Bat Activity at Nacelle Height Over Forest

Hendrik Reers, Stefanie Hartmann, Johanna Hurst and Robert Brinkmann

Abstract The number of wind power facilities (wind farms) has rapidly increased in Germany, with a number of these constructed in forested areas. As most bat species use forests to forage and roost, concerns have been raised in relation to the potentially higher collision risk with wind turbines in forests than in open landscapes. In addition, the standard curtailment algorithms used in open landscapes might not be appropriate in forests. An ample acoustic dataset derived from 193 nacelle height surveys of 130 individual turbines was used to investigate whether bat activity, phenology or species composition differ between forests and open landscapes. The data showed no significant differences between bats in forests and open landscape habitats, but revealed strong regional differences. Overall bat activity increases towards the east of Germany, which is mirrored by an increase of the dominant group of Nyctaloids, whereas the activity of common pipistrelles increases towards the south. These findings suggest that acoustic surveys must be interpreted on a regional and species-specific level. In summary, wind farms within forested areas do not seem not to inherently show higher bat activity at nacelle height, suggesting no increased collision risk for bats in general. However, future studies assessing bat activity at the lowest point of the rotor instead of at nacelle height are urgently needed, as well as studies that include additional variables such as proximity to bat roosts or the age of a forest.

Keywords Bat activity · Forests · Nacelle height · Wind farms · Germany · Collision risk · Acoustic surveys

H. Reers (✉) · S. Hartmann · J. Hurst · R. Brinkmann
Freiburg Institute for Applied Animal Ecology GmbH,
Dunantstraße 9, 79110 Freiburg, Germany
e-mail: reers@frinat.de

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Introduction

Renewable Energy and Increasing Wind Farms in Forests

The global trend in power being generated from renewable energy sources has led to increasing demands for wind power on a world-wide scale (Wang and Wang 2015; Valença and Bernard 2015; Bernard et al. 2014). In Germany, a new national energy concept was adopted in 2010. Therein, a target was defined: the renewable energy share of total electricity consumption should be increased to at least 35% by 2020 and 80% by 2050 (BMWI/BMU 2010). This target is well underway, in 2015 already 32.6% of total electricity consumption was produced from renewable energy sources, of which onshore wind farms provide 40.5% of the national renewable electricity production (Zentrum für Sonnenenergie- und Wasserstoff-Forschung Baden-Württemberg (ZSW) 2016). As a consequence, large numbers of wind power facilities are being installed all over Germany. While beneficial from an energy perspective, this can have severe consequences for wildlife, especially birds and bats (Voigt et al. 2015). Often, this leads to a typical "green-vs-green-dilemma" where sustainability and wildlife protection may not be compatible in all aspects (Köppel et al. 2014). The increasing demand for wind power requires decision-making despite the uncertainties that are involved.

So far, most wind farms have been constructed in northern Germany where wind yields are intrinsically higher due to geographical and climatic conditions. However, with an increasing demand for wind energy, more and more wind farms are being installed in middle and southern Germany. As the forested mountain ranges rank high among the sites due to a high wind resource, this leads to a larger proportion of wind farm developments in forested areas. However, information on the impacts of wind farms in forested areas is scarce compared to open landscapes. As forests play an important role for birds and bats, many experts claim that forested areas should be excluded completely from future wind farm planning (Richarz 2014) or claim that a minimum distance of 200 meters to forests should be preserved (Rodrigues et al. 2014). Such expert-opinions are so far mainly based on the precautionary principle and single case studies. For example, a study in the southern black forest found 35 dead bats of three species under 16 wind turbines in 2005 (Brinkmann et al. 2006), suggesting that collision risk with turbines might be high for bats in general.

The difficulty in predicting the impacts of wind farms in forests on bats is based mainly on two underlying uncertainties: the exact interaction of bats and wind farm infrastructure, and the role of forests for bat populations in general. Therefore, discussed below are both the knowledge and knowledge gaps with respect to these two topics.

Impacts of Wind Energy on Bats

The potential impacts of wind turbines on bats have been debated (Brinkmann et al. 1996; Rahmel et al. 1999) and studied when the first bat carcasses were found in Germany (Vierhaus 2000). However, it was not until wind farm construction increased significantly that awareness of the full potential impact of wind farms on bats arose, stimulating both initiatives in research and conservation (Brinkmann et al. 2011b; Arnett et al. 2008; Kunz et al. 2007; Behr et al. 2007). Many studies have provided evidence that large numbers of bats have died due to collisions with wind turbines world-wide (Barclay et al. 2007; Rydell et al. 2010a; Piorkowski and Timothy 2010; Lehnert et al. 2014; Baerwald et al. 2014; Barros et al. 2015).

