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Abstract

In this study parallel ground and canopy recordings of bat calls were compared in order to analyze the vertical stratification in a temperate forest in Central Europe. The recording effort was 48 nights, by sampling 16 sites three times during the year 2010. During this study, 2170 sequences were recorded with 40 % of these in the canopy level. Overall 16 bat species could be determined. On the ground level 13 species were recorded, compared to 14 species in the canopy. By calculating GLMMs for eight species with sufficient data, the effect of stratum, time period, temperature, and habitat structure on the bat activity was analyzed. The A clear preference for the ground level was proven for four bat species. *Myotis bechsteinii* was the only species, which had a significant preference for the canopy level in all three periods, whereas three further species showed a clear canopy preference in at least one period. Therefore, canopy sampling should be taken into account for certain species. For conservation measures and monitoring efforts it must be considered, that the canopy stratum of the forest is very important. Some target species will be underestimated by ground measurements alone.

Keywords

acoustic monitoring, bat community, batcorder, chiroptera, *Myotis alcathoe*, *Pipistrellus pipistrellus*, Thayatal National Park

Nutzung des Baumkronenbereichs durch Fledermäuse in den gemäßigten Wäldern Zentraleuropas

Zusammenfassung

Mithilfe von parallelen Aufnahmen von Fledermausrufen wurde der bodennahe mit dem Baumkronenbereich verglichen, um die vertikale Stratifizierung von Fledermäusen in den gemäßigten Wäldern Zentraleuropas zu untersuchen. Im Zuge von 48 Nächten wurden 16 Untersuchungsflächen während des Jahres 2010 dreimalig beprobt. Dabei konnten insgesamt 2170 Rufsequenzen aufgenommen werden, wovon 40 % auf den Baumkronenbereich entfielen. Insgesamt wurden dabei 16 Fledermausarten nachgewiesen. Während im bodennahen Bereich 13 Arten nachgewiesen werden konnten, waren im Baumkronenbereich 14 Fledermausarten aktiv. Mithilfe von GLMMs wurden acht Arten, welche eine ausreichende Datenlage boten, auf die Parameter Stratum, zeitliche Periode, Temperatur und Habitatstruktur analysiert. Dabei zeigte sich für vier Arten eine klare Bevorzugung des bodennahen Bereichs. *Myotis bechsteinii* war die einzige Art, welche über alle drei Perioden hinweg eine signifikant höhere Aktivität im Baumkronenbereich hatte. Weiter drei Arten zeigten in mindestens einer Periode eine signifikante Präferenz für den Baumkronenbereich. Aufgrund dessen sollte die Untersuchung des oberen Stratums des Waldes für bestimmte Arten in Betracht gezogen werden. Für Naturschutzmaßnahmen und Monitoringprogramme muss die Bedeutung des Baumkronenbereichs berücksichtigt werden. Besondere Zielarten würden durch eine Betrachtung mit reinen Bodenaufnahmen unterschätzt werden.

Schlagwörter

akustisches Monitoring, Fledermausgesellschaft, Batcorder, Chiroptera, *Myotis alcaethoe*, *Pipistrellus pipistrellus*, Nationalpark Thayatal

Introduction

Bats are one of the most endangered vertebrate groups in Austria. Many bats are listed in the red list of threatened mammals in Austria (Spitzenberger, 2005). Therefore they are very important for conservation measures and detailed information about the biology and ecology of single species is necessary (Racey & Entwistle, 2003). Since temperate forests in Central Europe are recently in the focus of many studies, the habitat selections of single species are in the point of interest. Due to its extend, the interior of the forest is the most important foraging habitat which also provides the highest bat species diversity (Celuch and Kropil, 2008).

This study focuses on vertical patterns of bat activity in the forest interior of the Thayatal National Park, in Lower Austria. Similar studies are very common in tropical ecosystems, due to the very complex vertical structure and species compositions in rainforests (Francis, 1994; Zubaid, 1994; Hecker & Brigham, 1999; Bernard, 2001; Kalko & Handley, 2001; Henry et al., 2004; Hodgkison et al., 2004; Kalko et al., 2008; Pereira et al., 2010; Voigt, 2010). All of these studies show a clear difference in the abundance and species compositions between the ground level and the canopy strata. Therefore a lot of species can be assigned to the canopy or to the ground, whereas others are able to use both strata. In temperate climate in North America (Bradshaw, 1996; Wunder & Carey, 1996; Kalcounis et al., 1999; Hayes and Gruver, 2000) and Australia (Adams et al., 2009) several studies on the vertical stratification of bats have been conducted. For Europe, only recently the first studies on the vertical stratification of bat communities have been published (Fichtner, 2004; Collins & Jones, 2009; Bach et al., 2010; Zeus, 2010). These studies in a temperate climate show the importance of the canopy as foraging habitat, because the activity of bats is similar to the ground level. A major weakness of these studies is the analyses on the genus level for certain taxa, especially for the genus *Myotis*. *Myotis* was handled as genus due to the lack of species discrimination (Anabat systems) or small sample sizes.

The studies in North America and Europe indicated, that species composition is similar within the strata, but there are significant differences in the activity level of certain species and species groups. Especially the vertical stratification of bats in temperate forest habitats in Central Europe is still poorly understood. Hence, the aim of this study was to get an insight

into the stratification of bats in a temperate forest in Central Europe. For some species, like ground gleaning bats and open space species, a clear stratification was expected. But in contrast to this, there are some bat species whose ecology is still poorly understood. In this study, whereas three time replications were conducted, following predictions have been analyzed:

- A clear stratification for ground gleaning bats and open space species occurs due to their foraging behavior, whereas bats which hunt close to the vegetation use both strata.
- Bat activity will differ during the three periods due to pregnancy, lactation, post-lactation and migration, respectively. The maximum activity will be reached during the lactation period due to high energy demands (Speakman & Racey, 1987; Ciechanowski et al., 2010).
- Bat activity will increase with the temperature, because the temperature is one main predictor for the activity of arthropods.
- The activity of bats is influenced by the forest structure. Species which hunt close to the vegetation will have an increased activity if the structure is more complex, whereas the other species will have a decreased activity.

Material and methods

In similar published studies from tropical areas, mostly canopy mist netting or bat call analyses were used. Studies from North America, Australia and Europe focus on the recording and identification of bat calls. Comparisons of acoustical and capture techniques show, that acoustical systems are more suitable to represent the species composition with the same time afford (Murray et al., 1999; O'Farrell & Gannon, 1999; MacSwiney et al., 2008) and the importance of acoustical analysis is pointed out (Flaquer et al., 2007). Therefore this study focuses on acoustical methods.

