Acoustic bat activity at wind turbines in temperate forests - Avoidance patterns and potential causes

Dissertation

„kumulativ“

zur Erlangung des Grades eines

Doktor der Naturwissenschaften

(Dr. rer. nat.)

des Fachbereichs Biologie der Philipps-Universität Marburg

Vorgelegt von

Julia Sophie Ellerbrok

Aus Berlin

Marburg, Juni 2023

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Illustration on front page: Echolocating greater mouse-eared bat (*Myotis myotis*). The illustration was created by Annika Wiedera.

Die vorliegende Dissertation wurde von Januar 2020 bis Juni 2023 am Fachbereich Biologie der Philipps-Universität Marburg unter Leitung von Prof. Dr. Nina Farwig angefertigt.

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Erstgutachterin:	Prof. Dr. Nina Farwig
Zweitgutachter:	PD Dr. Christian C. Voigt

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Declaration of the author contributions

The thesis 'Acoustic bat activity at wind turbines in temperate forests - Avoidance patterns and potential causes' is based on the work I carried out from January 2020 to June 2023 at the Philipps University of Marburg, under the supervision of Prof. Dr. Nina Farwig and PD Dr. Christian C. Voigt. Chapters 2 to 4 of this thesis consist of three independent scientific manuscripts, each with co-authorship, and have been published or will be published in peer-reviewed journals. The contributions of the authors for each manuscript are stated in the following:

Chapter 2 - Activity of forest specialist bats decreases towards wind turbines at forest sites (Published in *Journal of Applied Ecology*, 59, DOI: 10.1111/1365-2664.14249 (2022))

Julia S. Ellerbrok, Anna Delius, Franziska Peter, Nina Farwig, Christian C. Voigt

JE: Data collection, data curation, methodology, formal analysis, investigation, writing – original draft, writing – reviewing & editing, visualization.
AD: Data collection, data curation, methodology, writing – reviewing & editing.
FP: Funding acquisition, conceptualisation, supervision, writing – reviewing & editing.
NF: Funding acquisition, conceptualisation, supervision, writing – reviewing & editing.
CV: Funding acquisition, conceptualisation, methodology, supervision, writing – reviewing & editing.

Chapter 3 - Forest gaps around wind turbines attract bat species with high collision risk (In review at *Biological Conservation*)

Julia S. Ellerbrok, Finn Rehling, Franziska Peter, Nina Farwig, Christian C. Voigt

JE: Data collection, data curation, methodology, formal analysis, investigation, writing – original draft, writing – reviewing & editing, visualization.
FR: Formal analysis, writing – reviewing & editing.
FP: Funding acquisition, conceptualisation, supervision, writing – reviewing & editing.
NF: Funding acquisition, conceptualisation, supervision, writing – reviewing & editing.
CV: Funding acquisition, conceptualisation, methodology, supervision, writing – reviewing & editing.

Chapter 4 - Wind turbines operating at high wind speeds have a negative impact on the activity of forest bats (Not published)

Julia S. Ellerbrok, Nina Farwig, Franziska Peter, Christian C. Voigt

JE: Data collection, data curation, methodology, formal analysis, investigation, writing – original draft, writing – reviewing & editing, visualization.
FP: Funding acquisition, conceptualisation, supervision, writing – reviewing & editing.
NF: Funding acquisition, conceptualisation, supervision, writing – reviewing & editing.
CV: Funding acquisition, conceptualisation, methodology, supervision, writing – reviewing & editing.

Summary

Anthropogenic activities have caused two current major crises: biodiversity decline and climate change. Climate change mitigation is largely accepted as a societal goal and policy makers unite forces to substantially reduce carbon dioxide emission. However, the ongoing transition from fossil to renewable energy sources, such as wind energy, is not without impact on biodiversity, thereby creating a conflict of two sustainability objectives. Wind turbines are increasingly built in forest ecosystems, which present important foraging and roosting habitats for European bats. Forest bats may be affected by the deployment of wind turbines through collisions with the rotor blades, through habitat losses where forest is cleared, and through displacement effects. In this thesis, I investigated effects of wind turbines in forests as reflected in activity patterns of local bat communities. To this end, I performed an acoustic study across 22 wind turbines sites in temperate forests of Hesse, Central Germany. I determined bat activity levels at wind turbine clearings, at adjacent forest edges and in the surrounding forests at distances between 80 m and 450 m to the closest wind turbine. Recorded bat activity was investigated for three foraging guilds: narrow-space foraging bats specialized on flight in vegetation clutter, edge-space foraging bats specialized on flight in semi-open habitats like forest edges, and open-space foraging bats specialized on flight above forest canopies. I found that bats were negatively affected by wind turbines in forests. Specifically, narrow-space foraging bats avoided wind turbines over distances of at least 450 m, which presents an indirect habitat loss for these bats. The avoidance was at least partly explained by noise emissions of operating wind turbines which were amplified by high wind speeds. In contrast, the presence of cleared spaces around wind turbines did not contribute to the avoidance in narrow-space foraging bats. Edge-space and open-space foraging bats were less susceptible to displacements by wind turbines. Instead, they displayed higher activity levels at wind turbine clearings than in the surrounding forest canopies which might lead to increased collision rates for these bats in comparison to wind turbines in open landscapes. This thesis highlights the existence of forest-specific wind turbine effects on bat activity patterns which may affect local bat communities and populations. Consequently, when wind turbines are installed and operated in forests, forest-specific conservation measures are required, e.g., the exclusion or compensation of forest areas with heterogeneous vegetation structure and the reduction of turbine noise emissions. Such measures will contribute towards resolving the bat-wind energy conflict as an example of how objectives of climate change mitigation and biodiversity conservation can be reconciled.

Zusammenfassung

Anthropogene Aktivitäten haben zwei große, aktuelle Krisen verursacht: den Rückgang der Biodiversität und den Klimawandel. Der Kampf gegen den Klimawandel wird weitgehend als gesellschaftliches Ziel akzeptiert und politische Entscheidungsträger setzen sich mit vereinten Kräften für eine deutliche Verringerung der Kohlenstoffdioxidemissionen ein. Die aktuell stattfindende Energiewende von fossilen hin zu erneuerbaren Energieträgern, wie z. B. Wind, ist jedoch nicht ohne Auswirkungen auf die Biodiversität, wodurch ein Zielkonflikt zwischen zwei Feldern der Nachhaltigkeit entsteht. Windenergieanlagen werden zunehmend in Waldökosystemen errichtet, die wichtige Jagdhabitate und Quartiere für europäische Fledermäuse darstellen. Auf Waldhabitate spezialisierte Fledermäuse können durch die Errichtung von Windenergieanlagen beeinträchtigt werden, wenn sie mit den Rotorblättern kollidieren, Lebensräume bei der Rodung von Waldflächen verlieren oder Verdrängungseffekte erleiden. In dieser Arbeit untersuchte ich die Auswirkungen von Windenergieanlagen in Wäldern, wie sie sich in den Aktivitätsmustern der lokalen Fledermausgemeinschaften widerspiegeln. Zu diesem Zweck führte ich eine akustische Studie an 22 Windenergieanlagenstandorten in den gemäßigten Wäldern Hessens durch. Ich ermittelte die Fledermausaktivität über den Lichtungen um die Windenergieanlagen, an den angrenzenden Waldrändern und im umgebenden Wald in Entfernungen zwischen 80 m und 450 m zur nächstgelegenen Windenergieanlage. Die aufgezeichnete Fledermausaktivität untersuchte ich für drei Jagdhabitatgilden: Waldspezialisten, die auf Jagd in dichter Vegetation spezialisiert sind, Randstrukturjäger, die bevorzugt in halboffenen Habitaten wie z. B. an Waldrändern fliegen und Offenraumjäger, die bevorzugt über den Baumkronen fliegen. Ich fand heraus, dass Fledermäuse durch Windenergieanlagen in Wäldern negativ beeinflusst wurden. Insbesondere Waldspezialisten mieden Windenergieanlagen über Entfernungen von mindestens 450 m, was einem indirekten Lebensraumverlust für diese Fledermäuse gleichkommt. Dieses Meideverhalten ist zumindest teilweise auf die Lärmemissionen von in Betrieb befindlichen Windenergieanlagen zurückzuführen, welche durch hohe Windgeschwindigkeiten verstärkt werden. Im Gegensatz dazu trug das Vorhandensein von Freiflächen um Windenergieanlagen nicht zur Meidung durch Waldspezialisten bei. Randstrukturjäger und Offenraumjäger waren weniger anfällig dafür, von Windenergieanlagen vertrieben zu werden. Allerdings zeigten sie in den Lichtungen rund um Windenergieanlagen eine höhere Aktivität als in den Baumkronen des umgebenden Waldes, was zu erhöhten Kollisionsraten für diese Fledermäuse im Vergleich zu Windenergieanlagen an Offenlandstandorten führen könnte. In dieser Arbeit werden

waldspezifischen Auswirkungen von Windenergieanlagen auf die Aktivitätsmuster von Fledermäusen aufgezeigt, die sich auf lokale Fledermausgemeinschaften und -populationen auswirken könnten. Daher sind bei der Errichtung und dem Betrieb von Windenergieanlagen in Wäldern waldpezifische Schutzmaßnahmen erforderlich, z.B. der Ausschluss oder die Kompensation von Waldgebieten mit heterogener Vegetationsstruktur als Standorte oder die Reduzierung der Lärmemissionen durch Windenergieanlagen. Diese Maßnahmen werden dazu beitragen, den Fledermaus-Windenergiekonflikt zu lösen, und geben ein Beispiel dafür ab, wie die Ziele des Klimaschutzes und der Erhaltung der Biodiversität miteinander in Einklang gebracht werden können.

Chapter 1: General introduction

We are experiencing a global biodiversity crisis with around 25% of all known species being at risk of extinction (IPBES, 2019). The biodiversity decline is driven by human activities such as land use change and exploitation of natural resources, and increasingly exacerbated by climate change altering species distribution, disrupting interactions between species, and disturbing the balance of ecosystem functions (IPBES, 2019; Jaureguiberry et al., 2022). Because of the eminent threats that climate change moreover poses to human livelihoods, the global community has largely agreed to prioritize climate change mitigation and to achieve net-zero carbon dioxide emissions by 2050 (UNFCCC, 2015). Consequently, there has been a significant promotion of technologies that harness energy from renewable sources such as solar energy, wind energy, geothermal energy, hydropower, and bioenergy (Bull, 2001).

Renewable energies could cover two thirds of the global energy demand by 2050, which would contribute substantially to the targeted reduction of carbon dioxide emissions. Next to solar energy, especially the wind energy sector needs to grow to reach this target (Gielen et al., 2019). Wind energy is gained when wind sets the rotor blades and the connected hub of a wind turbine into motion, and mechanical energy is converted to electrical energy by the generator (Leishman, 2011). In some parts of the world, this technology is already the leading renewable energy on the market. For example, more than 15% of Germany's total energy consumption was already covered by wind energy in 2018 and prognoses state that nearly 100% could be covered if inter-annual variability of wind is accounted for (Jung & Schindler, 2018). Under this perspective, the deployment of onshore wind turbines is continuously increasing, in Germany and on a global level (in 2022: 3.6% increase to 66.242 MW and 10.5% increase to 934,443, respectively; WWEA, 2023). In conclusion, wind energy has a large potential, and the growth of the sector is expected to accelerate in order to meet the aims of the Paris Agreement (UNFCCC, 2015). However, although the use of wind turbines is carbon neutral and its high value regarding climate change mitigation is undisputable, it is not without problematic impacts on biodiversity (Kati et al., 2021; Saidur et al., 2011; Voigt et al., 2019).

Biodiversity, specifically flying animals, can be lethally affected when they come in close contact with wind turbines. Modern wind turbines reach hub heights of 103 m and rotor diameters of 120 m (global averages of 2020; GWEC, 2023). Thus, they present serious obstacles for birds and bats, which may collide with wind turbine rotors and die from their injuries (Thaxter et al., 2017). In birds, especially raptors with high space use and an association to agricultural habitats are susceptible to collisions with wind turbines (Bellebaum et al., 2013), e.g., common buzzards (*Buteo buteo*) and red kites (*Milvus milvus*) in Germany (LfU, 2022). In bats, species associated with open habitats and the ability to fly at rotor height have been identified to die most often at wind turbines (Rydell et al., 2010), e.g., common noctules (*Nyctalus noctula*) and common pipistrelles (*Pipistrellus pipistrellus*) in Germany (LfU, 2022). Collisions of birds and bats with wind turbines have rightfully received much attention, and technical solutions such as operation curtailments based on algorithms or automated detection cameras are currently tested to avoid them (Linder et al., 2022; Smallwood & Bell, 2020; Whitby et al., 2021). Yet, the underlying drivers have long been overlooked. Fatality rates at wind turbines are higher than expected considering the animals' abundances and can only partly be explained by species-specific flight styles (Cryan & Barclay, 2009; de Lucas et al., 2008; Rydell et al., 2010). This suggests that wind turbines influence the activity levels of birds and bats in their surroundings.

Increased activity levels at wind turbine rotors indicate that especially bats may be attracted to wind turbines (Cryan & Barclay, 2009). Possible explanations for the attraction include that bats feed on prey insects aggregating at wind turbines or that they mistake wind turbines for tree roosts (Guest et al., 2022). In birds, high collision rates are mostly attributed to landscape characteristics which for example increase the food availability close to wind turbines (Marques et al., 2014). In contrast to the attraction hypothesis, more and more studies on birds and bats present evidence that certain species avoid flying close to wind turbine sites which suggests an avoidance behaviour towards wind turbines. Specifically, studies on bat activity found reductions in the proximity of wind turbines in open landscapes and concluded that bats are displaced over several hundred meter distance (Barré et al., 2018; Minderman et al., 2017; Reusch et al., 2022). Similarly, occurrences of birds were reduced over distances of up to 800 m from onshore wind turbines in open landscapes (Drewitt & Langston, 2006; Pearce-Higgins et al., 2009). Further, reduced bird activity was found in the proximity of offshore wind turbines and over distances of several kilometres (Cook et al., 2018; Garthe et al., 2023; Larsen & Guillemette, 2007). The underlying causes for the observed displacements are still not understood but several possible explanations have been stated: bats and birds might avoid wind turbines due to a reduced availability of roosts and prey in the area, due to startling rotor movements, noises or lights associated with wind turbines, or due to turbulences compromising their flight (Gaultier et al., 2023; Langston, 2013). A thorough understanding of the factors that attract different bird and bat species or cause them to avoid wind turbines would enable us to predict activity patterns at wind turbines and take appropriate measures to protect them. Unfortunately, especially our understanding of avoidance behaviour in bats is still very basic because studies targeted on the topic only emerged in the last decade and focussed nearly exclusively on open landscapes.

In Germany, wind turbines used to be mostly deployed in manged open landscapes, e.g., agricultural fields, but suitable open areas have become scarce and land use conflicts increased (Frantál et al., 2023). As a result, the number of wind turbine deployments in forests increases and in 2022 a share of 11% of Germany's total wind energy capacity was already generated in forests (FA Wind, 2023). This development can be seen as representative of developments in other forest-rich countries, e.g., in North America and Scandinavia (Gaultier et al., 2020; Xiarchos & Sandborn, 2017). For the assessment of effects on biodiversity, analogies from wind turbines in open landscapes are often applied. Yet, such analogies might not be appropriate as forest ecosystems drastically differ from open landscapes in terms of vegetation cover, vegetation structure, microclimate, and ecological communities (Pretzsch, 2009). Thus, biodiversity in forests might react differently to wind turbine impacts than in open landscapes. Moreover, wind turbine deployment in forests requires the permanent clearing of 0,46 ha of woodland per turbine (German average; FA Wind, 2023) which presents a direct habitat loss for forest adapted species. Further, such wind turbine clearings in forests promote habitat fragmentation which presents barriers to some species while other species can gain foraging habitats in the cleared area or in the transition zone between clearing and forest (Fahrig, 2003). Either way, habitat changes related to wind turbine deployment are greater in forests than in open landscapes. Despite these habitat-specific features, studies on wind turbine effects in forests are still largely missing (Schöll & Nopp-Mayr, 2021). This poses the risk of forest-specific effects going unnoticed and impairing legally protected animals, such as bats.

Bats are the second most species-rich mammal order in the world, but the global biodiversity crisis does not spare them. In fact, for more than 20% of known bat species population trends are decreasing (Voigt & Kingston, 2016). Bats are particularly vulnerable because they live long and reproduce slowly. Thus, negative effects on individual level pose the risk of spill-over on population level from which bats may only recover slowly (Racey & Entwistle, 2000). Consequently, in Germany and further countries of the European Union, bats of all species are protected by law (Bundesnaturschutzgesetz, 2009; Council Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora, 1992). Being listed in the EU Habitat Directive, bats must not be deliberately killed, injured, or disturbed. To effectively protect bats, a good overview over their distribution ranges and abundantly used habitats is crucial. However, bats as small nocturnal animals are not easy to monitor, and their habitats are often cryptic (Voigt & Kingston, 2016). Therefore, it is important to understand what drives bat activity and where hotspots can be expected.

Habitat use of European bats varies among species. Some bat species find roosts in human settlements, e.g., common pipistrelles (*Pipistrellus pipistrellus*), while other species largely avoid urban areas, e.g., mouse-eared bats (*Myotis* ssp.; Jung & Threlfall, 2018; Lintott et al., 2016). Still, approximately 90% of all European bat species use forested areas for foraging and roosting, making forests a particularly important habitat in terms of bat conservation (Dietz & Kiefer, 2014; Russo et al., 2016). In general, bats prefer forests that offer roosts, e.g., tree cavities in standing deadwood, and a high availability of prey insects (Law et al., 2016). However, if and how bat species use different niches shaped by stratification, density and structure of forest vegetation depends on their foraging and flight mode. For example, common noctules (*Nyctalus noctula*) rather forage in spacious old-growth forests with low canopy cover, whereas mouse-eared bats (*Myotis* spp.) are also found in young stands with dense vegetation (Jung et al., 2012). High bat activity is usually associated with heterogeneous forests, but also forest monocultures can present valuable bat habitats (Buchholz et al., 2021). Besides, bat activity is subject to temporal variations because activity levels increase with increasing temperature and decrease with increasing wind speeds and air humidity (Bender & Hartman, 2015; Erickson & West, 2002; Voigt et al., 2011). In conclusion, bat activity levels depend on the species as well as biotic and abiotic environmental factors, which all need to be considered when wind turbines are deployed and operated in forest habitats in order to avoid negative impacts.

