



Full length article

From ground to above canopy—Bat activity in mature forests is driven by vegetation density and height



Jörg Müller^{a,b,*}, Roland Brandl^c, Johanna Buchner^{a,d}, Hans Pretzsch^e, Stefan Seifert^e, Christian Strätz^f, Michael Veith^d, Brock Fenton^g

^a Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany

^b Terrestrial Ecology, Technische Universität München Freising, Germany

^c Animal Ecology, Department of Ecology, Faculty of Biology, Philipps-Universität Marburg, Marburg, Germany

^d Department of Biogeography, Trier University, Germany

^e Forest Growth and Yield Science, Technische Universität München, Freising, Germany

^f Büro für ökologische Studien, Bayreuth, Germany

^g Department of Biology, Western University, London, Ontario, Canada

ARTICLE INFO

Article history:

Received 13 May 2013

Received in revised form 25 June 2013

Accepted 26 June 2013

Available online 20 July 2013

Keywords:

Batcorder

Bat fatalities

Foraging guilds

Terrestrial laser scanning

Wind farms

ABSTRACT

For several decades, forest managers have considered the effects of logging on the habitat quality of forests for bats. Concern about bat activity above the canopy has now been raised owing to rapidly increasing demands for wind energy and the ensuing placement of wind turbines over forests. We investigated the little-explored vertical stratification of bat activity in forests at ten sites on ten nights using five simultaneous bat-call recorders placed from near ground up to above the canopy. The vegetation-free space at each recorder position was measured with terrestrial laser scanning. We predicted that (1) the activity of *Pipistrellus*, *Myotis* and the open-habitat foraging guild will increase in mature forests with increasing height above ground, independent of local vegetation density and temperature, and (2) the activity of *Myotis* and the edge-habitat-foraging guild will decrease with height but increase with local low vegetation density. Our generalized linear mixed model indicated that *Myotis*, *Pipistrellus* and open-habitat foragers were increasingly active in higher strata, independent of temperature and local vegetation density. Activity of *Myotis* and *Pipistrellus* species and the edge-habitat foragers was higher along interior edges of forests. The activity of single species in the above-canopy stratum could be explained well by their Europe-wide wind-turbine risk assessment. Thus, we conclude that open-habitat bat species and *Pipistrellus* species not only forage regularly in clearings or forest meadows, but also above the canopy of closed mature stands, behaviour that may put them at risk from turbines.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

Naturally most of Europe would be covered by forests (Svenning, 2002). The extensive use of the existing forest remnants by bats shows that forests form the major natural habitat of insectivorous bats in Europe with a high phylogenetic diversity (Dietz et al., 2007; Riedinger et al., 2013). Bats are increasingly a focus of conservation planning in Europe and elsewhere (Jones et al., 2009). This means that foresters are increasingly confronted by implementations focusing on bat habitats and logging practices

(Patriquin and Barclay, 2003; Peters et al., 2006; Mehr et al., 2012). Recent work supports the view that bats may play a role in the control of forest insects (Kalka et al., 2008; Böhm et al., 2011).

The current energy situation has led to new considerations about bats in forests. The disaster at Fukushima dramatically accelerated demands for non-nuclear energy in Europe. In response, there are proposals to install commercial wind facilities (a.k.a. wind farms) including in forests. Such turbines in forests may be highly profitable for forest owners, but bat fatalities at wind turbines outside forests and in forest gaps demonstrate the threat these structures pose to bats (Rydell et al., 2010a; Arnett et al., 2011). Additional mortality threatens the survival of bats because of their life histories: they reproduce slowly, live a long time and suffer high levels of mortality in their first year (Barclay and Harder, 2003). However, decisions of European forest owners about whether or not to install wind turbines are hampered by

* Corresponding author at: Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany. Tel.: +49 8552 9600 179; fax: +49 8552 9600100.

E-mail addresses: joerg.mueller@npv-bw.bayern.de (J. Müller), brandlr@mailier.uni-marburg.de (R. Brandl), JBjoschi_b@hotmail.com (J. Buchner), hans.pretzsch@lrz.tu-muenchen.de (H. Pretzsch), stefan.seifert@lrz.tu-muenchen.de (S. Seifert), Christian.Stratz@bfoes.de (C. Strätz), MVveith@uni-trier.de (M. Veith), bfenton@uwo.ca (B. Fenton).

the limited data on bat activity in different strata of mature forests because of the difficulty of obtaining data about how bats use the area above the canopy.

The few studies have documented bat activity along the full vertical gradient of forests or above trees are restricted to single sites, mostly in North America (Kalcounis et al., 1999; Hayes and Gruver, 2000; Aschoff et al., 2006). This broad lack of knowledge is well mirrored in recent reports and regulations dealing with wind turbine risks to bats (Rydell et al., 2012). Monitoring bat activity using microphones deployed at or above ground level is hampered by the umbrella effect of leaves and loss of signal strength due to a combination of spreading loss and atmospheric attenuation (Adams et al., 2009; Lawrence and Simmons, 1982; Plank et al., 2011). Therefore, a full vertical assessment of forests as a habitat requires inclusion of the above-canopy stratum. Forests may act at two different scales on bat activity. First with increasing height above the ground the density of vegetation decreases. However, due to the architecture of trees and shrubs the vegetation density can vary considerably in different forest strata. Therefore to assess the bat activity in the different strata of mature forests, bat activity must be measured vertically to above the canopy, and the complex three-dimensional foliage structures of forests must also be assessed (Lefsky et al., 2002). These two data sets will allow researchers to distinguish between the effects of height above ground (as a measure of landscape vegetation density) and local vegetation density. New techniques such as light detection and ranging (LiDAR), allow rapid, high-resolution measurement of complex canopy structures (Jung et al., 2012).

