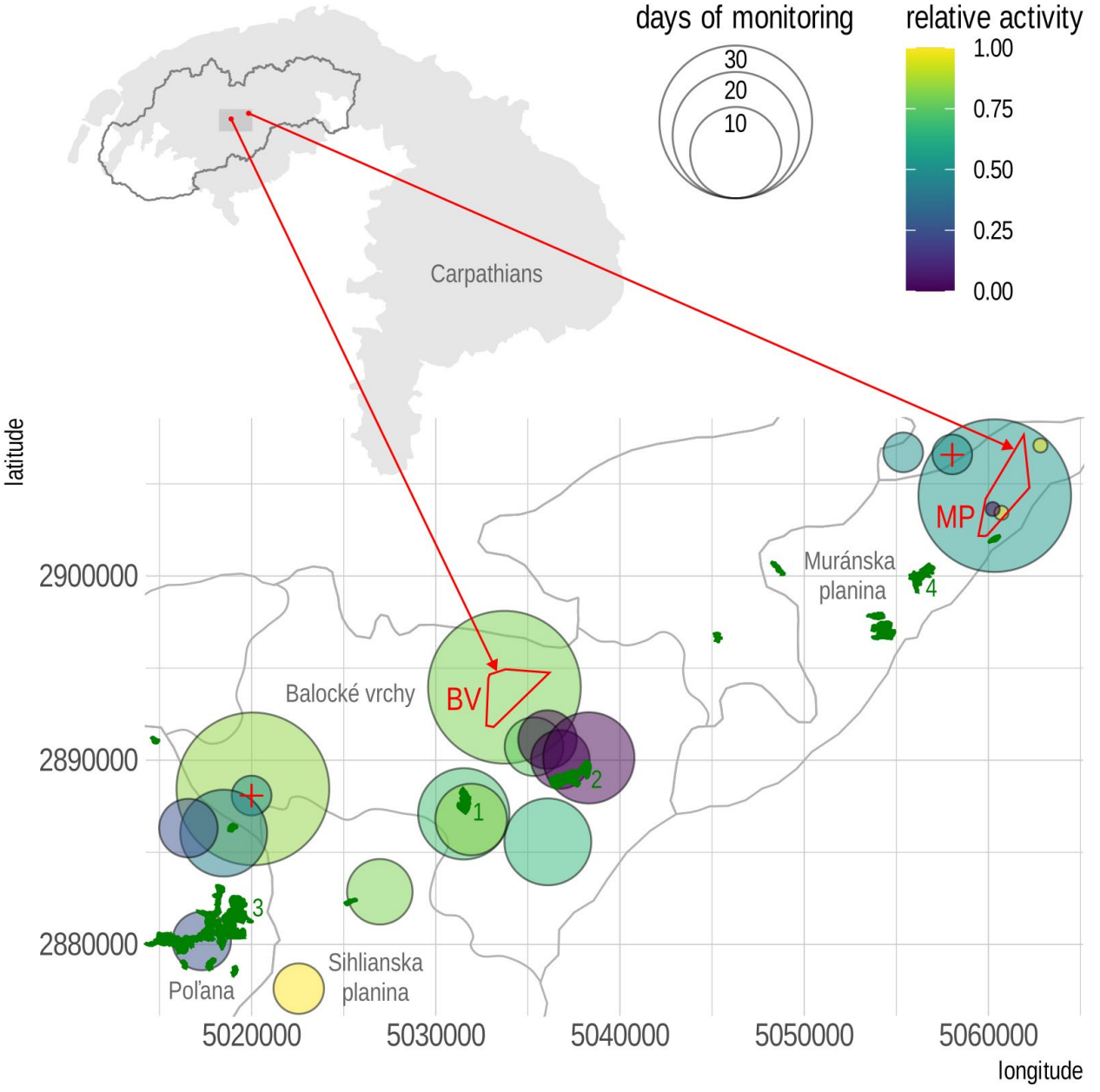

Fig. 1. Activity of the giant noctule, *Nyctalus lasiopterus*, as recorded by automatic ultrasonic detectors (circles) in central Slovakia (Western Carpathians), where two maternity colonies of the species have been established (BV – Balocké vrchy Mts, MP – Muránska planina Mts). The red polygons are convex hulls for tree roosts of bats. The red crosses show the sites where the first individuals were mist-netted in 2005 (Uhrin et al. 2006). The green polygons are remnants of primaeval forests: 1) Dobročský prales, 2) Klenovský Vepor, 3) Poľana, 4) Poludnica (source https://pralesy.sk). The coordinate reference system is ETRS89-extended/LAEA Europe (metres).

