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Nursery Roosts Used by Barbastelle Bats, *Barbastella barbastellus* (Schreber, 1774) (Chiroptera: Vespertilionidae) in European Lowland Mixed Forest Transformed by Spruce Bark Beetle, *Ips typographus* (Linnaeus, 1758) (Coleoptera: Curculionidae)

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Abstract: Białowieża Primeval Forest (BPF, approx. 1700 km²) is an important forest area in Europe from the point of view of the protection of natural diversity. BPF is covered with old mixed tree stands of mostly natural origin. Norway spruce is a tree species in BPF and covers approx. 27% of its area. Between 2012 and 2017 a large outbreak of the bark beetle *Ips typographus* (Linnaeus, 1758) took place in the forest, which transformed the stands and left many dead standing trees. At that time salvage logging had begun but was stopped due to protests by scientists and activists and for legal reasons. As a result of research conducted using a radiotelemetry method in 2020, we found that the Western barbastelle bat *Barbastella barbastellus* (Schreber, 1774) chooses nursery roosts in dead Norway spruce trees, showing ecological plasticity by colonizing a newly available resource. Based on this, we found that the Western barbastelle has a preference for a type of roost rather than a tree species. Insect outbreaks in forests of primary, natural, or semi-natural origin are one of the natural factors that shape the habitat. Removal of dead standing trees disrupts these processes, and in this particular case results in the disappearance of a newly appeared ecological niche.

Keywords: Western barbastelle bat; bark beetle outbreak; bat roosts; tree-related microhabitats; Białowieża Primeval Forest

1. Introduction

The natural resource of roosting places in old trees is endangered in countries with long-developed forestry, because hollows and cracks reduce the economic quality of wood, and typically, these trees are the first to be removed by forest management [1–3]. Natural roosts in trees are of great biocenotic value as they are tree-related microhabitats (TreMs) playing an important role in the forest ecosystem [4–6].

Providing shelter from predation and harsh weather, and serving as places to give birth to offspring, roosts play an essential role in bat reproduction and survival [7–11]. According to classification by [4], forest dwelling bats mostly use two types of TreMs: “woodpecker cavities” and “bark shelters”. The availability of potential roosting places (tree hollows, crevices, and dead trees) is one of the factors limiting the occurrence of tree-dwelling bats [1,12–14]. The number of trees with hollows has generally decreased in forest environments due to the activity of economic forestry, which involves the removal of dead or damaged trees, removing trees containing hollows as weakened [1–3]. The

Western barbastelle *Barbastella barbastellus* (Schreber, 1774) (Chiroptera: Vespertilionidae) is a species of bat that chooses summer roosts (maternity or nursery colonies) in tree trunk cracks and spaces under protruding bark in the Palearctic forests. Barbastelles have a highly specialized diet and hunts almost exclusively for moths [8,15,16]. In a forest-agricultural landscape, the Western barbastelle is able to establish roosts in old wooden buildings (behind protruding facade boards or under shutters) [17–20]. However, in the forest environment it is a species most commonly found in crevices and roosts under the bark of broadleaved trees (“bark shelters” [4]), which are probably first choice roosting places [21–24]. For this reason, Western barbastelles are considered as a species that chooses old deciduous forests, which, compared to coniferous stands, usually offer higher frequencies of this type of roosting place [25–27]. As Białowieża Primeval Forest (BPF) is a Natura 2000 Special Area of Conservation, within its borders, the Western barbastelle bat is subject to protection through Annex II of the Habitat Directive of the European Union (in addition to being protected under national law).

In the BPF, the Western barbastelle was poorly studied, and until recently, it was considered to be relatively rare in the area [28–30]. The latest data suggest that this bat may be one of the dominating bat species there [31,32]. The reason why BPF may be a mainstay and a place of numerous occurrences of the Western barbastelle is the natural or semi-natural character of forest stands, the forests species and age, and spatial structure. Old deciduous stands found here, considered to be preferred by barbastes, should provide good, stable conditions for the population of this bat. Apart from dominant deciduous trees, coniferous stands with Scots pine *Pinus sylvestris* L. (1753) and Norway spruce *Picea abies* (L.) H. Karst. (1881) are an important part of the BPF ecosystem. Norway spruce occurs natively in BPF as a boreal species, as well as a result of plantings carried out in the 20th century in economically used stands [33,34]. This makes spruce a significant species in the BPF ecosystem, especially where it is dominant in forest stands.