A key issue that must be understood is the proximate and ultimate causes of death at wind turbines. Proximately, bats may die due to direct collision and subsequent fractures (Voigt et al. 2015; Brinkmann et al. 2006) or indirectly because of barotrauma (Baerwald et al. 2008). Ultimately, bats could be killed not only because wind farms are constructed within their natural foraging area or migration route, but also because wind farms could even attract bats from surrounding areas into the wind farms. Reasons for such an attraction could be that insects (a main source of food for bats) are attracted to the turbines (Rydell et al. 2010b), or that bats tend to swarm at tall structures (Cryan et al. 2014). This behavior seems to play a major role for migrating bat species (Jameson and Willis 2014). In summary, bats are probably the group of vertebrates which is most severely affected by wind farms (Voigt et al. 2015).

The manifold effects which lead to collisions between bats and turbines are increased by the bats' special biology and life-history: bats, in contrast to other taxonomic vertebrate groups such as similar sized passerine birds, are characterized by a long life-span and low reproductive rates (Kunz and Fenton 2003; Bernotat and Dierschke 2015). The death of a bat individual thus has a much larger effect on the local population dynamics than the death of a single passerine. Collisions at wind farms therefore impact population dynamics both through an increased mortality and a decreased reproductive rate. Despite their urgent necessity, studies on the impact of wind farms on a bat population level are still lacking (Voigt et al. 2015).

The occurrence of bats at a wind turbine can depend on a variety of factors, such as weather or location, but also on species characteristics (Schuster et al. 2015; Cryan and Brown 2007; Martin 2015; Leopold et al. 2014). Species hunting at greater height and in open air space are of highest concern (Zahn et al. 2014): In Germany, the largest proportion of bat fatalities at wind turbines stems from noctule (*Nyctalus noctula)*, both from local populations as well as migrating individuals (Lehnert et al. 2014; Dürr 2015; Voigt et al. 2012; Niermann et al. 2011a). The species with the second highest share is Nathusius's bat *(Pipistrellus nathusii)*, with most mortalities occurring during migration (Voigt et al. 2012; Dürr 2015; Niermann et al. 2011a). This underlines the special importance of Germany as a migration corridor due to its central geographic position. Germany therefore has an important responsibility for the preservation not only of local but also foreign bat populations (Lehnert et al. 2014; Voigt et al. 2015). National and international migration routes are of high importance and many of these cross wind farms (Cryan and Brown 2007; Baerwald et al. 2014). However, not only migrating species are concerned: the species with the third highest share in collision fatalities is the common pipistrelle (*P. pipistrellus)*, where individuals come from local populations (Dürr 2015; Voigt et al. 2012; Dietz et al. 2007; Niermann et al. 2011a). Other species that often collide with wind turbines are Leisler's bat (*N. leisleri)* and parti-coloured bat (*Vespertilio murinus*) (Dürr 2015).

Studies have demonstrated that the number of bat fatalities is strongly correlated with acoustic bat activity recorded at nacelle height, and that bat activity is lower when winds become stronger and temperatures become lower (Brinkmann et al. 2011b). Generally, species composition of bat fatalities can differ to some degree between different regions in Germany (Niermann et al. 2011b). If wind farms are increasingly built in forests, it is of crucial importance to understand whether and which of the above phenomena and correlations could be mediated by a forested landscape.

Special Habitat Characteristics of Forests

Forests play an important role for most bat species, as a wide range of bat species depends on forests to forage and roost (Lacki et al. 2007; Barclay and Kurta 2007). Of all 25 bat species recorded in Germany, 22 species use tree roosts, and all species use forests during hunting activities (Hurst et al. 2015; Dietz and Kiefer 2014). Especially rare and sensitive species rely on undisturbed old-growth forest, such as Bechstein's bat (*Myotis bechsteinii*) (Kerth et al. 2002; Dietz and Pir 2011). Such forests can also lead to mass concentrations of more common species, for example 600 noctules were observed to gather for hunting in a Polish forest (Polakowski et al. 2014).

Due to the importance of forests for bats, it is often assumed that bat activity and therefore collision risk is higher at forest sites than in open landscapes. Furthermore, the presence of a wider diversity of bat species in forests could also lead to a different species composition above the forest canopy. In addition, bat phenology could differ from that in open landscapes, e.g. because some forest-specific insects could display different behaviour at wind turbines in forests compared to open landscape. However, studies assessing the complex interaction of forest, wind farms and bats are still scarce (Niermann et al. 2012; Segers and Broders 2014). Some studies indicate a correlation of bat activity at turbine height with proximity to forests (Niermann et al. 2011c; Rydell et al. 2010a), whereas other studies found the opposite (Johnson et al. 2004). A generalization is further complicated because activity patterns and species distribution vary according to forest stratification and recording height (Staton and Poulton 2012; Müller et al. 2013).