The complex three-dimensional structure associated with trees provides various potential roosting and foraging habitats for forest-dwelling bats (Kalcounis et al., 1999) and acts as a habitat filter for bat communities (Adams et al., 2009; Jung et al., 2012). Species-specific adaptations determine manoeuvrability and foraging ability (Müller et al., 2012), has led to the classification of bats into three foraging guilds. First, species hunting predominantly in open space (open-habitat foragers), second, species hunting along the edges of cluttered vegetation (edge-habitat foragers), and third, species that hunt in dense vegetation structures (closed-habitat foragers) (Fenton, 1989; Schnitzler and Kalko, 2001). In the context of risk assessment at wind turbines, the 'glint detection' (high-intensity, narrow-band, frequency-modulated calls) ability of bats has been used to identify species at risk of death by turbines (across north-western Europe, including studies in southern Germany): all species of the nyctaloid group and the genus *Pipistrellus* are assigned as high-risk species, while all species of *Myotis* are considered to be low-risk with respect to wind turbines (Rydell et al., 2010a).

The aim of our study was to document bat activity across the full vertical stratum of mature low-range montane forests. These areas are increasingly being considered for wind farms in Central Europe. In ten stands we surveyed bat activity by monitoring echolocation calls simultaneously with five bat-call recorders (batcorders) deployed between 1 m above the ground and 25.4–46.6 m above the ground in trees towering over the surrounding canopy. We measured bat activity within and above the forest canopy. All of our species have been recorded also within forest stands, but their relative use of the above canopy stratum is not well known. Specifically, we tested the predictions that the activity of open-habitat foragers and of the two high-risk taxonomic groups *Pipistrellus* and nyctaloids will increase in mature forests with increasing height above ground, independent of the local vegetation density and temperature, and the activity of edge-habitat foragers and of the low-risk *Myotis* species will decrease with height but increase with decreasing low vegetation density. Furthermore, we tested whether the activity of a species in the highest stratum

can be predicted by its classification as high or low risk at wind turbines.

2. Materials and methods

2.1. Study area

Data were collected in ten mature montane forest stands of the Bavarian Forest National Park, Germany (48°54'N, 13°29'E) (approx. 650–900 m a.s.l.) from May to October 2011. Stands were selected in beech forests of mountain ridges with a smooth relief. In each stand we selected the largest Silver Fir (*Abies alba*) tree as living pole exposing above the surrounding trees. Arborists cut off the top this Silver Fir tree in each stand at a diameter of 12 cm and a height of 26–47 m, depending from the maximum height of the tree (for details of sampling trees see Table S1). An aluminium construction with a mounted line was attached to the tree top, creating a "living pole" above the canopy (see Fig. S1). Each tree was divided into five sections, one for each bioacoustics device (batcorder 2.0; ecoObs, Nürnberg, Germany; Fig. 1). The lowest batcorder was positioned approximately 1 m above the ground, and the highest was placed at the top of the respective fir, between 25.4 and 46.6 m above ground, depending on the height of the tree. The other three batcorders were distributed evenly in between, thus forming five sections of equal height. Position 2 is located in the understorey between 7.1 and 12.4 m, position 3 is in the sub-canopy between 13.2 and 23.8 m and position 4 is in the canopy between 19.3 and 35.2 m. Due to this construction the highest batcorder was positioned above the canopy (Fig. S1). The individual height of each batcorder position was measured using the mounted line.

2.2. Bat sampling

To date, 16 species of bats have been recorded in the national park. All of them could be assigned to one of three foraging guilds and most of them to the groups *Myotis*, *Pipistrellus* and nyctaloid (Table 1). We mounted autonomous batcorders (batcorder 2.0; ecoObs, Nuernberg, Germany) on a rope, with the batcorder angled 10° upwards to prevent drops of water from collecting at the tip of the microphone. Batcorders use an omnidirectional exposed microphone. They are calibrated for a frequency of 40 kHz. These microphones record a *Nyctalus noctula* (~20 kHz) depending from its loudness and air moisture from 22 to 110 m and *Pipistrellus* spp. (40 kHz) calls between 42 and 13 m (<http://www.ecoobs.de>). Species producing low intensity echolocation calls, e.g., *Plecotus* spp., are always difficult to detect. This limits acoustic sampling for some species and we focused on species producing high intensity echolocation calls. We used the same recording mode ("Auto + Timer") and the same settings (quality: 20; threshold: -27 dB; post-trigger: 600 ms; critical call frequency: 16 kHz) during all surveys. Stationary sampling during a full night using calibrated and automatically triggered real-time recording devices lends itself to acoustic bat surveys because it produces unbiased and comparable data sets on the relative activity of bats (Stahlschmidt and Brühl, 2012). We ran acoustic surveys from 30 min before sunset until 30 min after sunrise during each sampling night at two trees with ten batcorders. Each tree was surveyed for 10 nights (survey campaigns). All trees were surveyed in each campaign during 1 week. Thus our data set comprised bat recordings from 10 trees × 5 positions × 10 replicated nights. To increase comparability among nights, we avoided surveying on moonlit nights and on nights with rainfall, minimum temperatures below 0 °C (mean temperature ranged from 6.8 to 22.1 °C) or high wind speed (wind was not measured).