The main non-anthropogenic factor that may change the structure of coniferous stands is large-scale disturbance, including mass outbreaks of insects such as the spruce bark beetle *Ips typographus* (Linnaeus, 1758) (Coleoptera: Curculionidae). The spruce bark beetle is a palearctic species. Adults are small (5 mm) diurnal beetles. It occurs periodically in forests, most often it is found in single species stands composed of Norway spruce. The tree’s death is caused by damage to the bark and phloem as a result of insects digging tunnels under the bark. The bark beetle usually does not inhabit healthy spruce trees, but instead inhabits those that have been weakened by disease, drought, or other insects. It gnaws at the bark and lays eggs from which the larvae hatch. These larvae dig tunnels, damaging the bark and phloem. After some time, the larvae develop into adults that bite their way outside the tree. The resulting changes in spatial characteristics, age, and species structure of stands affect all other organisms living in the transformed forest area. Due to the resulting initiation of many natural processes in the ecosystem, the spruce bark beetle is now considered a keystone species in forest biology [35]. In contrast to studies on birds [36–42] or even on ungulates [43,44], the impact of insect outbreaks on bats in forests has so far been studied fragmentarily [45–47]. However, recent data from Europe indicate that the impact of insect outbreaks can be significant and manifest itself in more than one way [32,48–50].

In 2012, a mass bark beetle outbreak started in the BPF area (Figure 1). This phenomenon lasted until about 2017–2018 and changed the structure of spruce stands within the forest [51]. Bark beetle outbreaks occur in BPF usually every 10–15 years and, depending on the intensity, they leave behind a larger or smaller number of dead standing spruce trees. The reason why the present outbreak was so large is not fully understood. Deterioration in the health of spruce trees in BPF due to the current change climate together with commercial forestry practices and lowering of groundwater levels due to previous management are considered to be important factors [52–55].



Figure 1. Mixed coniferous forest dominated by Norway spruce with dead trees as a result a bark beetle outbreak. On the left you can see the tree (marked with tape) in which a radio-tagged female barbastelle was found. There is also visible spruce undergrowth (in the background), which did not suffer from beetle infestation (photo A. Rachwald).

At the time of the outbreak salvage logging began (in the form of a clear-cuts over large areas) as a countermeasure. Due to the high international importance of BPF for European biodiversity and its protected status (Natura 2000 Special Area of Conservation PLC200004 “Puszcza Białowieska”, UNESCO Natural World Heritage Site and numerous nature reserves), logging was eventually ceased [56–61]. As a result, a large proportion of standing dead spruce trees remained in the forest, often in the mature age associated with large trunk dimensions, which allowed for research on the use of dead stands by various groups of organisms (including bats).

In 2020, a significant proportion of these standing trees were still partially covered with dead bark. Such trees create new microhabitats, the ecological resource for organisms that inhabit dead wood and bark, including those that prefer protruding bark as a roosting place [4,5,62]. The Western barbastelle is included in this group. In [50], a hypothesis was made that the increase in barbastelle density observed during the bark beetle outbreak was due to the change in conditions in spruce stands to those more favorable to this species of bat, mainly due to the appearance of new roosting places.

The aim of our research was to investigate if Western barbastelle bats exhibit ecological flexibility and, despite the permanent availability of appropriate roosting conditions in dominating old deciduous stands, choose places for nursery colonies in novel roost resources provided by the bark beetle outbreak.

2. Materials and Methods

2.1. Study Area

BPF is a mostly natural forest area and a remnant of the primeval European low-land forests that used to cover most of the continent [63]. The forest covers an area of approximately 1700 km² (divided between Poland and Belarus). In Belarus, the entire area is protected as a National Park. In Poland, the area is partially protected (100 km² as a National Park, plus 85 km² as nature reserves). However, most of this area is commercial

forest with varying degrees of naturalness and transformation. Some of these areas still show a relatively high degree of naturalness due to the special management rules applied in the commercial forest stands (e.g., keeping trees older than 100 years old and prohibiting the use of clear-cuts). The entire area is a cross-border UNESCO Natural World Heritage Site (it covers the BPF on the Belarusian side and on the Polish side), and in Poland the BPF is also protected as a Natura 2000 area. Most of these forms of protection (apart from the National Park) also cover the commercial forests.