Constructing wind farms in forests, which are special habitats for many bat species, generates further conservation issues which are less important in open landscapes. It can result in a loss, habitat deterioration or fragmentation of forested habitats. The clearance of forest patches at turbine construction sites and access roads thus leads to a loss and fragmentation of bat habitat (Farneda et al. 2015). The diversity of bats in forests decreases with an increasing degree of fragmentation (Lesinski et al. 2007). Recent studies show that habitat changes in forests due to wind farm construction can have species-specific effects on bats (Segers and Broders 2014; Morris et al. 2010). Studies that assess the interaction of bats, forests and wind farms on a larger scale and across a variety of bat species are therefore substantially required (BfN 2011; Wang and Wang 2015).

Implementation of European Law in Germany

The Birds and Habitats Directives are the cornerstones of the EU's biodiversity policy. According to the European Habitats directive, all 27 European member states have agreed to work together to conserve Europe's most valuable species and habitats across their entire natural range within the EU, irrespective of political or administrative boundaries. Article 12 and 13 of the Habitats Directive specify that it is prohibited for any member state to deliberately kill or disturb species in Annex IV. Since all European bats are protected by international and national legislation, any intentional killing is forbidden by law. Therefore, avoidance, or at least reduction to a minimum, of bat mortality by wind farms, is not only a priority for bat conservation, but also a legal obligation in Europe (Rodrigues et al. 2014). This implies an obligation to avoid or minimize bat collisions at wind turbines.

Researchers have provided some baseline information about bats and wind farms according to which avoidance and minimization measures have been developed. Guideline documents (European Commission 2010; Rodrigues et al. 2014) raise awareness amongst developers and planning agencies concerning the need to consider bats and bat conservation throughout the planning process of wind farms. These also prepare local and national authorities for the relevant steps in this process. Standardized impact assessments, such as post-construction monitoring, enable the design of a targeted avoidance and mitigation program. This program may include project abandonment, re-siting of the proposed turbines, site-specific use of blade feathering, higher turbine cut-in wind speeds and shutting down turbines temporarily to avoid or reduce bat mortality (Rodrigues et al. 2014). Key measures within these assessments are surveys of bat activity prior to and after wind farm construction (Hurst et al. 2015; Brinkmann et al. 2011b; Arnett et al. 2009; Willmott et al. 2015; Rodrigues et al. 2014).

Bat activity is heavily influenced by weather conditions, it decreases strongly with wind speeds above 6 m/s and temperatures below 10 °C (Brinkmann et al. 2011a). A model derived from a joint analysis of carcass searches, acoustic data and weather conditions now allows ecological consultants to predict the collision risk at specific wind farm sites. This can be used to develop turbine-specific curtailment algorithms that reduce bat mortality rates with a minimal loss of energy production

(Korner-Nievergelt et al. 2013). Following a national research project, site and weather-specific feathering (curtailment) strategies are now standard practice in Germany (Behr et al. 2015; Brinkmann et al. 2011a). Since 2008, the monitoring of bats at nacelle height has increased. By 2014, approximately 24,000 on-shore wind turbines have been installed in Germany (Berkhout et al. 2014), and the accompanying investigations have created an impressive dataset over the years. However, doubts remain whether these mitigation strategies derived from Brinkmann et al. (2011b) are effective in forests, as the underlying data used to develop the curtailment strategies stems mainly from wind farms in open landscapes (Behr et al. 2011b).

As part of this study, an extensive nation-wide dataset from nacelle surveys was gathered and analyzed in order to address the following questions:

1. Do bat species' compositions differ between forests and open landscapes?
2. Does bat activity and phenology differ between forests and open landscapes?
3. Does bat activity and composition differ between different regions in Germany?

Methods

Data Set

In total, data from 193 seasonal surveys (turbine-years) of 130 individual turbines were obtained (see Table 1).

Acoustic detectors, installed at the nacelle of the wind turbines, collected data during bat surveys to develop bat mitigation measures. The surveys were mostly run from April to October, with some exceptions whenever federal guidelines required different time periods or the detectors failed due to technical issues. Recording period spans across the years 2008 to 2014, with most survey data collected during the years 2012 to 2014. From 193 surveys, 106 surveys were conducted at wind turbines located in open landscapes and 87 facilities located in forests. Altogether, around 193,000 recordings were included in the analysis, of which around 93,000 have been recorded over open landscapes and around 100,000 over forests.

