

Selection of roosting habitats by *Nyctalus noctula* and *Nyctalus leisleri* in Białowieża Forest—Adaptive response to forest management?

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ABSTRACT

Tree dwelling bats select cavities in large, old, dying or dead trees. This inevitably brings them into direct conflict with the interests of forest managers, who are trained to fell such trees. Therefore the identification of forest stands providing optimal roosting opportunities for bats is crucial, in order to provide appropriate guidelines for forest management. It is also important to identify the extent to which the roosting ecology of bats changes in response to habitat modification. Białowieża Forest (BF) offers a unique opportunity, in the temperate zone, to observe differences between areas with no direct human intervention and managed areas and in particular to reveal the effect of forest management on the roosting ecology of forest dwelling bat species. We used GIS techniques to evaluate bats' spatial response to changes in forest structure and to test the hypotheses that the forest dwelling bats *Nyctalus noctula* and *Nyctalus leisleri* prefer roost sites within old deciduous or wet woodlands over young and coniferous ones and that roost site preferences reflect the extent to which dead and dying trees are removed. There was a significant difference in the selection of roosting habitat between the managed and pristine areas of the forest. Within the pristine forest, both species displayed a strong preference for roost trees located within old deciduous stands (>100 years), whereas in the managed part of the forest old wet woodland was preferred while all medium and young forest stands were avoided. Our data reveal a high degree of lability in the selection of roosting habitat by bats. It appears that bats are able to respond to changes in their environment by changing their roost site preferences and could therefore occupy habitat previously considered less suitable.

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1. Introduction

During the summer months, temperate zone bats can spend more than 20 h of each day within their roost (Jenkins, 1998). These roosts provide sites for hibernation, mating, and rearing young (Kunz and Lumsden, 2003), and may facilitate complex social interactions (Wilkinson, 1992; Kerth et al., 2001; Vonhof et al., 2004; Willis and Brigham, 2004), offer protection from inclement weather (Vaughan, 1987; Sedgeley, 2001) as well as minimising the risks of predation (Fenton, 1983; Fenton et al., 1994). Many of the 850 insectivorous bat species roost in trees (Menzel et al., 1998; Sedgeley and O'Donnell, 1999a; Boonman, 2000; Lacki and Schwierjohann, 2001; Kunz and Lumsden, 2003; Simmons, 2005) and the availability of suitable roost trees can affect not only the abundance and diversity of bat communities but also their spatial distribution (Crampton and Barclay, 1998; Russo et al., 2004). Therefore, an understanding of the roosting requirements of tree dwelling bat species is a vital component

for the conservation of bats, particularly within areas where forest management practices can lead to potentially important habitats being cleared, fragmented or extensively modified.

The selection of appropriate roost sites depends on both the physical characteristics of the roost (Kalcounis-Ruppell et al., 2005; Ruczyński and Bogdanowicz, 2005; Russo et al., 2004; Sedgeley and O'Donnell, 1999a) and its surrounding features (Humphrey et al., 1997; Kerth et al., 2001; Ruczyński and Bogdanowicz, 2008). Tree dwelling bats preferentially select cavities in old, dying or dead trees (Menzel et al., 2000; Kunz and Lumsden, 2003; Sedgeley and O'Donnell, 1999b; Ruczyński and Bogdanowicz, 2008), and studies have shown that bats roost preferentially within forest stands containing a high proportion of suitable roost trees (Crampton and Barclay, 1998; Sedgeley and O'Donnell, 1999b). Such selection may decrease the costs associated with finding new tree cavities or facilitate organization of fission–fusion groups when bats switch between alternate roost locations (Lewis, 1995; Ruczyński et al., 2007; Popa-Lisseanu et al., 2008).

Ancient forest stands offer greater densities of large and decaying trees, and therefore provide more suitable roosting sites than young or mature stands (Zielinski and Gellman, 1999; Crampton and Barclay, 1998). However, their dependence on dead

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wood brings tree dwelling bat species into direct conflict with the interests of forest managers, for whom dying and dead trees constitute a threat to timber production interests because they are perceived to form a possible source of disease for neighbouring living trees. Dead and dying trees also constitute a considerable fire-risk and provide wood of low quality (Ohlson et al., 1997; Lundquist, 2003). Forest management typically involves the removal of dead and dying trees as soon as they are detected, thereby minimizing the amount of dead wood within the forest (Nilsson et al., 2002; Löhmus et al., 2005; Czeszczewik and Walankiewicz, 2008). As a result, the management of forests for timber production could potentially have a detrimental effect on tree dwelling bat species. Current evidence indicates that such management reduces the availability of roosts for many tree roosting species (e.g. Vonhof and Barclay, 1996; Crampton and Barclay, 1998; Herr and Klomp, 1999; Law and Anderson, 2000). The reduction of available roost trees can, in turn, limit the distribution of bat species and reduce local abundance. Similarly, the reduction in the quality of roosts following habitat modification associated with forest management practices can influence levels of mortality and reproductive success (Brigham and Fenton, 1986). Therefore the identification of optimal roosting habitats for bat species is crucial in order to implement appropriate guidelines for forest management. However, roost switching is common in bats (Lewis, 1995; Kunz and Lumsden, 2003) and it has been shown that roost site preferences can change in response to ambient conditions (Kerth et al., 2001; Ruczyński and Bogdanowicz, 2008). Therefore, it is important to identify the extent to which the roosting ecology of bats changes in response to habitat modification, and particularly anthropogenic modification. In particular habitats previously identified as unimportant or marginal to bats may increase in importance with modified forest management practices.