Recording and analysis of bat calls

For the recording of bat calls we used two automated ultrasound recording units (“batcorder”, ecoObs, Nuremberg, Germany, www.ecoobs.de). Batcorder digitally records ultrasonic signals in real time (500 kHz, 16 bit). Furthermore, this system uses an online analysis to distinguish between bat calls and other ultrasound origins like locusts. Further advantages are the comparability of the results from different devices (calibrated sensitivity) and the omnidirectionality of the microphone. This system was originally designed for studies on microhabitat usage by bats in forests, therefore it is very suitable for this study (Runkel, 2008). The devices are calibrated and configured by ecoObs and no further adjustments of the settings have been made (400ms post trigger, -27 dB threshold level). The timers of the batcorders were always set to record the full night (two hours before sunset until two hours after sunrise).

In a first step, the bat calls recorded by the batcorder were automatically stored and measured with the software packages bcAdmin 2.0 (ecoObs, Nuremberg). In a next step the measurements were analyzed with the software batIdent 1.02 (ecoObs, Nuremberg).

After the automated classification each sequence was manually checked with the software bcAnalyze 1.11 (ecoObs, Nuremberg), using published descriptions for bat calls of the different species (Zingg, 1990; Russo & Jones, 2002; Pfalzer, 2002; Pfalzer & Kusch, 2003; Skiba, 2003; Obrist et al., 2004; Dietz et al., 2007; Pfalzer, 2007; Hammer et al., 2009). Each sequence which was classified as “Nyctaloid” or underlying taxa were also manually checked using the software BatSound 4.1 (Pettersson Elektronik AB, Uppsalla) and through a discrimination analysis using duration (D), start frequency, frequency at D/2, frequency at maximum energy and end frequency of single calls as classification criteria (Zingg, 1990; Sattler et al., 2007). These procedures resulted in a manual classification of each call sequence to the lowest possible operational taxonomic units (OTUs).

Study area

This study was conducted 2010 in the Thayatal National Park, which is situated in the northern part of Lower Austria. This small conservation area (1.330 ha) is a bilateral national park, the Czech part being called Podyji (6.260 ha). In the Austrian part three forest types are dominant: beech (*Fagus sylvatica*), hornbeam (*Carpinus betulus*), and oak forests (*Quercus*

sp.) (Grabherr & Willner, 2007). A previous study by Hüttmeir et al. (in press) proved 20 bat species for this study area in the year 2009. Therefore it was very suitable to study the stratification of bats, because assumptions for a wide range of species were expected.

Mounting technique

The technique to put batcorders in place was designed according to Humphrey et al. (1968), Munn (1991) and Kunz & Parsons (2009). To mount one batcorder (ecoObs, Nuremberg) at heights up to 20 m in the canopy, two suitable trees in a distance of approximately 10 m to each other were necessary. A tree was scored as suitable if strong branches in the upper canopy were available from the ground, with no branches or other structures beneath, which would interfere with the construction method. Furthermore trees with signs of damage, illness or recently fallen branches were avoided for safety reasons (Kunz & Parsons, 2009). At first it was necessary to pull a top support rope over the two chosen trees. To achieve that a commercial slingshot, a fishing reel, and a strong mainline with a plumb ball were used. The plumb ball, which was mounted to the mainline, was shot over the first tree and the top support rope was reeled in with the fishing reel. The next step was to shoot the plumb ball over the second tree and reel the top support rope in. In this stage, the pull rope between the two trees was still on the ground. Now the pull rope was mounted in the middle of the top support rope with a carabiner. After the pull rope was fixed at the ground, the top support rope was lifted up and both ends hog-tied to a tree nearby. The first batcorder was now lifted with the pull rope, and a stabilization rope was also tied to the batcorder, to make it more stable and prevent it from oscillation. As the batcorder was mounted in the canopy stratum, it was important to keep a minimum distance of 2.50 m to the trees and branches, to prevent problems with reflections of the ultrasound calls of the bats. The mean height of the upper batcorder was 13.9 m (SD = 2.1 m), with a range from 10.0 to 19.0 m. As last step the second batcorder, which recorded the bat calls near ground level, was mounted to the stabilization rope at a height of 2.30 m. At each measurement night the batcorder used for the canopy and the ground stratum were switched, to minimize the bias, if a single batcorder was more sensitive to bat calls than the other one. In addition to this, the recording sensitivity of both instruments was regularly checked.

Sampling design

For this study, 16 sampling sites in the Thayatal National Park were selected. The coordinates of these are listed in annex 1. Due to the small extend of the National Park, the mean minimum distance between two sites was 967 m with a range from 610 m to 1690 m. Each sampling site had to fulfill certain criteria to be comparable to the others. These sites had to be characteristic for the surrounding forest and it was important that no water bodies, forest roads or other possible flyways were located near the sampling site. Furthermore the sites needed to have a minimum distance of 50 m to the nearest forest edge. Thus, we were investigating the forest interior and no ecotones or sites where bat activity might be influenced by other factors.

At the sampling sites, two suitable trees for the mounting technique of the batcorder were chosen. For each of these 16 sampling sites, measurements of bat activity were made in three periods. Period 1, covered May and June and comprises the pregnancy phase. The second Period covered July and August during the lactation, and Period 3 was conducted in September during the post-lactation and migration phase. These periods should show the changes in the activity of the bats due to the different reproductive stages.

Table 1: List of the recorded habitat parameters for each site, which were used for further analyses.

parameter	scale	description
tree height	meter	mean height in a 15 m radius
height of the batcorder	%	height of the batcorder divided by the tree height
forest type	beech, hornbeam, oak	
distance to next forest edge	m	
distance to next settlement	m	
large tree trunks	rank scale: 1 – 3	trees > 50 cm diameter
variance breast-height diameter	m	all trees in a 30 m radius
basal tree area	m ²	all trees in a 30 m radius
density of the ground related stratum	rank scale: 1 – 5	very dense to very open

In addition to the recording of bat calls, important habitat parameters (Table 1) of the forest were measured (Ford et al., 2005; Kanuch et al., 2008). Here, only parameters are listed which were used for further analyses (full list see annex II). The structural parameters tree height, variance of the breast-height diameter, basal tree area and the density of the ground

related stratum (amount of tree trunks and bushes) are the most important parameters for the bats to influence the ability to fly and maneuver properly. Also, the distance to the next forest edge, and to the next human settlement were recorded since these are very important feeding or roosting sites. In addition to this, one button temperature logger (SL52T, ± 0.5 °C, Signatrol Ltd, Tewkesbury, www.signatrol.com) was mounted to each batcorder. These data loggers were configured to record the ambient air temperature every 15 minutes.