Most surveys were conducted with batcorders (n = 115) (ecoObs GmbH), followed by Anabat (n = 65) (Titley scientific) and Avisoft (n = 13) (Avisoft Bioacoustics). To analyse regional differences, data from these surveys was grouped into four regions. Those regions were derived from different Federal states as follows:

Table 1 Number of nacelle surveys per region, year and habitat type

	2008	2010	2011	2012	2013	2014	Open landscape	Forest	Total
North	0	0	0	7	14	13	34	0	34
East	0	0	15	7	12	12	27	19	46
South	0	0	0	3	5	8	8	8	16
West	6	1	3	31	45	11	37	60	97
Total	6	1	18	48	76	44	106	87	193

North: Lower Saxony (32 turbine-years) and North Rhine-Westphalia (2),
East: Mecklenburg-Vorpommern (2), Saxony-Anhalt (2), Brandenburg (38) and Saxony (4),
South: Bavaria (12) and Baden-Württemberg (4), and
West: Hesse (2), Rhineland-Palatinate (94) and Saarland (1).

As rotor radiuses have increased over time (>50 m for recent facilities), which may exceed recording capacities of the acoustic instruments (Behr et al. 2011a), this data does not cover the whole space impacted by the rotor blades. Further, because different bat species call at different intensities (Barataud 2015) not all bat calls across all species would have been fully captured equally. Thus, the results are to be interpreted as relative, not absolute activity data.

Data Processing

Recordings were identified to different levels for different taxa. Recordings belonging to genera that are hard to distinguish acoustically were lumped into groups. The Nyctaloids group consists of recordings that belong to bats from the genera *Eptesicus, Nyctalus* or *Vespertilio*. Recordings from species of the genus *Myotis* were lumped together. Recordings from the species of the genus *Plecotus* were similarly lumped into a *Plecotus*-group. Recordings from the genus *Pipistrellus* that were not identified to a species level were lumped into a group called Pipistrelloids. 144 recordings from the soprano bat *(P. pygmaeus)* were also placed in this Pipistrelloid group. Recordings from the Nathusius's pipistrelle and the common pipistrelle were considered at species level.

To level out differences between detector types, detector settings and recording sensitivities, we used presence-absence data for 10 min intervals. This was necessary to allow for a comparison between different detector types and detector settings, taking into consideration that information on absolute activity levels within 10 min intervals was lost. However as mentioned above, because the data was acquired through automated acoustic surveys, the number of calls cannot be interpreted absolutely anyway. For example, it is not possible to differentiate whether 20 recordings within 10 min stem from one hunting individual or 20 different individuals passing by. The 193,000 recordings translate into around 25,000 and 19,000 10 min intervals with activity over open landscape and forest, respectively.

Linear Mixed Effects Model

First, to investigate the impact of forest cover on bat activity using location as a gradual variable, we used a mixed effects model including forest cover in a 500 m radius in percent, latitude in degrees and longitude in degrees as covariates (fixed effects). Second, to investigate the impact of forest cover on bat activity for each region separately, we used a mixed effects model for each region including forest cover in a 500 m radius in percent. Initially, closest distance to large water bodies (more than 20 m wide ponds or more than 10 m wide streams) was included into the model, but was omitted in the final models due to insignificance. To account for non-independent data we included turbine identity, wind farm identity, survey year and detector type as random effects in all models. Prior to the analysis, the bat activity (as a percentage of 10 min intervals of bat activity, ranging from 0 to 100) was increased by 1 and log-transformed to approach normality of the residuals. The analyses were done by using the R-function *lmer* from the package *lme4* (Bates et al. 2015) using R.3.1.1 (R Core Team 2014).

Results

Descriptive Statistics

Species Composition

Between 50 and 60% of all 10 min intervals with bat activity could be attributed to the group of Nyctaloids, followed by Nathusius's bat and the common pipistrelle (Table 2).

Pipistrelloids and recordings from unidentified bats contributed to up to 8% of the 10 min intervals with bat activity. Interestingly, species that are strongly associated with forest as their feeding and/or roosting habitat (i.e. *Myotis*-group and *Plecotus*-group) were recorded in only a very small number of 10 min intervals. Only 22 10 min intervals with bat activity for the *Myotis*-group and only 37 for the *Plecotus*-group were registered during the entire surveys.

Table 2 Number of 10 min-intervals with bat activity for the different species and habitat types open landscape (N = 106 turbine-years) and forest (N = 87 turbine-years)

	Open habitat number of 10 min-intervals	Percentage	**Forest** number of 10 min-intervals	Percentage
Myotis group	15	0.06	7	0.04
Nyctaloids	15,555	62.80	9,262	48.93
Nathusius's bat	3,341	13.49	2,220	11.73
Common pipistrelle	4,390	17.72	5,060	26.73
Pipistrelloids	856	3.46	1,548	8.18
Plecotus group	7	0.03	30	0.16
Spec.	605	2.44	801	4.23
Total	24,769		18,928	

While looking at all data lumped together firstly, the following statistics also focus on the Nyctaloids, Nathusius's bat and common pipistrelle on a species group or a species level.

Overall Bat Activity Levels

In both habitats Nyctaloids contributed most to overall bat activity, while the Nathusius's bat appears to be recorded more often in open landscapes than in forests (Fig. 1).