In BPF there are deciduous forests (mainly common hornbeam *Carpinus betulus* L. (1753), European oak *Quercus robur* L. (1753), and small-leaved lime *Tilia cordata* Mill. (1768), as well as common alder *Alnus glutinosa* (L.) Gaertn. (1791) and a minority of coniferous stands (mostly Norway spruce *Picea abies* and to a lesser extent Scots pine *Pinus sylvestris*). Spruce account for about 27% of the managed BPF area (except the Białowieża National Park, where it is 13%, [64]), both in the form of one-species stands (especially in the North of the BPF) and as an important admixture to deciduous forest. Larger areas covered with spruce occur in the BPF in commercial forests (this is the result of forest management carried out over the last 100 years, which has promoted this species). For this reason, we conducted our research outside the area of the National Park, in a mixed deciduous–coniferous forest with an important share of Norway spruce that is common in the managed part of BPF, which was affected by the bark beetle outbreak (Figure 1).

2.2. Study Design and Collecting Data

In our research, we used the method of netting bats on their possible flight routes and foraging sites (forest roads), fitting bats with radio transmitters and then making bearings during the day in search of their daily roosting sites. It is an established method in studies that require locating a colony of roosting bats [65]. Two nets were installed at one location at a distance of about 20–30 m from each other. A single net set up consisted of two nets, each approx. 2.5 m high, placed one on top of the other (with the use of telescopic poles). The purpose of such an installation was to increase the chance of catching bats flying closer to the tree canopies. The length of the mist net depended on the available space, most often it was 9 m. Monofilament nets (ECOTONE, <https://www.ecotone.pl>, accessed on 6 July 2022) were used because of their efficiency for barbastelles.

Netting was carried out in order to catch lactating females. The choice of the time of the research work (second half of July) was selected to avoid catching pregnant females (earlier) and volant offspring (later). This is in line with the adopted methodology for the inventory of this species [61]. We also considered that the chosen date of field work would also prevent the potential negative effect of installing transmitters on the hair cover of barbastelle females after their last moult before hibernation [66]. It was considered that installing the transmitters on females during the lactation period was the safest solution for animals, and at the same time, it is the best method of locating them in the place where they form nursery colonies with other females. Bats were netted for a total of four nights (16–19 July 2020) at four plots in total.

Bats were measured and weighed. Transmitters were attached to the dorsal side with surgical glue, directly to the skin under the hair coat (i.e., no hair cutting, Figure 2). The animal was held for 15 min (to fix the transmitter attachment) and then released. The search for radio-tagged bats in the field was carried out by three teams of two people, each equipped with a receiver and a directional antenna. Titley Australis receivers (Titley Scientific, Brendale QLD 4500, Australia, <https://www.titley-scientific.com/eu/> accessed on 6 July 2022) with Yagi antennas were used. The transmitters (Holohil LB2, Holohil Systems, Ottawa, ON, Canada, <https://www.holohil.com/> accessed on 6 July 2022) were selected specifically to suit the average body weight and size of the animals [67]. Bats were radio-tracked every day until transmitter failure or loss.



Figure 2. Western barbastelle female tagged with radio transmitter Holohil LB2, ready to release (photo A. Zapart).

We chose four netting points located in stands with both coniferous and deciduous trees. Netting was conducted in a commercially managed forest. Forest plot locations were identified using publicly available detailed forest maps (Forest Data Bank, <https://www.bdl.lasy.gov.pl/portal/mapy>, accessed on 6 July 2022) that show the boundaries of forest sub-compartments with similar species composition and age (thereafter referred to as “forest plots”). We recorded the following roost characteristics: tree species, nearest four trees (N, S, E, W), dominant tree species, and age in the forest plot, as well as the distance to the nearest forest plot with a dominance of deciduous trees. The exact roost locations were measured using GPS (Garmin GPS64Map). The selection of the research site was preceded by a research project conducted in 2011–2017, during which, using ultrasonic detection, high activity of the Western barbastelle was observed in BPF stands (one of the two most frequently recorded species [32]).

Appropriate permits were obtained from the Regional Directorate for Environmental Protection in Białystok (number WPN.6205.36.2020.ML).