The present study was carried out in the Białowieża Forest (BF) (NE Poland), where patches of primeval lowland temperate forest, untouched by forestry operations, have survived (Tomiałojć et al., 1984; Faliński, 1986). This offers a rare opportunity, in the European temperate zone, to observe differences between areas with no direct human intervention (which can therefore act as 'controls') and managed areas (which can act as 'experimental' sites), and can therefore give an indication of the effect that forest management has on the roosting ecology of forest dwelling bat species. The present study focused on two particular bat species found in the study area: *Nyctalus noctula* (Schreber, 1774) and *Nyctalus leisleri* (Kuhl, 1817).

N. noctula and *N. leisleri* are closely related species (Salgueiro et al., 2007) which are sympatric over much of their ranges. *N. noctula* is one of the most common forest dwelling species in Europe, whereas *N. leisleri* is relatively rare (Bogdanowicz, 1999; Bodanowicz and Ruprecht, 2004; Shiel, 1999) except in Ireland, where *N. noctula* does not occur (O'Sullivan, 1994). *N. leisleri* is also more limited to ancient forests (Bodanowicz and Ruprecht, 2004). In both taxa, pregnant and lactating females typically roost in tree cavities (Gebhard and Bogdanowicz, 2004; Strelkov, 2000).

The aims of the present study were to investigate: (1) roost site selection by *N. noctula* and *N. leisleri* in relation to tree species dominance, and age of forest stand surrounding roost trees, (2) interspecific differences in roost site selection and (3) differences in the selection of roosting habitat by bats roosting within managed and pristine areas (strict reserve of Białowieża National Park) within the forest. We tested the following hypotheses: *N. noctula* and *N. leisleri* will select roost trees within forest stands offering the highest proportion of available roosting cavities, i.e. old, deciduous stands. Bats will alter their roost site preferences in response to anthropogenic modification that reduces the proportion of available roosting cavities, i.e. the removal of dead and dying trees.

2. Materials and methods

2.1. Study area

Białowieża Forest (BF) is located at the Polish–Belorussian border (approximately 52°43'N, 23°54'E) and covers an area of 1450 km². It is the largest remnant of original temperate forest in Europe. The study area (approximately 100 km²) covers the well-preserved stands of the strict reserve within Białowieża National Park (BNP, hereafter referred to as pristine stands) (47.5 km²) and an extensive area (>570 km²) of managed forests with old growth remnants (trees > 100 years old) within them. Large-scale timber extraction began in the forest less than a 100 years ago, and the currently managed fragments did not initially differ from the retained parts in terms of climate, soil, history or plant and animal communities at this time (Faliński, 1986; Bobiec et al., 2000; Tomiałojć and Wesołowski, 2004). The old-growth stands preserved in the strict reserve of BNP consist of multi-storied, unevenly aged, mixed tree species (the tallest spruces grow up to 57 m and several other species reach 42–45 m). The old growth stands are further characterised by large amounts of dead timber and uprooted trees (Wesołowski and Tomiałojć, 1995). These stands are dominated by oak *Quercus robur* (20% of the area), hornbeam *Carpinus betulus* (19%), spruce *Picea abies* (16%), alder *Alnus glutinosa* (12%), pine *Pinus sylvestris* (11%), lime *Tilia cordata* and maple *Acer platanoides* (9%), birch *Betula* spp. and poplar *Populus tremula* (7%), and ash *Fraxinus excelsior* (6%). In the managed part of the forest, there is a lower percentage of deciduous trees: oak (11% of the area), hornbeam (2%), alder (20%), lime and maple (0%), birch and poplar (12%), ash (2%), and a greater proportion of conifers: pine (26%) and spruce (28%; Jędrzejewska and Jędrzejewski, 1998). In addition, there are fewer older trees and many areas where trees have a similar upper age-limit in the managed forest, reflecting when they were previously harvested.

2.2. Capture of bats and location of roost trees

Roost sites were located from May to August 1998–2000 and 2002 (*N. leisleri*), and in 1999–2002 (*N. noctula*). Bats were captured in mist nets (2 m × 6 m and 2.5 m × 4 m) set across small rivers in the forest and at one pond (6 capture sites in total). Captured bats were classified by species, sex, age (juvenile or adult), and reproductive status. Roost trees were located by tracking bats with radio-transmitters (0.5 g – Biotrack, Wareham, UK, and Titley Electronics, Ballina NSW, Australia; or 0.7 g – Titley Electronics and Holohil Systems, Carp, ON, Canada) affixed to the inter-scapular region with rubber adhesive (Skin-Bond, Smith and Nephew[®], Largo Florida, USA). Transmitter mass represented <5% of the body mass of bats (Aldridge and Brigham, 1988). Altogether, 26 *N. noctula* and 25 *N. leisleri* were tracked using 2-element Yagi antennae and receivers (Yupiteru MVT-700, Javiation, Bradford, West Yorkshire, United Kingdom; Yaesu FT-290R, Vertex Standard, Cypress, California). Bats emerging at dusk were counted to determine the number of individuals in each roost. In most cases each species roosted separately. Tagged bats were located daily for the life of transmitters (up to 14 days). Methods conformed to guidelines approved by the American Society of Mammalogists (Gannon and Sikes, 2007).