For my studies, I investigated bat activity patterns along distance gradients from wind turbines in twelve mixed and ten coniferous forests in Hesse, Central Germany, thereby capturing a variety of environmental and wind turbine characteristics. Hesse is located in the low mountain ranges with many wind-exposed slopes where energy production from wind would be efficient (LEA Hessen, 2012). At the same time, 42% percent of the state area is covered with forest, of which 59% is characterized by mixed tree stands, 29% by deciduous stands and 12% by coniferous stands (BMEL, 2012). Due to these landscape features, wind turbines are regularly deployed in Hessian forests, resulting in a total number of 485 forest wind turbines at the end of 2022 (FA Wind, 2023). Additionally, forests in Hesse harbour a number of bat species, typically *Barbastella barbastellus*, *Eptesicus serotinus*, *Myotis bechsteinii*, *M. brandtii, M. daubentonii*, *M. myotis*, *M. mystacinus*, *M. natterii*, *Nyctalus noctula*, *N. leisleri*, *Pipistrellus nathusii*, *P. pipistrellus*, *P. pygmaeus* and *Plecotus auritus* (Dietz & Kiefer, 2014; HessenForst, 2006). I assessed acoustic activity of these bats at increasing distances from the closest wind turbine using ultrasonic recorders. Acoustic studies are non-invasive and allow the collection and standardised evaluation of large data sets of bat activity (Froidevaux et al., 2014). Therefore, acoustic studies are the best approach to uncover general activity patterns around wind turbines. However, it is an often-occurring problem of acoustic studies that bat calls cannot be identified on species level, so that a coarser degree of taxonomic identification must be accepted for certain groups (Frick, 2013; Froidevaux et al., 2014). Consequently, for this thesis I analysed the acoustic bat activity on the level of foraging guilds, a commonly used concept in bat ecology (Denzinger & Schnitzler 2013). Foraging guilds comprise bat taxa which are using the same habitat niches and evolved similar morphological and echolocation features (Denzinger & Schnitzler 2013). Therefore, I assumed that bats of the same foraging guild respond to wind turbines in similar ways. I distinguished between narrow-space foraging bats that hunt preferably in dense vegetation and are especially adapted to flight in forests, edge-space foraging bats hunting along linear structures like forest edges and open-space foraging bats hunting most efficiently above the canopy and in forest clearings (Denzinger & Schnitzler 2013). In this way, my thesis investigates habitat-specific effects of wind turbines on forest biodiversity as reflected in the activity patterns of forest-associated bats.

Aims of the thesis

In this thesis, I investigated the acoustic activity of forest-associated bats close to wind turbine sites in temperate forests of Central Germany. Overall, I aimed to provide comprehensive scientific evidence on the effects of wind turbines in forests on the local bat community. Thereby, I hope to contribute towards shaping a sustainable development of wind energy in Germany and beyond which factors in the conservation of bats and forest biodiversity.

Specifically, I wanted to find out if activity patterns indicating avoidance towards wind turbines, which were observed in open landscapes, also apply in forest ecosystems. To this end, in chapter 2, “Activity of forest specialist bats decreases towards wind turbines at forest sites”, I investigated general trends in the echolocation activity of three bat foraging guilds in forests along a distance gradient towards wind turbine sites. I expected to see activity levels increase with increasing distance to wind turbines and decrease with increasing size of wind turbine rotors. I also expected varying activity levels in response to the ratio of deciduous to coniferous trees, average tree height, vertical vegetation heterogeneity and season. Moreover, I expected differences among bat foraging guilds and particularly strong impacts of wind turbines on forest-specialized narrow-space foraging bats. This chapter is based on bat activity which I recorded from May to September 2020 at 22 wind turbines.

Further, I asked if avoidance of wind turbines in forests by bats can be explained by the creation of new habitat types where forest is cleared for wind turbine deployment. Thus, in chapter 3, “Forest gaps around wind turbines attract bat species with high collision risk”, I investigated the activity of three bat foraging guilds in different habitat types around wind turbines in forests. Specifically, I recorded bat activity in the forest clearings around wind turbines, at the adjacent edge habitat between clearings and forests and in the canopy of the surrounding forests. The aim was to infer shifts in the echolocation and foraging activity of bats when forest areas are cleared for wind turbine deployments. I expected to see that edge-space and open-space foraging bats but not narrow-space foraging bats are most active in the open habitats created around wind turbines and that this may depend on wind turbine size and forest type. This chapter is based on bat activity which I recorded from May to September 2021 at 22 wind turbines.

Lastly, I asked if avoidance of wind turbines in forests by bats can be explained by the operation mode of wind turbines. Therefore, in chapter 4 “Wind turbines operating at high wind speeds have a negative impact on the activity of forest bats”, I analysed if bats were more inclined to avoid wind turbines at times when they were operating than at times when they were not operating. I expected an interactive effect between operation mode and wind speed, because I suspected noise emissions as underlying driver, which are perceived louder and further with increasing wind speeds. This chapter is based on bat activity which I recorded from May to September 2020 and 2021 at a subset of 12 wind turbines for which I was able to obtain operation protocols for recording nights from the responsible companies.

Being a cumulative dissertation, chapters 2 to 4 are presented in the format of scientific articles. These chapters can be read independently as the necessary context, the applied methods and the results are presented and discussed independently in each chapter.

Chapter 2: Activity of forest specialist bats decreases towards wind turbines at forest sites

2.1 Abstract

Worldwide, wind turbines are increasingly being built at forest sites to meet the goals of national climate strategies. Yet, the impact on biodiversity is barely understood. Bats may be heavily affected by wind turbines in forests because many species depend on forest ecosystems for roosting and hunting and can experience high fatality rates at wind turbines. We performed acoustic surveys in 24 temperate forests in the low mountain ranges of Central Germany to monitor changes in the acoustic activity of bats in relation to wind turbine proximity, rotor size, vegetation structure and season. Call sequences were identified and assigned to one of three functional guilds: open-space, edge-space and narrow-space foragers, the latter being mainly forest specialists. Based on the response behaviour of bats towards wind turbines in open landscapes, we predicted decreasing bat activity towards wind turbines at forest sites, especially for narrow-space foragers. Vertical vegetation heterogeneity had a strong positive effect on all bats, yet responses to wind turbines in forests varied across foraging guilds. Activity of narrow-space foragers decreased towards turbines over distances of several hundred meters, especially towards turbines with large rotors and during midsummer months. The activity of edge-space foragers did not change with distance to turbines or season, whereas the activity of open-space foragers increased close to turbines in late summer. Synthesis and applications: Forest specialist bats avoid wind turbines in forests over distances of several hundred meters. This avoidance was most apparent towards turbines with large rotors. Since forests are an important habitat for these bats, we advise to exclude forests with diverse vegetation structure as potential wind turbine sites and to consider compensation measures to account for habitat degradation associated with the operation of wind turbines in forests.

2.2 Introduction

Global carbon dioxide emission is the main driver of climate change (Solomon et al., 2009), threatening biodiversity and human economies worldwide (Bellard et al., 2012; Walther et al., 2002). To mitigate this threat, many countries are promoting wind energy production as a sustainable form of energy from renewable sources (Gielen et al., 2019). However, a growing body of literature indicates that the construction and operation of wind turbines may lead to habitat loss and an increased mortality risk for wildlife (Kuvlesky et al., 2007; Saidur et al., 2011). For instance, past studies documented high fatality rates of bats and birds at wind turbine rotors (Arnett et al., 2016; Thaxter et al., 2017). Indeed, it was suggested that wind turbines may be the most significant anthropogenic factor causing multiple mortality events in bats (O'Shea et al., 2016). Consistent with this notion, past studies estimated that annual losses of bats at wind turbines may reach several hundred thousand in countries of the temperate zone (Hayes, 2013; Voigt et al., 2015; Zimmerling & Francis, 2016). This is mirrored in observed and modelled population declines of high collision risk species in North America and Europe (Frick et al., 2017; Friedenberg & Frick, 2021; Printz et al., 2021).

Our current understanding of the wind energy-bat conflict is based almost exclusively on studies conducted at wind turbines operating in open landscapes. However, over recent years turbines have been increasingly built at forest sites throughout Europe, particularly in Central and Northern Europe (Gaultier et al., 2020), despite guidelines recommending the contrary when alternative sites are available (Rodrigues et al., 2014). For instance, in Germany more than 2,000 wind turbines (7.5% of all onshore turbines) operate currently at forest sites (FA Wind, 2023; Mackensen, 2019). To reduce further greenhouse gas emissions, recent pledges aimed at doubling the share of renewable energy production by increasing the area assigned for wind energy development from 0.8% (as of 2021) to 2.0% of the total surface area until 2030 (BMWK, 2022). Since land use pressure on open landscapes is already high and critical distances between wind turbines and settlements need to be maintained, several German federal states expand wind energy production in forests.

Although non-primary forests of the temperate zone are usually managed for timber production, they offer valuable habitats for many species (Götmark, 2013; Hilmers et al., 2018; Spiecker, 2003). Forests constitute important hunting grounds for forest specialist bats and provide shelter for many more bat species (Dietz & Kiefer, 2014; Müller et al., 2013; Plank et al., 2012). Thus far, it is largely unknown how wind turbines in forests affects forest-associated bats. Although not at high risk of colliding with turbine rotors, forest specialist bats foraging below the canopy may be impacted by indirect wind turbine effects (Hurst et al., 2020). For instance, studies in open landscapes documented a reduced bat activity close to wind turbines compared to control sites without turbines, suggesting an avoidance behaviour and an indirect habitat loss for several species (Millon et al., 2015). Another study documented decreased bat activity along transects towards turbines (Barré et al., 2018), an observation that was confirmed for small wind turbines (Minderman et al., 2017). The underlying cause for this avoidance remains unclear, but bats may respond to turbine-generated noise (Allen et al., 2021; Finch et al., 2020) or potentially to artificial light (Bennett & Hale, 2014). Turbine construction in forests is further accompanied by fragmentation and degradation (Lesiński et al., 2007), while the creation of clearings and aisles is leading to a loss of foraging habitats and daytime roosts in trees (Hurst et al., 2020). However, forest fragmentation may also lead to increased activity of those bats which are more adapted to open and edge habitats and to an increased collision risk for these species at forest wind turbines (Kirkpatrick et al., 2017).

In temperate forests, diverse vegetation structure and vertical stratification facilitate the cohabitation of three foraging guilds: open-space foragers which hunt insects above the canopy and in clearings, edge-space foragers which hunt along structures like forest edges or within gaps, and narrow-space foragers which hunt in dense vegetation and are especially adapted to life in forests (Denzinger & Schnitzler, 2013). The effect of habitat changes related to turbine construction and operation on bats may be guild-specific due to different ecological requirements. The activity of open- and edge-space bats could even increase towards wind turbines caused by their attraction to clearings and forest edges (Kirkpatrick et al., 2017). Conversely, narrow-space foragers might respond negatively or not at all to the turbine-related habitat changes as they do not profit from open or semi-open habitats. In addition, a structure-rich forest vegetation could influence how far turbine effects on bats may extend into the surrounding forest, as dense vegetation may block visual signals and mitigate noise pollution. Lastly, turbine effects on bats may depend on the season, since bat activity varies throughout the year (Heim et al., 2016). For instance, most fatalities at turbines have been reported in late summer, coinciding with the post-weaning period of juveniles and the migration season (Kruszynski et al., 2022). Here, we asked how wind energy production affects bat assemblages in non-primary forests of Central Europe. This is a critical question since all bat species are protected by national and international legislation. Knowledge of factors that impact forest-associated bats is key to formulate adequate mitigation and compensation measures to protect bats when expanding wind energy production in forests.

In our study, we used call activity as a proxy for the abundance of bats and thus conducted acoustic surveys along distance-gradients towards wind turbines in 24 forests. Compared to earlier distance-gradient studies on bat activity at wind turbines, our focus on forest sites is novel and offers new insights about the consequences of wind turbine integration in forests accounting for vegetation structure. We predicted (I) that bat activity decreases with increasing proximity to the nearest turbine and that this effect will be stronger at larger wind turbines, where sensory pollution is presumably stronger. Moreover, we expected (II) that bat responses differ across functional guilds with strongest impacts for the activity of forest specialists, i.e., narrow-space foragers and (III) that bat responses may vary across seasons and with vertical vegetation heterogeneity as a measure of forest structure. Our study aims to contribute to a sustainable wind energy development in forests from the perspective of bat conservation. Ultimately, this will help to reconcile the two important environmental goals of mitigating climate change and protecting biodiversity.

2.3 Material & Methods

Study area

We conducted our study in Hesse, a federal state in Central Germany characterized by temperate low range mountains and a forest cover of 42% (316 m to 545 m a.s.l., 50°81' North, 8°81' West, Fig. 2.1). We selected 24 forests ranging from coniferous monocultures to mixed and deciduous stands. Forest patch size varied between 184 ha and 6,337 ha (1,798 ha ± 1,745 ha; mean ± standard deviation, hereafter). Wind turbines in our study sites had been erected between 2006 and 2017 (6 ± 3 years). Tower height ranged between 145 m and 212 m (194 m ± 16 m; N=24) while rotor diameter ranged between 82 m and 126 m (mean: 112 m ± 11 m). Studied turbines were located individually in cleared forest patches that ranged in size between 0.16 ha and 11.77 ha (median: 1.75 ha). To minimize confounding effects of other anthropogenic disturbances and edge effects, we excluded study sites adjacent to highways and factories and established all transect points at a distance of more than 473 m (median) to the forest edge (91 m - 1,884 m). Fieldwork permits were obtained from the respective forest owners. Ethical approval was not required.

Sampling of bat echolocation calls

At each forest site, we used a distance-gradient study design with sampling points at 80 m, 130 m, 250 m and 450 m distance to our focal turbine at the edge of the wind farm. In one study site each, one 80 m, 130 m and 250 m point had to be skipped because of smaller clearings. For acoustic monitoring we used automated bat recorders (BATLOGGER A+, Elekon, Lucerne, Switzerland). At each sampling point, we installed one recorder per forest stratum: near-ground in the clutter-free understorey (approx. 2.5 m height) and a second recorder in the lower canopy, where height varied according to forest succession stage (range: 4 m – 22 m; 13 m ± 4 m). Recordings were conducted in 45 nights between mid-May and mid-September 2020, from 9pm to 5am. Per night, we recorded simultaneously at two geographically close transects and at each sampling point in the two designated forest strata.

At every recording point, we recorded bat calls once per sampling period (1: May 17 – June 5; 2: June 8 – July 7: 3: July 13 – August 15; 4: August 18 – September 17) with intervals of 17 to 58 days (33.29 ± 11.26 days) in between. Some exceptions were caused by technical failures and unforeseeable logging activities (four recording nights at 156 recording points, three at 15 points, two at 1 point, and one at 14 points). We employed BATLOGGER default settings with a trigger frequency between 15 kHz and 155 kHz, thus covering the call frequency range of species expected in the local bat assemblage. We set a pre-trigger time of 500 ms, a post trigger-time of 1,000 ms and a recording intersection time of 20 s. We used the CrestAdvanced trigger algorithm to enhance the recording probability of quiet calls and minimize sensitivity towards disturbing noise (Elekon AG, 2020).

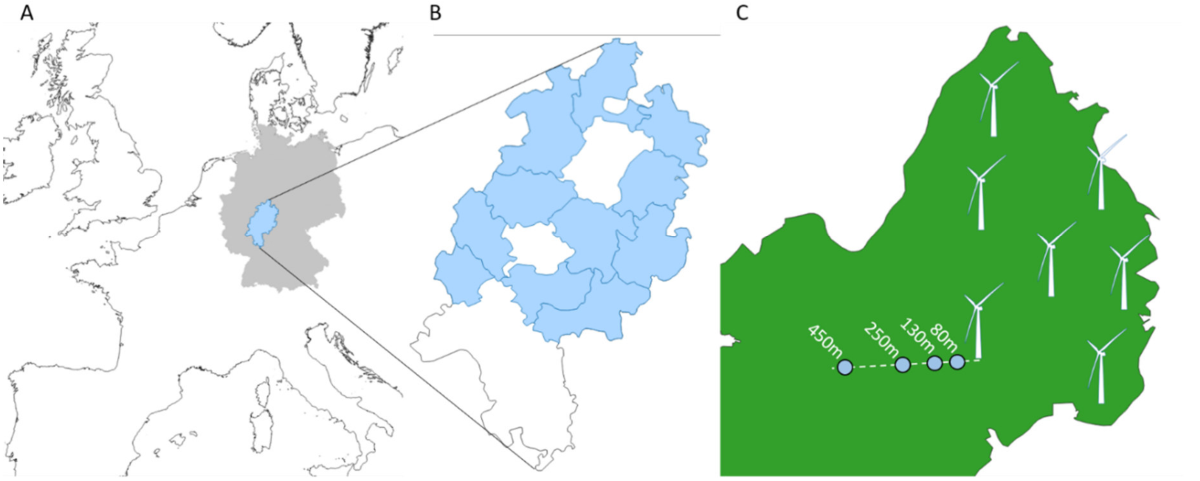

Figure 2.1: Map of the study area. *Location of the sampling sites in (A) Germany and (B) Hesse are marked in blue. (C) Example transect at the edge of a forest wind farm with sampling points set up in increasing distances to the focal turbine.*

Sampling of covariates

At each sampling point, we assessed four environmental variables that were assumed to influence bat activity: As a proxy for habitat heterogeneity, we estimated vegetation cover at heights of 0 m, 0.5 m, 1 m, 2 m, 4 m, 8 m, 16 m, and 32 m to the nearest 5% within a 10 m radius around distance points. We then calculated the diversity of the layers at each distance point using the Shannon-Weaver index to obtain vertical vegetation heterogeneity (Bibby et al., 2000). Furthermore, as a proxy for age structure we measured the average tree canopy height in the immediate surrounding of sampling points with the help of a laser rangefinder (Forestry 550, Nikon, Tokyo, Japan) and used aerial photographs (Google Ireland Limited, Dublin, Ireland) to measure the distance between sampling points and the nearest outer forest edge. Finally, we calculated the proportion of deciduous and coniferous trees based on the Copernicus land cover map (ESA, 2018) within a 200 m radius around distance points, hereafter called tree composition. To capture differences in turbine characteristics we retrieved the rotor diameter of each turbine from the publicly accessible data base of Hessian environmental agency (HLNUG, 2019).