For the common pipistrelle there appear to be more 10 min intervals with activity over forests than over open landscape. When investigating the species composition across the different regions, Nyctaloids contributed most to overall bat activity across all regions, but their contribution was more pronounced in the east and least in the west (Fig. 1). Similar differences can be found for Nathusius's bat and common pipistrelles. Whereas Nathusius's bats showed a higher presence than common pipistrelles in the north and east, common pipistrelles had a higher presence than Nathusius's bats in the west and south. These results give first indications towards regional differences in overall bat activity and species composition, with a lower effect of habitat on bat activity and species composition. However, since the data set consists of more wind farms in open landscape for the regions north and east and more wind farms in forests in the region west, the effects of habitat and region are intermingled. Therefore, the following mixed effects models address the statistical tests of these intermingled effects.

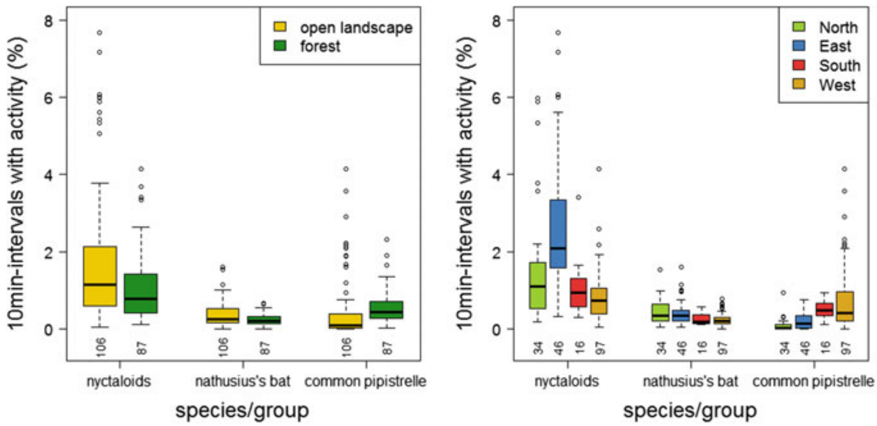

Fig. 1 Bat activity measured in percent of 10 min intervals for Nyctaloids, Nathusius's bat and common pipistrelle for the entire recording time period, depending on habitat and region. The *number* below the *boxplots* indicates the number of turbine-years

Annual Phenology of Bat Activity

Phenology patterns for all groups and species were very similar in open landscapes and forests. Activity in spring and autumn was very low with <1% activity in all recorded 10 min intervals. In both habitats and for all groups and species bat activity peaked in late summer and early autumn with up to 5% of all recorded 10 min intervals showing bat activity (Fig. 2).

In general, common pipistrelle activity was highest in July in both habitats, with a higher variance in open landscapes than in forests. Activity levels of Nathusius's bats were generally lower and later in the year than activity peaks of Nyctaloids and common pipistrelles. Both habitat types showed quite large variances between