2.3. Data sources

Geographical position of roost sites was recorded using a GPS-receiver in 2008, with an accuracy of <15 m (Garmin GPSmap60cSx). Habitat data were extracted from the official inventory and management plans of the local forestry authorities (Białowieża, Hajnówka) and those of BNP (map scale 1:20 000).

Maps were referenced into 1965–2 ordinations and entered into a geographic system (GIS) created in ArcView GIS 3.3. Once entered into the GIS, forest habitats were divided into three classes based on the tree species composition, structure and environmental conditions. These were:

1. Deciduous Woodland (DW): DW strands are composed of about a dozen main tree species, including hornbeam *C. betulus*, lime *T. cordata*, pedunculate oak *Q. robur*, continental maple *A. platanoides* and spruce *P. abies*. As well as having a wide variety of tree species, DW stands are the most structurally diverse and consist of trees that vary greatly in both age and size.
2. Wet Woodland (WW): These are deciduous stands (*Circaeo-Alnetum*, *Carici elongate-Alnetum*) that are more uniform than DW, with a canopy composed mostly of alder *A. glutinosa*, ash *F. excelsior* and spruce *P. abies*. Other species occur more rarely. These stands are subject to temporary flooding of local rivers or from rainwater, which gathers and stagnates within depressions with inadequate drainage. These stands contain the largest amount of fallen timber, as the use of heavy machinery to transport wood from these areas is limited due to the marshy soil and presence of water throughout the majority of the year.
3. Coniferous Woodland (CW): Within these stands (*Quercus-Piceetum*, *Pineto-Quercetum*, *Peucedano-Pinetum*) the canopy is composed of spruce and Scots pine *P. sylvestris* with a small admixture of birches *Betula* spp. and some oaks. Coniferous stands in the managed forest are mostly cleared by cutting all trees from 2 to 5 ha patches and replanting them with Scots pine. Clear felling is less frequently undertaken in the managed oak-hornbeam and wet stands than in coniferous ones.

Within each class, stands were further sub-divided by age into stands dominated by young (1–79 years), medium (80–99 years), and old (>100 years) trees, giving a total of nine habitat combinations. Eighty and 100 years were selected as divisions between age classes due to the fact that it is a common management practice for forest stands to be cut at this age (e.g. alder stands 60–80 years, pine and spruce stands; 80–100 years) so by using this criterion we could test whether forest stands, considered to have reached a terminal age from a management point of view, are selected by bats to the same extent as young and old stands. Białowieża Forest stands which are older than 100 years, are generally recognized as pristine (Jędrzejewska and Jędrzejewski, 1998). The mature stands in the managed forest are still similar to those in strict reserve of BNP and are mostly of natural origin (self-sown), multi-species and of an uneven age, but snags and fallen trees are no longer left.

2.4. Habitat selection

In order to determine whether *N. noctula* and *N. leisleri* were selecting roost trees according to the composition of surrounding local habitat, 100 m radius plots (roost plots) centred on each identified roost tree were generated in the GIS. The proportion of each defined habitat category, within these roost plots, were then compared to the habitat available for roosting. We used roost trees, rather than individual bats, as the sampling unit to both facilitate the computation of habitat usage and to preserve potentially important variations in habitat around individual trees. This information may have been lost if bats roosted in more than one tree and an average value for habitat use calculated for each individual bat. In any study of habitat selection one of the most difficult decisions is the definition of what habitat is available for an animal to use. Throughout the present study, individual bats of either species were caught and subsequently tracked from one of six distinct capture sites throughout the forest (Fig. 1). Clearly the

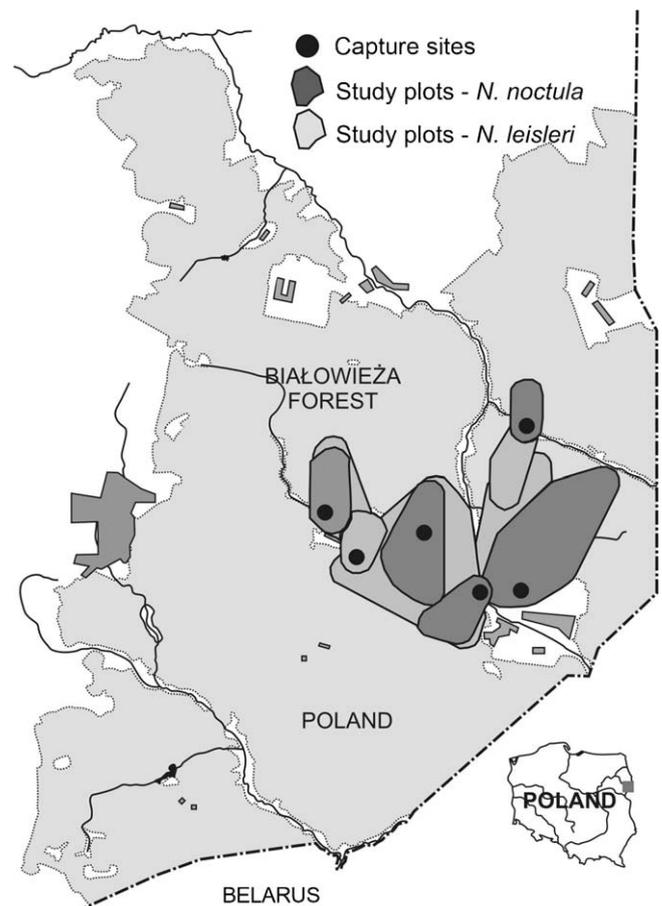


Fig. 1. The study area.