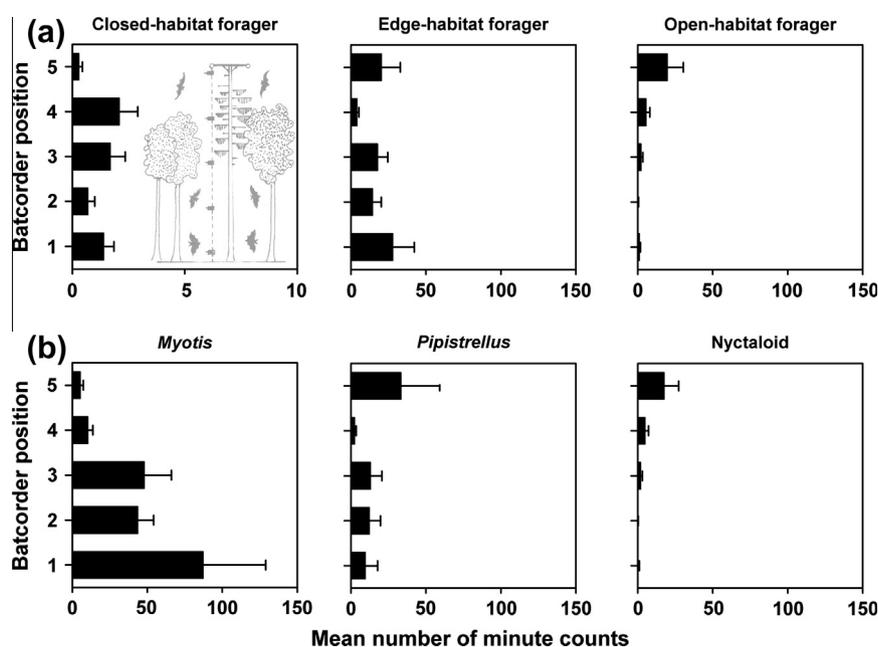


Fig. 1. Mean and standard errors of the minute counts at the ten trees summed up across the 10 samplings of the three foraging (a) and the three taxonomic (b) groups at one batcorder position (Table 1).

We used echolocation calls to identify the species of bats we recorded using the software *bcDiscriminator1.14* (ecoObs, Nuernberg, Germany). This software assigns probabilities to calls that indicate the species or species group (operational taxonomical unit; OTU) to which the call may belong (minimum probability 60%). Our analysis included all recorded calls, unlike studies that assessed only selected calls (e.g. Walters et al., 2012). As far as possible, these OTUs were assigned to one of three foraging guilds (40% of recordings) and to one of the three taxonomic groups [*Pipistrellus*, *nyctaloid* (*Vespertilio*, *Eptesicus*, *Nyctalus*), and *Myotis*] (97% of recordings). In line with previous studies, we used an activity index to quantify activity (Müller et al., 2012). We defined bat activity as the number of 1-min intervals per night in which at least one call of one of the three guilds or taxonomic groups was recorded. This length of interval has been proofed as superior to longer intervals, when measuring differences in the bat activity in forest habitats (Müller et al., 2012).

2.3. Temperature, and local vegetation density and height

Temperature at night affects bat activity in our study area (Müller et al., 2012). Therefore, during all acoustic surveys, we measured the temperature every hour using a Data Logger EL-USB-2 (LASCAR Electronics, Salisbury) mounted at the batcorder (Table 2). Mature stands vary in their vegetation density across the strata. Therefore, to precisely and continuously measure the vegetation-free foraging space (for simplicity referred to as space in the following) for bats at all 50 batcorder positions, we used a terrestrial laser scanner (LiDAR, LMS-Z420i, Riegl) as in a previous study on the influence of vegetation density on bats (Müller et al., 2012). From three to four positions at the ground level, the reflection of laser beams by vegetation was measured in a virtual cylinder with a radius of 20 m. The cylinder was divided into equal sections by the position of the batcorder. Inside the cylinder, all laser beams were followed until they hit a target. The scans were done when trees had foliage and at an angular resolution of $0.06^\circ \times 0.06^\circ$, resulting in a 3-cm point-to-point spacing at a distance of 30 m from the scanner. The volume from scanner to target was marked as free and the target space as occupied. Marking is based on spherical voxels (svoxel) in polar coordinates with a

resolution of $1^\circ \times 1^\circ \times 0.5$ m, separately for each of the three to four scan positions. The svoxels from all scan positions were then aggregated in a $1 \times 1 \times 1$ m cubic grid in Cartesian coordinates, giving the free, occupied and unmarked volume for each cube. Based on this information, the percentage of vegetation-free space was calculated.