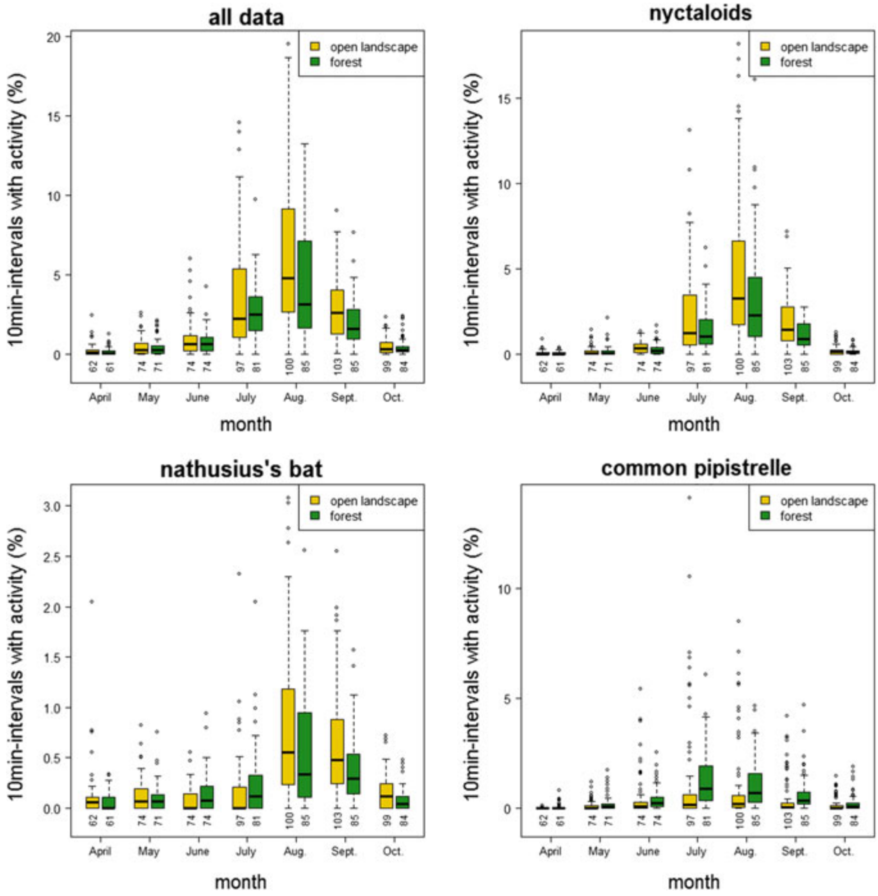

Fig. 2 Bat activity measured in percent of 10 min intervals with activity from April to October for all bat data, Nyctaloids, Nathusius's bat and common pipistrelle in open landscape and forests. The *number* below the *boxplots* indicates the number of turbine-years

different wind farms, but did not show different phenological patterns for any species in the two habitat types.

Annual phenology was also similar across regions, where highest activity was reached in all regions in late summer for all groups and species (Fig. 3).

However, the highest values for southern regions occurred in September, whereas for all other regions highest activity levels occurred in August. The activity levels for the Nyctaloids and the common pipistrelle also demonstrated the differences in species composition across regions. Highest overall Nyctaloid activity levels were found in the east, whereas the common pipistrelle showed highest activity levels in the south.

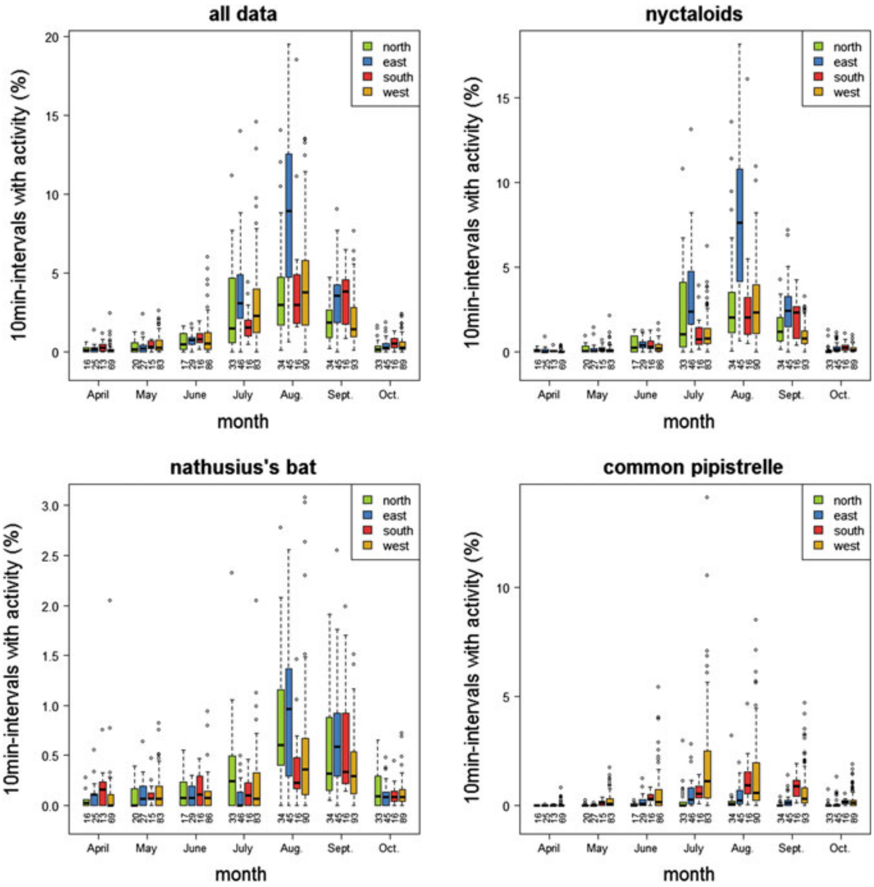

Fig. 3 Bat activity measured in percent of 10 min intervals with activity from April to October for all bat data, Nyctaloids, Nathusius' bat and common pipistrelle across all four regions. The *number* below the *boxplots* indicates the number of turbine-years

Linear Mixed Effects Model

The linear mixed effects model found no significant differences in overall bat activity between forests and open landscapes (Table 3).

Similarly, neither activity levels for Nyctaloids, Nathusius's bats nor common pipistrelle differed between forests and open landscapes (Table 3). The only factor that correlated with both overall bat activity as well as activity levels of specific species groups were longitude or latitude. Overall bat activity increased towards the east, which is mirrored by an increase in Nyctaloid activity towards the east (Table 3). In contrast, no east-west gradient was found for Nathusius's bats and common pipistrelles. In common pipistrelles, however, activity significantly increased towards the south. Activity levels of the Nathusius's bat were not correlated with geography at all.