habitat composition of the forest may be substantially different in the vicinity of any of these points. Therefore, in order to test whether bats were selecting their roosts according to specific habitat requirements or whether the selection of roost trees was independent of surrounding habitat, it was important that comparisons (used vs available habitat) were carried out within clearly demarcated catchment areas. For each species, the minimum convex polygon (MCP) enclosing all roosts identified from each catching point was defined as a roosting area (Fig. 1). As the apices of each MCP were defined by roost trees a buffer zone representing the average distance travelled between roost trees, by both species, was added to the MCP. This area defined a roosting area associated with the catching points.

Within each roosting area, we calculated the average proportion of each habitat category within 100 m circular plots (random 'roost' plots) of 100 randomly positioned points (see below for a validation of using a sample size of 100 points to quantify the average habitat availability within each roosting area). This was then compared to the habitats found around the trees which were used as bat roosts. This was defined as the proportion of each habitat category within 100 m circular plots (roost plots) around roost trees used by each bat. By using this approach, the habitat within 100 m of all selected roost trees was directly compared to the habitat available within the same roosting area.

2.5. Were sample sizes obtained sufficient to separate real habitat preferences from random variation due to small sample sizes?

In any study of habitat preferences it is important to establish that the sample sizes used in the analysis are sufficient to separate

real habitat preferences of a species from those generated by artefacts of the sample sizes used. This will be determined by the answers to two questions:

1. Was the sample size used to quantify the habitat availability within the study area sufficient to do so given the variation within it?
2. Was the sample size of the bat roosts sufficient to determine the actual habitat usage given the variation in habitat usage within the bat data?

In both cases, habitat preferences can be detected with smaller sample sizes in more homogenous study areas (either in terms of that available or that used by the bats, which equates to a narrower habitat niche), while larger sample sizes will be required for more heterogeneous study areas. To address this, we conducted a power analysis using repeated random sampling of the study area to define the variation in average habitat for different sample sizes. One thousand randomly positioned points were plotted within each roosting MCP (generated using ArcView Random Point Generator v 1.3 extension) and randomly selected points from this data set for sample sizes between 1 and 250 points. This was repeated 250 times to allow an estimate of the variation in average habitat values to be calculated for each possible sample size. This variation can be identified by estimating the 95% confidence interval of the average habitat availability for each habitat category from the 250 repeats by sorting the average values in ascending order and plotting the 7th and 243rd values for each sample size. If the sample sizes used in this study were sufficient to detect a real habitat preference, the average value for the actual bat roosts should lie outside the 95% confidence intervals for the relevant sample size, and outside that for 100 randomly positioned points. This analysis showed that the variation within the random 'roost' plots decreased markedly as sample size increased until a relatively stable range of values was obtained with the sample size >100 (Fig. 2). Therefore, 100 random points were found to be sufficient to accurately classify the available habitat within each roost area. Consideration is given below to whether the sample size of bat roosts was sufficient to ensure that any observed differences in habitat use were not considerably influenced by random variation.

2.6. Data analysis

Methods for analysing patterns of habitat use are reviewed by Alldredge and Ratti (1986), White and Garrott (1990) and Manly et al. (1993). In the present study, compositional analysis (Aitchison, 1986), following Aebischer et al. (1993a), was selected to investigate the selection of roosting habitat by *N. noctula* and *N. leisleri* and to rank habitats in order of preference. Analysis was conducted using an Excel macro (Smith, 2004) specifically written to carry out all calculations described in Aebischer et al. (1993a). Intra-specific tests compared the proportions of habitats within all selected roost plots ($n = 50$) against the habitat available within roosting areas (as indicated by 100 randomly selected potential 'roost' plots). To overcome problems arising from departure from multivariate normality of log-ratio difference distribution, we calculated the significance of Wilk's Λ and t statistics by randomisation tests (Aebischer et al., 1993a). To enable calculations of logarithms, where the calculated proportion for a specific habitat category within an individual roost plot was zero, it was replaced by 0.01, as suggested by Aebischer et al. (1993a), which was at least an order of magnitude less than the smallest measure and represented use too small to be detected.