2.3. Data Analysis

For each roost ($n = 21$), the four nearest trees (one per cardinal direction) with a DBH exceeding 25 cm were found, and the tree species and condition (living/dead) were recorded (according to a point-centered quarter method, [68]). Trees were divided into a 2×2 contingency table (coniferous/deciduous; live/dead). The dead coniferous category was represented solely by the Norway spruce. We used a one-sided Fisher’s exact test and the Chi^2 test with Yates correction. Subsequently, the value of the correlation coefficient r was calculated to evaluate the effect size for the Chi^2 test. Data analysis was carried out with two separate online calculators (<https://www.socscistatistics.com/tests/fisher/default2.aspx>, <https://www.campbellcollaboration.org/escalc/html/EffectSizeCalculator-R5.php>, accessed on 1 May 2022).

The distances between subsequent roosts and netting sites were calculated using QGIS tool (ver.3.16 Hannover). Distances were tested for normality of distribution (Shapiro–Wilk

test). Differences in distances between the two groups were compared with the Mann–Whitney U test. Additionally, biodiversity indices were calculated for the trees surrounding the roost. This part of the analysis was performed in the PAST 4.3 statistics software package [69].

3. Results

During the four nights of netting, a total of nine Western barbastelle females were caught. All females were adult and lactating. Nine radio transmitters were attached, including four on 16 July and a further five on 18 July. All tagged females were subsequently found roosting in trees, most of them (seven out of nine) the day after the night they were tagged (Table 1). The other two females were located one day later. The netting sites and trees where the females were found are shown in Figure 3.

Table 1. The time of contact with individual bats and the time spent in their roosts. 1–9: individual bats with transmitters. 1–16: consecutive days, each cell stands for one day. The same colour indicates days spent in one roost. Example: bat number 1 inhabited five roosts consecutively, while bat number 7 was only observed in one roost. The dotted boxes represent the days spent together by bats no. 2 and 3 in the same tree. The boxes with diagonal lines represent the days spent together by bats 5 and 9 in the same tree.

Bat	Day in Roost															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	Red	Blue	Yellow	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green
2	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red
3	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red
4	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red
5	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red
6	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red
7	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red
8	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red
9	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red

We found that the vast majority of lactating female barbastelles chose roosting places in dead spruce trees (Figure 1, Table 2), in the vicinity of the netting location where they were caught (Figure 3). We found that bats used 18 unique roost trees (Tables 1 and 2). Of the nine radio-tagged females, we observed two females nesting in the same tree on two occasions, accounting for 6 of the roosting days (Table 1). In addition, one tree was also used by two bats, but not at the same time. This was taken as 21 roosting observations of nine individuals. Of these 21 roosting cases, 20 were in dead Norway spruces and 1 was in a dead black (European) alder (Table 2). We did not observe any cases of a tagged animal roosting in a living tree. When field conditions allowed it, we conducted observations of bats leaving these roosts. In all five observed locations, the emergence of several barbastelles was confirmed, with the number ranging between 6 and 10 individuals. On this basis (and taking into account that all tagged females were lactating), we assumed that in all cases they were barbastelle nursery roosts.