Statistical analyses

In a first step, the data was exported from bcAdmin 2.06 and a species-sampling point matrix was created, with the number of sequences in each cell. For the identification of the most important habitat parameters for further analysis, this matrix was converted in a standardized Bray-Curtis distance matrix using PRIMER-E (Clarke & Gorley, 2006). With this matrix a non-linear multidimensional scaling (NMDS) was performed. For this purpose, the three replicate bat surveys for each site were summed up to achieve a more complete local species abundance list. In the resulting NMDS ordination plot the sampling sites gradually distributed along the first ordination axis (Figure 1). No clustering of different forest types occurred. Thus, Pearson correlations of the first and second ordination axis values drawn from the NMDS with the standardized habitat parameters from the field survey were calculated. To achieve normality of the variables, they were transformed if necessary (log, sqrt or arc-sin-sqrt transformations). All parameters which were correlated significantly with the position of the bat communities in reduced ordination space were identified as important and were thus considered for further analyses. The first ordination axis of the NMDS plot was mainly correlated with forest structural parameters (tree height, variance of the breast-height diameter, basal tree area, density of the ground related stratum, distance to next forest edge, distance to next settlement). Many of these important habitat parameters were multicollinear to each other, so a principle component analyses (PCA) was performed to condense the information contained in these parameters. The first and second principal components of this PCA were then used for further analysis. All analyses above were conducted with the software Statistica 9 (StatSoft GmbH). Furthermore, for each night and each batcorder, the mean temperature recorded by the temperature data-logger was calculated. For three nights no temperature data were available, due to problems with the

data-logger. Therefore a linear regression of the other recorded nights to the temperature data of the weather-station in Retz was calculated and the mean temperature for these three nights estimated.

With the data prepared during these steps, generalized linear mixed models (GLMM) were calculated with the software R 2.12.0 (R Development Core Team, 2010) using the package lme4 (Bates, 2005). For each bat species (or OTU) with more than 30 call sequences recorded a GLMM was constructed. In addition to this, a GLMM was calculated for all recorded sequences of all species summarized as OTU Spec to show overall effects of stratum and season on calling activity amongst Chiroptera in the study region. The OTUs Mkm, *Myotis* and Chiroptera sp. indet were excluded from further analyses, because different, acoustically inseparable species are united within these OTUs which nevertheless may show diverging habitat use. With these GLMMs it was possible to analyze the effects of stratum, period, and the most important habitat parameters on the frequency of recorded calls. In each GLMM the dependent variable was the number of call sequences for the respective species in each night and batcorder ($n = 96$), the independent variables were stratum (ground or canopy), period (1, 2 or 3), mean temperature (standardized), PCA1 and PCA2 of the habitat variables, and the interaction term between stratum and period. Sampling site (because of the three repetitions per site) and the measure night (because of the parallel recordings) were used as random factors. As family function a Poisson distribution and a log-link was used. After the full GLMM had been calculated for each species, a stepwise backward reduction was performed. If the interaction of stratum and period was not significant, it was dropped. In the next steps, the parameter with the highest p-value was removed (p-value at reduction point is always listed) and a new GLMM was calculated. The GLMM was reduced, till only parameters with a p-value < 0.05 were included. This final GLMM was used for further interpretation. Due to this model building approach, no Bonferroni correction was adopted (Moran, 2003). Since the package lme4 offers no single p-value for factors with more than two steps, it is only listed in the table if at least one value for period was significant or not. If the interaction of stratum and period was significant, the effect of stratum was analyzed by re-calculating the final GLMM with a subset for each period. Furthermore it is listed if the stratum was significant in at least one period.

Results

Overall 2170 call sequences were recorded in 48 nights with two batcorders (Table 2). In the first period 1151 sequences were recorded, 636 in the second period, and 380 in the last period. In these three periods, 1301 call sequences were recorded on the ground level and 869 in the canopy stratum. 65 % of all calls could be determined to the lowest possible level. In most cases this was the species level, except for *Myotis brandtii* (EVERSMANN, 1845) and *Myotis mystacinus* (KUHL, 1817), which were determined to an OTU termed Mbart hereafter, because these two related species cannot be distinguished through acoustical analysis of their search calls. The other 35 % (Table 3) of the call sequences could only be determined to OTUs at more coarse resolution, of which the OTU Mkm, which consists of *Myotis daubentonii*, *Myotis bechsteinii* and Mbart (n = 446 sequences) was the most important. Further 279 sequences could only be determined to the genus *Myotis* (Table 2).

Table 2: Numbers of recorded call sequences per OTU. Only for OTUs in bold letters further analyses were performed. Ground level is indicated as "G" and canopy level as "C". Mbart consist of *Myotis brandtii* and *Myotis mystacinus*. Mkm is an OTU of calls of *M. alcaethoe*, *M. daubentonii*, *M. bechsteinii* and Mbart.

OTU	period 1		period 2		period 3		overall		sum
	G	C	G	C	G	C	G	C	
<i>Pipistrellus pipistrellus</i> (LEACH, 1825)	481	26	35	100	52	56	568	182	750
Mkm	128	89	75	88	9	57	212	234	446
<i>Myotis</i> sp.	94	55	34	66	0	30	128	151	279
Mbart	70	25	36	36	6	19	112	80	192
<i>Myotis alcaethoe</i> (HELVERSEN & HELLER, 2001)	23	25	6	35	6	31	35	91	126
<i>Pipistrellus pygmaeus</i> (LEACH, 1825)	6	5	1	3	57	22	64	30	94
<i>Myotis daubentonii</i> (KUHL, 1817),	43	10	11	2	0	0	54	12	66
<i>Myotis bechsteinii</i> (KUHL, 1817)	14	25	6	11	0	4	20	40	60
<i>Barbastella barbastellus</i> (SCHREBER, 1774)	8	1	21	9	9	3	38	13	51
<i>Eptesicus serotinus</i> (SCHREBER, 1774)	3	1	23	4	0	0	26	5	31
Chiroptera sp. indet.	3	2	7	10	4	4	14	16	30
<i>Myotis myotis</i> (BORKHAUSEN, 1797)	5	0	5	0	3	0	13	0	13
<i>Myotis emarginatus</i> (GEOFFROY, 1806)	4	1	0	1	0	3	4	5	9
<i>Myotis nattereri</i> (KUHL, 1817)	0	0	3	0	4	0	7	0	7
<i>Eptesicus nilssonii</i> (KEYSERLING & BLASIUS, 1839)	0	1	5	0	0	0	5	1	6
<i>Nyctalus leisleri</i> (KUHL, 1817)	0	3	1	0	0	1	1	4	5
<i>Rhinolophus hipposideros</i> (BECHSTEIN, 1800)	0	0	0	0	0	2	0	2	2
<i>Nyctalus noctula</i> (SCHREBER, 1774)	0	0	0	2	0	0	0	2	2
<i>Vespertilio murinus</i> (LINNAEUS, 1758).	0	0	0	0	0	1	0	1	1
sum	882	269	269	367	150	230	1301	869	
	1151		636		380		2170		

In Table 3 the proportions of sequences which could not be determined to the lowest possible OTUs are listed. The percentages of undetermined sequences were higher in the canopy stratum and this effect was equal for all three periods. Only 1.4 % of all recorded sequences could not be determined to genus or species level.

Table 3: Proportion of sequences which could not be determined to the lowest possible OTU

	period 1	period 2	period 3	overall
ground	25.5 %	43.1 %	8.7 %	27.2 %
canopy	54.3 %	44.7 %	39.1 %	46.1 %
sum	32.2 %	44.0 %	27.2 %	34.8 %

The mean nightly temperature during the first period was 12.4 °C (\pm 2.63 SE) and in 5 out of the 32 measurements, the mean night temperature was below 10 °C. In the second period the mean temperature was 16.4 °C (\pm 2.33 SE). The third period was the coldest one, with a mean temperature of 10.5 °C (\pm 2.78 SE) and 9 measurements of the mean nightly temperature below 10 °C. Between the two strata no difference in the mean temperature was detectable (paired t-test: $t = -0.86$, $p = 0.39$).