Inter-specific comparisons between *N. noctula* and *N. leisleri* followed the same procedure, by directly comparing the composi-

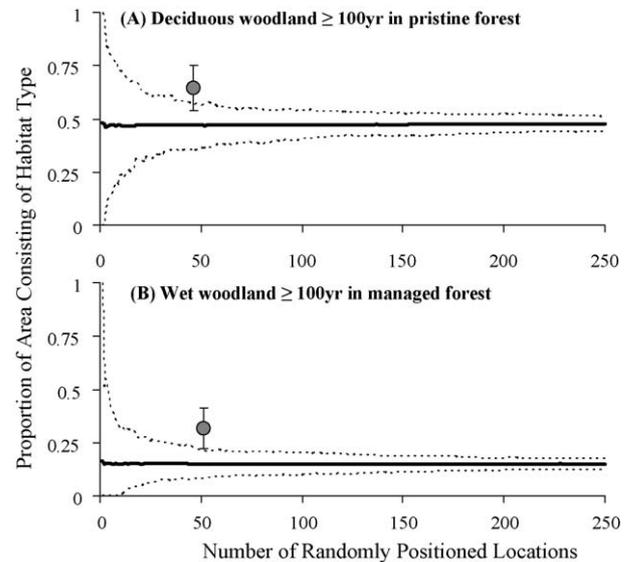


Fig. 2. The effect of sample size on the average proportion of available habitat within 100 m radius buffers around randomly positioned locations in pristine (A) and managed (B) forest areas used by *Nyctalus* spp. In each case, only the data for the habitat type most preferred by bats is presented (see composition analysis). Solid line: average value for 250 randomly chosen sets of points of a given sample size of randomly positioned locations; dotted lines: estimated 95% confidence interval around the mean value for these randomly chosen sets of points. Grey circle: actual mean value for 100 m radius buffers around roost trees utilised by bats with 95% confidence interval for this mean value for that specific habitat type.

tion of habitats within roost plots selected by either species, similar to the survival analysis carried out by Aebischer et al. (1993b) but using the proportion of habitats within roost plots rather than the proportion of radiolocations. In the absence of significant differences in habitat use between the two species, all roosts were grouped into a single data set and compositional analysis was used to identify whether habitat selection was occurring within the managed and pristine parts of the forest, and in each case to rank habitats in order of preference.

Differences in the selection of roosting habitat between the pristine and managed parts of the forest were further investigated by calculating the niche breadth of roosting habitat (proportion of habitat within roost plots) within the managed and pristine parts of the forest using a standardized version of Levins index (Hurlbert, 1978):

$$B_A = \frac{(1/\sum p_j^2) - 1}{n - 1}$$

where B_A = Levins' standardised niche breadth, p_j = proportion of times habitat class j was used ($\sum p_j = 1.0$), n = number of possible habitat classes.

However, niche breadth analysis only considers each habitat variable individually, while in reality niche preferences among different variables may interact within the n -dimensional hyper-space defined by them. Therefore, to assess which habitat variable was most important for separating the habitat preferences in the managed and pristine areas, a principal components analysis (PCA) was conducted (Fig. 3). Each roost plot was treated as a separate data point and the proportion of each habitat category within roost plots used as the habitat variables. The principal component scores for each roost plot for the first principal component axis (which will determine the most important sources of variation within the data) for roosts in managed and preserve areas were then compared using the total number of bat roosts for each management regimen in increments of 0.5 of the full range of PC scores for the first PC axis. The eigenvalues for this component

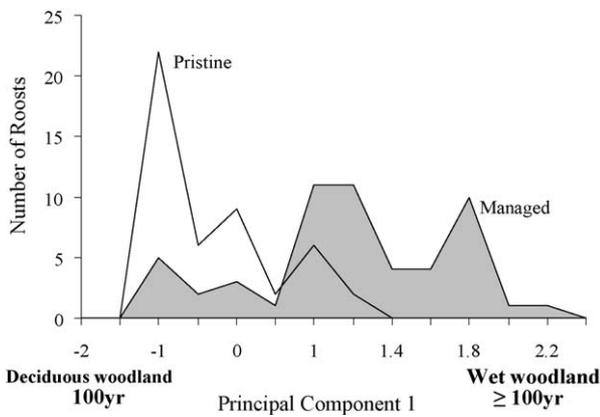


Fig. 3. Variation in proportions of different habitat types in 100 m radius buffers around *Nyctalus* spp. roosts in managed and pristine forests along the first principal component axis. The most important variables for determining variation along this axis were the proportion of deciduous woodland (DW) > 100 years (eigenvector: -0.738) and proportion of wet woodland (WW) > 100 years (eigenvector: 0.500). This axis explained 17.9% of the variation in the data and provided the greatest separation between the two management regimens.

were then used to infer which habitat categories were most important for separating the habitat preferences of bats in the two areas, and therefore, where they most differed.

3. Results

3.1. Radio telemetry

Twenty-six *N. noctula* and 25 *N. leisleri* were radio-tracked from May to August 1998–2002. Tagged bats were located daily for the life of transmitters. The average tracking period was 6.5 days for *N. noctula* (range 1–14) and 7.5 days for *N. leisleri* (range 2–13). The distance travelled between roost trees was similar for both species: *N. noctula* – average 0.7 km, range 0.05–2.5 km; and *N. leisleri* – average 0.7 km, range 0.03–1.7 km.