2.4. Statistical analyses

All statistical analyses were carried out using R 2.15.2 (<http://www.r-project.org>). Surveying the activity of each of three bat guilds or three taxonomic groups at one position are not multiple independent observations, similar to the replicated measurement during the campaigns at the same tree. Furthermore the minute counts at each night were typical count data. To account for these circumstances, we modelled bat activity using a generalized linear mixed model with a Poisson distribution, using the function *glmer* in the add-on package *lme4* in R 2.15.1 (<http://www.r-project.org>), with tree and sampling as random factors (see also [Supplementary material](#)). To account for over-dispersion in the generalized mixed model, we used an observation-specific random intercept (Elston et al., 2001). We estimated and tested group (taxonomic group and foraging guild) and temperature as fixed effects and the group-specific effects of free space and height above ground.

To test for differences throughout the survey nights in the highest stratum, we again used a generalized linear mixed model with a Poisson distribution for all bat activities with a sequential post hoc test to test between subsequent samplings. We finally modelled the species-specific proportion of activity in the highest stratum using the risk category of Rydell et al. (2010a) as predictor. To avoid inflation of degrees of freedom due to relatedness of species (Garland et al., 1992), we applied a generalized least-square (GLS) model in the add-on package *picante* (Kembel et al., 2011) with a phylogenetic tree of Riedinger et al. (2013) as correlation matrix using Pagel's λ .

3. Results

Our sampling at 10 trees at 5 positions and in 10 nights each (500 samplings) provided 3762 bat recordings (17,599 calls)

Table 1

Sum of minute counts of operational taxonomic units across the five strata, each with ten replicates and ten sampling nights from May to October 2011. Operation taxonomic units which could not be unambiguously assigned to a guild are marked as group. These data were not used in the respectively guild analysis later.

Operational taxonomic unit	Foraging guild	Taxa	Position				
			1	2	3	4	5
Minute counts with recordings			1120	601	875	224	707
Bat not further identified			61	12	38	18	84
Recordings not identified			14	3	180	20	20
<i>Myotis</i> ^L	Open/Edge/Closed	<i>Myotis</i>	175	91	76	20	13
<i>Myotis bechsteini</i> ^{L, b}	Closed	<i>Myotis</i>	13	5	16	19	3
<i>Myotis nattereri</i> ^L	Closed	<i>Myotis</i>	1	2	1	2	0
<i>Barbastella barbastellus</i> ^L	Edge		2	0	3	0	5
<i>Myotis daubentoni</i> ^L	Edge	<i>Myotis</i>	13	14	16	0	0
<i>Myotis myotis</i> ^L	Edge	<i>Myotis</i>	3	4	0	2	0
<i>Myotis brandtii/mystacinus</i> ^L	Edge	<i>Myotis</i>	183	46	110	23	16
<i>Pipistrellus pipistrellus</i> ^H	Edge	<i>Pipistrellus</i>	79	80	48	18	191
Mkm ^{a, L}	Edge/Closed	<i>Myotis</i>	551	294	294	44	25
<i>Pipistrellus pipistrellus</i> ^H	Edge/Open	<i>Pipistrellus</i>	14	56	111	4	196
<i>Eptesicus nilssonii</i> ^H	Open	Nyctaloid	1	0	11	24	107
<i>Eptesicus serotinus</i> ^H	Open	Nyctaloid	0	0	0	0	2
<i>Nyctalus leisleri</i> ^H	Open	Nyctaloid	2	1	4	9	31
<i>Nyctalus leisleri</i> ^H	Open	Nyctaloid	1	1	5	15	53
<i>Nyctalus leisleri</i> ^H	Open	Nyctaloid	2	0	0	0	1
<i>Nyctalus noctula</i> ^H	Open	Nyctaloid	0	0	0	2	17
<i>Pipistrellus nathusii</i> ^H	Open	<i>Pipistrellus</i>	0	0	0	1	4
Ptie ^{a, H}	Open	<i>Pipistrellus</i>	6	1	3	3	2
<i>Vespertilio murinus</i> ^H	Open	Nyctaloid	0	0	0	8	19

^a The OTU Mkm could be *M. daubentoni*, *M. brandtii/mystacinus* or *M. bechsteini*; Nycmi could be *N. leisleri*, *Eptesicus serotinus* or *Vespertilio murinus*, and Ptief could be *P. nathusii*, *P. kuhlii* or *Hyposugo savii*.

^b The letters ^L and ^H indicate OTUs that have been assessed at low and high risk, respectively, for bat fatalities at wind turbines (see Rydell et al., 2010a).

Table 2

Results of a generalized linear mixed model for bat activities measured by minute counts of the three foraging guilds (left), and the three taxonomic groups with identical risk assessment (right), using *glmer* in package *lme4*. Tree and survey night were random factors, an observation-specific random intercept accounted for possible over-dispersion, and temperature, group, height and space were fixed factors. For temperature, the overall effect was tested. For space and height, the varying effects for each taxonomic and foraging guild were estimated. Boldface indicates significant predictors.