Data analyses

The ultrasound recordings were analysed with the BatExplorer software (Elekon, Switzerland) using identification criteria of the giant noctule call characteristics (e.g. Barataud 2015, Bartonička et al. 2019) with manual control. The relative activity in the acoustic data was calculated as the proportion of days on which some echolocation calls of the species were recorded out of the total number of days on which activity was monitored at the site. To estimate the size of the roosting territory, we calculated the 95% home range and the 50% core range from the roost locations using two methods, minimum convex polygon (MCP) and kernel density estimation (KDE), implemented in the package 'adehabitatHR' (Calenge 2023a) in the R 4.1.2 environment for statistical computing (R Core Team 2021). The digital terrain models (source DMR3.5, resolution 10 m, https://www.geoportal.sk/) and the linear distances between neighbouring roosts (each roost was joined to its nearest neighbours using Delaunay triangulation) were created with the software QGIS 3.22.4 (https://qgis.org/). Trajectories of individuals during roost switching were calculated using the R package 'adehabitatLT' (Calenge 2023b).

Table 1. Sizes of roosting territories of two maternity colonies of the giant noctule, *Nyctalus lasiopterus*, in central Slovakia (Western Carpathians), were calculated using two different methods (MCP – minimum convex polygon, KDE – kernel density estimation).

Area (km^2)	Balocké vrchy Mts	Muránska planina Mts
MCP		
95% home-range	3.45	3.47
50% core-range	0.29	0.86
KDE		
95% home-range	16.03	22.71
50% core-range	2.98	4.81

For non-parametric statistical tests, functions of the R core package 'stats' were used, and plots were made with the package 'ggplot2' (Wickham 2016).

Results and Discussion

In the period 2017-2022, acoustic monitoring with a follow-up radio-tracking survey led to the localisation of two maternity colonies of the giant noctule in the study area, namely in the Balocké vrchy (hereafter BV) and Muránska planina (hereafter MP) mountains. The centres of roosting ranges of these two colonies were 29 km apart as the crow flies. The relative activity of the giant noctules recorded by the ultrasonic detectors (58% of the monitored days were positive for the species' calls) did not correlate with the distance from the colonies' roosting ranges (Spearman's rank correlation test, $\varrho = -0.03$, $P = 0.89$; Fig. 1). It is therefore not possible to deduce from the acoustic data whether there are other colonies in this mountain area or whether this pattern only shows that the species also forages far away from the roosts (e.g. Camprodon & Guixé 2013, Naďo et al. 2019, Pineda 2023). However, based on the acoustic data, it may be possible to prioritise other sites for further surveys (cf. O'Malley et al. 2023) if the research is extended to a larger region of the Western Carpathians.

Bats roosted in cavities of large trees in different decay stages (21 trees in BV, 18 trees in MP). The cavities were all excavated by woodpeckers (Fig. 2). In BV, they were located at a height of 5-20 m (mean 11 m) above the ground, which was slightly higher than in MP (4-17 m, mean 8 m; Naďo et al. 2019). The 95% MCP home-range was approx. 3.5 km^2 for both colonies (Table 1), and this conservative measure appears to be more relevant for this system than the KDE method, which likely overestimates roosting areas there (Fig. S1). Tree species composition and forest management in the surveyed areas differ substantially. The MP colony is located in the Muránska planina National Park in relatively well-preserved limestone beech and mixed forests (105-150, mean 145 years old), 83% of which are unmanaged and in which the processes of natural forest dynamics are protected. In contrast, 100% of the stands (85-110, mean 90 years old) in which the BV colony has survived have been converted into Norway spruce (*Picea abies*) monocultures in the past. There is almost no Eurasian aspen (*Populus tremula*) in the monocultures of BV, but the bats roosted in this tree whenever possible (Fig. 3). Otherwise, the bats there roosted mainly in Norway spruce (76%), in contrast to the preserved stands in MP, where aspen accounted for 100% of roosts (Naďo et al. 2019). Therefore, the absence of aspen and/or the abundance of cavities in a dominant tree species could explain the selection of beech in natural mountain beech forests in the nearby Mátra Mts in northern Hungary (Estók et al. 2007). Despite the great diversity of tree species that can serve as nursery roosts for *N. lasiopterus* throughout its range (e.g. Estók et al. 2007, Popa-Lisseanu et al.

Table 2. Distances between two neighbouring roosts (d), given as medians or values less than and maximum distances between the most distant tree roosts (d_{max}) in different populations.

