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

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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*, nyctaloids 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 nyctaloids, *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.

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

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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 subcanopy 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).