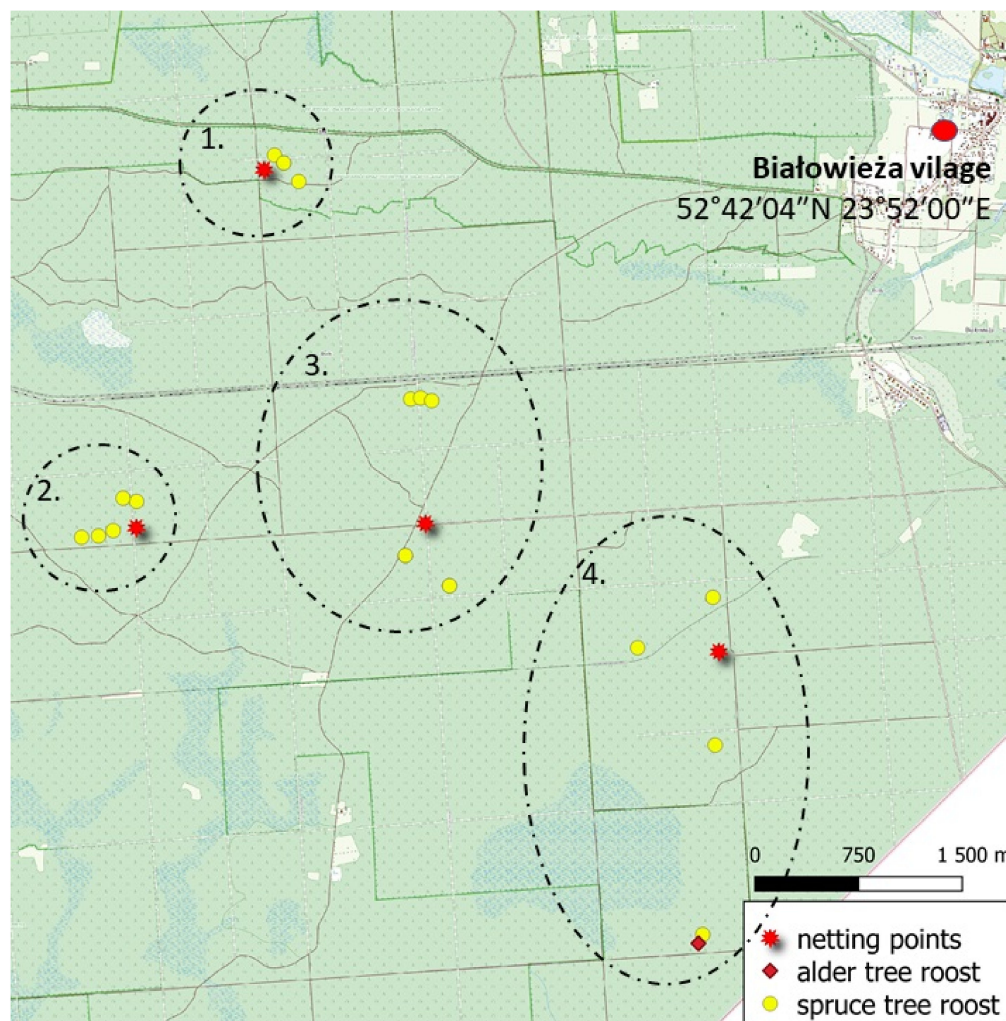


Figure 3. Study area. Bat netting sites (four) marked with asterisks. Spruce roosting trees marked with yellow circles. Alder roosting tree marked with diamond. The ovals with a dotted line surround the respective netting points (1–4) along with the roosts used by the bats captured at these points. They are drawn for reference only.

Table 2. The main parameters of the trees in which the bat roosts were found.

Tree No.	Species	DBH (cm)	Height (m)	DistDecid (m)	Dom./Age (yrs)	Four Trees	Status
1	<i>P. abies</i>	42	22	963	Psyl/101	Pabi/Pabi/Pabi/Pabi	D/D/D/D
2	<i>P. abies</i>	60	28	915	Psyl/101	Psyl/Pabi/Pabi/Pabi	L/D/D/D
3	<i>P. abies</i>	50	25	903	Psyl/40	Bver/Pabi/Pabi/Pabi	L/D/D/D
4	<i>P. abies</i>	53	29	1088	Pabi/120	Pabi/Pabi/Pabi/Pabi	D/D/D/D
5	<i>P. abies</i>	51	17	1126	Psyl/90	Pabi/Pabi/Pabi/Pabi	D/D/D/D
6	<i>P. abies</i>	65	22	373	Pabi/155	Pabi/Pabi/Pabi/Qrob	D/D/D/L
7	<i>P. abies</i>	53	22	208	Pabi/150	Pabi/Pabi/Pabi/Qrob	D/D/D/L
8	<i>P. abies</i>	55	25	89	Psyl/105	Pabi/Pabi/Psyl/Psyl	D/D/L/L
9	<i>P. abies</i>	62	30	85	Pabi/160	Pabi/Pabi/Psyl/Pabi	D/D/L/D
10	<i>P. abies</i>	47	23	145	Pabi/160	Pabi/Pabi/Qrob/Pabi	L/D/L/D
11	<i>P. abies</i>	55	27	240	Pabi/160	Pabi/Pabi/Pabi/Pabi	D/D/D/D
12	<i>P. abies</i>	62	29	250	Pabi/180	Pabi/Pabi/Bver/Pabi	D/D/L/D

Table 2. Cont.