Foraging guilds			Taxonomic groups (risk assessment)		
	z Value	p Value		z Value	p Value
(Intercept)	-2.86	0.004	(Intercept)	-5.86	<0.001
Temperature	6.82	<0.001	Temperature	6.18	<0.001
Edge	-0.80	0.420	Nyctaloid	-1.40	0.041
Open	-0.24	0.811	<i>Pipistrellus</i>	-3.59	<0.001
Closed: height	-0.78	0.436	<i>Myotis</i> : height	-6.64	<0.001
Edge: height	-1.57	0.116	Nyctaloid: height	7.24	<0.001
Open: height	5.15	<0.001	<i>Pipistrellus</i> : height	2.98	0.002
Closed: space	-0.26	0.793	<i>Myotis</i> : space	4.45	<0.001
Edge: space	3.64	<0.001	Nyctaloid: space	-0.874	0.382
Open: space	-1.21	0.222	<i>Pipistrellus</i> : space	5.49	<0.001

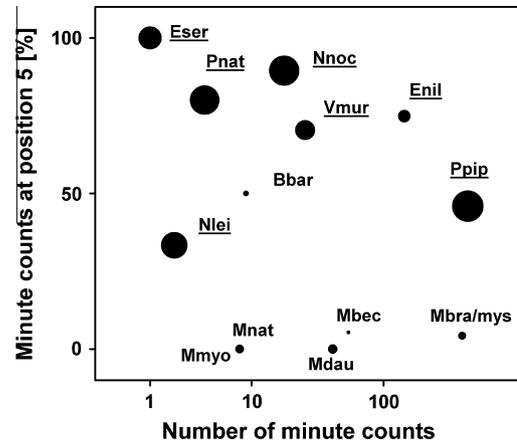


Fig. 2. Scatterplot of percentage of minute counts in the highest stratum (position 5) compared to the total minute counts of a species versus the log-transformed total number of minute counts at all of our trees. Symbol size is scaled to the number of bat fatalities in Europe under wind turbines (Dürr, 2012). The underlined species are assessed as at high risk of death by wind turbines in Rydell et al. (2010a). Eser *E. serotinus*, Pnat *P. nathusii*, Nnoc *N. noctula*, Vmur *V. murinus*, Enil *E. nilssonii*, Ppip *P. pipistrellus*, Bbar *B. barbastella*, Nlei *N. leisleri*, Mmyo *M. myotis*, Mnat, *Myotis nattereri*, Mdau *M. daubentoni*, Mbec *M. bechsteini*, Mbra/mys *M. brandtii/mystacinus*.

representing 3527 min counts (=8% of all minutes sampled)/We assigned 2919 of these calls to one of three taxonomic groups and 1280 to one of three foraging guilds (Table 1). The probability of identification of species or higher operational taxonomic unit varied considerably across the OTUs (Figs. S2, 3). In our generalized linear mixed model with Poisson distribution temperature had a positive overall effect on bat activity in both the foraging-guild model and the taxonomic-group model (Table 2). The model for the activity of foraging guilds revealed a positive effect of height above ground for open-habitat foragers and a positive effect of local space for edge-habitat foragers (Fig. 1a, Table 2). The model for taxonomic groups showed that nyctaloid and *Pipistrellus* activity increased significantly with height (Table 2). Activity of *Myotis* species decreased significantly with height. Furthermore the activity of *Myotis* and *Pipistrellus* species significantly increased with increasing locally free space, independent of height and temperature (Table 2; Fig. 1b). Temperature and height did not significantly interact (not shown).

The generalized least-square model for single species revealed that the proportion of species activity in the highest stratum (above the trees) could be significantly explained by the risk assessment of the species in Europe, despite the control for phylogeny ($p = 0.008$; Pagel's $\lambda = 0.45$; Fig. 2). When we used minute counts of all bat recordings, the seasonal distribution among our ten sampling periods during the frost-free period from May to October differed among the strata (Fig. 3; positions 1–5). Batcorder reported slightly higher bat activity from the end of June to the beginning of September in the highest stratum (dominated by *Eptesicus nilssonii* and *P. pipistrellus pipistrellus*, Fig. 3; position 5), but the differences were not significant. A peak in the lowest stratum in mid of July was dominated by *Myotis brandtii*/*Myotis mystacinus* follow by *P. pipistrellus*.

4. Discussion

Our results clearly indicated that open-habitat foragers and nyctaloids (which broadly overlapped; Table 1), but that *Pipistrellus* species also regularly foraged in the highest strata, and throughout the growing season. All nyctaloid species belong to the open-habitat foraging guild, species whose morphology and behaviour is clearly constrained for foraging in the open. Horizontally, they

are excluded from dense stands with free space <80% (Müller et al., 2012). Only these open-habitat foragers have to cover longer distances to find ephemeral food sources (Safi and Kerth, 2007), and in forests, they are the only foraging guild that shows an aggregative predator response (Müller et al., 2012). These findings provide two important pieces of information about bats in forests. First, open-habitat foragers seem to regularly use also closed mature stands, but above the trees. Therefore, any kind of monitoring within the stand typically will fail to reliably measure the activity of these open-sky specialists above trees. This can result in an underestimation of the relevance of larger closed forests for these species. Second, their biased activity above the trees would potentially place them at risk at turbines located above the trees. This is underlined also by the large concordance of our finding and the risk assessment of the species based mostly on bat fatalities at wind turbines outside forests. Also in line with our prediction, we found a significant higher activity of *Pipistrellus* species with increasing height (Rydell et al., 2010a), which also underlines their assessment as being at risk and with high numbers of fatalities at windturbines (Fig. 2; Dürr, 2012). We found a higher activity of *Pipistrellus* species only at one site (Fig. 1b). Even ten sites, as we monitored, may be too few to detect the irregular peaks of *Pipistrellus* species as revealed by permanent monitoring with batcorders in gondolas of turbines at the highest strata outside forests (Collins and Jones, 2009). Another explanation for infrequent high bat activity may be lack of insect-attracting effects of wind turbines

in our pre-construction study. The natural forest stands of our study have nocturnal prey density in dense vegetation generally higher than in open patches, which may provide more attractive habitats for *Pipistrellus* species (see Müller et al., 2012).