Altogether, 16 bat species (including Mbart) were detected in this study (Table 3). Of these, 13 species were found on the ground level, with the exception of *Rhinolophus hipposideros*, *Nyctalus noctula* and *Vespertilio murinus*. In contrast, *Myotis myotis* and *Myotis nattereri* were never recorded in the canopy level.

In the NMDS (Fig. 1), calculated with sampling-point matrix, the different forest types did not clearly segregate from each other. The first ordination was significantly correlated with various habitat parameters. The second ordination of the NMDS correlated but weakly with the height of the batcorder. A PCA for the important habitat parameters, identified in the NMDS, was calculated. The first principal component (PCA 1) described 56.04 % of the variance, the second principal component (PCA 2) 16.41 %, and the third principal component contained less than 10 %. The PCA 1 was mainly composed of tree-height, variance of the breast-height diameter, basal tree area, density of the ground related stratum, large tree trunks and the distance to the next forest edge (factor loadings in this order). In contrast, PCA 2 was based on the distance to the next settlement and the amount of large tree trunks.

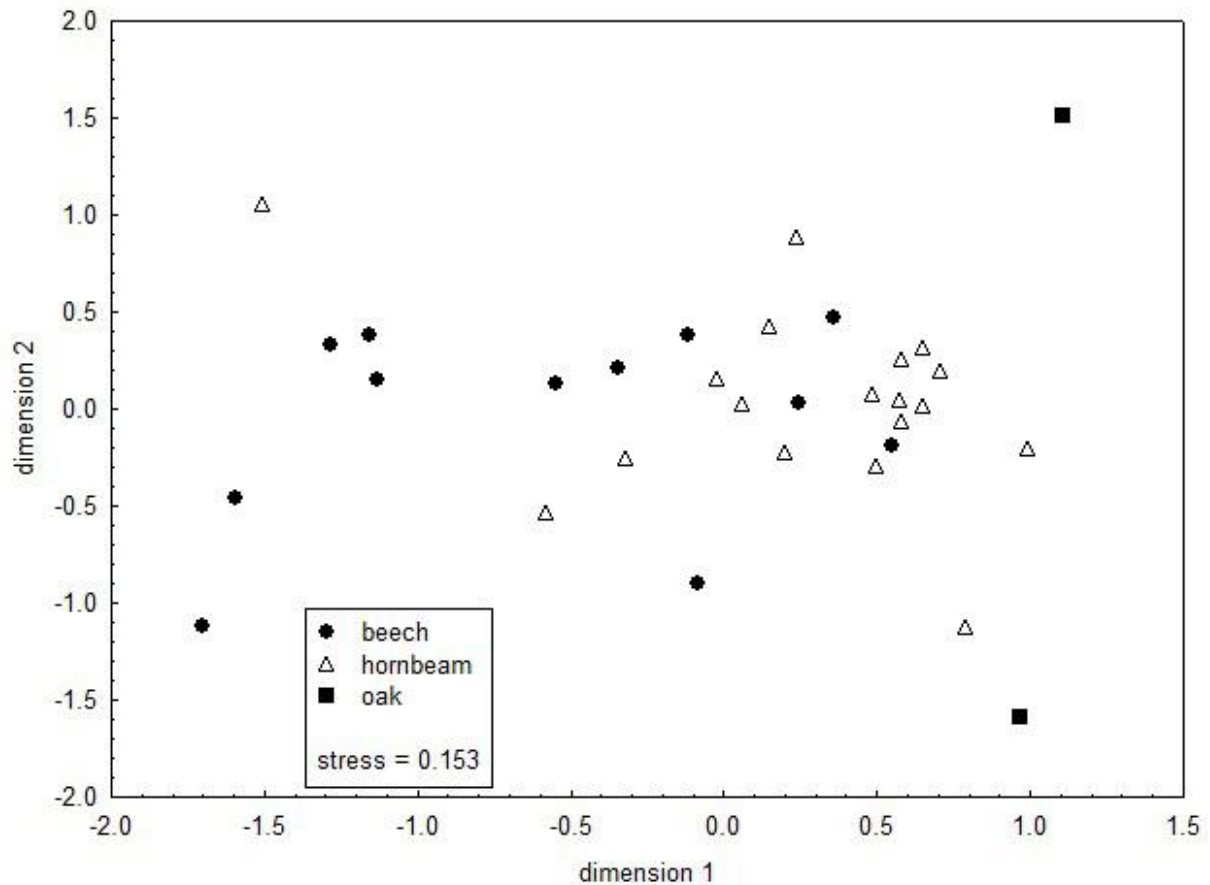


Fig. 1: NMDS ordination plot of bat communities based on Bray-Curtis distance matrix of call sequences. Each dot depicts one site, divided in ground or canopy stratum. The forest types did not clearly segregate from each other.

For all nine OTUs (Table 4), a significant overall effect of the stratum was found with the GLMMs, i.e. the calling activity of these species was not evenly distributed between canopy and understory. Over the three periods, a significant difference in the calling activity was found for six OTUs. Also, the significant interaction of period and stratum shows that calling activity varied across space and time for all bats combined and the OTUs *Myotis alcaethoe*, *Mbart* and *Pipistrellus pipistrellus*. Thus, all bat species with sufficiently large sample sizes showed at least some differentiation in their calling activity between the two forest strata. The forest structure, measured as PCA 1 and PCA 2, had a significant influence on call numbers only for all bats combined, *M. daubentonii*, *P. pipistrellus* and *Mbart*. Surprisingly, ambient air temperature had no significant positive influence on call frequencies, except for *M. alcaethoe*.