Call analysis

We used the software BatExplorer (version 2.1.7.0, Elekon, Lucerne, Switzerland) to manually assign echolocation calls to bat species, only relying on the automatic call identification for *Pipistrellus pipistrellus*. We identified bat species based on echolocation call characteristics such as peak frequencies and call shapes from the literature (Barataud, 2020; LFU Bayern, 2020; Skiba, 2009). We subsequently grouped all call sequences into one of three ecological guilds (Denzinger & Schnitzler, 2013): open-space foragers (consisting of the genera *Eptesicus, Vespertilio* and *Nyctalus*), edge-space foragers (*Pipistrellus* ssp. and *Barbastella barbastellus*) and narrow-space foragers (genera *Myotis* and *Plecotus*). Sequences that could not be identified because of poor recording quality were discarded (0.4%). To obtain a proxy for the local bat abundance and prevent overestimation of single bats, we calculated the number of bat activity minutes for each of the three ecological guilds per night, sampling point and stratum. We divided recordings of all nights into 60 second intervals and counted minutes with at least one echolocation call, hereafter called activity minutes (Heim et al., 2016). If calls of more than one bat species appeared in one interval, they were considered as two separate activity minutes. Recordings with only social calls were discarded to avoid a bias towards species with higher detection and identification probability for social calls. In the following, we use the amount of activity minutes as a metric measure to describe bat activity.

Data Analysis

We conducted all statistical analyses with the software R (version 4.0.3; R Core Team, 2021). First, we split the data set into three subsets, one for each foraging guild, because recorded activities were quantitatively too different between guilds to be fitted in the same model. For each guild, we tested if bat activity (response variable) decreases with increasing proximity to wind turbines. Due to the nested structure of our data, we used generalized linear mixed models (glmmTMB package; Brooks et al., 2017) with sampling points nested in study site as random effects. We used a negative binomial distribution to account for overdispersion (nbinom1 for open- and edge-space foragers, nbinom2 for narrow-space foragers) and, apart from that, applied the same model structure for all guilds. Models included turbine distance, vertical vegetation heterogeneity, canopy height, tree composition, rotor size, forest stratum and sampling period as fixed effects. Moreover, we added forest edge distance as fixed factor to correct for its potential influence on the distribution of bats in the studied forests, as well as the interactions of turbine distance with sampling period and rotor size. We checked the variance-inflation factor (VIF) of the regression, which assesses for each coefficient whether a correlation with other predictors may lead to an increased variance. VIF was below 2 for all predictors and we thus excluded multicollinearity (car package; Akinwande et al., 2015; Fox & Weisberg, 2019). All numerical predictors were standardized to allow direct comparison of estimates (Schielzeth, 2010). We worked with full models (Tredennick et al., 2021) and ensured their goodness-of-fit with the DHARMa package for residual diagnostics (Hartig, 2020). We checked that all models were informative looking at the difference in AIC value compared to null models and marginal R^2 values (Appendix Table S1 in Supporting Information). Rotor diameters were not randomly distributed across forest sites and small rotors were biased towards deciduous forests. To exclude misinterpretations, we repeated above described analyses with only the data obtained from deciduous forests, thereby obtaining a balanced representation of rotor sizes. Additionally, we tested for potential confounding edge effects of the turbine clearing on bat activity by applying our model to a subset including only data sampled at 250 m and 450 m distance to the wind turbine. Results did not qualitatively change in the additional analyses compared to models based on the complete data set (Table S2 - S3). Accordingly, we considered our original results to be robust.

2.4 Results

During five months of data sampling, we obtained 678 recordings of complete nights, out of which 17 did not contain any bat calls. In total, we recorded 61,988 activity minutes of which 83% belonged to edge-space foragers, 12% to narrow-space foragers and 5% to open-space foragers (Tab. 2.1).

The activity of narrow-space foragers was almost halved at the distance points closest to wind turbines (80 m) compared to 450 m distance points (Fig. 2.2, Fig. S1). This distance effect showed temporal variation, as it was apparent for the first three sampling periods (mid-May to mid-August) and absent for the last sampling period (mid-August to mid-September, Fig. 2.3). Furthermore, the activity decrease was only observed towards turbines with rotors larger than 93m diameter (Tab. 2.2, Fig. 2.4). Activity increased with vertical vegetation heterogeneity, but no difference was observed between recordings made at the canopy and ground level. Bats were most active between mid-July and mid-September (Tab. 2.2, Figs S4 – S8).

Tab. 2.1: *Absolute and median numbers of activity minutes for each foraging guild at the distance points and pooled across recording levels.*

		All bats		Open-space foragers		Edge-space foragers		Narrow-space foragers	
Turbine distance [m]	N sites	N activity minutes	Median (per recording)	N activity minutes	Median (per recording)	N activity minutes	Median (per recording)	N activity minutes	Median (per recording)
80	23	13,879	3	688	2	8609	26	1263	2
130	24	15,686	4	588	1	9452	35	1821	5
250	24	13,161	3	665	2	7935	35	1088	4
450	24	18,958	4	700	1	12838	36	1989	5

The activity of edge-space foragers did not vary with turbine distance or rotor size (Fig. 2.2, Fig. S2). However, activity was higher at the canopy level than at ground level and increased with vertical vegetation heterogeneity and with tree height. Edge-space foragers were most active between mid-July and mid-August (Tab. 2.2, Figs S4 – S8).

The overall activity of open-space foragers did neither change with the distance to the wind turbine (Fig. 2.2, Fig. S3) nor with rotor size. Yet, in the last sampling period (mid-August to mid-September) we observed an increase in activity minutes close to turbines (Fig. 2.5). Activity of open-space foragers was higher at canopy than ground level and increased with the proportion of coniferous trees in the forest. Bats were most active between mid-July and mid-August (Tab. 2.2, Figs S4 – S8).

Tab. 2.2: *Estimates and p-values of the effects on call activity of three foraging guilds. Significant effects (p-value < 0.05) are shown in bold.*

Variables	Df	Open-space foragers		Edge-space foragers		Narrow-space foragers	
		Chi^2	p-value	Chi^2	p-value	Chi^2	p-value
turbine distance	1	1.6	0.202	0.4	0.521	18.0	**< 0.001**
recording level ‘canopy’	1	27.5	**< 0.001**	35.5	**< 0.001**	3.1	0.080
% conifers in forest	1	8.9	**0.003**	3.6	0.057	0.1	0.765
vertical vegetation structure	1	1.3	0.258	21.1	**< 0.001**	10.9	**0.001**
rotor diameter	1	0.3	0.560	1.4	0.238	0.2	0.898
canopy height	1	1.6	0.201	14.5	**< 0.001**	0.4	0.733
forest edge distance	1	0.7	0.387	1.2	0.288	2.6	0.106
sampling period	3	51.1	**< 0.001**	41.9	**< 0.001**	75.7	**< 0.001**
turbine distance x sampling period	3	10.9	**0.012**	0.3	0.955	19.4	**< 0.001**
turbine distance x rotor diameter	1	1.99	0.158	3.6	0.057	4.7	**0.0295**

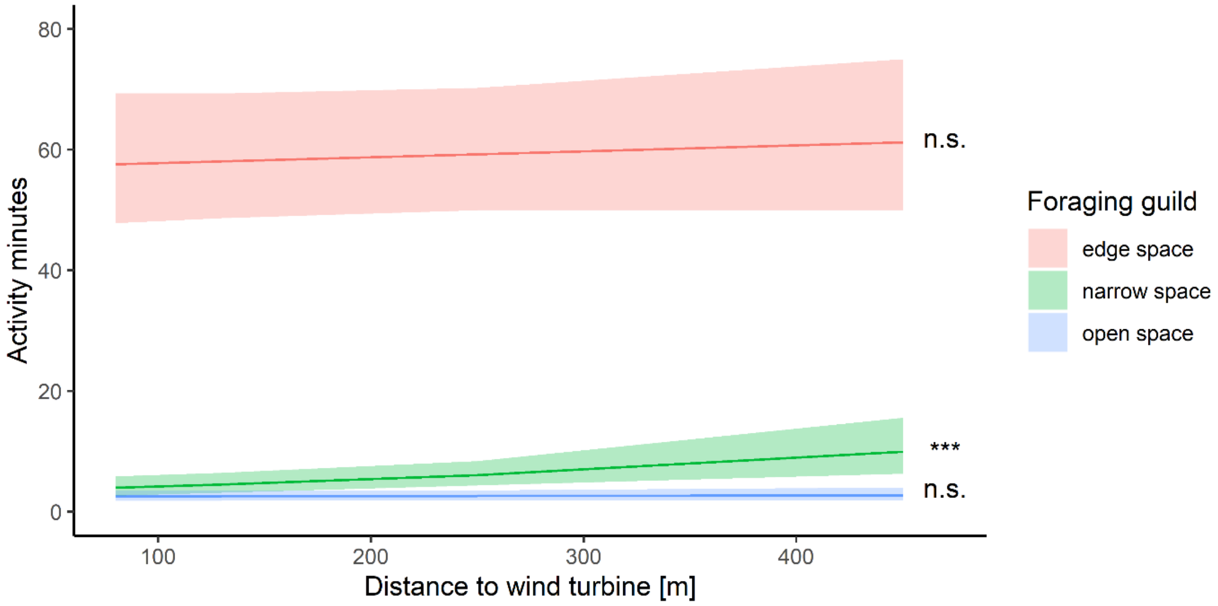

Fig. 2.2: *Effects (lines) and 95%-confidence intervals (shades) of wind turbine distance on activity of three foraging guilds. Asterisks denote the significance level of effects (*** <0.001 < ** <0.01 < * <0.05< n.s.).*

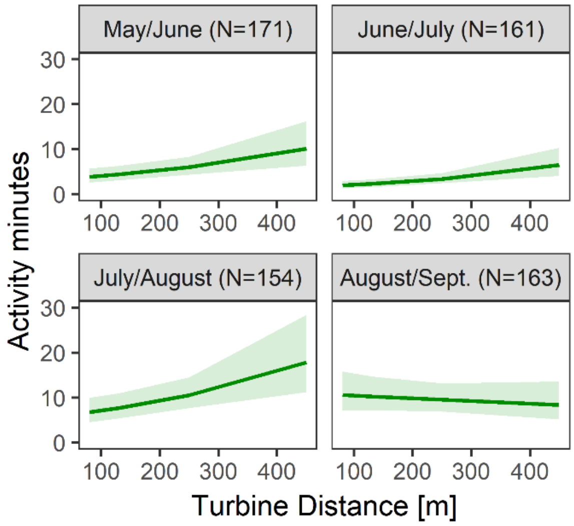

Fig. 2.3: *Interactive effect (lines) and 95%-confidence intervals (shaded area) of turbine distance and sampling period on the activity of narrow-space foragers.*

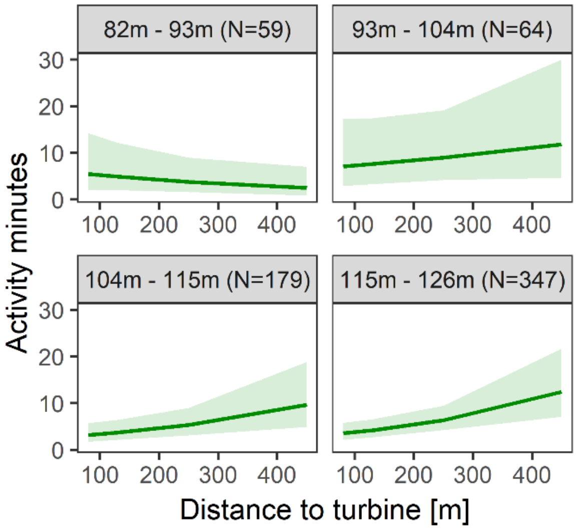

Fig. 2.4: *Interactive effect (lines) and 95%-confidence interval (shaded area) of wind turbine distance and rotor size on the activity of narrow-space foragers.*

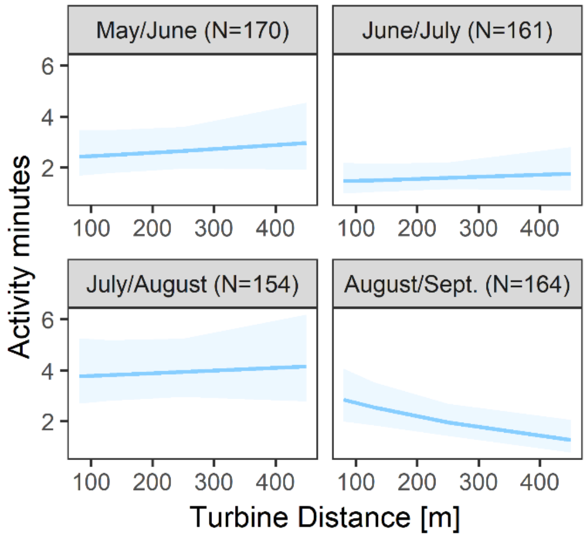

Fig. 2.5: *Interactive effect (lines) and 95%-confidence intervals (shaded area) of turbine distance and sampling period on the activity of open-space foragers.*

2.5 Discussion

We studied bat activity at wind turbines in 24 temperate forests in Central Germany and discovered a relationship with turbine distance, season and turbine size, but different patterns depending on bat foraging guild. Strikingly, activity of narrow-space foragers decreased with increasing proximity to turbines. This effect was notable over distances of several hundred meters. Our findings highlight that forest-dwelling bats, being at low risk of colliding at turbines, might still be affected by wind turbines in forests. This complements research from open landscapes, where narrow-space foraging bats showed a similar negative response towards wind turbines (Barré et al., 2018; Millon et al., 2015). However, our study is the first to confirm this pattern for forests, a highly important habitat from the perspective of bat conservation.

Narrow-space foragers: avoidance of large wind turbines

We found that the activity of narrow-space foragers, mainly *Myotis* bats in our study area, decreased significantly towards turbines. This is in line with earlier studies on *Myotis* activity in open landscapes (Barré et al., 2018), even when focussing on small wind turbines (Minderman et al., 2012), highlighting the sensitivity of narrow-space foragers to wind turbines both in forests and open landscapes. Furthermore, we found that the activity decline of narrow-space foragers towards wind turbines was weaker in late summer, which confirmed the results of another open landscape study comparing wind turbine sites to control sites (Millon et al., 2015). In our study, we observed a distance effect particularly at turbines with large rotors. This suggests that avoidance might be caused by turbine-generated noise, which is presumably related to turbine size and diminishes over distance (Katinas et al., 2016). An adverse effect of noise on *Myotis* activity is also implied by a study on small wind turbines, where bats were particularly repelled by operating turbines (Minderman et al., 2012). Many narrow-space foragers locate their prey passively by detecting acoustic cues (Denzinger & Schnitzler, 2013). Therefore, these bats tend to avoid noisy environments, suggesting either a masking of prey sounds by anthropogenic sound emissions (Schaub et al., 2009) or a startling effect (Luo et al., 2015). In conclusion, we found a hitherto unknown avoidance behaviour of narrow-space foragers towards wind turbines in forests, indicating an indirect habitat loss for bats of this functional guild, possibly caused by noise.

Edge-space foragers: no effect of wind turbines

For edge-space foragers, which were mostly *P. pipistrellus* in our study, we neither found support for avoidance of, nor attraction towards wind turbines in forests. In contrast, recent open landscape studies observed a strong decrease in the activity of *P. pipistrellus* at hedgerows with decreasing distances to turbines on the one hand (Barré et al., 2018), and an increased activity at wind turbine sites in comparison to control sites on the other hand (Richardson et al., 2021). Possibly, the discrepancy between findings may be explained by different habitat matrices. Specifically, the erection of wind turbines in forests creates clearings and a network of edge structures which is an ideal foraging habitat for edge-space foragers. Indeed, it was observed that members of the edge- and open-space foraging guild were more active in spruce plantation after clear-cuttings (Kirkpatrick et al., 2017). In conclusion, clear-cutting for turbine construction probably poses a spatially restricted benefit for edge-space foragers.

Open-space foragers: seasonal attraction to wind turbines

Activity of open-space foragers did not change in relation to turbine distance except for an activity increase with increasing turbine proximity in late summer. Our overall findings contrast with a previous open-landscape study that showed decreased activity for *N. leisleri*, but not for *N. noctula* and *E. serotinus* close to turbines (Barré et al., 2018), suggesting that open-space foragers might not be coherent in their responses to wind turbines. Different responses may even be related to intra-species variation across bat individuals, as was suggested by GPS tracking studies on *N. noctula* around wind turbines (Reusch et al., 2022; Roeleke et al., 2016). In contrast, our finding of open-space foragers being attracted to wind turbines in late summer aligns with numerous previous studies suggesting an attraction effect of wind turbines on open-space foragers, hypothesizing various, yet untested causes (Guest et al., 2022). Given the seasonality of the attraction, open-space foragers possibly confuse forest turbines with tall trees, when searching for orientation points or stop-over roosts during fall migration (Cryan et al., 2014; Jameson & Willis, 2014). However, a recent study from Northern Germany shows an avoidance behaviour of *N. noctula* in late summer towards wind turbines, which argues against a general attraction of open-space foragers towards turbines in this season (Reusch et al., 2022). In conclusion, we could not confirm avoidance behaviour towards turbines for the entire guild. Yet, our findings of a seasonal attraction to turbines in forests is of high relevance in context of collision risks for open-space foragers.

Diverse vegetation structure enhances bat activity

High activity of edge- and narrow-space foragers coincided with heterogeneous vertical vegetation structure. Similar positive effects of different measures of vegetation structure on forest associated bats have been shown before and can be explained by a higher availability of microhabitats (Adams et al., 2009; Langridge et al., 2019; Müller et al., 2013). Furthermore, activity of edge-space foragers increased with tree height, suggesting a preference for more mature forest stands, probably due to their dependency on semi-open foraging habitats which rarely occur in early succession stages. In contrast, activity of open-space foragers was not affected by vertical vegetation structure or tree height, indicating that forest vegetation parameters are less important for aerial hawkers. For most bats, we observed a higher activity in the canopy than near-ground, confirming that the forest canopy is an important bat habitat (Adams et al., 2009; Erasmy et al., 2021; Müller et al., 2013; Plank et al., 2012). Lastly, we found a similar activity of most bats in mixed and coniferous forests which is consistent with a recent study suggesting that bats can find suitable roosts even in monocultural forest plantations (Buchholz et al., 2021). In conclusion, our findings indicate that forests with diverse vegetation structure present valuable habitats for a variety of bats, while forest type alone seems to be less important. The high activity of open-space foragers in conifer-dominated forests is likely related to high proportions of standing deadwood and clearances in these forests, leading to reduced attenuation of echolocation call and an increased recording probability (Lawrence & Simmons, 1982).