Our finding of a positive response of edge-habitat foragers and *Myotis* species to free space within the vertical expanse of a forest stand, independent of height and temperature confirms that that these bats forage along forest edges and in forests can efficiently localize prey also in a background-cluttered space (Schnitzler and Kalko, 2001). Their shorter echolocation calls (3–10 ms) and their frequency-modulated (FM) broadband and quasi-constant frequency (QCF) narrowband components (Fenton, 1989) seem well suited. In our study area, the *Myotis* group is dominated by the species pair *M. brandtii*/*M. mystacinus*, both typical edge-foraging species. On the single species level, none of the *Myotis* species showed a higher risk through high occurrences in the upper stratum, independent from abundance (Fig. 2).

A general problem in the evaluation of negative impacts of wind turbines on bats is the question whether fatalities only mirror the abundance of a species in a region or are result of a higher species-specific risk. Our full vertical assessment is one of the few studies that allow the effect of activity to be separated from the effect of stratification on potentially placing bat species at risk in a mature forest (Fig. 2). In line with bat fatality counts, the three species foraging most pronouncedly at the upper level in our study (*N. noctula*, *Eptesicus serotinus*, *Pipistrellus nathusii*) are listed as having very high fatalities in Europe (Fig. 2; Dürr, 2012). Only *E. nilssonii* is listed as having few fatalities, but in our study, this species was pronounced active above the canopy. In Germany, this species is not yet on any list of protected species, whereas in Sweden, where it already co-occurs with wind turbines, it is the species most often killed (Dürr, 2012). This underlines that regional species pools and their population sizes have to be considered in fatality assessments. Among the three Natura 2000 species—*Myotis bechsteinii*, *Myotis myotis*, *Barbastella barbastellus*—only the latter showed increased activity in the highest stratum, but this species is assessed as low risk. Unfortunately, our data for this species were too few to allow any implications. More detailed studies of how this species uses the highest stratum and how high it flies are still required.

Several studies have demonstrated strong effects of weather conditions on bat activity and fatality. Bats are killed at wind turbines almost exclusively at low wind speeds and higher temperatures (Brinkmann et al., 2011). Our vertical study added information that increasing activity of nyctaloids with height is independent of temperature during the vegetation period. Additionally, we confirmed previous near-ground surveys that recorded bats from temperatures above 5 °C (Mehr et al., 2012). High peaks of fatalities in late summer had been linked to migration, but Rydell et al. (2010b) argue that bat fatalities are not driven by migration activity but rather by weather conditions. In our study, bat activity was slightly but insignificantly higher from July to the end of August, which would be in line with the high peaks of fatalities (Brinkmann et al., 2011). Since most carcass surveys have not been strictly standardized and were not conducted in forested terrain (only in meadows set up in forests), the activities detected in our study are a clear warning signal that bats may be at risk even earlier in the year.

The use of trees as poles limits the implications of our study for higher turbine tower heights (>100 m). To judge whether taller turbines would still endanger bats foraging over forests, bat activity measured with batcorders placed at the top of high towers (without turbines) and the use of more sensitive systems as the Petterson D1000X from exposed positions (e.g. canopy trails, towers), or batcorders mounted in balloons would be necessary (Griffin and Thompson, 1982; Fenton and Griffin, 1997). Owing to the intense pressure to rapidly set up more wind turbines in forests, lack