Table 4: Results of the final GLMM's for all bats combined, *Barbastella barbastellus* (Bbar), *Eptesicus serotinus* (Eser), *Myotis alcathoe* (Malc), *Myotis brandtii* & *Myotis mystacinus* (Mbart), *Myotis bechsteinii* (Mbec), *Myotis daubentonii* (Mdau), *Pipistrellus pipistrellus* (Ppip) and *Pipistrellus pygmaeus* (Ppyg). Given are z- and p-values for the variables included in the models and the respective sample-size corrected value of Akaike's Information Criterion (AICc). s. indicate that a least one factor was significant, otherwise it is marked as n.s. For models with a significant interaction, no single p-value for stratum can be shown.

species	stratum		temperature		PCA 1		PCA 2		period ×		final AICc
	z	p	z	p	z	p	z	p	period	stratum	
all		s.	0.34	0.74	2.03	0.043	1.75	0.080	s.	s.	1264.7
Bbar	-3.19	0.001	0.62	0.54	0.49	0.62	1.08	0.28	n.s.	n.s.	131.8
Eser	-3.30	0.001	1.35	0.18	0.70	0.48	0.03	0.98	n.s.	n.s.	66.0
Malc		s.	1.98	0.047	1.41	0.16	0.89	0.37	s.	s.	220.0
Mbart		s.	1.64	0.10	0.05	0.96	2.12	0.034	s.	s.	292.8
Mbec	2.44	0.015	0.33	0.74	0.83	0.41	0.07	0.95	s.	n.s.	159.7
Mdau	-4.66	<0.001	1.84	0.66	2.99	0.003	0.75	0.45	s.	n.s.	86.2
Ppip		s.	0.51	0.61	2.30	0.021	0.13	0.90	s.	s.	318.1
Ppyg	-3.40	<0.001	0.08	0.94	-0.33	0.74	0.09	0.93	n.s.	n.s.	96.2

Fig. 2 shows the effect of the stratum for five bat species in which no significant interaction with period was observed. *Barbastella barbastellus*, *Eptesicus serotinus*, *Myotis daubentonii* and *Pipistrellus. pygmaeus* were significantly more active near ground level compared to the canopy. For *Myotis bechsteinii* a significantly higher activity in the canopy stratum level was found.

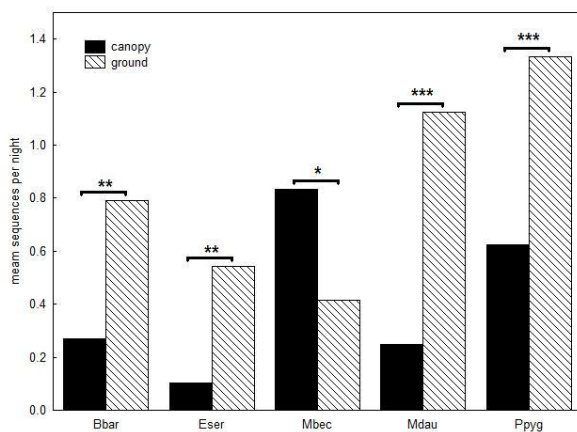


Fig. 2: Mean number of sequences per night in the canopy and ground level. Abbreviations see Table 4. * = 0,05 – 0,01, ** = 0.01-0.001, *** = <0.001

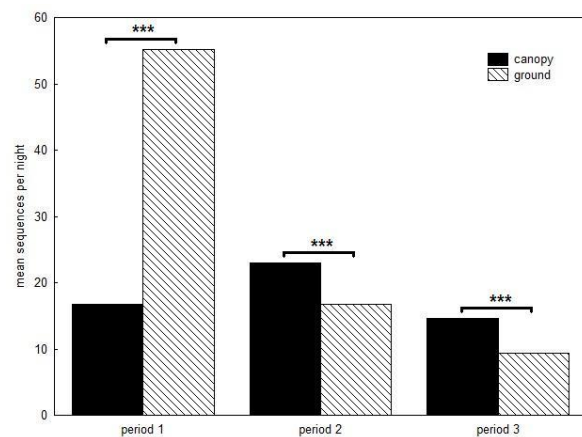


Fig. 3: Mean number of sequences per night in the canopy and ground level across all three periods for all bats combined. * = 0,05 – 0,01, ** = 0.01-0.001, *** = <0.001

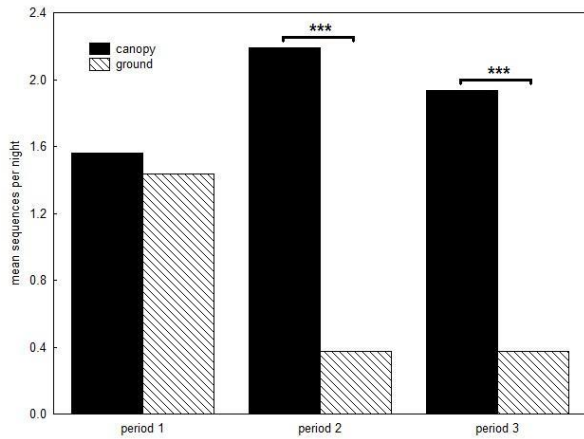


Fig. 4: Mean number of sequences per night in the canopy and ground level across all three periods for *Myotis alcaethoe*. * = 0,05 – 0,01, ** = 0.01-0.001, * = <0.001**

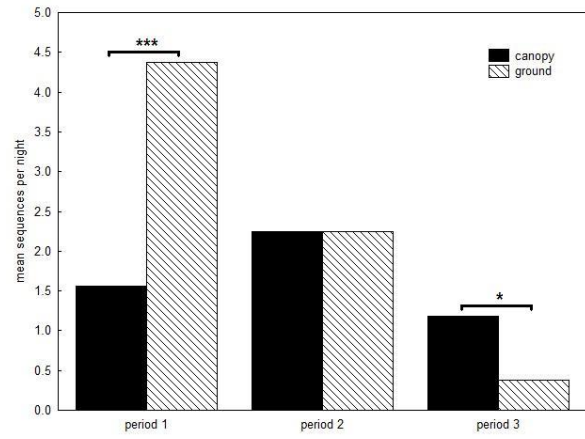


Fig. 5: Mean number of sequences per night in the canopy and ground level in all periods for *Myotis brandtii* & *Myotis mystacinus* (Mbart). * = 0,05 – 0,01, ** = 0.01-0.001, * = <0.001**

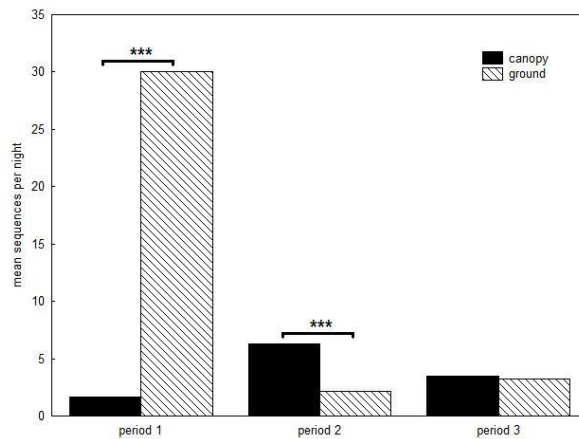


Fig. 6: Mean number of sequences per night in the canopy and ground level in all periods for *Pipistrellus pipistrellus*. * = 0,05 – 0,01, ** = 0.01-0.001, * = <0.001**

For all bats combined, *M. alcaethoe*, Mbart and *P. pipistrellus*, which had a significant interaction between stratum and period, the reduced GLMM was calculated separately for each period. Bats in general (Fig. 3) showed a significantly higher activity in the understory in the pregnancy period ($z = -17.05$, $p < 0.001$). In the lactation ($z = 3.87$, $p < 0.001$), and in the post-lactation and migration period ($z = 4.20$, $p < 0.001$) the activity in the canopy stratum was clearly higher. *M. alcaethoe* (Fig. 4) showed a significant stratification in periods 2 ($z = 3.92$, $p < 0.001$) and 3 ($z = 3.61$, $p < 0.001$) with a strong preference for the canopy stratum. In period 1 ($z = 0.28$, $p = 0.78$) no stratification occurred. The OTU Mbart (Fig. 5), which comprises the two species *M. brandtii* and *M. mystacinus*, revealed a strong preference for the ground

level in period 1 ($z = -4.39$, $p < 0.001$), no difference in period 2 ($z = 0.00$, $p > 0.99$), and a less pronounced preference for the canopy stratum in period 3 ($z = 2.39$, $p = 0.017$). *P. pipistrellus* (Fig. 6), the most active bat species during this study, showed a very clear preference for the understory level in period 1 ($z = -14.48$, $p < 0.001$), in period 2 more activity in the canopy stratum ($z = 5.32$, $p < 0.001$), and no difference in period 3 ($z = 0.38$, $p = 0.70$).