4.6 Conclusion

Our study highlights that the activity of forest-associated bats declines towards wind turbines at forest sites. Narrow-space foragers such as *Plecotus* spp. and *Myotis* spp. seemingly avoid wind turbines in forests and show reduced activity by about 50% from 450 m to 80 m turbine distance. This avoidance is possibly caused by habitat degradation triggered by turbine-generated noise, since it was strongest towards turbines with large rotors. Consequently, legally protected forest bat specialists lose large habitat areas when wind turbines are erected at forest sites. Hence, we argue that this habitat loss should be compensated by taking nearby old forest stand out of forestry use, thus creating refugia for forest specialist bats. We also plead for a general caution when siting wind turbines in forests, since the response of bats was independent of vegetation structure and tree composition. We do not necessarily argue for a complete ban of wind energy production in forests, because in some countries there is little other option for renewable energies. Where absolutely necessary, turbines should only be built in managed forests with low vertical vegetation heterogeneity, as bat activity is expected to be low in these forests. This approach would most likely also account for birds and insects, which have been reported to die in considerable numbers through wind turbines (Thaxter et al., 2017; Voigt, 2021). However, as forest-related studies on birds and insects are still lacking, we urge to fill these research gaps to provide a basis for comprehensive recommendations on wind energy development in forests.

4.7 Acknowledgements & declarations

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Data availability

Data is available via the Dryad Digital Repository https://doi.org/10.5061/dryad.m0cfxpp66 (Ellerbrok et al., 2022)

Authors contributions

Nina Farwig, Franziska Peter and Christian C. Voigt conceived the ideas and designed the methodology. Julia S. Ellerbrok and Anna Delius collected data; Julia S. Ellerbrok analysed the data and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Our study relied on local authors and research assistants. We frequently presented our research progress to stakeholders and sought their feedback.

Conflict of interest

None of the authors have conflicting interests.

Chapter 3: Forest gaps around wind turbines attract bat species with high collision risk

3.1 Abstract

The global demand for renewable energy has led to an expansion of wind energy production at forested sites. The deployment and operation of turbines requires the clearing of forest areas, resulting in significant habitat changes. To assess the consequences of these changes for forest-associated bats, we measured the acoustic activity of three foraging guilds at turbine clearings, adjacent forest edges, and above nearby closed forests. Open-space and edge-space foraging bats were more active at turbine clearings and forest edges than above closed forests. Similarly, narrow-space foraging bats tended to be more active at turbine clearings than above closed forests. Open-space and edge-space foraging bats are known to be at high risk of colliding with wind turbines and their increased activity at forest gaps around turbines may increase casualties for these guilds. Operation of wind turbines in forests may therefore require longer shutdown periods to prevent legally protected bats from colliding with turbines. Although this may impair the energy yield of wind turbines in forests, such preventive conservation measures will ultimately contribute to a sustainable transition from fossil to renewable energy sources which factors in biodiversity conservation.

3.2 Introduction

Between 2000 and 2012, a total of 2.3 million km^2 of global forest ecosystems were lost (Hansen et al., 2013). The quality of remaining forests is severely threatened by human activities such as logging, fragmentation, and construction of infrastructures (Grantham et al., 2020; Ibisch et al., 2016). In many parts of the world, anthropogenic pressure on forest ecosystems is now increasing due to the expansion of wind turbines to forested sites (EEA, 2009). Alone in Germany and in the USA, two of the largest markets for wind energy, several thousand turbines are operating in forests already (FA Wind, 2023; REN21, 2018; Xiarchos & Sandborn, 2017). Particularly countries with a high percentage of forest cover, where open areas for wind energy production are scarce, may need to place turbines in forests to meet the international goal of net zero carbon dioxide emissions by 2050 (Gaultier et al., 2020; UNFCCC, 2015). This development is relevant for biodiversity conservation because wind turbine deployment in forests will inevitably create forest gaps and alter sensitive ecosystems. In Germany, the construction of a single turbine at a forested site involves clear-cutting of about 0.9 ha. Half of the cleared area is permanently converted into gravel areas with compacted soil for maintenance of turbines (FA Wind, 2023). Ultimately, this alteration of vegetation and soil results in habitat changes, which can affect the biodiversity and community composition of forest animals, and their trophic networks (Ellerbrok et al., 2022; Fahrig, 2003; Scholz & Voigt, 2022). Yet, the ecological impacts of creating forest gaps for wind turbines on animals are poorly known to date, specifically for bats that are vulnerable at wind turbines (Schöll & Nopp-Mayr, 2021).

Temperate forests are important habitats for a wide range of species, among them bats. For example, 90% of European bat species use forest structures at least temporarily for foraging and roosting (Dietz & Kiefer, 2014; Russo et al., 2016). Specifically, bats require tree cavities and standing deadwood for roosting as well as resource-rich foraging areas, which they use according to strata, structure, and vegetation density (Jung et al., 2012; Law et al., 2016; Müller et al., 2013). When forests are partially cleared for wind turbines, bats can be affected in several ways depending on their foraging and flight behaviour (Aldridge & Rautenbach, 1987; Denzinger & Schnitzler, 2013). Open-space foraging bats are long-range echolocators with pointed wings foraging mostly in spaces with few or no obstacles (Denzinger & Schnitzler, 2013). They hunt above treetops and in larger clearings, while they avoid dense vegetation and small clearings (Voigt & Holderied, 2012). Thus, open-space foraging bats may explore and use forest gaps associated with wind turbines in forests. Edge-space foraging bats are mid-range echolocators, which are specialized on hunting prey close to background objects (Denzinger & Schnitzler, 2013). Hence, they are often found at forest edges (Kirkpatrick et al., 2017), which are created when forest patches are clear-cut for wind turbines. Finally, narrow-space foraging bats are short-range echolocators with rounded wings that facilitate foraging in forest understorey (Denzinger & Schnitzler, 2013). Although narrow-space foragers can fly outside of forests (Heim et al., 2018), they mostly occur in the forest interior and might therefore suffer from the creation of forest gaps for wind turbines. In conclusion, open-space and edge-space but not necessarily narrow-space foraging bats can be expected to increase their activity where forest gaps are created for wind turbines.

Fatalities of bats after collisions with wind turbines are a known global problem (O'Shea et al., 2016; Thaxter et al., 2017). Bat casualties at wind turbines are not equally distributed across species. In Europe, for example, 95% of bats found dead under wind turbines belonged to 6 out of 11 assessed genera (*Nyctalus, Vespertilio, Pipistrellus, Hypsugo, Miniopterus, Tadarida*; LfU, 2022). Accordingly, bat species from these genera are commonly recognized as high-collision risk species (Rodrigues et al., 2014), which is associated with their ability to fly at the operation range of wind turbines (Reusch et al., 2022, Reusch et al., 2023; Roeleke et al., 2016; Roemer et al., 2017). Noticeably, all bat species recognised as high-collision risk species at wind turbines are members of the open-space or edge-space foraging guild, while bat species of the narrow-space foraging guild are usually considered to be at low risk of colliding with wind turbines (Rodrigues et al., 2014). Consequently, deployment of wind turbines at forested sites might lead to more casualties at wind turbines if bat species of high-collision risk are attracted to the open and edge habitats which were created for the deployment and operation of wind turbines. Besides, bats may also respond to the operation of wind turbines. Indeed, past studied confirmed that wind turbines repel certain bat species in open landscapes (Barré et al., 2022; Leroux et al., 2022) and in forests (Ellerbrok et al., 2022; Gaultier et al., 2023; Reusch et al., 2023), depending on the size of the wind turbines.

Here, we investigated how bats of three foraging guilds respond to habitat changes associated with the creation of forest gaps for wind turbines deployment and operation. We monitored acoustic bat activity at 22 forest wind turbines, specifically at turbine clearings, at the edge between turbine clearings and forests, and above the adjacent closed forest. We estimated echolocation call activity as the number of minutes with bat calls and foraging activity as the occurrence of stereotyped call sequences associated with hunting events (hereafter: feeding buzzes, in sensu Skiba, 2009). We predicted that (i) echolocation activity and (ii) foraging activity of open-space and edge-space foraging bats but not those of narrow-space foraging bats is highest at forest gaps adjacent to wind turbines. Finally, we expected (iii) that the activity patterns of bats in the different habitats is influenced by the size of turbines, since our previous work suggested a reduced activity of some bat species at turbines with large rotors (Ellerbrok et al., 2022). With this study, we aim to contribute to evidence-based schemes for a sustainable use of wind energy which incorporates the protection of forest-associated bats.

3.3 Material & Methods

Study area & design

We conducted acoustic surveys in 22 managed forests in the low-mountain ranges of Hesse, Central Germany. We chose twelve mixed deciduous and ten predominantly coniferous forests, which represent structurally rich and poor forests. We surveyed wind turbines of varying sizes, ranging in rotor diameter between 82 and 126 m (111 ± 11 m, mean ± one standard deviation) and in tower height between 145 and 212 m (193 ± 16 m; HLNUG, 2019). Turbines were located at the margins of multi-turbine facilities in clearings ranging from 0.2

to 6.5 ha (median: 1.0 ha). Around these focal wind turbines, we established three sampling points in distinct habitats: one at the centre of the wind turbine clearing, one at the adjacent forest edge and one in the canopy of the surrounding closed forest. Sampling points in the closed forest were chosen as close to focal wind turbine as possible without entering the forest edge zone to avoid the confounding effects of the edge habitat. As a result, sampling points in closed forests were all located at approximately 80 m distance to focal wind turbines. We did not survey the availability of tree roosts close to our sampling points. However, we do not anticipate a systematic bias caused by the presence of roosts but rather an increased unexplained variation in the recorded acoustic data. Acoustic surveys were conducted four times during the active season between May and September 2021 at each sampling point between 9 pm and 5 am, resulting in a total of 264 full night recordings (22 study sites x 3 habitat types x 4 sampling periods). Sampling points were chosen to be at a minimum distance of 150 m (one exception at 90 and two at 120 m, 540 ± 360 m) from the outer edge of the forest patch and a minimum distance of 250 m from other than the focal wind turbines to exclude edge and cumulative effects.

Bat call sampling and analysis

We used automated ultrasonic recorders (BATLOGGER A+, Elekon, Lucerne, Switzerland) with a trigger frequency between 15 and 155 kHz to cover typical call frequencies of expected local bat species. At sampling points of forest edges and closed forests, recorders were placed at canopy level, as we were particularly interested in the activity of open-space and edge-space foraging bats which occur mostly above the forest canopy (Ellerbrok et al., 2022). Additionally, most species of these two guilds are considered high-collision risk species at wind turbines (Rodrigues et al. 2014). We placed recorders in clearings adjacent to wind turbines, at the top of 2 m poles.

We used the software Batexplorer (ELEKON, Luzern, Switzerland) to convert audio recordings into spectrograms. We manually checked all sequences to identify bat calls based on typical call shape, end frequencies and peak frequencies from the literature (Barataud, 2020; LFU Bayern, 2020; Skiba, 2009) and assigned them either to the open-space (*Eptesicus* ssp., *Vespertilio* ssp., *Nyctalus* ssp.), edge-space (*Pipistrellus* ssp., *Barbastella barbastellus*) or narrow-space foraging guild (*Myotis* spp., *Plecotus* spp.). For each foraging guild, we determined bat activity minutes by dividing recording nights into 1 min intervals and counting intervals with at least one echolocation call for each foraging guild. Activity minutes were used as a proxy for the echolocation activity (Miller, 2001). Additionally, we identified call sequences with increasingly short intervals and a final drop in frequency as so-called feeding buzzes (e.g., Skiba, 2009). The presence of feeding buzzes per guild and night were used as a proxy for foraging activity.

Data analysis

All analyses were performed in R (version 4.1.3; R Core Team, 2022). We used generalized mixed models (GLMMs, glmmTMB package; Brooks et al., 2017) with a binomial error distribution and a logit link function for each bat guild separately. We analysed the effect of habitat (turbine clearing, forest edge, closed forest), forest type (deciduous, coniferous) and rotor diameter as well as the interaction of rotor diameter and habitat on echolocation and foraging activity. We did not include tower height in our model because it was strongly correlated with rotor diameter (Spearman correlation: $r = 0.72$; $p < 0.001$). Month of sampling (May, June, July, August, September) was added as fixed effect to account for temporal autocorrelation. Recording points were nested in plots, i.e., the sites of focal wind turbines (random effect). Models were checked for homoscedasticity and normally distributed residuals with help of the DHARMa package for residual diagnostics (Hartig, 2020). As models for foraging activity were highly zero-inflated, we resorted to assessing the presence/absence of feeding buzzes (more details on methodology provided in Supporting information A).

3.4 Results

Overall, we recorded 28,155 activity minutes of which most corresponded to edge-space foraging bats (84% of activity minutes), followed by open-space and narrow-space foraging bats (each 8%). We documented foraging activity of edge-space foraging bats in 130 nights, of narrow-space foraging bats in 26 nights and of open-space foraging bats in 13 nights. Levels of echolocation and foraging activity varied across seasons (Supporting information B).

Open-space foraging bats were 111% (95% confidence interval [21%, 270%]) more active at turbine clearings and 71% (CI [-3%, 202%]) more active at forest edges than at closed forest sampling points (Figure 3.1A, Table 3.1). Foraging activity of open-space foraging bats was neither influenced by habitat nor any other predictor (Figure 3.1D, Table 3.1). Edge-space foraging bats were 60% (CI [15%, 122%]) more active at forest edges and 51% (CI [8%, 109%]) more active at turbine clearings compared to closed forests (Figure 3.1B, Table 3.1), while the foraging activity was 113% (CI [34%, 180%]) higher at forest edges compared to closed forests (Figure 3.1E, Table 3.1). Echolocation and foraging activity of narrow-space foraging bats was similar across the three habitats, but echolocation activity tended to be 42% (CI [9%, 122%]) higher in the turbine clearing than at closed forest sampling points (Figure

3.1C & 1F, Table 3.1). Neither echolocation nor foraging activity of the three guilds were influenced by an interactive effect of habitat type and rotor size. However, the overall echolocation and foraging activity of narrow-space foraging bats, but not those of edge-space and open-space foraging bats, decreased by 85% (CI [73%, 91%]) and 74% (CI [5%, 95%]) respectively with increasing rotor diameter (Figure 3.2, Table 3.1). The effect of rotor diameter was not confounded by forest vegetation structure, distance to the outer forest edge or forest patch size (Supporting information C).

Table 3.1: *Estimates and p-values of the effects on echolocation and foraging activity of three foraging guilds. Significant effects (p-value <0.05) are shown in bold.*

			Open-space foragers		Edge-space foragers		Narrow-space foragers	
	Predictors	Df	Chi^2	p-value	Chi^2	p-value	Chi^2	p-value
Echo-location activity	Habitat	2	27.391	**<0.001**	17.102	**<0.001**	5.361	0.069
	Forest type	1	0.157	0.692	2.068	0.150	0.951	0.330
	Month	4	65.247	**<0.001**	38.524	**<0.001**	7.113	0.130
	Rotor Size	1	2.137	0.144	0.357	0.550	10.75	**0.001**
	Habitat x Rotor size	2	0.993	0.609	3.134	0.371	0.808	0.668
Fora-ging activity	Habitat	2	0.635	0.728	12.68	**0.002**	0.176	0.916
	Forest type	1	0.142	0.707	0.258	0.612	0.166	0.684
	Month	4	2.353	0.671	9.258	0.055	2.989	0.560
	Rotor Size	1	1.370	0.242	0.346	0.557	4.335	**0.037**
	Habitat x Rotor size	2	1.281	0.527	1.682	0.431	0.318	0.853

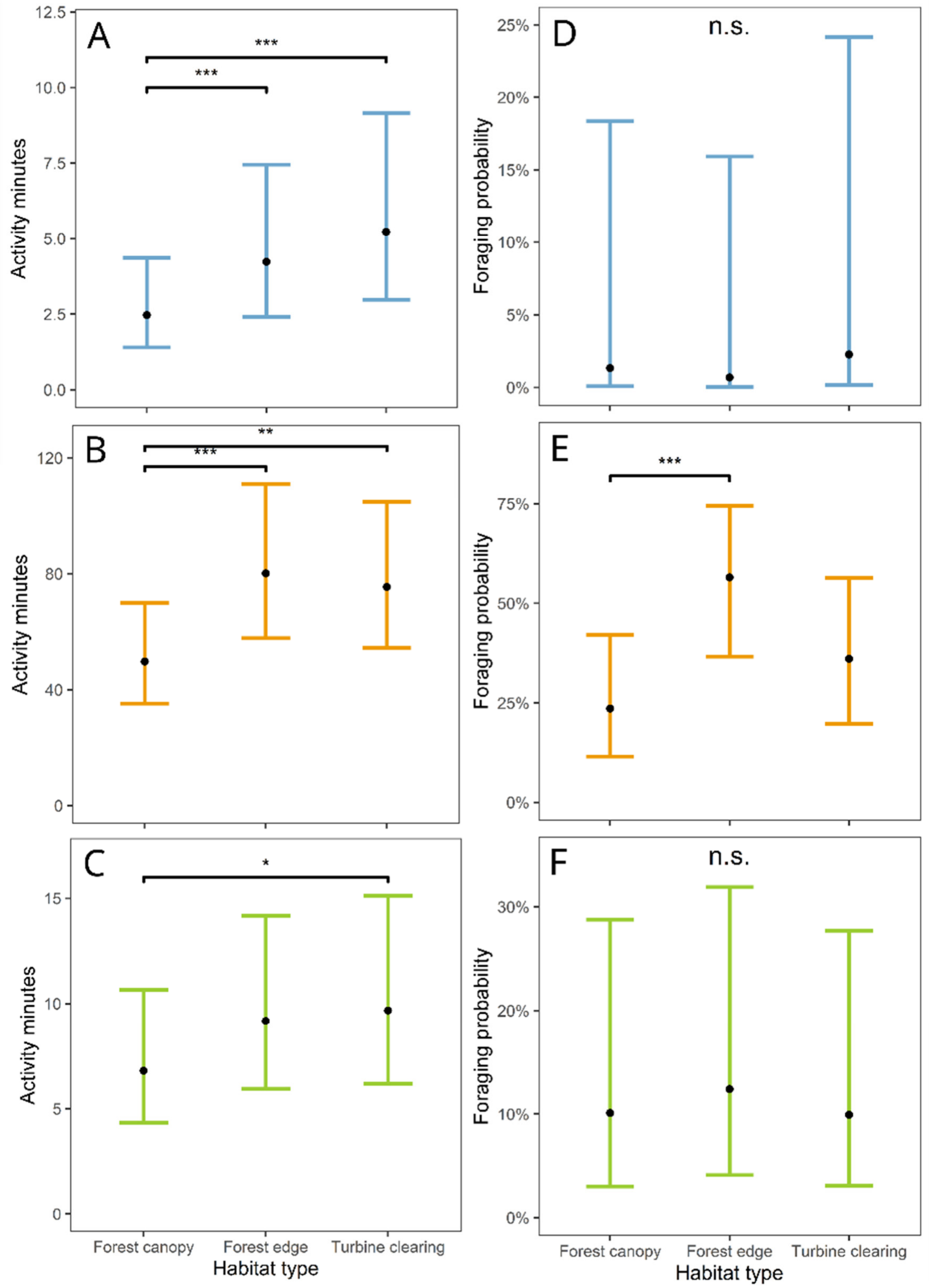

Fig. 3.1: *Effect of habitat on (A-C) echolocation activity and (D-F) foraging activity of open-space (blue; A, D), edge-space (yellow; B, E) and narrow-space foraging bats (green; C, F). Black dots and coloured bars indicate mean ± 95% prediction intervals. Asterisks denote the significance level of effects (***< 0.001< **<0.01< *< 0.05< n.s.).*