3.2. Intra-specific roost site selection

In total, 50 trees used as roosts by *N. noctula* and 50 by *N. leisleri* were included in the analysis. Compositional analysis indicated a highly significant difference between the proportion of each habitat category within 100 m circular plots around roost trees (roost plots) and the average proportion of habitats available within randomly positioned potential roost trees ($n = 100$) for both species (Wilks lambda $\lambda = 0.2171$, $P < 0.0001$, $P_{\text{randomisation}} = 0.001$, for *N. noctula*. Wilks lambda $\lambda = 0.3531$, $P < 0.0001$, $P_{\text{randomisation}} = 0.001$, for *N. leisleri*). A ranking matrix comparing all available habitat categories for *N. noctula* is shown in Table 1, and can be summarised as follows: old deciduous woodland \ggg old wet woodland > medium wet woodland > old coniferous woodland > medium coniferous woodland > young wet woodland > medium deciduous woodland > young deciduous woodland > young coniferous woodland. Old deciduous woodland (≥ 100 years) was significantly selected above all other habitat categories, followed by a preference for old wet woodland. In general *N. noctula* showed a strong preference for roost trees surrounded by older forest stands (≥ 100 years) in preference to younger stands (< 80 years), which were selected less than predicted from their availability. The habitat ranking matrix for *N. leisleri* is shown in Table 2 and can be summarised as follows: old deciduous woodland > old wet woodland > old coniferous woodland > medium deciduous woodland > young deciduous woodland > medium coniferous woodland > young wet woodland > young coniferous woodland > medium wet woodland. Once again old

Table 1 Log-ratio differences derived from compositional analysis on habitat within 100 m radius of *Nyctalus noctula* roosts.

	CW < 80 years	DW < 80 years	DW 80–99 years	WW < 80 years	CW 80–99 years	CW ≥ 100 years	WW 80–99 years	WW ≥ 100 years	DW ≥ 100 years	Rank
DW ≥ 100 years	***	***	***	***	***	***	***	***	n/a	8
WW ≥ 100 years	***	***	***	***	a	a	a	n/a	n/a	7
WW 80–99 years	***	a	a	a	a	a	n/a	n/a	n/a	6
CW ≥ 100 years	***	a	a	a	a	n/a	n/a	n/a	n/a	5
CW 80–99 years	***	a	a	a	a	n/a	n/a	n/a	n/a	4
WW < 80 years	***	a	a	a	n/a	n/a	n/a	n/a	n/a	3
DW 80–99 years	***	a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	2
DW < 80 years	a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	1
CW < 80 years	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	0

Habitats are ranked from most (8) to least (0) preferred.

^a A positive log-ratio difference.

*** A significant difference, $P < 0.05$ by randomisation.

Table 2
Log-ratio differences derived from compositional analysis on habitat within 100 m radius of *Nyctalus leisleri* roosts.

	WW 80–99 years	CW < 80 years	WW < 80 years	CW 80–99 years	WW < 80 years	DW 80–99 years	CW ≥ 100 years	WW ≥ 100 years	DW ≥ 100 years	Rank
DW ≥ 100 years	***	***	***	***	***	***	***	a	n/a	8
WW ≥ 100 years	***	***	***	a	a	a	a	n/a		7
CW ≥ 100 years	***	***	a	a	a	a	n/a			6
DW 80–99 years	***	***	a	a	a	n/a				5
DW < 80 years	a	a	a	a	n/a					4
CW 80–99 years	a	***	a	n/a						3
WW < 80 years	a	a	n/a							2
CW < 80 years	a	n/a								1
WW 80–99 years	n/a									0

Habitats are ranked from most (8) to least (0) preferred.

a A positive log-ratio difference.

*** A significant difference, $P < 0.05$ by randomisation.

deciduous woodland was significantly selected above all other habitat types, with the exception of old wet woodland, which was also used disproportionately to its availability. For both species there is a clear preference for roost trees located within older forest stands (≥ 100 years) with the youngest stands (< 80 years) selected less than would be expected based on their availability.

3.3. Inter-specific roosting comparisons

Compositional analysis revealed no significant difference in the proportion of habitat categories within the roost plots of either species (Wilks lambda $\lambda = 0.9035$, $P_{\text{randomisation}} = 0.795$) indicating that both species are selecting roost trees with a similar composition of surrounding habitat.

3.4. Roost site selection within managed and pristine areas of the BF

There is a clear difference in the selection of roosting habitats by *Nyctalus* spp. within the managed and pristine areas of the BF (Fig. 4). Within the managed area of the park, bats predominantly selected roosts located within old wet woodland stands (WW3); and the proportion of this habitat category within roost plots greatly exceeded its availability (Fig. 4). In contrast the proportion of all young woodland categories within roost plots (DW1, WW1, CW1) was less than would be expected based on their availability.

Within the pristine area of the park, bats predominantly selected roosts located within old deciduous woodland stands (DW3); and the proportion of this habitat category within roost plots greatly exceeded its availability. The proportion of all young woodland categories within roost plots (DW1, WW1, CW1) was less than would be expected based on their availability.

3.5. Niche breadth of roosting habitat

Within the pristine area of the forest, the proportion of habitats within roost plots of *Nyctalus* spp. was dominated by old deciduous woodland (64%), all other categories ($< 10\%$), resulting in a narrow niche breadth $BA = 0.16$. In contrast, roost plots within the managed area of the forest were not dominated by a single habitat type: old wet woodland (34%), old coniferous woodland (23%) and old deciduous woodland (17%) all other categories ($< 10\%$) resulting in a broader niche breadth $BA = 0.46$.