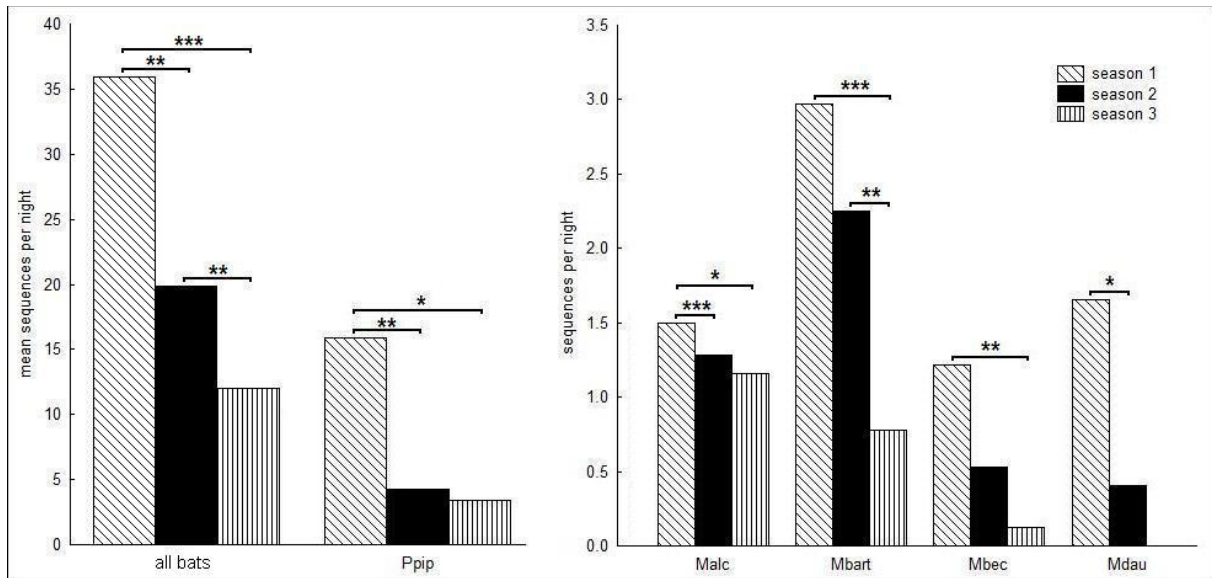


Fig. 7: The effect of the period on the mean calling activity of all bats combined, Ppip, Malc, Mbart, Mbec, and Mdau. Abbreviations see Table 4. * = 0,05 – 0,01, ** = 0.01-0.001, *** = <0.001

Six OTUs exhibited distinct periodic patterns in their calling activity (Fig. 7, Table 5). In all these cases activity declined from spring to autumn. For *Barbastella barbastellus*, *Eptesicus serotinus* and *Pipistrellus pygmaeus* no significant periodic changes were recorded.

Table 5: Differences of the recorded sequences between the periods. In all cases, the activity is declining from the first period to the last period. Mbart consist of *Myotis brandtii* and *Myotis mystacinus*.

species	period 1 vs period 2		period 1 vs. period 3		period 2 vs. period 3	
	z	p	z	p	z	p
all	-2.59	0.001	-5.15	<0.001	-2.60	<0.001
<i>Myotis alcathoe</i>	-3.48	<0.001	-2.26	0.024	1.22	0.22
Mbart	-1.26	0.21	-4.20	<0.001	-3.20	0.001
<i>Myotis bechsteinii</i>	-1.35	0.18	-2.93	0.004	-1.9	0.06
<i>Myotis daubentonii</i>	-2.15	0.032	-0.01	0.99	-0.01	0.99
<i>Pipistrellus pipistrellus</i>	-2.81	0.005	-2.51	0.012	0.21	0.84

All bats combined, *P. pipistrellus* and *M. daubentonii* were the only OTUs which showed a significant response of their calling activity to the forest structure described as first dimension of the PCA (Table 4). In sites where the forest was denser and the amount of obstacles increased, their calling activity declined. The second dimension of the PCA was significant for Mbart, thus the activity increased with the distance to the next settlement and the amount of large tree trunks.

Discussion

During this study, 15 bat species and one OTU (Mbart) were recorded. In the study of Hüttmeir et al. (in press) 20 bat species in the Thayatal National Park and Podyji National Park were registered by mist netting, acoustic surveys, and checking of roosts. Of these 20 species 18 OTUs are possible to be discriminated with the batcorder system (Runkel, 2010). Compared to Hüttmeir et al. (in press) *Pipistrellus nathusii* (KEYSERLING & BLASIUS, 1839), *Plecotus auritus* (LINNAEUS, 1758), and *Plecotus austriacus* (FISCHER, 1829) were not detected in this study.

By studying the activity of bats only on the ground level in closed forest, some species which use the upper canopy or which fly above the forest will be missed. In this study, three species were only recorded in the canopy stratum. In the study of Collins and Jones (2009) some species were found only on the canopy level too. But this effect was only dominant in closed canopy woodland, whereas in other habitat types they registered all species if only recorded from the ground.

Two species were only recorded on the ground level. *Myotis myotis* is a species which is hunting for ground living arthropods (Dietz et al., 2007) and therefore this species was expected to be active dominantly on the ground level. In this study, all recordings were made on the ground level. But with only 13 sequences in 48 nights no further analyses have been conducted. All five species, which were only recorded in one stratum, accounted only for 1.2 % of all sequences. Therefore it is not possible to make any statement about their habitat selections and their occurrence in only one stratum is probably an effect of the small sampling size. However, stratification could be expected and needs further investigation.

The community analyses with the NMDS revealed that the bat assemblages do not depend on a special forest type. The three forest types did not clearly segregate from each other. Moreover the forest types are very much interlaced in the survey area, therefore it was not expected to find completely different species communities in these sites. On the community level, the structural parameters of the forest are more important. Differences between the forest types occur, because a typically beech forest has another structural environment than a typical hornbeam forest. It is possible that major distinctions occur, if the species are sampled in larger areas of single forest types. Therefore further studies are recommended.