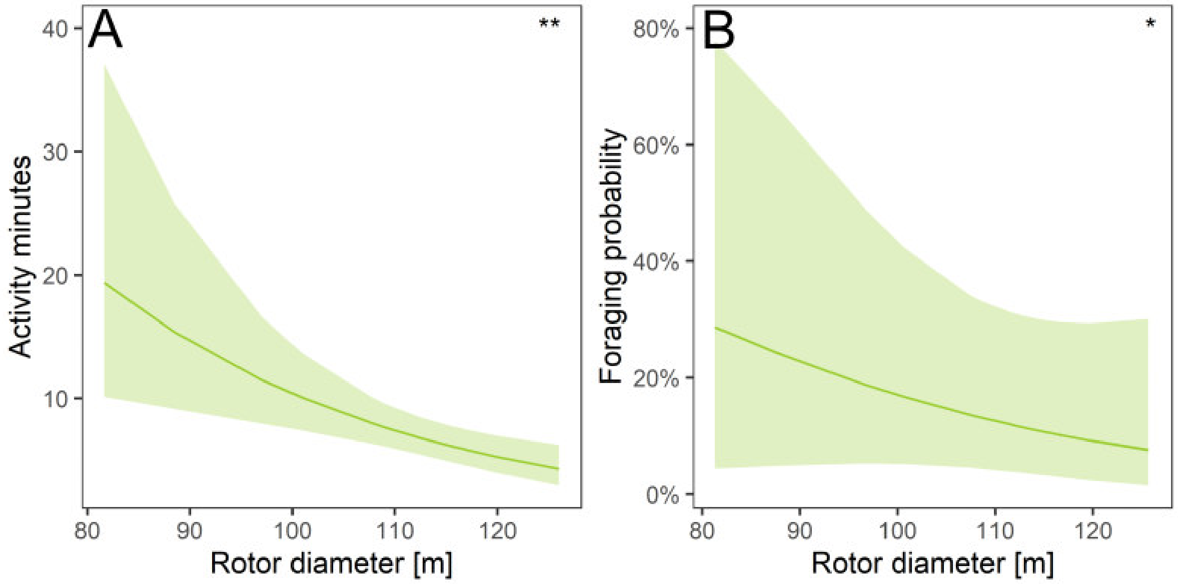

Fig. 3.2: *Effect of wind turbine rotor size on (A) echolocation activity and (B) foraging activity of narrow-space foraging bats. The green line depicts predicted mean values, green shades indicate mean ± 95% prediction intervals. Asterisks denote the significance level of effects (***< 0.001< **<0.01< *< 0.05< n.s.).*

3.5 Discussion

We conducted acoustic surveys at wind turbines in forests to investigate the effects of habitat conversion for turbine construction and operation on the activity of bats belonging to three foraging guilds. Bats used the forest gaps created for wind turbines, with open-space and edge-space foraging bats being more active above turbine clearings and at forest edges than above nearby closed forests. The activity of narrow-space foraging bats tended to be higher at turbine clearings than above closed forests, but the difference was less pronounced compared to those of other guilds.

Our findings are consistent with studies from managed forests without wind turbines where forest gaps created by clear-cutting were more frequently used by bats than surrounding or preceding forest habitats (Grindal & Brigham, 1998; Maki et al., 2021), especially by open-space and edge-space foraging bats (Kirkpatrick et al., 2017). In contrast to the study by Kirkpatrick and colleagues, our data also indicates an increased use of clear-cuttings by narrow-space foraging bats compared to nearby closed forests. This slight difference might be due to our recorders being installed at the canopy level of the forested sampling points but not those at the turbine clearing. We likely missed some echolocation calls of narrow-space foraging bats flying in the forest understorey, since echolocation calls of narrow-space foraging bats are emitted at lower intensities than calls of edge-space and open-space foraging bats, and they also attenuate faster in vegetation (Denzinger & Schnitzler, 2013; Holderied &

Helversen, 2003). Accordingly, echolocation calls of narrow-space foraging bats are more likely to be recorded by ultrasonic detectors at the clearing than at the forested sampling points. In contrast, open-space and edge-space foraging bats emit echolocation calls with a high sound pressure level (Currie et al., 2020; Holderied & Helversen, 2003). Additionally, echolocation calls of these species are less attenuated in the open space, where open-space and edge-space foragers typically fly, than those of narrow-space foraging bats within the vegetation. Therefore, it is likely that we detected open-space and edge-space foraging bats with similar probability in all three habitats. Consequently, we consider our results to be robust and in line with our hypothesis that forest-associated open-space and edge-space foraging bats are more active in forest gaps next to turbines than above the canopy of nearby closed forests.

As predicted, edge-space foraging bats were more active hunting insects at forest gaps at wind turbines than above the adjacent closed forest, suggesting that edge-space foraging bats use turbine clearings and adjacent edge habitats as a hunting ground. Increased foraging of edge-space foraging bats especially at forest edges is in line with their elevated echolocation activity at forest edges but might be additionally promoted by a high abundance of insect prey accumulating in proximity of wind turbines (Cryan et al., 2014; Foo et al., 2017). In conclusion, we showed that edge-space foraging bats predominantly use forest gaps at wind turbines for foraging. However, we cannot disentangle the causal factor behind this pattern because we did not measure prey abundance. Although increased foraging at forest gaps is likely for open-space-foraging bats as well, it was not confirmed by our data, possibly due to the low number of feeding buzzes recorded for this foraging guild. Based on the presence of echolocation activity but relatively low number of feeding buzz recordings of narrow-space foraging bats at forest gaps around wind turbines, we suggest that narrow-space foraging bats may use forest gaps around wind turbines mainly for commuting, but not necessarily for hunting. All in all, our study shows that the activity of open-space and edge-space foraging bats is high at forest gaps created by the clear-cutting of forests for wind turbine deployments. Contrary to our expectation, this was also the case at wind turbines with large rotors, although bats of these foraging guilds are known to be repelled by turbine operation in open landscapes (Leroux et al., 2022; Reusch et al., 2022). Accordingly, we conclude that clearings around wind turbines in forests are highly attractive for open-space and edge-space foraging bats and increase the probability that these bats fly in the immediate proximity of turbines.

Bats of the open-space and edge-space foraging guild are known to fly at heights at which wind turbines operate (e.g., Rodrigues et al., 2014). In our study area, the average ground clearance of the lower rotor tips of wind turbines was 82 m. The bat species with the highest mortality at wind turbines in Germany, *N. noctula* of the open-space foraging guild, flies on average below 60 m above ground but can also reach several hundred meters height (O'Mara et al., 2019; Reusch et al., 2023). *Pipistrellus pipistrellus* of the edge-space foraging guild, a species with similarly high fatalities at wind turbines in Germany, is regularly recorded at 85 m heights (Roemer et al., 2017). Consequently, edge-space and open-space foraging bats may experience increased casualties at wind turbines in forests compared to those operating in open landscapes. Based on morphology, *B. barbastellus* is grouped with the edge-space foraging guild but is usually not considered a high-collision risk species at wind turbines. However, since *B. barbastellus* only comprised 8% of recorded activity minutes in the edge-space foraging guild, their influence on our results can be neglected. In contrast, the activity of narrow-space foraging bats increased less clearly at forest gaps. Furthermore, they usually do not fly high above treetops and are rarely found dead below wind turbines (Rodrigues et al., 2014; Rydell et al., 2010). Therefore, we consider it unlikely that narrow-space foraging bats experience increased collisions at wind turbines in forests. Bats of this foraging guild are likely more affected by the direct loss of habitat caused by the clear-cutting, and by the indirect displacement that is caused by turbine operation. In fact, we confirmed our previous work that showed a reduced activity of narrow-space foraging bats in the proximity of wind turbines with large rotors (Ellerbrok et al., 2022).

3.6 Conclusion

Clear-cutting of forests for wind turbine construction and operation increased the activity of bats of all local foraging guilds in the newly created forest gaps. While all species might lose relevant habitat features like tree roosts as a result of clear-cutting, activity of open-space and edge-space foraging bats in particular seems to be promoted by the opening of the canopy when the forest is clear-cut for the deployment of wind turbines. Consequently, wind turbines in forests may lead to an increased number of collisions for these high-flying bat species (Rodrigues et al., 2014; Rydell et al., 2010). This might affect bat populations on the long run, because of the low reproduction rates of bats (Racey & Entwistle, 2000). To prevent this, we recommend that the operation of wind turbines in forests should be curtailed at times of high bat activity, by using algorithms that are specifically developed for wind turbine operation at forested sites. Curtailments of wind turbine operations have proven to be a promising solution to reconcile biodiversity conservation and the production of wind energy (Adams et al., 2021; Arnett et al., 2016; Whitby et al., 2021) and thus should be practiced, whenever wind turbines need to be placed in forests. Although operation curtailments may impair the efficacy of wind energy generation, such preventive measures may ultimately help to reconcile the two important goals to protect the global climate and the global biodiversity.

3.7 Acknowledgements & declarations

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Data availability

Data will be made available via the Dryad Digital Repository.

Authors Contributions

Nina Farwig, Franziska Peter and Christian C. Voigt designed the study and acquired funding. Julia S. Ellerbrok collected the data and wrote the original draft. Julia S. Ellerbrok and Finn Rehling analysed the data. All authors contributed critically to the writing of the manuscript.

Conflict of interest

None of the authors have conflicting interests.

Chapter 4: Wind turbines operating at high wind speeds have a negative impact on the activity of forest bats

4.1 Abstract

The increasing use of onshore wind energy is leading to an expansion of wind turbines in structurally rich habitats such as forests. Forest bats, in turn, are at risk of colliding with the rotor blades. Due to the legal protection of bats in Europe, it is imperative to restrict the operation of wind turbines to periods of low bat activity. However, bats can also be displaced from turbines by indirect influences like noise emission, a largely neglected disturbance factor. Therefore, we investigated whether bat activity is influenced by operation mode (on/off) under variable wind conditions along transects between 80 and 450 m from wind turbines. We divided recordings by foraging guilds, grouping activity of bats that preferentially forage either in the narrow, edge or open space of the forest habitat and analyzed them with autoregressive mixed effects models. We found that overall bat activity was not related to turbine operation. Yet, the acoustic activity of narrow-space foraging bats (*Myotis, Plecotus*) decreased significantly by 91% with increasing wind speed when wind turbines were operating, while bat activity remained unaffected by wind speed when turbines were not operating. This was neither observed for open-space foraging bats (*Nyctalus, Eptesicus, Vespertilio*) nor for edge-space foraging bats (*Pipistrellus, Barbastella*), which however, still avoided the proximity of wind turbines (8% activity decrease). In conclusion, wind turbine operation mode had a guild-specific negative effect on some forest-affiliated bats. The interactive effect of wind speed and operation mode suggests that noise emissions may have caused the observed avoidance response of sensitive bat taxa. We call for the implementation of low-noise wind turbines and strict curtailment schemes at forest sites to prevent long-term effects on noise-sensitive wildlife. Additionally, habitat loss has to be compensated by setting aside forests for bat conservation.

4.2 Introduction

Wind energy is globally promoted because more and more governments are committing to ambitious political targets with the aim to reduce greenhouse gas emissions (UNFCCC, 2015). As of June 2022, wind turbines with a capacity of 874 GW had been installed worldwide, presenting a 13% increase to the year before (WWEA, 2022). As a consequence of this rapid increase, wind turbines are nowadays more often established in remote areas such as forests

(FA Wind, 2023; Xiarchos & Sandborn, 2017). This may impact local wildlife, e.g., when habitats are lost or fragmented for the construction of wind turbines (Schöll & Nopp-Mayr, 2021). Furthermore, forest birds and bats may die by colliding with the blades of wind turbine rotors (Arnett et al., 2016; Thaxter et al., 2017). These obvious negative impacts of wind turbines on wildlife are well documented. Recent studies, however, have found that some bird and mammal species show also a decreased activity in the vicinity of wind turbines which cannot be explained by changes in habitat structure with distance to wind turbines (birds: e.g., Garthe et al., 2023; Rehling et al., 2023; mammals: e.g., Barré et al., 2018; Ellerbrok et al., 2022; Millon et al., 2018; Reusch et al., 2022; Skarin et al., 2018). Until now, the underlying causes for the avoidance behavior towards wind turbines remain unknown. One possible driver for avoidance is that animals could be affected by noise emissions from wind turbines (Teff-Seker et al., 2022).

Noise emissions from operating wind turbines are broadband and non-continuous, with most sound pressure in the frequency range below 200 Hz (Deshmukh et al., 2019; Katinas et al., 2016; Møller & Pedersen, 2011). Modern wind turbines may generate more noise than old turbines because of larger rotors that are designed to generate a higher energy yield (Møller & Pedersen, 2011; Xu et al., 2021). Wind turbine-induced noise can be counteracted to a certain extent by modifications to the rotor blades, e.g., brushes on the trailing edge, or to the drivetrain, e.g., dampers (Deshmukh et al., 2019; Hansen & Hansen, 2020; Xu et al., 2021). In general, the extent and profile of noise emissions from wind turbines vary considerably depending on wind turbine type and size. In addition, the spatial dispersion of wind turbine noise depends on the topography of the landscape and especially on atmospheric conditions, with wind turbine noise being perceived further and louder at high wind speeds and on the leeward side, whereas high wind speeds on the windward side can impair the propagation of wind turbine-generated noise (Heimann, 2018; Katinas et al., 2016). Therefore, a general characterization of the impacts of wind turbine noise is challenging and depends not least on the auditory capabilities of animals (Francis & Barber, 2013).

Acoustic stimuli can affect wildlife in various ways, for instance by overlapping in frequencies with the sounds of prey or predators, with calls of conspecifics or the animal itself, thereby acoustically masking important cues and signals. In addition, broadband noise can startle the receiving animal, causing it to flee from perceived threats, or it can distract animals that would otherwise focus their attention on important tasks such as foraging (Francis & Barber, 2013). As a result, animals may move away from the source of noise (Perillo et al., 2017) or alter their behavior (Zwart et al., 2016). Sensitive species can also develop chronic stress in response to anthropogenic noise (Kleist et al., 2018). Such adverse effects of anthropogenic noise, mostly originating from traffic, have already been documented in a variety of animals such as birds (Perillo et al., 2017), crickets (Orci et al., 2016), hermit crabs (Chan et al., 2010) and marine mammals (Erbe et al., 2019). Due to taxon-specific, context-specific, and sometimes elusive impacts, the effects of anthropogenic noise on wildlife can easily be overlooked or underestimated. However, it is likely that animals that rely on the acoustic rather than the visual and olfactory senses are particularly sensitive to anthropogenic noise. This brings bats into focus, which rely heavily on echolocation for orientation, foraging and communication (Griffin, 1958; Middleton et al., 2014).

Bats are highly sensitive to anthropogenic noise, as has often been shown for exposure to traffic noise emissions. Bats avoid crossing roads with heavy traffic (Bennett & Zurcher, 2013), and on the landscape level, bat activity decreases towards busy roads (Berthinussen & Altringham, 2012; Claireau et al., 2019; Voigt et al., 2020). Road avoidance by bats is most likely caused by multiple effects, including changes in food availability and modified habitats adjacent to roads (Berthinussen & Altringham, 2012). However, a past study also demonstrated a direct link between avoidance of bats and the sound pressure level of traffic noise (Zurcher et al., 2010). Lastly, experimental studies demonstrated that foraging success is impaired and prey search prolonged when bats are exposed to the playback of traffic noise (Finch et al., 2020; Luo et al., 2015; Schaub et al., 2009; Siemers & Schaub, 2011). Adverse effects on bats were observed no matter whether the frequencies of played noise overlapped with the frequencies of bat calls or prey rustling sounds. Thus, bats are not necessarily affected by masking of relevant sounds from the environment but rather startled by unexpected noises (Francis & Barber, 2013; Siemers & Schaub, 2011). Sound emissions of road traffic and wind turbines share certain acoustic features. Specifically, both generate non-continuous sounds in broadband frequencies, often with an unpredictable onset. Therefore, bats might react to noises from both sources in similar ways, i.e., bats may be negatively affected by wind turbine noise. In a natural setting, the effect of wind turbine noise on local wildlife may vary depending on the local propagation of noises from wind turbines, e.g., being more intense at high wind speeds and on the leeward side of wind turbines.

Convergent research from various countries demonstrated an avoidance behavior of various bat taxa towards wind turbines over up to several kilometer distance (Barré et al., 2018; Leroux et al., 2022; Millon et al., 2015, 2018; Minderman et al., 2017). However, effects vary among habitats and foraging guilds, i.e., between bat taxa specialized on different foraging niches (Denzinger & Schnitzler, 2013). For example, bats foraging preferentially in dense vegetation and bats foraging in the open airspace, so-called narrow-space and open-space foraging bats, respectively, avoid wind turbines in forests over several hundred meters (Ellerbrok et al., 2022; Gaultier et al., 2023; Reusch et al., 2023). Bats hunting along linear structures, so-called edge-space foraging bats, have so far only been observed avoiding wind turbines in open landscapes over more than one kilometer distance (Barré et al., 2018). Only one study on small wind turbines (< 50 kW) demonstrated that the avoidance response of bats towards wind turbines depends on the operation status. In that study, bats of all foraging guilds avoided small wind turbines but only when they were operating at high wind speeds (Barré et al., 2018; Minderman et al., 2012). Here we ask whether the avoidance behavior of bats towards large wind turbines depends also on the operation mode, assuming that bats may be repelled by increased noise emissions at high wind speeds.