Tree No.	Species	DBH (cm)	Height (m)	DistDecid (m)	Dom./Age (yrs)	Four Trees	Status
13	<i>A. glutinosa</i>	24	15	0	Aglu/70	Aglu/Aglu/Aglu/Aglu	L/D/L/L
14	<i>P. abies</i>	62	30	37	Pabi/150	Ptre/Pabi/Cbet/Ptre	L/D/L/L
15	<i>P. abies</i>	58	28	105	Pabi/90	Psyl/Pabi/Pabi/Pabi	L/D/D/D
15	<i>P. abies</i>	46	25	15	Pabi/105	Psyl/Pabi/Pabi/Pabi	L/D/D/D
17	<i>P. abies</i>	52	27	248	Pabi/105	Bver/Pabi/Pabi/Bver	L/D/D/L
18	<i>P. abies</i>	56	25	148	Pabi/160	Psyl/Pabi/Pabi/Pabi	L/D/D/D

DBH—Diameter at Breast Height (cm), Height—the height of the tree (m), DistDecid—the distance to the nearest forest division with dominant deciduous trees (m), Dominant/Age—the dominant tree species and its average age in the forest plot where the roost tree was located, Four Trees—four nearest located trees (North, South, East, and West of the roost tree), Status—tree live (L) or dead (D). Pabi—*Picea abies* (L.) H. Karst. (1881), Psyl—*Pinus sylvestris* L. (1753), Bver—*Betula verrucosa* Roth (1788), Qrob—*Quercus robur* L. (1753), Aglu—*Alnus glutinosa* (L.) Gaertn. (1791), Ptre—*Populus tremula* L. (1753), Cbet—*Carpinus betulus* L. (1753).

All tracked females moved between their roosts during the research period. During the entire period (16 days, determined by the time of operation of radio transmitters), one individual female occupied up to five roosts. One female (number 7) after 4 days of observation disappeared from her first roost and was not found again. The minimum observed time spent in one roost was 1 day, the maximum was 11 days (median = 4, 0.25 = 2; 0.75 = 7) (Table 1).

We observed two separations of colonies. Females no. 2 and 3 roosted together in one tree for 2 days before switching roosts (at different times). Females number 5 and 9 roosted together in one tree for 4 days before female no. 9 switched roost to another tree for the remaining tracking days (Table 1).

Trees around the roost trees were dominated by dead spruces (Fisher's exact test: $p < 0.00001$; Chi-square with Yates correction— $\chi^2 = 37.029$, $df = 1$, $p < 0.0001$) (Table 1). The effect size was estimated as large ($r = 0.6639$). The Simpson (0.424) and Shannon (0.9735) biodiversity indices were calculated for the trees nearing roosts. There was a total of 84 trees representing seven taxa: *Picea abies* ($n = 63$), *Pinus sylvestris* (7), *Betula verrucosa* (4), *Alnus glutinosa* (4), *Quercus robur* (3), *Populus tremula* (2), and *Carpinus betulus* (1).

The minimum distance between roost and nearest deciduous plot was 0 m (roost in black alder) and the maximum distance was 1126 m, whereas median value was only 240 m; 0.25 percentile = 97 m; 0.75 percentile = 638 m ($n = 21$) (Table 2).

The minimum distance between subsequent roosts was 68 m, the maximum distance was 645 m, and the median value = 136.5 m; 0.25 percentile = 93 m and 0.75 percentile = 349.75 m. The distances between subsequent roosts ($n = 12$) and the valid distances between all four netting sites ($n = 6$) were significantly different (Mann–Whitney U Test $Z = 3.33$, $p > 0.0001$). The close proximity of subsequent roosts comparing to distances between netting points suggests that barbastelles in BPN have relatively small home ranges (Figure 3), which, however, requires further research.

4. Discussion

In recent years, some studies have shown that the Western barbastelle can enter and colonize Norway spruce stands under certain conditions [49,70]. In these cases, serious large-area disturbances occurred as a result of an outbreak of the spruce bark beetle. The authors of [50] showed a significant effect of a spruce bark beetle outbreak on the barbastelle population density and suggested that it may be due to the use of a new resource for bats as a result of an insect outbreak (roosts under protruding bark of a dead trees).