Effect of the stratum on the bat activity

The results of this study emphasize the importance of the canopy stratum as foraging habitat. Like similar studies (Kalcounis et al., 1999; Collins & Jones, 2009; Bach et al., 2010; Zeus, 2010) in the northern hemisphere no clear stratification of the communities appeared. Compared to the previous studies, I was also able to make assumptions for the single species of the genus *Myotis*.

The stratification of all bats summarized, show the importance of the canopy stratum. In the first period, the activity on the ground was significantly higher. But in the second and third period, the canopy stratum was found to be more important. By analyzing single species, a more complex pattern is shown. Some species show a clear stratification in all three periods, with a preference for the ground (*Barbastella barbastellus*, *Eptesicus serotinus*, *Myotis daubentonii*, *Pipistrellus pygmaeus*) or the canopy (*Myotis bechsteinii*). Also three species (*Myotis alcathoe*, *M. bart*, *Pipistrellus pipistrellus*) showed a switch of their foraging habitat preference during the year. It seems that every species is very special, and that an evaluation on the genus level will be very misleading. Especially for the genus *Myotis*, which consist of species with very distinctive foraging strategies.

All species, which have a significant higher activity on the ground level, are also found in the canopy stratum regularly. Around 75 % of all calls from *Barbastella barbastellus* were recorded on the ground level. This species typically inhabits woodlands of all kinds, with a preference to highly structured habitats. The main diet is small tympanate moths (Sierro, 1999; Dietz et al., 2007). Radiotracked individuals observed by Sierro & Arlettaz (1997) are described to forage typically near to the vegetation and above the forest canopy. In the

study of Zeus (2010), the main activity of *B. barbastellus* was also on the ground. In the third period of her study the stratification was significant. The results of Zeus (2010) are in good accordance with this study. These findings indicate that *B. barbastellus* prefer the ground level of the forest in contrast to the canopy level. In addition to this, the study of Siervo & Arlettaz (1997) was conducted in a pine forest, which could also lead to a different habitat selection. But it must also be considered, that individuals who were foraging above the canopy were possible not recorded by the batcorder within the canopy.

For *Eptesicus serotinus* only five sequences were recorded in the canopy stratum, so a significant preference for the ground level was found. The main hunting habitats reported for this species are pasture areas, orchard meadows, parks and edges of water bodies (Dietz et al., 2007). The interior of the forest is not the typical hunting area of *E. serotinus*, but nonetheless it was regularly recorded (31 sequences). The results of this study are similar to the study of Bach et al. (2010) in a mature beech forest. There, the activity of *E. serotinus* was also higher in the lowest strata than in the upper two surveyed strata. The temporal distribution of the recorded sequences show, that 65.4 % of the sequences on the ground level were recorded between 8.30 pm and 9.30 pm. This indicates, that *E. serotinus* uses the more open ground related habitat for commuting from its roosting sites to the feeding grounds. *Myotis daubentonii* had also a significant preference for the ground level in this study (54 sequences on the ground versus 12 sequences in the canopy stratum). *M. daubentonii* is reported to use mainly open water bodies for its foraging activities. But it is also able to use the interior of the forest as feeding ground. Individuals which are hunting in the forest, at forest edges or above marsh areas or reported to fly in heights of 1 to 5 m (Dietz et al., 2007). In this study, these reported data can be confirmed.

Pipistrellus pygmaeus, which is morphologically very similar to *P. pipistrellus*, had also a higher activity on the ground level than in the canopy stratum over all three periods. In contrast to *P. pipistrellus* it is known to be more selective in the use of the habitats (Davidson-Watts & Jones, 2006; Davidson-Watts et al., 2006), which are often related to water bodies. *P. pygmaeus* is also hunting closer to the vegetation than *P. pipistrellus* (Arnold et al., 2003). In addition to this, our study indicates, that *P. pygmaeus* also has a different habitat preference in the forest interior, where both species occur. At least in the

second and third season, the main activity of *P. pipistrellus* was in the canopy stratum. The findings in this study are comparable to the results from Collins & Jones (2009) in England. There the activity of *P. pygmaeus* was also significantly higher on the ground level.

Only one species had a significant preference for the canopy stratum in all three periods. *Myotis bechsteinii* is a species which is restricted to woodlands, especially to old growth broadleaved forests (Dietz & Pir, 2009; Zahn et al., 2010). They prefer the interior of the forest with high canopy cover (Napal et al., 2010). Therefore the Thayatal National Park is a suitable habitat for this annex two FFH-RL species (Hüttmeir et al., in press). *M. bechsteinii* is reported to fly in a height of 1 to 5 m very close to the vegetation, but depending on the habitat structure, it can also forage close to the ground or in the canopy stratum (Dietz et al., 2007). It is able to detect prey hidden in the vegetation only due to the sounds of the prey itself (Siemers & Swift, 2006). The results of this study are indicating a different habitat preference. The activity in the canopy was twice the activity on the ground (40 versus 20 recorded sequences).

Three species (incl. Mbart) had a varying preference for the stratum during the year. This variation was different within the species, no similar pattern turned up. *Pipistrellus pipistrellus* is a very common species in Europe (Dietz et al., 2007) and it can use a large variety of habitats (Oakeley & Jones, 1998; Russo & Jones, 2003; Sattler et al., 2007). In this study it was the most active species with 34.6 % of all sequences. In the first period a significant preference for the ground level was recorded. This effect is comparable to the studies of Collins & Jones (2009) and Bach et al. (2010), which also had a higher activity of *P. pipistrellus* on the ground level. But in the second period the effect was in opposite direction and in the third period there was no difference in the use of the strata (Fig. 4). In the study of Zeus (2010), which was conducted in open patches near water bodies, also a switch in the usage of the strata was found. In her first period, April to Mai 2010, also a significant preference for the ground level could be detected. And later in the period, there were no significant differences. In consideration of the flexibility in the selection of the habitat and their broad range of prey species (Arnold et al., 2003; Dietz et al., 2007) it seems, that their main hunting habitat is near to the ground. But they can also have high activities in the canopy stratum, because they are very flexible depending on the availability of insects.