We investigated the acoustic activity of bats towards twelve wind turbines in forests of Central Germany. We hypothesized that bats are negatively affected by the noise emissions of operating wind turbines, yet this effect may vary among foraging guilds. In Germany, the operation of modern wind turbines is curtailed at times of predicted high bat activity. Widely applied algorithms trigger the starting and stopping of wind turbines in 10-minute intervals throughout the night, depending on season and environmental conditions (Behr et al., 2017). This offers the opportunity to relate the acoustic activity of bats to the actual operation mode (on/off) of the wind turbines. Because of the curtailment algorithms, a low bat activity can be expected at times of wind turbine operation, independent of wind turbine effects. However, operating wind turbines emit more noise than non-operating wind turbines and noise attenuates with increasing distance from the source (Katinas et al., 2016). Therefore, we predicted (1) that the acoustic activity of bats is reduced towards wind turbines when they are operating, but not when they are not operating. Since sound propagation is also defined by ambient conditions, we further predicted (2) that bat responses to operating wind turbines depend on wind speed and wind direction, with stronger adverse effects at high wind speeds and at the leeward side of wind turbines.

4.3 Material & Methods

Study Area

Our study took place in the temperate low mountain ranges of Hesse in Central Germany (316 m to 509 m a.s.l.). Based on previously published datasets (Ellerbrok et al., 2022), we selected a subset of twelve study sites for which we had obtained comprehensive data on the operation mode of wind turbines. The chosen study sites were located in predominantly deciduous (seven sites) or coniferous forests (five sites) of a patch size between 184 ha and 2,595 ha (1,127 ha ± 691 ha; mean ± standard deviation, hereafter). Study sites were as far as possible from anthropogenic infrastructure other than wind turbines and from forest edges to prevent confounding effects on bat activity. Each study site consisted of one wind turbine built on a cleared forest patch of 44 ha to 315 ha (115 ha ± 76 ha) and positioned at the margins of wind farms. Focal wind turbines ranged in net energy production between 1.5 MW - 3.3 MW (2.8 MW ± 0.4 MW) and in rotor size between 97 m - 126 m diameter. The rotor diameter correlated with the tower height (182 m - 212 m, mean: 199 m ± 8 m; $r = 0.59$, $p<0.005$) and age of wind turbines (time since start-up at the beginning of the study: 1.5 - 19.0 years, mean: 4.8 ± 3.4 years; $r = -0.25$, $p<0.005$). Information on focal wind turbines were retrieved from the publicly accessible data base of Hessian environmental agency (HLNUG, 2019).

Bat call sampling and analysis

At each study site, we recorded acoustic bat activity along a distance gradient, starting at the wind turbine and leading into the forest, away from other turbines of the wind farm. At fixed distances of 80 m, 130 m, 250 m, and 450 m from the focal wind turbine we installed automated bat recorders (BATLOGGER A+, Elekon, Lucerne, Switzerland) in the lower tree canopy (height: 5 m - 29 m, mean: 16 m ± 6 m) and recorded for whole nights from 9 pm to 5 am. Recordings were carried out between May and September 2020 and 2021. Within each year, every recording point was covered four times in randomized order with intervals of 17 to 61 days (33 ± 12 days) in between. We used BATLOGGER default settings with a trigger frequency between 15 kHz and 155 kHz, which covered the typical call frequency range of expected bat species. With the software BatExplorer (version 2.1, Elekon, Lucerne, Switzerland), we manually identified recorded bat call sequences based on their call shape, end frequencies and peak frequencies (Barataud, 2020; LFU Bayern, 2020; Skiba, 2009). Bats of different foraging guilds are known to sometimes react differently to influences from the environment. Therefore, call sequences were either assigned to the functional guild of narrow-space foraging bats (*Myotis* ssp., *Plecotus* ssp.), edge-space foraging bats (*Pipistrellus* ssp., *Barbastellus* ssp.) or open-space foraging bats (*Eptesicus* ssp., *Nyctalus* ssp., *Vespertilio* ssp.; Denzinger & Schnitzler, 2013). To match the temporal resolution of wind turbine operation data, we divided recording nights into 10-min intervals and determined for each time interval in how many minutes bat calls were present.

Sampling of covariates

In Germany, the operation of modern wind turbines is usually curtailed at nights with high expected bat activity levels to reduce casualties. Automated curtailments are based on algorithms which are fine-tuned for individual wind turbines (Behr et al., 2017). Due to legal requirements, wind energy companies need to document these curtailments. We harmonized different operation protocols, resulting in a documentation of nightly wind turbine operation and standstill phases in a 10-min resolution for each focal wind turbine. Further, climate data simulated for each study site were downloaded from Copernicus Climate Change Service in hourly resolution (Muñoz Sabater, 2019). Based on the simulated data, we calculated air temperature, wind speed and wind direction in relation to the geographic orientation of the recording transect for each study site. Wind conditions were classified as downwind when the wind was blowing from the wind turbine down the transect and as upwind when the wind was blowing the opposite direction (with an accepted deviation of ± 22.5°). All other relations of wind direction and transect orientation were classified as crosswind. Lastly, to account for variations in the forest habitat structure and its effects on bat activity at each recording point, we estimated vegetation cover at ground level, 0.5 m, 1 m, 2 m, 4 m, 8 m, 16 m, and 32 m above ground to the nearest 5% within a 10 m radius. Subsequently, we calculated vertical vegetation heterogeneity across the layers using the Shannon-Weaver index (Bibby et al., 2000).

Data analysis

All statistical analyses were performed with R (version 4.2.2; R Core Team, 2021). Using generalized mixed models (GLMMs, package glmmTMB; Brooks et al., 2017) we assessed how bat activity as response variable was affected by the operation mode of wind turbines ('on' or 'off'), while controlling for differences in wind turbine features, habitat structure and weather conditions (predictor variables). All continuous fixed factors were standardized with a z-transformation. Recording points were nested in study site and recording night (random effects).

We performed a model selection process to determine which predictor variables were relevant and to be included in the final analysis. To this end, we constructed full models with all plausible predictor variables potentially influencing bat activity, being wind turbine rotor size, air temperature, wind speed, wind direction in relation to recording transects ('upwind', 'downwind' or 'crosswind'), vertical vegetation heterogeneity of the forest habitat and time of night. Additionally, we included wind speed as a quadratic term to account for the fact that low wind speeds might reduce wind turbine noise propagation, while very high wind speeds could mask wind turbine noise, implying a non-linear relationship with bat activity. Based on the full models, we tested all possible combinations of predictors using the dredge function of MuMIn package (Bartoń, 2022) and selected the model with the smallest AICc as final model (Appendix S4). Turbine operation was set as a fixed predictor so that we could test our hypotheses.

Following the described model selection process, final models were selected for each bat foraging guild separately, because activity levels differed considerably among guilds. In our main models, we tested for effects of predictor variables on bat activity within each 10-min interval, the finest temporal resolution possible. However, bat activity in consecutive 10-min intervals was temporarily autocorrelated (Durbin-Watson test for narrow-space foraging bats: DW = 0.86, $p<0.005$; for edge-space foraging bats: DW = 0.24, $p<0.005$; for open-space foraging bats: DW = 0.58, $p<0.005$). Thus, we included an autoregressive covariance structure in the GLMM, thereby performing a time series model accounting for the correlation. Only a comparably small percentage of all 10-min intervals contained more than one minute of bat activity (4.2% in narrow-space foragers, 27.0% in edge-space foraging bats, 2.6% in open-space foragers). Therefore, we resorted to more robust binomial GLMMs assessing presence and absence of bat activity within each interval for narrow-space and open-space foraging bats. The model residuals for edge-space foraging bats deviated severely from normal distribution, which is why we performed a truncated poisson (hurdle) model for this guild.

In addition to the time series models, we performed negative binomial GLMMs assessing effects on total number of bat activity minutes per night. With this model, we tested for cumulative effects of total turbine operation time per night assuming that responses in bat activity might only become visible, when conditions persist over longer periods. To this end, we summed up the time intervals with and without turbine operation and calculated mean wind speed and air temperature for the corresponding period. Predictor variables were chosen with the model selection process described above, but without time of night or wind direction in relation to transects as potential predictors, because a meaningful averaging was not possible.

Full models and selected final models were checked for multicollinearity by calculating variance inflation factors with the car package (Fox & Weisberg, 2019), as well as for homoscedasticity and normally distributed residuals with the DHARMa package (Hartig, 2020). P-values and estimates for fixed effects, calculated with Wald-$\chi 2$-tests from the car package, were compared between full and selected models (Appendix S5). For significant interactive effects with wind turbine operation status we calculated the within-group p-values with least-squares means (package lsmeans; Lenth, 2016).

4.4 Results

In total, we recorded 28,856 minutes with bat presence over 297 full night recordings within two years. Narrow-space foraging bats made up 14% of all recorded bat activity minutes. Bats of this foraging guild were active in 12% of all recorded 10-min intervals. Edge-space foraging bats made up 78% of activity minutes and were active in 42% of 10-min intervals. Open-space foraging bats made up 8% of activity minutes and were active in 8% of 10-min intervals. Bat activity levels varied in the course of the night and between foraging guilds (Appendix S1). Wind turbines were operating during 49% of all recorded 10-min intervals, with highest number of operation periods in June and lowest in September (Appendix S2).

The time series model revealed that the acoustic activity of bats did not correlate with the operation mode of wind turbines, regardless of foraging guild. However, acoustic activity of narrow-space foraging bats decreased by 91% (95% confidence interval [-95%, -82%]) with increasing wind speed when wind turbines were operating ($p = 0.048$), while the activity remained unaffected by wind speed when wind turbines were not operating ($p = 0.50$; Fig. 4.1). This interaction appeared in the full model as a marginally significant trend ($p = 0.062$; Appendix S5). Additionally, narrow-space foraging bats were less active close to wind turbines than far from wind turbines (-48%, CI [-48%, -47%]; Fig. 4.2a). The activity of bats decreased around wind turbines with large rotors compared to turbines with small rotors (-78%, CI [-76%, -78%]) and it increased at locations of high vertical vegetation heterogeneity compared with places of low vertical vegetation heterogeneity (+172%, CI [+165%, +176%]; Tab. 4.1).

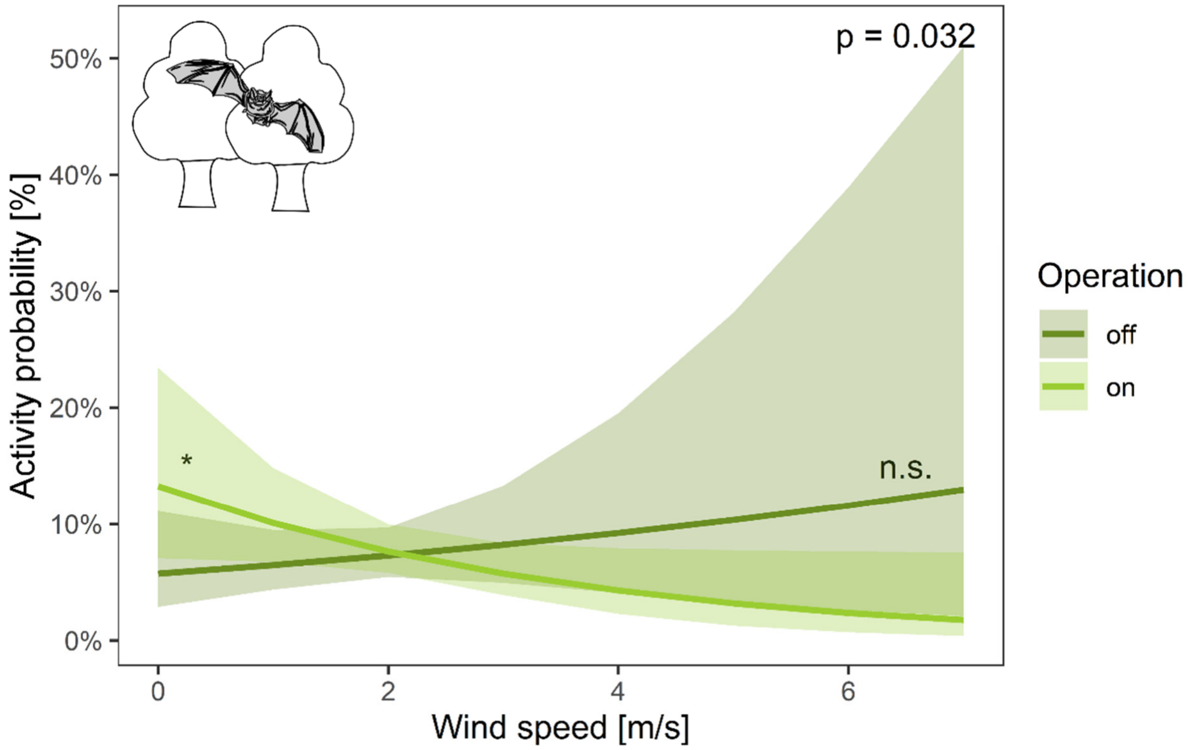

Fig. 4.1: Activity probability of narrow-space foraging bats in relation to wind speed around operating and non-operating wind turbines. *Mean estimates (lines) and 95%-confidence intervals (shades) of activity probability in narrow-space foraging bats depending on wind speed at times of wind turbine operation ('on') and standstill ('off') in 10-min intervals of the night. Asterisks denote the significance level of the effect for different turbine operation modes (*** < 0.001 < ** < 0.01 < * < 0.05 < n.s.).*

Acoustic activity of edge-space foraging bats recorded closest to wind turbine decreased by 8% (CI [-8%, -8%]) in comparison to the recording point most distant to wind turbines (Fig. 4.2b). In addition, acoustic activity increased with decreasing vegetation heterogeneity (13%, CI [-2%, +12%]) and decreased over the course of the night (-28%, CI [-27%, +8%]; Tab. 4.1). All but the effect of time was supported by the full model (Appendix S5).

Open-space foraging bats were more active at study sites where wind turbines had large rotors than at sites with small rotors (+167%, CI [+117%, +228%]) and at recording sites with high vertical vegetation heterogeneity compared to sites of low heterogeneity (+499%, CI [+485%, +510%]). Additionally, we observed a marginally significant trend of a reduced activity in open-space foraging bats with increasing proximity to wind turbines, especially when wind turbines were operating (Fig. 4.2c, Tab. 1, Appendix S3). Only in the full model we found a positive effect of air temperature on the activity of open-space foraging bats (Appendix S5).

The GLMMs at the resolution of full nights did not reveal any further effects of turbine operation on summed bat activity. Still, these models showed that high mean air temperature had a positive effect on the activity of narrow-space (+614%, CI [+596%, +633%]), edge-space (+170%, CI [164%, +176%]) and open-space foraging bats (+3681%, CI [+3488%, +3883%]). High mean wind speed reduced the activity of narrow-space (-97%, CI [-99%, -93%]) and edge-space foraging bats (-82%, CI [-68%, -90%]; Tab. 4.1). In the full model, the negative effect of high wind speed on edge-space foraging bats was only marginally significant (Appendix S5).

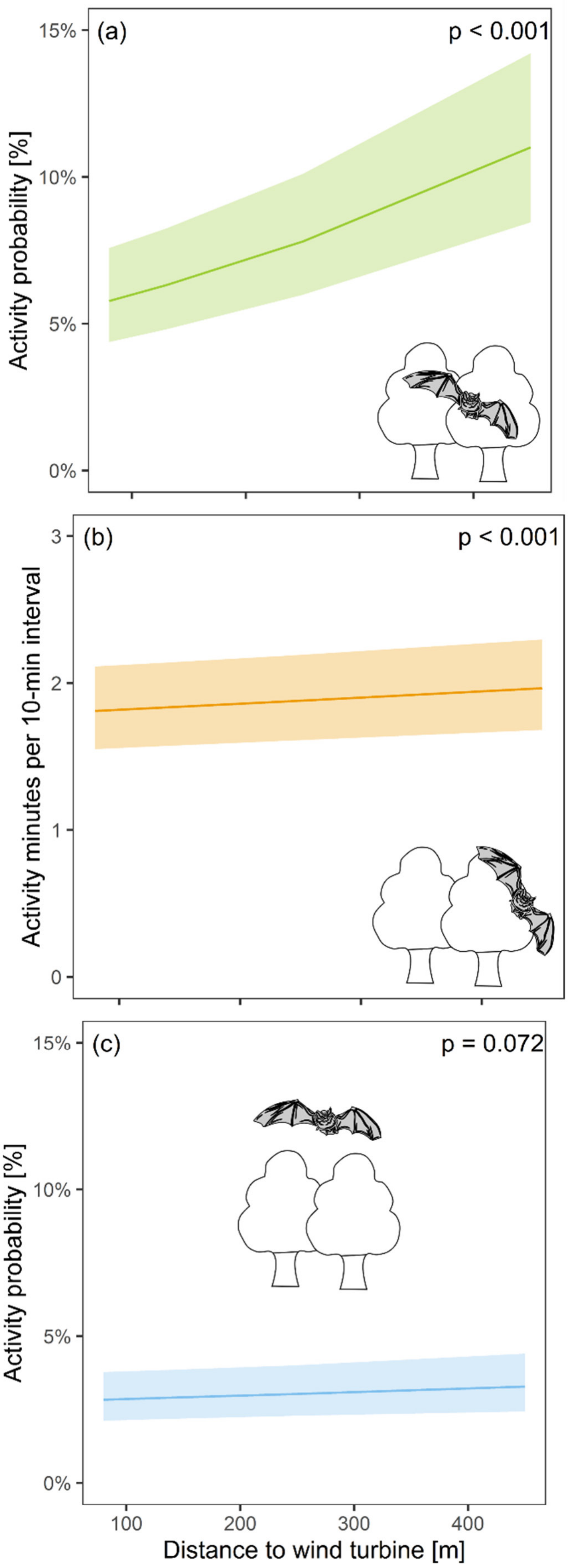

Fig. 4.2: Bat activity at increasing distance to wind turbines regardless of operation mode. *Mean estimates (dots) and 95%-confidence intervals (lines) of bat activity depending on the distance to wind turbines for (a) narrow-space, (b) edge-space, and (c) open-space foraging bats in 10-min time intervals of the night.*

Tab. 4.1: *Results of selected GLMMs at 10-min and nightly resolution. Estimates and p-values of the effects on bat echolocation activity of three bat foraging guilds. Significant effects (p-value < 0.05) are shown in bold. Predictors from the full model which were not included in the top AICc model are marked with an "x". Time of night and wind direction could not be assessed in the models for full nights (shaded).*

			Temporal resolution			
			10 min intervals		full nights	
Foraging guild	Predictors	Df	Chisq	p-value	Chisq	p-value
Narrow-space	turbine operation	1	1.350	0.245	1.821	0.177
	turbine distance	1	104.595	**< 0.001**	14.540	**< 0.001**
	wind speed - linear	1	1.192	0.275	8.931	**0.003**
	wind speed - quadratic	1	x	x	x	x
	air temperature	1	x	x	7.481	**0.003**
	rotor diameter	1	9.572	**0.002**	8.001	**0.005**
	vertical vegetation heterogeneity	1	41.266	**< 0.001**	x	x
	wind direction	2	x	x		
	time of night	1	3.565	0.059		
	turbine operation x turbine distance	1	x	x	x	x
	turbine operation x wind direction	4	x	x		
	turbine operation x wind speed - linear	1	4.592	**0.032**	x	x
Edge-space	turbine operation	1	1.563	0.211	0.376	0.540
	turbine distance	1	13.653	**< 0.001**	x	x
	wind speed - linear	1	0.107	0.743	6.482	**0.011**
	wind speed - quadratic	1	x	x	x	x
	air temperature	1	x	x	6.064	**0.014**
	rotor diameter	1	3.527	0.060	2.819	0.093
	vertical vegetation heterogeneity	1	5.007	**0.025**	9.428	**0.002**
	wind direction	2	4.4743	0.107		
	time of night	1	4.543	**0.033**		
	turbine operation x turbine distance	1	x	x	x	x
	turbine operation x wind direction	4	x	x		
	turbine operation x wind speed – linear	1	x	x	x	x

			Temporal resolution			
			10 min intervals		full nights	
Foraging guild	Predictors	Df	Chisq	p-value	Chisq	p-value
Open-space	turbine operation	1	0.290	0.590	0.013	0.911
	turbine distance	1	3.235	0.072	x	x
	wind speed - linear	1	2.102	0.147	2.532	0.112
	wind speed - quadratic	1	x	x	x	x
	air temperature	1	x	x	21.136	**< 0.001**
	rotor diameter	1	3.934	**0.047**	1.660	0.198
	vertical vegetation heterogeneity	1	82.931	**< 0.001**	22.496	**< 0.001**
	wind direction	2	x	x		
	time of night	1	x	x		
	turbine operation x turbine distance	1	3.732	0.053	x	x
	turbine operation x wind direction	4	x	x		
	turbine operation x wind speed - linear	1	x	x	x	x

4.5 Discussion

In this study, we investigated bat activity around wind turbines at 12 forested sites in Germany to elucidate the causal mechanisms driving avoidance of wind turbines by bats. We argued that noise emissions of operating wind turbines might be responsible for the avoidance and assessed differences between bat activity at operating and non-operating wind turbines. We found no overall correlation of wind turbine operation mode and activity levels in any bat foraging guild, regardless of distance to wind turbines. However, narrow-space foraging bats were less active around operating wind turbines at high wind speeds over a distance of at least 450 m, whereas their activity was not affected by non-operating wind turbines at high wind speeds. Narrow-space and edge-space foraging bats additionally reduced their activity towards wind turbines, regardless of wind turbine operation mode.