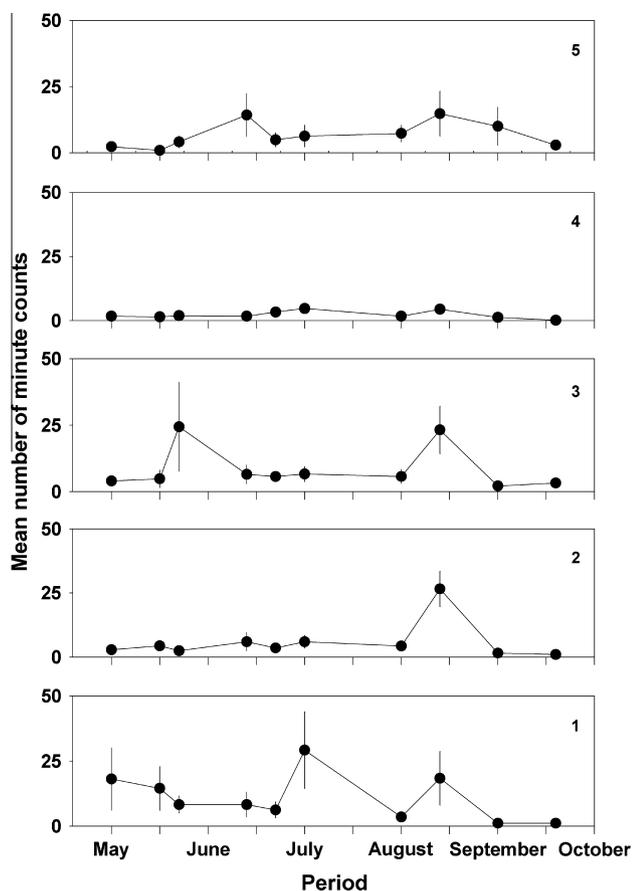


Fig. 3. Seasonal pattern of mean minute counts of bat calls per sampling period in the five forest strata. Bat calls were recorded for one-week sampling periods from May to the beginning of October in the five strata from near ground (1) to above canopy (5) from ten sampling trees. Data points indicate the mean minute counts on the mean sampling date of each sampling campaign. Bars indicate standard errors. Note that the scale of the y-axis of the upper two layers is smaller than that of the lower layers.

of knowledge of bat activity above forests, and promising results in reducing bat fatalities through timing and speed reduction of existing wind turbines (Arnett et al., 2011), most studies now seem to focus on post-construction gondola monitoring. Such speed-altering modes are developed from models based on bat carcasses found in meadows under wind turbines and batcorder-measured activities (Oliver Behr, personal communication). This is certainly a promising method, but we have to keep in mind that real bat fatalities at wind turbines in forests cannot be measured because searches for bat carcasses in the heterogeneous environment of the forests ground are impossible.

Our data, combined with difficulties in assessing actual mortality of bats at turbines together suggest that those charged with making decision about installing turbines in forests pay more attention to data about bat activity in and above the canopy. Our study was conducted in a “pristine” forest habitat without wind turbines. Therefore, bat activity in our study was not influenced by habitat alteration, such as linear clearings for the installation and service of wind turbines; attracting lights, pale colours and roosting opportunities of wind turbines; and potential attraction of flying insect prey by wind turbine acoustics or heat (Kunz et al., 2007). Such reinforcing attraction effects of wind turbines would only boost our findings.

In closing, we point out that the lack of knowledge of bat activity above the forest canopy should no longer be used as an argument allowing the building of wind turbines in forests without any preconstruction studies. We urge forest managers, conservationists and those involved with the wind-energy industry to finance and conduct more pre-construction surveys above the canopy and not only post-construction surveys, thereby emulating the Bats and Wind Energy Cooperative in the USA (<http://www.batsandwind.org>).

Acknowledgements

We thank Jens Rydell, Amanda Adams and two anonymous reviewers, for important comments on previous versions of the manuscript and Karen A. Brune for linguistic revision of the manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.06.043>.