Other parameters like interspecific competition with other bats like *Pipistrellus pygmaeus* can also be important. During this study, *Myotis alcathoe* also had a varying stratification. This species was first described in the year 2001 (von Helversen et al., 2001). Since then it has been shown that it is distributed all over Europe in an island like pattern (Dietz et al., 2007; Niermann et al., 2007). In Lower Austria the first record of *M. alcathoe* was in the Thayatal National Park (Hüttmeir et al., in press). Nematocera are one of the main components of their diet (Lucan et al., 2009). No data have yet been published about the vertical stratification of *M. alcathoe*, but it is known to use the lower canopy of broadleaf trees (Dietz et al., 2007). The roosting sites of *M. alcathoe* seem to be fissures or small cavities in the canopy, up to 16 m above the ground (Dietz et al., 2007; Lucan et al., 2009). In this study, a clear stratification in the second and third period was found (Fig. 4). In the first season the stratification was not significant, but the activity in the canopy was also slightly higher. *M. alcathoe* seems to have a preference for the canopy stratum, but it is also able to have comparable activities near the ground. The third OTU Mbart, which consists of the two species *M. brandtii* and *M. mystacinus*, also had a varying stratification. In the Thayatal National Park both species are occurring in comparable densities, as shown in the study of Hüttmeir et al. (in press) by mist netting. *M. brandtii* is described to use open forests with a varying high from the ground level up to the canopy (Dietz et al., 2007; Lustig, 2010). *M. mystacinus* is reported to prefer more open habitats, and to use forest predominantly in the proximity of rivers and other water bodies. It uses mainly foraging heights of 1 to 6 m but it is reported to fly also up to the canopy of the trees (Dietz et al., 2007). In the first period the main activity was on the ground level, whereas in the second period no difference between the strata use occurred, and in the third period the stratification was in the opposite direction (Fig. 3). With the acoustical analysis of Mbart, we are not able to tell, if this variation in the stratification is maybe depending on a species shift from *M. mystacinus* in the early periods to *M. brandtii* in September.

The influence of the forest structure on the bat activity

The activity of all bats combined decreased as the density of the forest increased. In sampling sites with an open structure, and a low amount of interfering obstacles the activity was higher. This effect was also significant for *Pipistrellus pipistrellus* and *Myotis daubentonii*. The clear preference for the ground level of *M. daubentonii* indicates that it

prefers open forest patches on the ground level and avoids the dense canopy stratum. This results are according to Siemers & Schnitzler (2004), since *M. daubentonii* is not able to detect prey as successfully in front of an background compared to other *Myotis* species.

The period effect

In the pregnancy period (Mai – June) 53.0 % of all sequences were recorded compared to 29.3 % in the lactation period (July – August) and 17.5 % in the post-lactation and migration period (September). Also the activities of all bats combined and five OTUs (*P. pipistrellus*, *M. alcaethoe*, *M. bart*, *M. bechsteinii* and *M. daubentonii*) were significantly different within the three periods. The third period was the coldest period with a mean temperature of 10.5 °C compared to 12.4 °C in the first and 16.4 °C in the second period. The temperature can only explain the low activity in the last period, but not the lower activity in the second period. It was expected to have the highest bat activity in the lactation period due to the high energy demand of the females (Speakman & Racey, 1987; Ciechanowski et al., 2010). Results of mist netting in the year 2009 by Hüttmeir et al. (in press) and 2010 (own data) in the study area revealed, that the proportion of the females captured is low. Thus, their contribution to the recorded activity is also expected to be low. A further explanation of the reduced activity in the forest in the second period is that some bat species have switched their foraging habitat. So, *Pipistrellus pipistrellus* is known to forage at human settlements, *Myotis daubentonii* primary at water bodies and *Myotis bechsteinii* also at orchard meadows (Dietz et al., 2007). These alternative habitats had maybe a better prey availability than the forest habitat. In addition to the overall decrease of activity during the year, the results (Fig. 3) indicate that the activity in the canopy is more stable in the three periods, whereas the activity on the ground is varying more. Maybe the prey species in the canopy habitat have similar abundances in the tree periods, whereas the occurrence of prey on the ground level is driven by mass occurrences of special arthropods (e.g. swarming of ants). To really understand these changes, it is inevitable to have additional studies about the abundance and seasonal changes of the prey species.

Conclusion

For inventory studies, it is important to detect all occurring bat species. With the acoustic survey from the ground 13 of the 16 species were recorded, compared to 14 species in the canopy stratum. In consideration of the high amount of work which is necessary to establish the batcorder in the canopy, it is not recommended to use this method for a simple inventory of bat species. Maybe, another technique with telescope bars is more suitable. Overall, it seems more important to use the available recourses to sample different habitats like water bodies and ecotone areas for a full-fledged species list.

In monitoring studies, the stratification of bats must always be considered. In our study, 50 % of the analyzed species showed a significant higher activity in the canopy in at least one period. In dependence of the species, which are monitored, it is recommended to consider recordings also in the canopy level. Especially for permanent plots, as the infrastructure in the tree only has to be established once.

For conservation measures, red listed species and species of community importance are the most suitable. At least 16 species which are listed in the annex IV and five species of the annex II of the FFH directive were recorded during this study. For two of these five annex II species a sufficient sampling size was reached. *Barbastella barbastellus* showed a higher activity on the ground level, conservation measures focussing on the ground level are adequate. But *Myotis bechsteinii* is an annex II species, which has a higher activity in the canopy stratum compared to the ground level. For conservation studies, it must be considered, that the activity will be underestimated, if the data are only collected on the ground level. Since it is a specialized forest species (Meschede & Heller, 2002), which has its main activity in the interior of near-natural woodlands, these findings are very important. The results of this study have also to be considered in establishing management plans, especially in working forests. If *Myotis bechsteinii* would be monitored only from the ground, its conservation status would be estimated on biased data.

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Appendix

Annex I: Coordinates of the sampling sites

	North	Esat
site 01	48.84324	15.85373
site 02	48.82453	15.91381
site 03	48.84825	15.85165
site 04	48.83804	15.83208
site 05	48.85219	15.87602
site 06	48.82789	15.88698
site 07	48.84455	15.89609
site 08	48.85637	15.84259
site 09	48.85819	15.87624
site 10	48.83654	15.88740
site 11	48.81726	15.92783
site 12	48.61100	15.83850
site 13	48.85068	15.86430
site 14	48.86772	15.84253
site 15	48.81626	15.95031
site 16	48.83463	15.90052

Annex II: Full list of all habitat variables which have been recorded

parameter	scale	description
basal tree area	m ²	all trees in a 30 m radius
canopy-closure	%	5 vertical pictures, ImageJ analyses (Abramoff et al., 2004)
cover of herb-layer	%	15 m radius, visually
cover of shrub-layer	%	15 m radius, visually
dead wood	1 – 5	visually, amount of dead wood on a scale
density of the ground related stratum	rank scale: 1 – 5	visually, very dense to very open
distance to next forest edge	m	GPS, Google Earth
distance to next settlement	m	GPS, Google Earth
distance to the next water body	m	GPS, Google Earth
distance to the river Thaya	m	GPS, Google Earth
exposition	N – NO – O ...	compass
forest type	beech, hornbeam, oak	dominating tree species
fraction of broad-leafed trees	%	15 m radius, visually
height of the batcorder	%	height of the batcorder divided by the tree height
inclination	°	visually
large tree trunks	rank scale: 1 – 3	trees > 50 cm diameter
number of tree size classes	1 – 2 – more	visually
texture of the forest	1 – 4	visual interpretation of the texture richness of the forest
tree height	meter	mean height in a 15 m radius
variance breast-height diameter	m	all trees in a 30 m radius

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Grundwehrdienst: Abgeleistet von 06.09.04 bis 04.05.05

Weitere Qualifikationen: BatSound; BC Admin; Statistica; R; Arc-GIS; MS Office, MS Excel,
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Fremdsprache: Englisch, (Latein)