The most important variables determining differences among managed and pristine stands along the first principal component axis were in proportion of old deciduous woodland (DW3; eigenvector: -0.738) and proportion of old wet woodlands (WW3; eigenvector: 0.500). Along this PC axis, roost plots in the managed forest are primarily grouped at the old wet woodland end of the axis, while the roost plots in the pristine stands are primarily grouped at the old deciduous end of the axis (Fig. 3). The greater spread and lower peak values in the frequency distribution of PC one scores for the managed forest also indicate a broader niche breadth in the managed than the pristine forest stands. Therefore, there is a clear difference in the composition of the habitat surrounding roosts in managed and pristine forest. However, it is possible that this is due to differences in the composition of these stands and not differences in habitat selection by the bats. In order to separate these two possibilities, the proportions of these two main habitat types surrounding roost trees was compared to repeated sampling of a similar number of randomly positioned potential roost trees in managed and pristine stands (Fig. 2). In the pristine stands, the average proportion of old deciduous woodland around bat roosts was above the 95% confidence intervals for the proportion of this type of habitat in a similar number of randomly positioned plots. Similarly, in the managed plots, the average proportion of old wet woodland around bat roosts was above the 95% confidence interval

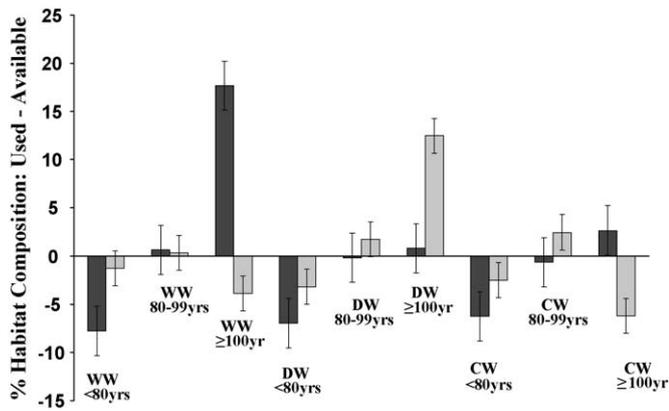


Fig. 4. The selection of roosting habitat by *Nyctalus* spp. within managed (black bars) and pristine (grey bars) areas of the BF. The y-axis illustrates the average proportionate differences between habitat within 100 m radius of roosts plots (used) and random plots (available). Bars above the axis indicate selection and below avoidance. Habitat categories used were wet woodland (WW) deciduous woodland (DW) and coniferous woodland (CW).

for the proportion of this habitat in these stands in general. As a result, the identified preferences in pristine stands for roost trees surrounded by a higher proportion of old deciduous woodland, and for roost trees surrounded by a higher proportion of old wet woodland in managed stands, are unlikely to be a result of the sample sizes of bat roosts or random variation in habitat compositions within the stands themselves.

4. Discussion

4.1. Roost site selection by *N. noctula* and *N. leisleri*

The results of the present study reveal the importance of both age and structure of forest stands in the selection of roost trees by both *N. noctula* and *N. leisleri*. Both species demonstrated a clear preference for roost trees located within old forest stands (≥ 100 years) in comparison to young ones (< 100 years) and roost trees were most commonly located within stands of either deciduous or wet woodland. Furthermore, results indicate that the roosting preferences of either species are driven by the degree to which the environment has been subject to anthropogenic modification. Within the managed area of the BF, bats exhibited a distinct preference for roost trees within wet forest stands, in contrast to a preference for deciduous stands in the pristine area of the park. We suggest that within the managed area of the forest, bats respond to the decreasing amount of suitable roost trees by selecting habitats that offer the highest potential number of roosts, a behavioural response very similar to that described for the endangered white-backed woodpecker *Dendrocopos leucotus* in the same area (Wesołowski, 1995; Czeszczewik and Walankiewicz, 2006). In addition, we suggest that current management regimens within the old deciduous stands, in particular the removal of dead and dying trees, are responsible for the observed differences in roost site selection.

During the present study, the selection by *Nyctalus* spp. for forest stands dominated by old deciduous and wet woodland, in preference to either younger or coniferous stands, can be explained by the higher presence of suitable roost trees within these areas, typically large broad-leaved trees (Bobic, 2002; Nilsson et al., 2002). By selecting forest stands that offer the highest number of suitable roost trees, both *N. noctula* and *N. leisleri* can reduce some of the costs associated with roost switching. Breeding bat colonies of *N. noctula* and *N. leisleri*, have been described as demonstrating a fission–fusion structure (Kerth and König, 1999), where group composition within individual tree roosts changes on a daily basis

but social cohesion to a larger group is preserved. Recent studies suggest that this behaviour acts to maintain social bonds between bats belonging to a colony that is spread over a large area of forest (O'Donnell, 2000; Willis and Brigham, 2004; O'Donnell and Sedgely, 2006), and could also serve to enhance information transfer, regarding roost location, between both individuals and sub-groups (Kerth and Reckardt, 2003; Russo et al., 2005; O'Donnell and Sedgely, 2006).