When linear mixed effects models were used for each region separately, only assessing the effect of forest cover, there was a significant effect of higher common pipistrelle activity recorded over forests than over open landscapes within the west region, from which the largest data set was available (linear mixed effects model: coefficient: 0,00288; standard error: 0,00077; t-value = 3745; P-value = 0001).

Discussion

Bat Activity Over Open Landscape and Forests

The study revealed only small differences between bat activity at nacelle height over forest and open landscapes. Species composition was very similar between the

Table 3 Estimated effect sizes of forest cover in a 500 m radius, latitude and longitude on bat activity (logarithm of percentage 10 min intervals with activity increased by 1) for all bats, Nyctaloids, Nathusius's bat and common pipistrelle

	Variable	Estimate	Std. error	t-value	P-value
All data	Forest in 500 m (%)	−0.001	0.001	−1.362	0.177
	Latitude (°)	−0.040	0.033	−1.242	0.219
	Longitude (°)	**0.071**	**0.020**	**3.476**	**0.001**
Nyctaloids	Forest in 500 m (%)	−0.002	0.001	−1.921	0.058
	Latitude (°)	−0.002	0.030	−0.076	0.939
	Longitude (°)	**0.096**	**0.019**	**5.094**	**<0.0001**
Nathusius's bat	Forest in 500 m (%)	−0.001	0.000	−1.716	0.089
	Latitude (°)	0.015	0.013	1.158	0.251
	Longitude (°)	0.007	0.008	0.902	0.371
Common pipistrelle	Forest in 500 m (%)	0.000	0.001	−0.074	0.941
	Latitude (°)	**−0.009**	**0.024**	**−3.693**	**<0.001**
	Longitude (°)	−0.002	0.016	−1.420	0.162

In the model, we included turbine, wind park, year and detector type as random factors. Bold letters indicate significant effects as assessed by a t-test of the nullhypothesis that the effect is zero two habitat types. Nyctaloids had a higher level of bat activity in both forest and open landscapes, followed by common pipistrelles and then Nathusius's bats. However, as both noctule as well as Leisler's bat rank among the bat species with the highest call intensity levels, they can be detected across a much larger distance (80–100 m) than Pipistrelloids (30 meters) (Barataud 2015; Rodrigues et al. 2014), and might thus be overrepresented in the dataset. Typical forest bat species of the genera *Myotis* and *Plecotus* have been registered extremely rarely despite their common occurrence at the forest floor, as revealed by acoustic surveys and mist-netting (own data). However, a medium to low call intensity (Barataud 2015) might have led to an underrepresentation in the data. This study shows that typical forest species are equally rare at nacelle height (mean height 140 m in this data set, thus a minimum of 100 m above the forest canopy) in forests as in open landscapes.

Given that the rotor radius and thus the lowest turbine outreach are increasing in modern wind farms and approaching the forest canopy, future acoustic surveys at the lowest turbine outreach will be furthermore adequate to model collision risk than nacelle height recordings. Studies which employ simultaneous acoustic surveys at forest floor, at the lowest turbine outreach and at nacelle height are therefore important to better assess potential differences in activity and subsequent collision risks over forests versus over open landscapes (Hurst et al. 2015).

As this dataset was based on existing acoustic surveys, data sampling was not equally distributed across regions (see Table 1). The inferences derived from this study thus warrant some caution. Despite pronounced similarities in bat activity between forests and open landscapes, overall variance within each habitat type was very high. This suggests that some variables, which could not be assessed in this study, could have a strong influence on bat activity at nacelle height. Probably, the proximity to bat roosts could explain differences in bat activity levels (Ferreira et al. 2015), as could proximity to important foraging sites, such as mass concentrations of insects (McCracken et al. 2008) or sites where major migration routes concentrate. Another important factor could be the age and type of forest around the wind farm (Niermann et al. 2011c). Future studies should therefore aim to include a variety of environmental factors, as they might influence bat composition and abundance (Humes et al. 1999; Meschede and Heller 2000; Bach et al. 2012; Müller et al. 2013).

Regional Differences Versus Differences in Forest Cover

A comparison of differences in bat activity between forests and open landscapes revealed that differences between regions were much more pronounced. The differences that emerge concern both bat activity as well as species composition. Overall activity levels are much higher in the east, which is probably due to the dominant group of Nyctaloids, as they have highest activity levels in the east. Higher Nyctaloid activity levels in the east are attributed to the noctules, because the nursery roosts of this species concentrate in the north-east of Germany

(Dietz et al. 2007). Regional differences are similarly pronounced for the common pipistrelle where activity levels decrease significantly towards the north. Interestingly the common pipistrelle was the only species or group to be affected by the forest cover surrounding the wind turbines and this only in the west region. The locations of the turbines from this region varied very strongly in their surrounding habitat as such that most turbines were placed either in agricultural areas with no forests for several kilometers or in densely forested hillsides. This suggests that forests can in fact have a direct or indirect effect on bat activity in nacelle height, however, this effect might be regional and limited to specific species.