Population	d (km)	d_{max} (km)	n	Source
Slovakia (Balocké vrchy Mts)	0.46	4.47	21	this study
Slovakia (Muránska planina Mts)	0.81	5.99	18	this study
Spain (Andalusia)		0.55	> 70	Fortuna et al. (2009)
Spain (Catalonia)*	1.7	7.90	19	Camprodon & Guixé (2013)
France (Aveyron)		1.10	2	Dubourg Savage et al. (2013)
Corsica*	< 0.20		49	Beuneux et al. (2010)
Hungary (Mátra Mts)	< 1.40		9	Estók et al. (2007)
Belarus (Pripyat)		4.60	18	Dombrovski et al. (2017)

* Non-breeding population.

Fig. 2. (a-c) Examples of tree cavities occupied by the giant noctule in the Western Carpathians. (d, e) Typical locations of tree roosts (circles) in managed spruce forests during a bark beetle infestation.

2008, Camprodon & Guixé 2013, Dombrovski et al. 2017, Russo et al. 2023), we suggest that aspen plays an important role for the species under the local conditions of the Western Carpathians. In general, aspen trees (*P. tremula* and *P. tremuloides*) are critical resources for tree-dwelling bats in forests with a continental climate in the Northern Hemisphere (e.g. Crampton & Barclay 1998, Michaelsen 2016, Jarolímek & Vierling 2019). Aspen is a light-demanding, fast-growing and short-lived pioneer tree species with soft wood (Caudullo & de Rigo 2016) and a high incidence of stem rot (Liepiņš et al. 2023), which can promote the formation and thus high availability of cavities (Carlson et al. 1998). Although aspen is undoubtedly of conservation biological importance, little information is available on its abundance in forests (Kivinen et al. 2020).

Similar to the sparse natural forests in MP, where the roost trees were often located at the edge of escarpments (Naďo et al. 2019), the bats in BV preferred to roost at the edge of the forest stands on steep slopes, which also offered a free exit from the roost into the open space. Such suitable open patches in the managed forests resulted from the clearing of infested sites (small-extent salvage logging) during the current massive bark beetle (*Ips typographus*) outbreak (Fig. 2). This confirms that structured stands with an open space in front of the roost entrance (but see Russo et al. 2023) and its position high above the terrain are important for this fast-flying but poorly manoeuvring bat with high wing loading and large aspect ratio (Ibáñez & Juste 2023). While the forest decline in secondary spruce monocultures can also provide suitable habitats for this rare species, deadwood should be considered integral to the forest ecosystem during timber harvesting (Rachwald et al. 2022a, b). Interestingly, the convex hulls of the colonies' roosts were larger than any substantial remnant of primaeval forests in the surrounding area (Fig. 1). On the other hand, the