Overall, we did not find that bats were more active at times when wind turbines were not operating, neither at 450 m nor at 80 m distance, which is surprising given that wind turbines are switched off when bat activity is predicted to be high (Behr et al., 2017). However, narrow-space foraging bats were negatively affected at high wind speeds around operating wind turbines, which was not observed at non-operating wind turbines. Bats in general are known to fly less with increasing wind speeds (e.g., Erickson & West, 2002; Voigt et al., 2018) but the interactive effect with wind turbine operation mode argues that it is not the wind speed as such that causes the reduced activity of narrow-spaced foraging bats. Rather, high wind speeds amplify negative impacts of operating wind turbines on the acoustic activity of bats. This finding is consistent with that of a previous study conducted at small wind turbines (< 50 kW net energy production) in open habitats (Minderman et al., 2012). In that study, bats of all foraging guilds avoided operating wind turbines at a distance of at least 25 m. These convergent results suggest that the operation of wind turbines at high wind speeds can indeed negatively affect bat activity in both forest and open habitats. Moreover, the strength of the adverse effect seems to increase with turbine dimensions, as we observed a stronger effect at the large wind turbines of our study sites, suggesting an impact of operating wind turbines over at least 450 m. Yet, for edge-space and open-space foraging bats we could not confirm a negative effect of wind turbine operation at high wind speeds over similar spatial scales.

In line with our findings, several recent studies show that bats are less active around wind turbines than in distance to them (e.g., Barré et al., 2018; Ellerbrok et al., 2022; Gaultier et al., 2023; Millon et al., 2018; Reusch et al., 2022). The underlying causes remained unknown, but several potential explanations have been put forward, including noise, visual disturbances and turbulences originating from the wind turbine as well as habitat changes associated with wind turbine construction in forests. Based on our observation that narrow-space foraging bats avoid operating wind turbines only at high wind speeds we can rule out several of potential explanations. First, visual disturbances cannot explain our findings because visual stimuli are not perceivable in the darkness of the night, e.g., the moving blades, or they do not depend on wind conditions, e.g., aviation security lighting. Second, turbulences in the tailwind of wind turbines are unlikely to affect bats below the tree cover and are strongly influenced by wind direction (Porté-Agel et al., 2013), a factor which was not explaining variation of bat activity in our analysis. Third, trophic effects probably do not underlie the observed pattern, because we saw a decrease in bat activity only when performing analyses at a temporal resolution of 10 minutes but not at larger temporal resolutions. This points towards a causal factor that can change swiftly, and insect availability is very unlikely to vary between 10-min intervals. Lastly, bat activity may decrease in proximity to wind turbines depending on differences in the vegetation structure, especially when wind turbines are constructed in complex ecosystems such as forests. However, in our analyses we accounted for variation in vegetation structure between sampling points and can therefore exclude that a reduced bat activity is driven by the habitat. In conclusion, we consider noise emissions from operating wind turbines generated during strong winds as the most parsimonious explanation that causes certain bat taxa to avoid operating wind turbines.

Wind turbine noise emissions are the most likely cause for the observed avoidance of operating wind turbines at high wind speeds in narrow-space foraging bats, since wind turbine noise is stronger and spread farther at high wind speeds than at low wind speeds (Heimann, 2018; Katinas et al., 2016). As a result, narrow-space foraging bats may avoid wind turbines more strongly in high winds than in low winds. Yet, we could not confirm that the effect of turbine operation at high wind speeds is stronger on the leeward side of wind turbines, where noise should propagate more efficiently than on the windward side (Heimann, 2018). Unfortunately, we were not able to measure turbine generated sounds in relation to increasing distances to wind turbines at our study sites. We can only speculate how far wind turbine-related sounds propagate locally and how loud these sounds are perceived by bats of different foraging guilds. However, some studies suggest that bat taxa differ in their sensitivity to anthropogenic noises and that specifically narrow-space foraging bats are more likely avoiding anthropogenic noise emissions than bats from other foraging guilds (Bonsen et al., 2015; Leroux et al., 2022). Therefore, it is possible that narrow-space foraging bats are startled by turbine-related noise at high winds over the 450 m range of our transect, regardless of wind direction, while edge-space and open-space foraging bats are less affected. Differences in the response of bats from different foraging guilds to wind turbine operation might additionally be confounded with their preferred use of habitat niches in forests. For example, open-space foraging bats fly above the tree canopy where they could be exposed to additional visual cues. This may explain why open-space foraging bats tend to be less active close to operating wind turbines independent of wind speeds, while this was not observed for narrow-space and edge-space foraging bats, that fly lower and prefer foraging habitats in forests and at forest edges (Denzinger & Schnitzler, 2013). To conclude, noise emission of wind turbines is of ecological relevance and may negatively affect local bats, particularly of the narrow-space foraging guild. We recommend conducting playback experiments and evaluate the effect of wind turbine-related noise emission more directly on the activity of forest-associated bats.

Noticeably, climate factors, i.e., wind speed and ambient temperature, did not explain the variation in bat activity in our main models. At first sight, this seems to contradict a series of studies which showed that bat activity strongly depends on wind speed, ambient temperature, and precipitation (e.g., Behr et al., 2017; Erickson & West, 2002; Voigt et al., 2018). The unexpected results might have been caused by inaccuracies in our meteorological data, since we made use of simulations at a horizontal resolution of 9 km. Consequently, smaller scaled variations in wind and temperature were not captured in these models although they are highly likely to occur due to the local topography and variable forest structure of our study area. However, our additional models which were based on averaged wind speed and ambient temperature of whole nights confirmed the relevance of climate variables as a factor explaining bat activity. Thus, the simulated weather data used for our analyses are robust. The absence of any climate effects in our original analyses is most likely caused by the high temporal resolution of 10-min intervals which leads to very small variations in climate parameters between consecutive intervals. Further, bats possibly only react to unfavorable weather conditions when they persist over a longer time period.

4.6 Conclusion

Our study shows that bats in temperate forests generally avoid wind turbines and that sensitivity to wind turbine operation varies between foraging guilds. In particular, narrow-space foraging bats, that are especially dependent on the forest habitat, significantly reduced their activity when wind turbines were in operation during high wind speeds. To the best of our knowledge, our study is the first to describe a relationship between bat activity, turbine operation and wind speed for wind turbines of standard industrial sizes. Notably, we did not observe any significant changes in activity of edge-space and open-space foraging bats in response to the operating mode of wind turbines. Consequently, guild-specific sensitivity of bats towards wind turbine operation may influence the composition of local bat communities. In addition, the observation of stronger avoidance effects at high wind speeds suggests that bats respond more strongly when turbine noise is perceived louder and at greater distances from wind turbines. In order to clarify the relevance of wind turbine noise for bats detached from correlating factors, we propose to conduct playback experiments similar to previous studies on birds (Szymański et al., 2017; Zwart et al., 2016).

Our study design focused on the short-term effects of wind turbine operation on bats. However, long-term effects beyond the timeframe of our study are possible and likely where noise is emitted (Francis & Barber, 2013). For example, increased chronic stress and resulting fitness costs could impact individual bats or populations, respectively, as previously shown for birds (Kleist et al., 2018). It is also possible that even occasional turbine-related noises may startle bats, causing them to avoid the affected area over extended periods. Bats are known to have an excellent spatial memory and therefore, bats may remember areas with noise pollution at the landscape scale over long periods of time (Mueller & Mueller, 1979). Consequently, conservation actions should be considered following the mitigation hierarchy (Arlidge et al., 2018). Wind turbines that produce loud noises should be avoided, specifically in forests that are suitable as habitats for sensitive bat taxa. Wind turbines in forests should operate under stricter curtailment criteria than wind turbines in open areas. Effective compensatory measures include the designation of protected forests to compensate for indirect habitat loss for forest bats due to the displacement of bats by wind turbines.

4.7 Acknowledgements & declarations

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Data availability

Data will be made available via the Dryad Digital Repository.

Authors contributions

Nina Farwig, Franziska Peter and Christian C. Voigt designed the study and acquired funding. Julia S. Ellerbrok sampled and analysed the data and wrote the original draft. All authors contributed critically to writing and revising the manuscript.

Conflict of interest

None of the authors have conflicting interests.

Chapter 5: Synthesis

Biodiversity is in crisis, not least because climate change compromises habitats and ecological networks (IPBES, 2019; Jaureguiberry et al., 2022). Policy makers push towards mitigating the consequences of climate change which includes the promotion of wind energy as a renewable energy source (Gielen et al., 2019). In countries with a high forest cover, it may be inevitable to deploy wind turbines in forests in order to reach the goal of net zero carbon dioxide emissions (Gaultier et al., 2020; UNFCCC, 2015). However, wind turbines in forests may, in turn, conflict with the conservation of biodiversity in the forest ecosystems (Schöll & Nopp-Mayr, 2021). This conflict of objectives will only be resolved through evidence-based trade-offs. Specifically, we must aim for the most possible efficiency in wind energy generation while preventing or minimizing adverse effects on forest wildlife at the same time. In this thesis, I investigated the activity patterns of bats from three foraging guilds in forests with wind turbines. With my work, I aimed to unravel if and how bat activity is affected in the proximity of wind turbines and how this is influenced by distance to wind turbines, their size and operation schemes, as well as forest vegetation structure and the presence of clear-cut areas around wind turbines. Ultimately, I want to provide evidence-based approaches contributing towards a reconciliation of the bat-wind energy conflict in forests. The focus of this chapter will be on narrow-space foraging bats, which I found to be most affected by wind turbines in forests.

5.1 Distance to the closest wind turbine determines activity levels of narrow-space foraging bats in forests

Increasingly, wind turbines are not only deployed in open landscapes but also in forest areas (FA Wind, 2023; Xiarchos & Sandborn, 2017). As a consequence, bats might be displaced by wind turbines in forests, which would be reflected in reduced activity levels towards wind turbines. Activity patterns implying avoidance at wind turbines sites have been observed in open landscapes (Barré et al., 2018; Leroux et al., 2022), but little is known about the effects of wind turbines on bats in forests. In Chapter 2, I investigated differences in the echolocation activity of three bat foraging guilds in relation to wind turbine distance and rotor size in forests of different vegetation structure. I found strong evidence that bats of the narrow-space foraging guild were less active towards wind turbines and concluded that they are most likely displaced by wind turbines or associated factors. This is in line with research from agricultural landscapes in France following the same study design (Barré et al., 2018; Leroux et al., 2022) and has in the meantime been confirmed by a study on forest-based wind turbines in Finland (Gaultier et al., 2023). The proximate causes for bats to avoid wind turbines are still unclear. I found that narrow-space foraging bats are particularly less active around wind turbines with larger rather than smaller rotors and towers and concluded that the avoidance in narrow-space foraging bats is likely caused by a factor related to the size of turbines. However, wind turbine size could not be examined separately from the age of turbines, as both factors were correlated. Although some recent studies from forests observed avoidance behaviour around wind turbines also in bats of the open-space foraging guild (Gaultier et al., 2023; Reusch et al., 2023), I could not confirm this for forests in Hesse. Instead, I found an activity increase in open-space foraging bats in late summer, which coincides with the autumn migration and mating season (Dietz & Kiefer, 2014). This seasonal attraction supports the hypothesis that bats might orientate towards wind turbines because they mistake them for large trees which they use as landmarks or roosting sites (Guest et al., 2022). In conclusion, I saw that bats can be displaced especially by large wind turbines, but activity patterns depend on foraging guild and season and are stronger influenced by vertical vegetation structure than by wind turbine parameters.

5.2 Wind turbine clearings attract edge-space and open-space foraging bats but are not avoided by narrow-space foraging bats

Forests are receding worldwide as more and more areas are cleared to gain space or material for anthropogenic needs (Hansen et al., 2013). Also for the deployment of wind turbines in forests a certain area needs to be cleared of trees (FA Wind, 2023; Schöll & Nopp-Mayr 2021). The creation of open habitats in the forest interior can be expected to have varying impacts on bats from different foraging guilds, because edge-space and open-space foraging bats are adapted to more open spaces while narrow-space foraging bats are rather adapted to dense vegetation clutter (Kirkpatrick et al., 2017). In chapter 3, I compared activity levels of three bat foraging guilds between turbine clearings, adjacent forest edges and the canopy of the surrounding forest. I differentiated between echolocation activity, based on echolocation calls used for orientation, and foraging activity, based on typical buzz-like calls emitted during hunting (Skiba, 2009). As expected, edge-space and open-space foraging bats were more active at the wind turbine clearing or the adjacent forest edge than in the surrounding forest canopies. Bat species from these guilds are known to be susceptible to collisions with wind turbines due to their typically high flight altitude (Rodrigues et al., 2014; Rydell et al., 2010). Consequently, the deployment of wind turbines in forests may increase fatality rates for these high-risk species compared to deployments in open landscapes due to the creation of contrasting habitats. In contrast to expectations, I did not observe that narrow-space foraging bats were less active at wind turbine clearings compared to the surrounding forest canopy. Consequently, the avoidance behaviour I found and described for this guild in chapter 2 cannot be explained by the presence of cleared spaces around wind turbines and the associated loss of the forest habitat they are specialized on.

5.3 Narrow-space foraging bats are repelled by wind turbine operation at high wind speeds

Anthropogenic infrastructures are steadily expanding, resulting in noise pollutions perceivable even in remote areas and most conservation areas (Barber et al., 2011). Also wind turbines emit noise and, when deployed in forests, this might affect local wildlife (Teff-Seker et al., 2022). Bats are known to be sensitive towards broadband noise (e.g., Schaub et al., 2009) Therefore, wind turbine noise emission seem to be a plausible explanation why bats avoid the proximity of turbines. Yet, evidence is still pending. Higher sound pressure levels can be measured at operating wind turbines than at non-operating wind turbines (Katinas et al., 2016). Thus, in chapter 3, I compared activity levels of three bat foraging guilds between times when wind turbines were operating and times when they were not operating. Moreover, I analysed how the bats' responses to operation modes was influenced by wind speed and wind direction. I found that the activity of neither bat foraging guild was generally affected while wind turbines were operating. However, narrow-space foraging bats were less active when wind turbines were operating, and strong winds were prevailing at the same time. This effect was noticeable over the whole 450 m length of the recording transect. Noise emissions are the most likely link between wind speed and turbine operation because noise emissions generally propagate further in leeward direction at high wind speeds (Heimann, 2018; Katinas et al., 2016). Nevertheless, open questions remain regarding the exact mechanisms of avoidance. For example, contrary to what I expected under the assumption that bats are repelled by turbine noise, I did not see that the negative effect of wind turbine operation was influenced by wind direction or distance to turbines. Still, my findings are a promising start towards understanding the mechanisms of avoidance in bats towards wind turbines. Additionally, in this chapter general avoidance patterns in bat activity towards wind turbines were confirmed not only for narrow-space foraging bats but to a lesser extent also for edge-space foraging bats, where the effect was small but significant, and open-space foraging bats, where the activity decrease towards wind turbines was marginally significant.

This suggests that all bats might be affected by wind turbines in forests but sensitivity varies among foraging guilds.

5.4 General conclusions

In this thesis, I present three major achievements that will be helpful for sustainably designing the wind energy development in forests with regard to bats.

(1.) I found that bats are repelled by wind turbines in forests and therefore experience an indirect habitat loss. This confirms that wind turbine in forests can be treated as point sources of disturbances (Ellis & Schneider, 1997), whose negative influence on bats is strongest close to the turbine itself and attenuates over distance. This holds especially true for narrow-space foraging bats which reduced activity levels by approximately 50% along the 450 m distance gradient towards wind turbines. Accordingly, wind turbines in forests should be kept away from habitat structures important for narrow-space foraging bats to avoid displacements. Currently, it is best practice in Germany to maintain minimum distances of 200 m to confirmed bat roosts (Hurst et al., 2020). Although a good approach, such minimum distances to roosts do not necessarily prevent indirect habitat loss as some bat species have home ranges of several square kilometres (Dietz & Kiefer, 2014). Consequently, forest areas used for foraging and commuting may become unsuitable in the vicinity of wind turbines. Such indirect habitat losses for forest bats need to be avoided, minimized, or compensated (see chapter 5.5).