The regional differences in species composition and activity levels confirm the findings of a past carcass search study (Niermann et al. 2011b). Remarkably, the Nathusius's bat ranks among the top bat fatality species across all regions, despite their small percentage in acoustic surveys. This observation is in line with Brinkmann et al. (2011b), where a disproportionally large amount of Nathusius's bats were found dead compared to their acoustic occurrence at wind farms.

Consequences for Future Wind Park Planning

The study found hardly any differences in bat species composition or activity at nacelle height between forests and open landscapes. Thus, forested areas must not per se be excluded from future wind farms development. However, suitability of sites might differ depending on forest type, age or other environmental factors, which were not assessed in this study. Strong regional differences in species composition, as revealed by this study, suggest that an interpretation of bat activity must occur within the frame of the specific region where acoustic surveys took place. Based on this study's findings, it is advocated that the curtailment algorithms developed (Behr et al. 2011c; Korner-Nievergelt et al. 2013) can be applied to wind farms in forests. This should lead to a similarly effective reduction of collision risk as in open landscapes. Further, the strong geographic differences in activity levels and species composition stress the importance of using regionally adapted algorithms, currently under development (Behr, personal communication).

Open Questions and Future Research Needs

The results strengthen the value of a scientific collection and analysis of large, standardized datasets. This study reviews the extensive dataset of 193 individual, standardized acoustic surveys stretching across a large spatial scale, thus allowing a simultaneous assessment of regional and environmental effects. Given that acoustic surveys are recommended or obliged for most wind farms in Germany, the size of the dataset will rapidly increase in the years to come. To fully tap the potential of such a dataset, it is recommended that the existing dataset continues to be maintained within the framework of a national-wide database, and to regularly evaluate this dataset scientifically. This study shows that already a relatively small proportion of the existing acoustic surveys can help to unravel some of the unknowns concerning wind farms and bats. Furthermore, the knowledge gained through such an investigation will increase tremendously with its sample size.

Future investigations for example could address the stratification of bat activity from forest floor to the uppermost turbine outreach. As rotor radiuses have increased over time, acoustic surveys from nacelle height capture less of the entire turbine radius, which severely limits their extrapolation concerning collision risk. Especially in wind farms of lower nacelle height combined with a large rotor radius, the lowest turbine reach can affect the forest canopy area, where bat activity is known to be higher than at nacelle height (Niermann et al. 2011c).

What further hinders the development of optimized mitigation measures is the lack of knowledge on the underlying reasons for the presence of bats at nacelle height. Basic research should therefore address the different hypotheses of why bats occur at different heights and how this phenomenon depends on weather conditions, time of the year or species-specific characteristics. A differentiation between the different hypotheses that are currently employed (social reasons, hunting behavior, etc.) would allow a better prediction and extrapolation across different sites. Furthermore, the large variance we find in this study points to the importance of some variables that so far remain unstudied. A larger dataset could allow for an increase in the number of investigated variables, for example: studying habitat quality in much finer detail than the forest cover in the surrounding area such as the type of forest or proximity to key structures such as roosts. The better we understand the complex interactions between meteorology, regional and site-specific characteristics, and the bat species itself, the more effective future mitigation strategies will become.

To further understand whether and to what extent habitat quality may decrease due to the proximity of wind farms, it is recommended that long-term studies be conducted across Germany. These studies should measure bat activity and behavior before and after wind farm construction. In this study, we have assessed activity at the nacelle as a proxy for collision risk only. However, it is known from other vertebrate groups such as birds that individuals can be displaced from their home-range in order to avoid wind farms (Gonzalez and Ena 2011). This suggests that disturbances or fragmentation effects due to wind farm construction might have negative influences on wildlife, including bats. Future studies could therefore assess whether bat activity and home-range use differ as a response to the construction of a wind farm and whether a subsequent decrease in habitat quality must be taken into account during the planning process.

Conclusions

Very small differences between forest and open landscape in terms of species composition, level of bat activity and phenology of bat activity were found in this study. Regional differences in bat activity and species composition outweigh the effect of differences in forest cover in the immediate surroundings of a wind turbine. This result therefore suggests that mitigation measures developed primarily on data from wind turbines in open landscape are also applicable to wind turbines in forests, as wind speed and temperature still seem the dominant factors determining bat activity. This study highlights the value of a compilation and analysis of a comprehensive central dataset, as the large sample size of the dataset provides an opportunity to address more complex questions than single case studies. The dataset generated through this study should thus be extended and be made available for future studies.

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