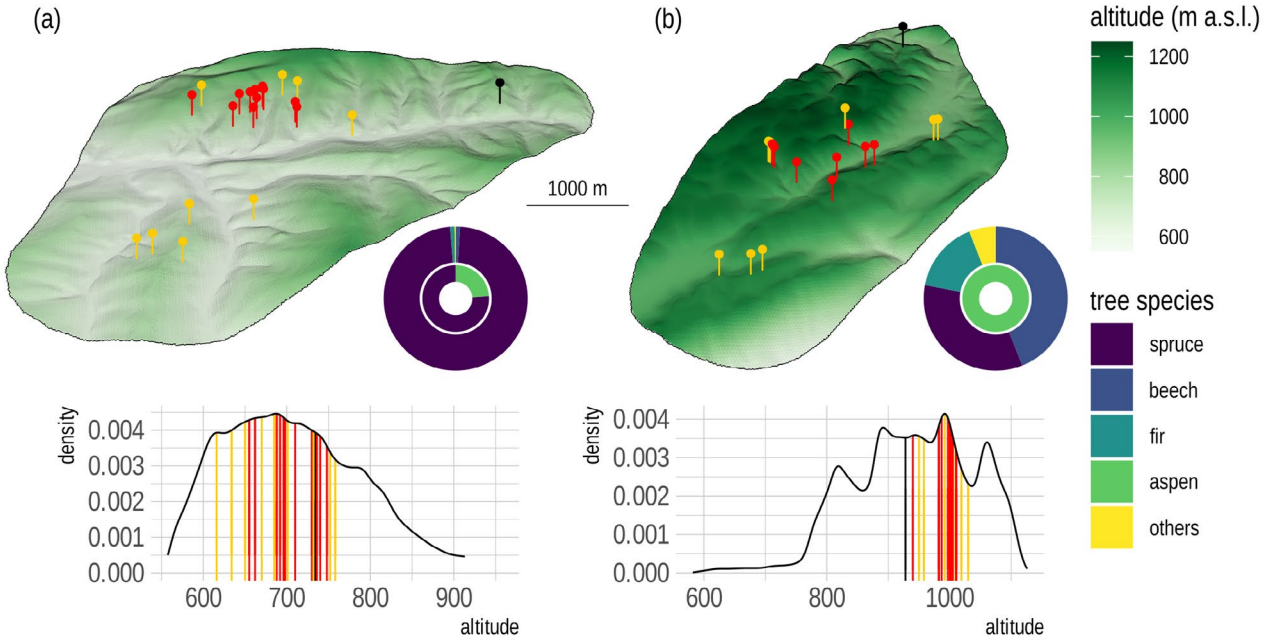

Fig. 3. Relief maps (digital terrain models) for the areas of maternity colonies in the (a) Balocké vrchy Mts (disturbed spruce monocultures) and (b) Muránska planina Mts (preserved forests in the national park). The colour of the tree roosts of bats (pins) indicates their 95% home range (yellow) and 50% core range (red) based on the maximum convex polygons (outliers are in black). The doughnut charts summarise the proportion of tree species in the surrounding forest stands (outside) and the bat roosts (inside). The proportion of the Eurasian aspen in the forest stands is generally very low, so it was only included in the category of other species. Density plots give an overview of the distribution of local altitudes with altitudes of bat roosts (vertical lines colour-coded as above).

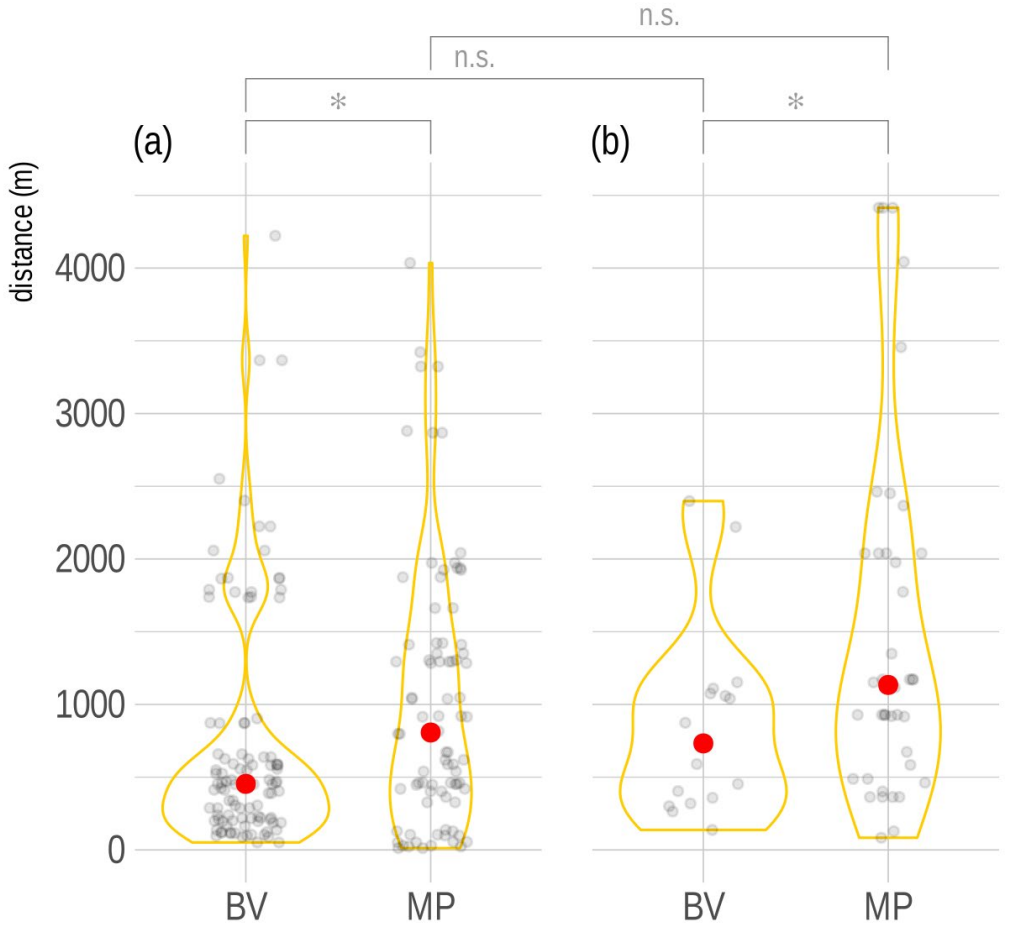

Fig. 4. (a) Distances between neighbouring tree roosts calculated by Delaunay triangulation and (b) roost switching distances of bats recorded by telemetry in two maternity colonies. The kernel density estimates of the data (small dots) distribution are accompanied by medians (red dots).