The results of our study confirm the hypothesis that, in instances of increased availability of shelters in conifers (“bark shelters”, [4]), female barbastelles use these shelters as nursery colony sites, despite the fact that old deciduous trees are present in close vicinity. Our work is a continuation and completion of research that started at the beginning of the last substantial outbreak of the bark beetle in BPF, when we first observed changes in the population of bats in this area and linked this with the progression of a beetle

outbreak [32,50]. Our results agree with the data of [49] and [70], which were studies conducted in the conditions of submontane and mountain forest. Our work was conducted in a lowland old growth mixed forest with a high predominance of deciduous trees (about 70% in the entire area, [64]). This is an important difference to Bavarian Forest, where the general proportion can even be reversed in favor of the Norway spruce [71]. Białowieża Primeval Forest is widely considered to be the reference area of European natural forest and biodiversity hotspot. The phenomena that take place here can be considered as a reference for other lowland forests [34,63,72,73].

Barbastelles (due to their preferences regarding specific roosting places [21–24]) show a very distinct reaction to a change in forest environment caused by the bark beetle outbreak. Our results show how flexible the response of the population to such a change can be. Our results indicate that a species that is numerous in a favorable environment [32] may at the same time be active in searching for new niches, if only a change in the environment allows it. In the case of barbastelles, the availability of roosting places is a factor that limits the population due to the behavior of this species, consisting of regular roost switching [20,22,74,75]. Another species of European forest bat known to have similar behavior is *Myotis bechsteinii* (Kuhl, 1817) [19,76]; however, this species does not occur in BPF due to its restricted geographic range. The forest habitat of the BPF (especially its most natural fragments) is dense with trees with fissures and thick, cracked bark (hornbeams *Carpinus betulus*, oaks *Quercus robur*), which meets the needs of barbastelles well [21,77]. On the other hand, the relatively quick appearance (within a few years) of new available roosting places in the area resulted in the colonization of coniferous stands that were previously unattractive for this species [25–27]. It therefore follows that barbastelles in a forest habitat have a preference for a specific type of roost (microhabitat) rather than for specific tree species, and that the dynamics of the species population are related to the dynamics of changes taking place in the ecosystem, which in the case of insect outbreaks means periodical variability.

The appearance of new roosting places is a spectacular effect of changes taking place in forest stands, but not the only one that affects the population of forest vertebrates. Both the outbreak of insects and possible subsequent salvage logging change the structure of the forest (e.g., gaps, clearings) and promote the growth of shrubs and young trees. Changes in food resources (insects), local climate, and increased habitat heterogeneity modify the occurrence of groups of vertebrates such as birds and bats [41,42,78–80]. The impact of these factors on the population of bats in the BPF requires further research.

Tree-related microhabitats are among those resources that are particularly quickly damaged or removed by intensive forestry practices. In Europe, this has been driven by policy change initiated as a result of the Convention of Biological Diversity, requiring explicit consideration of environmental, economic, and social objectives and a multi-purpose approach to forestry [81]. In some areas in the BPF, in the initial period of the beetle outbreak, clear felling was carried out over large forest areas (also with the removal of natural regeneration and undergrowth). Large-scale clear-cuts were also carried out in the Šumava National Park (part of the Bohemian Forest in the Czech Republic) during a bark beetle outbreak. Bayerische Wald NP, on the other side of the border, adopted the opposite strategy in most cases [82] (http://sumava.tadytoje.cz/info/studieadokumenty/studieainfo/podklad_pro_iucn_en.pdf, accessed on 6 July 2022). It is now known that salvage logging in many cases did not stop the bark beetle outbreak, and it did have a severe impact on biodiversity [83,84]. On the other hand, forest dieback caused by insects in protected areas (such as the Białowieża Primeval Forest) may lead to the restoration of species typical of the primeval forest [85]. In our work, we proved that under natural conditions in an old mixed forest with spruce, barbastelles will make full use of its roosts in dead or damaged conifers. Dead trees occupied by the nursery colonies of a rare and protected mammal, such as barbastelle, are an example of such a natural resource that could be easily destroyed. It is especially worth emphasizing this is the case for Białowieża

Primeval Forest, one of the most valuable forested areas in Europe, whose future as a natural forest is still under threat [86].

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