Roost selection is species dependent and may change during a breeding season (Kerth et al., 2001; Ruczyński and Bogdanowicz, 2008). However, bats in temperate forests generally select similar trees for roosting, predominantly large and old ones (Miller et al., 2003). *N. noctula* and *N. leisleri* show a striking similarity in their selection of individual roost trees in terms of both tree species, and the size and structure of the tree itself (Ruczyński and Bogdanowicz, 2005, 2008). The results of the present study also demonstrate the similarity between the species in their selection of forest stands and indicates that primary forest stands fulfill the roosting requirements of both *N. noctula* and *N. leisleri* within the study area.

It is probable that the majority of forest dwelling bats, living in the temperate zone, evolved in an environment that was replete with suitable tree cavities, a situation still observed in the pristine area of the BF. Therefore the selection of roosting habitat within this area can be considered as pristine. Due to the ongoing natural processes of regeneration and death, the availability of suitable roost trees is high within pristine forest stands (Bobic, 2002; Nilsson et al., 2002). But even within these pristine stands, natural processes can lead to a dynamic mosaic of developmental phases and an uneven distribution of large or dead trees (Bobic, 2002). Therefore, bats may be pre-adapted to spatial changes in forest structure, although the extent of these adaptations is not known.

Within the managed area of the BF, the removal of dead and dying trees as soon as they are identified minimises the number of trees available to tree dwelling bats and birds (Wesołowski, 1995; Wesołowski et al., 2005; Ruczyński and Bogdanowicz, 2008). This may explain the observed difference in the selection of roosting habitat by *Nyctalus* species within the managed and pristine areas of the park. Within the pristine area of the park, bats exhibited a clear preference for roosts surrounded by old deciduous woodland. However, within the managed area of the forest, bats preferentially roosted within trees surrounded by old wet woodland. It seems probable that the intensive exploitation of old deciduous stands, within the managed area of the forest, may explain this difference. Within the managed area of the park, wet woodland stands are typically the least intensively managed and are often left to be thinned, or cut last of all (Wesołowski, 1995). Therefore, they may provide a valuable roosting refuge for bats within this managed area. This shift in roosting preferences, within a relatively small geographical area, indicates a clear behavioural response by bats to changes in the forest ecosystem. By choosing forest stands that offer the highest proportion of suitable trees and by utilizing different forest stands, bats are able to minimize the negative effects of forest management. The results of the present study are similar to the changes in habitat use that were observed for the highly endangered *D. leucotos*. This species associates with forests containing a lot of dead wood where large deciduous trees are present (Angelstam et al., 2002; Gjerde et al., 2005). Wesołowski (1995) revealed that *D. leucotos* selected deciduous stands in pristine forests, while in managed forests it almost exclusively used wet woodland (Wesołowski, 1995; Czeszczewik and Walankiewicz, 2006). It appears that this may be the first level of response by these species to changes in their habitat and is very similar for both the white-backed woodpecker and bats. As predicted by other studies, the removal of dead wood may completely exclude this woodpecker from certain areas (Czeszczewik and Walankiewicz, 2006), which is not the case for *N. noctula* and *N. leisleri*. In contrast to white-backed

woodpeckers, bats are more able to respond to the removal of old or dead trees. They may compensate by selecting lower quality roosts or by altering their roosting behaviour, e.g. changing group size or reducing roost switching (Willis and Brigham, 2007; Metheny et al., 2008).

4.2. Conservation implications

Russo et al. (2005) suggest that in logged areas, selective timber harvesting protocols that preserve large and dead trees, and a significant fraction of mature trees, should be adopted. The high level of roost lability observed in many species of tree roosting bats, and the social organization of large colonies through fission–fusion behaviour, would seem to necessitate a concentration of suitable trees in patches of forest. This would be more beneficial for bats than leaving individual old trees that may become isolated. When patches of old-growth are still available, protection of these areas would favour bats. Therefore, we recommend that logging in old-growth stands in the managed part of BF should be greatly reduced or stopped completely. Similarly, in younger commercial forests the preservation of large dead trees throughout the forest would be beneficial. Additionally, a high concentration of large and old trees in selected patches of woodland seems to be beneficial to bats. Such a concentration could potentially reduce the costs of colonial breeding. Concentration of suitable trees could be attained by the exclusion of forest patches from management. However, such conservative protection may not be sustainable. It may be more effective to adopt an active management plan such as maintaining a high density of potentially suitable trees or even “killing” trees. Besides *N. noctula* and *N. leisleri*, several other woodland species of bats would benefit from these management procedures (Mayle, 1990; Hutson et al., 2001; Russo et al., 2004). Old growth within the managed forests of BF covered around 20% of the area and appears to fulfill the requirements of bats within that area. It is difficult to imagine excluding such large areas from traditional management in commercial forests. Patches of old growth used by bats in the managed forest of BF exceed 0.035 km² (with 1 tree roost), are typically larger than 0.230 km² (more than 3 roosts) and are connected or lie close to other old-growth patches. Therefore we suggest maintaining a high density of suitable trees in a system of patches connected by corridors with an overall area in excess of 10 ha. This concept however still demands tests and monitoring in commercial forests.

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