Balocké vrchy Mts are one of the most affected regions in Slovakia, where bark beetles are currently damaging spruce forests on an unprecedented scale, with habitat disturbance exacerbated by windstorms and extensive salvage logging (Potterf et al. 2023). However, if the natural forest dynamics are respected during the restoration of such former plantation-transformed stands and a sufficient amount of standing deadwood with cavities remains, such an irretrievable forest decline should not have a severe impact on the giant noctule and other tree-dwelling bat species there (Law et al. 2016, Rachwald et al. 2022b).

Regarding relief and roost location, the colonies were situated at altitudes that were predominant in their surroundings (616-758 m a.s.l. in BV, 928-1,030 m a.s.l. in MP). The roosts in the core range were located along some central valleys (Fig. 3), which could be related to spatial navigation when changing roosts over long distances. Bats can easily find a swarm of conspecifics at a new roost site at dawn if they fly the same fixed routes every night when returning from their hunting grounds (flyways along linear landscape elements); however, there must also be a more sophisticated, cognitive map-based navigation strategy when searching for the tree roost in such a sizeable roosting range (Yovel & Ulanovsky 2017). The median distance between two neighbouring roosts was 457 m in BV and 807 m in MP (mean values 746 m and 1,019 m, respectively; Fig. S2). The distances between roosts and/or the home-range size in the Western Carpathians were similar to other breeding populations at the species' northern range, e.g. in the Mátra Mts (Estók et al. 2007) or in Pripyat (Dombrovski et al. 2017). However, such roost density is significantly lower than populations in the species' Mediterranean range (e.g. Fortuna et al. 2009, Beuneux et al. 2010). It is likely that these measures are locally specific and depend mainly on population size (Table 2).

We observed 40 (MP) and 16 (BV) roost-switching events of seven (MP) and six (BV) radio-tracked individuals, respectively (for the remaining individuals, we were unable to determine more than the location of a single roost). The distances between neighbouring roosts and the distances flown by bats when changing roosts were significantly greater in MP than in BV (Mann-Whitney U-test, $P < 0.05$; Fig. 4), but observation periods for individuals in MP were longer than in BV (Fig. S3). Furthermore, there was no statistically significant difference when comparing these two values within a colony (Fig. 4). This suggests that the tracked bats moved between roosts within the entire roosting area of the colony. On average, the bats changed their roost every third day, staying in one roost for one to six days. The mean distance travelled between roost trees was 1.3 km (0.08-4.41 km), almost twice as long as in the related but smaller species *Nyctalus noctula* and *N. leisleri*, which travelled an average of 0.7 km between roosts (Ruczyński et al. 2010).

Conclusions

In the forests of the Western Carpathians, old or dead aspens with numerous cavities proved the most suitable trees for the maternity roosts of the giant noctule, while dead wood provides an alternative habitat even in disturbed plantations. Therefore, conservation measures should aim to increase the proportion of aspen in managed stands, which will positively impact the target species and other tree-dwelling bats. The question arises whether the extensive roosting ranges of both colonies are related to the current scarcity of this resource. Our observations in distinct forest habitats also suggest that stand structure, openness and the location of roost trees in relation to the slope of the terrain are essential features of the species' habitat in mountainous areas. However, extensive salvage logging without preserving forest patches with cavity trees (standing deadwood) destroys any chance of survival for this species in disturbed spruce monocultures.

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Author Contributions

P. Kaňuch and D. Lőbbová designed the study, P. Kaňuch, D. Lőbbová, R. Ružinská, B. Jarčuška, A. Krištín and A. Kaňuchová conducted fieldwork, P. Kaňuch, C. Bovin and R. Ružinská analysed data, and P. Kaňuch wrote the manuscript. All authors commented and agreed on the manuscript.

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Supplementary online material

Fig. S1. Roosting ranges represented by (a) minimum convex polygons and (b) kernel density estimation (yellow, 95% home-range; red, 50% core-range). The coordinate reference system is ETRS89-extended/LAEA Europe (metres).

Fig. S2. Lines connecting roosts so that each roost is joined to its nearest neighbours.

Fig. S3. Trajectories of *Nyctalus lasiopterus* individuals when changing roost sites. The initial and final locations of each individual are indicated in the yellow triangles and red squares respectively.

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