References

- Adams, M.D., Law, B.S., French, K.O., 2009. Vegetation structure influences the vertical stratification of open- and edge-space aerial-foraging bats in harvested forests. *Forest Ecology and Management* 258, 2090–2100.
- Arnett, E.B., Huso, M.M.P., Schirmacher, M.R., Hayes, J.P., 2011. Altering turbine speed reduces bat mortality at wind-energy facilities. *Frontiers in Ecology and the Environment* 9, 209–214.
- Aschoff, T., Holderied, M.W., Marckmann, U., Runkel, V., 2006. Forstliche Maßnahmen zur Verbesserung von Jagdlebensräumen von Fledermäusen. Abschlussbericht für die Vorlage bei der Deutschen Bundesstiftung Umwelt.
- Barclay, R.M.R., Harder, L.D., 2003. Life histories of bats: life in the slow lane. In: Barclay, R.M.R., Harder, L.D., Kunz, T.H., Fenton, M.B. (Eds.), *Bat Ecology*. The University of Chicago Press, Chicago, pp. 209–253.
- Böhm, S.M., Wells, K., Kalko, E.K.V., 2011. Top-down control of herbivory by birds and bats in the canopy of temperate broad-leaved oaks (*Quercus robur*). *PLoS One* 6, e17857.
- Brinkmann, R., Behr, O., Niermann, I., Reich, M., 2011. Methods to assess and reduce collision risk of bats at onshore wind energy turbines (in German). Cuivillier Verlag, Göttingen, Germany.
- Collins, J., Jones, G., 2009. Differences in bat activity in relation to bat detector height: implications for bat surveys at proposed windfarm sites. *Acta Chiropterologica* 11, 343–350.
- Dietz, C., von Helversen, O., Nill, D. (Eds.), 2007. *Handbuch der Fledermäuse Europas und Nordwestafrikas*. Kosmos, Stuttgart.
- Dürr, T., 2012. Fledermausverluste an Windenergieanlagen. Daten aus der zentralen Fundkartei der Staatlichen Vogelschutzwarte im Landesumweltamt Brandenburg. <<http://www.tobias.duerr@lua.brandenburg.de>>.
- Elston, D.A., Moss, R., Boulinier, T., Arrowsmith, C., Lambin, X., 2001. Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. *Parasitology* 122, 563–569.
- Fenton, M.B., 1989. The foraging behaviour and ecology of animal-eating bats. *Canadian Journal of Zoology* 68, 411–421.
- Fenton, M.B., Griffin, D.R., 1997. High-altitude pursuit of insects by echolocating bats. *Journal of Mammalogy* 78, 247–250.
- Garland, T., Harvey, P.H., Ives, A.R., 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* 41, 18–32.
- Griffin, D.R., Thompson, D., 1982. High altitude echolocation of insects by bats. *Behavioral Ecology and Sociobiology* 10, 303–306.
- Hayes, J.P., Gruver, J.C., 2000. Vertical stratification of bat activity in an old-growth forest in western Washington. *Northwest Science* 74, 102–108.
- Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R., Racey, P.A., 2009. Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research* 8, 93–115.
- Jung, K., Kaiser, S., Böhm, S., Nieschulze, J., Kalko, E.K.V., 2012. Moving in three dimensions: effects of structural complexity on occurrence and activity of insectivorous bats in managed forest stands. *Journal of Applied Ecology* 49, 523–531.
- Kalcounis, M.C., Hobson, K.A., Brigham, R.M., Hecker, K.R., 1999. Bat activity in the boreal forest: importance of stand type and vertical strata. *Journal of Mammalogy* 80, 673–682.
- Kalko, M.B., Smith, A.R., Kalko, E.K.V., 2008. Bats limit arthropods and herbivory in a tropical forest. *Science* 320, 71.
- Kemmel, S.W., Ackerly, D.D., Blomberg, S.P., Cornwell, W.K., Cowan, P.D., Helmus, M.R., Morlon, H., Webb, C.O., 2011. Picante - R tools for integrating phylogenies and ecology. Version: 1.3-0.
- Kunz, T.H., Arnett, E.B., Erickson, W.P., Hoar, A.R., Johnson, G.D., Larkin, R.P., Strickland, M.D., Thresher, R.W., Tuttle, M.D., 2007. Ecological impacts of wind energy development on bats: questions, research needs, and hypotheses. *Frontiers in Ecology and the Environment* 5, 315–324.
- Lawrence, B.D., Simmons, J.A., 1982. Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *Journal of Acoustical Society of America* 71, 585–590.
- Lefsky, M.A., Cohen, W.B., Parker, G.G., Harding, D.J., 2002. Lidar remote sensing for ecosystem studies. *Bioscience* 52, 19–30.
- Mehr, M., Brandl, R., Kneib, T., Müller, J., 2012. The effect of bark beetle infestation and salvage logging on bat activity in a national park. *Biodiversity and Conservation* 21, 2775–2786.
- Müller, J., Mehr, M., Bässler, C., Fenton, M.B., Hothorn, T., Pretzsch, H., Klemmt, H.-J., Brandl, R., 2012. Aggregative response in bats: prey abundance versus habitat. *Oecologia* 169, 673–684.
- Patriquin, K.J., Barclay, R.M.R., 2003. Foraging by bats in cleared, thinned and unharvested boreal forest. *Journal of Applied Ecology* 40, 646–657.
- Peters, S.L., Malcolm, J.R., Zimmerman, P.I., 2006. Effects of selective logging on bat communities in the southeastern Amazon. *Conservation Biology* 20, 1410–1421.
- Plank, M., Fiedler, K., Reiter, G., 2011. Use of forest strata by bats in temperate forests. *Journal of Zoology* 286, 154–162.
- Riedinger, V., Müller, J., Stadler, J., Brandl, R., 2013. Phylogenetic diversity of bats decreases in urban environments. *Basic and Applied Ecology* 14, 74–80.
- Rydell, J., Bach, L., Dubourg-Savage, M.-J., Green, M., Rodrigues, L., Hedenström, A., 2010a. Bat mortality at wind turbines in northwestern Europe. *Acta Chiropterologica* 12, 261–274.
- Rydell, J., Bach, L., Dubourg-Savage, M.-J., Green, M., Rodrigues, L., Hedenström, A., 2010b. Mortality of bats at wind turbines links to nocturnal insect migration? *European Journal of Wildlife Research* 56, 823–827.
- Rydell, J., Engström, H., Hedenström, A., Larsen, J.K., Pettersson, J., Green, M., 2012. The Effect of Wind Power on Birds and Bats – A Synthesis. Swedish Environmental Protection Agency, Report 6511, p. 152.
- Safi, K., Kerth, G., 2007. Comparative analyses suggest that information transfer promoted sociality in male bats in temperate zones. *American Naturalist* 170, 465–471.
- Schnitzler, H.U., Kalko, E.K.V., 2001. Echolocation by insect-eating bats. *Bioscience* 51, 557–569.
- Stahlschmidt, P., Brühl, C.A., 2012. Bats as bioindicators – the need of a standardized method for acoustic bat activity survey. *Methods in Ecology and Evolution*. <http://dx.doi.org/10.1111/j.2041-210X.2012.00188.x>.
- Svenning, J.-C., 2002. A review of natural vegetation openness in north-west Europe. *Biological Conservation* 104, 133–148.
- Walters, C., Freeman, R., Collen, A., Dietz, C., Fenton, M.B., Jones, G., Obrist, M.-K., Puechmaile, S.J., Sattler, T., Siemers, B.M., Parsons, S., Jones, K.E., 2012. A continental-scale tool for acoustic identification of European bats. *Journal of Applied Ecology* 49, 1064–1074.