(2.) I showed that bats of different foraging guilds differ in their responses to wind turbines with narrow-space foraging bats being more likely to be displaced than edge-space and open-space foraging bats. This is in line with studies on *Myotis* bats, the bat genus of which the narrow-space foraging guild mostly consists in my study area, showing them to be especially sensitive to anthropogenic disturbances such as noise (e.g., Schaub et al., 2009) or light (Lewanzik & Voigt, 2017; Zeale et al., 2018). Yet, so far it had not been observed that bats of different foraging guilds are more likely than others to be displaced by wind turbines (e.g., Barré et al., 2018). A possible explanation is that distinct levels of sensitivity among foraging guilds are specific to the forest habitat. Consequently, narrow-space foraging bats deserve special attention when wind turbines are deployed in forests, not least because they depend strongly on the forest habitat for roosting and hunting and may therefore be particularly affected when these habitats are lost or degraded (Dietz & Kiefer, 2014). Yet, bats of the edge-space and open-space foraging bats should not be neglected. Although they are not strongly repelled by wind turbines in forests they are still affected since for these foraging guilds I could infer an increased risk for collisions with the rotor blades compared to open landscapes. In conclusion, effective conservation measures must aim at all forest bat species and account for the different ways in which wind turbines in forests affect bats of different foraging guilds.

(3.) So far, several studies had indicated that bats avoid wind turbines, but none could explain the underlying mechanisms. With this thesis, I narrowed down the causes which can potentially contribute to the avoidance of wind turbines in forests particularly by narrow-space foraging bats. First, I could infer that narrow-space foraging bats are likely repelled by wind turbine noise emissions, based on the observation that they are less active at operating than at non-operating wind turbines during high wind speeds. So far, this correlation had only been shown for much smaller wind turbines of up to 50 kW energy generation capacity (Minderman et al., 2012). Second, I found that the presence of open habitats around wind turbines does not explain the avoidance of narrow-space foraging bats towards wind turbines. Instead, I found that narrow-space foraging bats make use of the open habitats created around wind turbines, although their morphology gives them a competitive advantage when foraging in closed forests (Voigt & Holderied, 2012). This is in line with a recent study on bat activity around wind turbines in boreal forests, where bat activity was not related to canopy cover either (Gaultier et al., 2023). Third, it remains unclear if wind turbine effects on prey insects may drive the avoidance patterns of narrow-space foraging bats towards wind turbines. In a preliminary analysis I found a marginally significant reduction of arthropod biomass towards wind turbines but no correlation to bat activity. Yet, more extensive research on this topic will be needed (see chapter 6). Lastly, earlier studies hypothesized that avoidance in bats might be caused by aviation lights or turbulences originating from wind turbines (Barré et al., 2018; Gaultier et al., 2023). I did not investigate effects of light and turbulences, but it is unlikely that they explain the avoidance observed in my study system, because narrow-space foraging bats typically fly under the tree canopy which physically shields them from such impacts. In conclusion, although the effects of wind turbines are possibly multifactorial, noise emission is likely an essential driver. This is an important finding, because modern wind turbines are built increasingly larger to raise energy yields and noise emissions tend to increase at the same time, if no silencing adjustments are made (Hansen & Hansen, 2020; McKenna et al., 2016; Møller & Pedersen, 2011). Appropriate conservation measures should therefore be established without delay.

5.5 Conservation implications

Based on the findings of my thesis, there is clearly a need for forest-specific conservation measures and adapted siting guidelines to protect bats from negative effects where wind turbines are deployed in forests. Particularly, we need to take action to avoid that indirect habitat losses, which are caused when bats avoid wind turbine sites, may come to affect populations on a larger scale. To this end, it will be useful to apply the mitigation hierarchy for nature conservation which provides that environmental impacts are either avoided, mitigated, remediated or offset (Arlidge et al., 2018). Remediation means the restoration of biodiversity or ecosystems after the ceasing of an environmental impact and is outside the scope of my research. For the three remaining hierarchical levels, I summarize in the following which conservation measures can be inferred from my findings.

Avoiding impacts: To avoid indirect habitat loss for forest bats, wind turbines should be placed away from habitat structures where high bat activity can be expected. According to calculations for Germany, it would be possible to deploy all wind turbines needed to reach net-zero carbon dioxide emissions solely in open landscapes (Tafarte & Lehmann, 2023). However, countries with a higher forest cover may not be able to afford a complete exclusion of forest sites (Gaultier et al., 2020) and also in Germany the costs would be high. For example, collision risks of large raptors that mostly forage in agricultural landscape (e.g., *Milvus milvus*) would increase as well as the probability for conflicts with residents (Spatz et al., 2022; Tafarte & Lehmann, 2023). In contrast, the costs of a partial forest ban, e.g., by permitting wind turbine deployments only in coniferous forests, might be acceptable (Tafarte & Lehmann, 2023). However, in my study area I did not find bat activity to be significantly different between predominantly deciduous and predominantly coniferous forests which is in line with a study comparing forest monocultures to mixed deciduous forests (Buchholz et al., 2021). Consequently, a general exclusion of only deciduous forests would be too simplistic. Alternatively, high vertical vegetation heterogeneity, which I found to be strongly positively correlated to local bat activity, could be a useful tool to identify forest areas with high habitat value for bats. To apply this measure to the larger scale, e.g., Germany, remote sensing data such as LiDAR data could be used to infer vertical structural diversity of forests (Zimble et al., 2003). Remote sensing techniques are already used to make large-scale predictions on species richness in forests (e.g., Wallis et al., 2017) and my findings imply that via the correlation with vertical vegetation heterogeneity they would enable predictions on bat activity levels as well. Once identified, forest areas with diversely structured vertical vegetation should be excluded as wind turbines sites. Since bat activity was overall higher in forest areas of high vertical vegetation heterogeneity, bats of all foraging guilds would benefit from an exclusion of such areas as wind turbine sites. On the one hand, indirect habitat loss for narrow-spacing foraging bats could be avoided. On the other hand, less collisions of high-risk species from the edge-space and open-space foraging guild can be expected when wind turbine deployments were effectively limited to forest areas of low bat activity.

Mitigating impacts: In my studies, I found that wind turbine size, operation mode and most likely noise emissions can influence bat activity and avoidance towards turbines. An adjustment of these wind turbine parameters could achieve the mitigation of indirect habitat loss for narrow-space foraging bats in the area of forest wind turbines. For example, wind turbines with small rotors might have a lesser negative impact on bats than wind turbines with large rotors. However, wind turbines with larger rotors usually also have higher towers and are equipped with more modern technology than wind turbines with small rotors. These correlations are a challenge for designing effective mitigation measures as desired results might be missed as long as the actual mechanism linking turbine size to bat activity remains unknown. Therefore, it might be more reasonable to limit the operation of wind turbines to times of low bat activity. This can be achieved with algorithms which predict bat activity levels based on variables like wind speed, month, and time of night, and autonomously curtail wind turbine operation when predicted bat activity passes a threshold (Behr et al., 2017). In Germany, curtailment algorithms have been implemented since 2015 and effectively reduced collision numbers of bats with wind turbines (Adams et al., 2021; Behr et al., 2017; Whitby et al., 2021). It is however questionable how well currently employed curtailment algorithms can predict activity levels of narrow-space foraging bats, which fly close to ground, as they assess bat activity at hub height with a focus on high-collision risk species. Therefore, curtailment algorithms might need to be adjusted to serve the new purpose of mitigating indirect loss of forest habitat for narrow-space foraging bats. Lastly, reducing noise emissions of wind turbines may mitigate negative effects on bats. This can be achieved by technical adjustments that make wind turbine operation quieter in terms of mechanical noise, e.g., with drivetrain dampers, and aerodynamic noise, e.g., with trailing edge brushes or pointed blade tips (Deshmukh et al., 2019; Hansen & Hansen, 2020; Xu et al., 2021).

Offsetting impacts: If not possible to avoid or mitigate displacements of narrow-space foraging bats, the area of indirect habitat loss should be offset by elsewhere setting aside forest areas which are suitable as bat habitats. Ideally, the size of the compensatory forest area should be measured according to the size of the lost habitat. According to my findings, narrow-space foraging bats avoided wind turbines over at least 450 m distance. However, since this was the entire length of the recording transect, we cannot know if bats are affected over even greater distances. Indeed, there is evidence that narrow-space foraging bats still can be affected at a one-kilometre distance from wind turbines (open landscapes: Barré et al., 2018; forests: Gaultier et al., 2023). Therefore, compensatory forest areas with a radius of one kilometre or more might be necessary to completely offset the indirectly lost habitat around a one wind turbine. Yet, in countries like Germany, where forests are heavily fragmented (Mann et al., 2023), implementing forest compensations on this scale may be unrealistic. Consequently, conservation measures to avoid or mitigate wind turbine impacts on bats should be preferred.

Although scientific studies often concentrate on single species for practical reasons, biodiversity and its conservation should be considered holistically as all components are intertwined. In this thesis, I recommend conservation measures for the protection of bats against adverse effects of wind turbines in forests. However, the recommended conservation measures will benefit a number of species which are usually not assessed for wind energy projects but may still be negatively affected. Specifically, the exclusion of richly structured forests as wind turbine sites will ultimately conserve these habitats for a range of species that thrive at places of high vertical vegetation heterogeneity, e.g., songbirds (Rehling et al., 2023) and arthropods (Knuff et al., 2020). In this way, bats can serve as umbrella species for forest biodiversity. Further, the reduction of noise emission could benefit other disturbance sensitive animal species such as the black stork (*Ciconia nigra*; Rosenvald & Lõhmus, 2003). In conclusion, the consideration of negative effects on bats and appropriate conservation measures may indeed contribute to designing a more biodiversity-friendly wind energy sector.

Chapter 6: Research perspectives

The wind energy sector is expanding worldwide and in more and more countries wind turbines are deployed in forests which has consequences for forest biodiversity (Schöll & Nopp-Mayr, 2021). My thesis revealed that bats are negatively affected by wind turbines in forests, but it also demonstrated that important pieces of knowledge about how wind turbines affect bats are still missing. These knowledge gaps present promising starting points for future research, which I describe in the following.

My analyses based on bat foraging guilds (Denzinger & Schnitzler, 2013) showed that bats with different morphology and habitat use respond differently to wind turbines in forests. This is convenient for implications beyond the study area because the foraging guild concept is widely applicable and therefore findings for wind turbine effects on bat foraging guilds in Germany can be transferred to other parts of the world. This transferability is for example illustrated by research on bat activity at forest clearings, as studies conducted in Scotland (Kirkpatrick et al., 2017) and Japan (Maki et al., 2021) both found that open-space foraging bats are attracted to cleared spaces in forests. Analogously, narrow-space foraging bats in forests with wind turbines may be displaced across climate zones. Still, it would be worthwhile to compliment my results from temperate forests with studies in other climate zones, e.g., in countries of the global south, where knowledge on the wind energy-wildlife conflict is overall scarce.

Additional research needs to be conducted to understand the exact mechanisms that lead to an avoidance of forest wind turbines by bats and to subsequently be able to infer concrete conservation measures including specifications of thresholds and spatial scales. First, we need to ask over what distances narrow-space foraging bats are displaced by wind turbines. To this end, studies will be necessary that investigate bat activity over distances of more than kilometre from wind turbines, which is the maximum at which displacement effects on bats have been considered and found so far (Barré et al., 2018; Gaultier et al., 2023). Countries in North America or Scandinavia offer suitable study sites for such large-scale studies as forests areas are large enough and already contain wind turbines (Gaultier et al., 2020; Xiarchos & Sandborn, 2017). Further, it be will important to determine if and until what distances from wind turbines bats are affected in terms of roosting and reproducing. This data may inform us over what distances wind turbine effects on bats are ecologically relevant and may be helpful to establish exclusion zones and offset forest areas of reasonable minimum sizes. To this end, investigations on the use of available bat roosts and on reproduction rates in different distances to wind turbines will be helpful. First, catches with mist nets should be performed to quantify the number of reproductive bats and juveniles at a given sampling distance (Battersby, 2014; Hurst et al., 2020). Second, the tracking of reproductive female bats fitted with radio or GPS transmitters may enable the localisation of bat roosts and in particular maternity roosts in the proximity of wind turbines (Battersby, 2014; Hurst et al., 2020). Additionally, transect walks with ultrasonic bat detectors can reveal the location of mating roosts where typical social calls are emitted (Battersby, 2014; Hurst et al., 2020).

Future studies should look more closely at the role of wind turbine noise emissions in repelling bats. As a first step, we should aim to prove that bats directly react to wind turbine noise exposure and investigate how this is influenced by sound pressure level. Here, studies showing that bats avoid traffic noise playbacks (Schaub et al., 2009) or that birds modify their call structure in the presence of wind turbine noise playbacks (Szymański et al., 2017; Zwart et al., 2016) can serve as an inspiration. In a second step, we should ask until what distance from wind turbines noise emissions are likely to affect bats. This question is best addressed under controlled conditions to exclude impacts of other noise sources. Inspired by another playback study on traffic noise (Siemers & Schaub, 2011), bats could be treated with simulations of wind turbine noise as perceived at increasing distances to wind turbines. It should be noted, however, that under natural conditions the perceptibility of noise is influenced by factors such as vegetation, wind speed and wind direction (Heimann, 2018; Katinas et al., 2016). Insights from wind tunnel measurements could help designing realistic wind turbine noise playbacks at different distances and wind conditions (e.g., Boorsma & Schepers, 2017).

Moreover, the role of trophic interactions in displacing bats in forests with wind turbines needs to be clarified. All bats in Hesse are insectivorous and their activity is therefore related to insect abundance (Bender & Hartman, 2015; Dietz & Kiefer, 2014). Wind turbines could influence the bat-insect interactions, e.g., on the one hand, when insects swarming at wind turbines attract foraging bats which may lead to collisions with the rotor blades (Foo et al., 2017; Jansson et al., 2020). On the other hand, insects have been found to die in large numbers at wind turbine rotors (Trieb, 2018). Consequently, it is conceivable that wind turbine sites are biodiversity sinks and that the surrounding forest areas may become depleted of flying insects (Voigt, 2021). In this case, reduced prey availability close to wind turbines could be an additional driver for bats to avoid these areas. Accordingly, we would be able to see a positive correlation between bat activity and insect abundance at different distances to wind turbines.

Finally, observations from the tropics suggest that prey abundance in proximity of wind turbines could increase when their predators are displaced from the area and trophic control is reduced (Thaker et al., 2018). Accordingly, we would see a negative correlation between bat activity and insect abundance, with most bat activity far from turbines and most insect abundance close to turbines. In my study area, malaise traps were attached at 80 m and 450 m distance to wind turbines to sample arthropod biomass in June and July 2020 and 2021. A preliminary analysis of the data showed that arthropod biomass tended to increase with distance to wind turbines (Fig. 6). This could hint towards prey availability as one driver for bats avoiding wind turbines, however there is still no evidence of a correlation with bat activity. Therefore, for future studies a methodology should be conceived which allows sampling of insect biomass parallel to bat monitoring in a way that data from both groups can be investigated for correlations. For example, this could be achieved with suction traps which can be programmed to operate during a certain time slot only (de Jong et al., 2021).

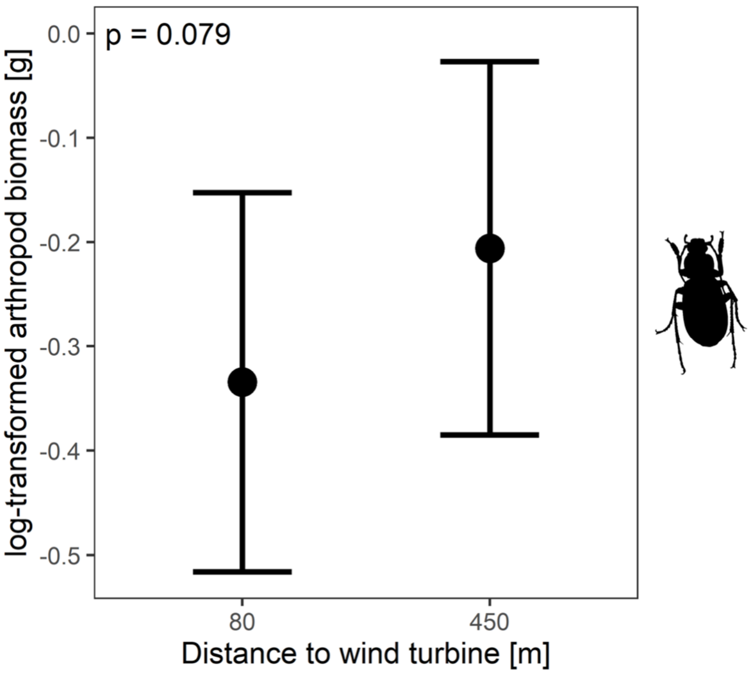

Fig. 6: Result of a preliminary study on arthropods in forests with wind turbines. *Mean estimates (dots) and 95% confidence intervals (bars) of arthropod biomass at close (80 m) and far (450 m) distance from wind turbines in forests.*

In conclusion, research targeted on wind turbine noise emissions and altered trophic interactions as potential causes for wind turbine avoidance by bats as well as consequent effects on reproduction rates should be conducted. Such research will not only advance our understanding of how bats are affected by wind turbines in forests, it will hopefully also allow us to establish concrete conservation actions that safeguard bats from adverse effects. However, time is pressing as according to recent German and European laws new wind energy priority areas are to be designated soon (Gesetz zur Erhöhung und Beschleunigung des Ausbaus von Windenergieanlagen an Land, 2022; Council Regulation Laying down a Framework to Accelerate the Deployment of Renewable Energy, 2022). Therefore, it is of uttermost importance to identify forest areas most valuable for forest bats and prevent them from falling within the area of influence of wind turbines. In this context, studies determining over what spatial scale wind turbine effects have an ecologically relevant effect on bats, e.g., regarding reproduction rates, should be prioritized.

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Appendix Chapter 2

Table S1: *Comparison of AIC values for null models and full models and marginal R^2 for each foraging group.*

Subset	Null model AIC	Full model AIC	Delta AIC	R^2 full model
Open-space foragers	2983.2	2855.2	128	0.60
Edge-space foragers	6586.7	6363.3	223.4	0.64
Narrow-space foragers	4082.1	3922.0	160.1	0.52

Table S2: *Results of subset analysis only for plots in deciduous forests. Estimates and p-values of the effects on call activity of three foraging guilds. Significant effects (p-value < 0.05) are shown in bold.*

		Open-space foragers		Edge-space foragers		Narrow-space foragers	
Variables	Df	Chi^2	p-value	Chi^2	p-value	Chi^2	p-value
turbine distance	1	1.1	0.299	0.1	0.754	5.9	**0.015**
recording level ‘canopy’	1	16.0	**< 0.001**	16.2	**< 0.001**	3.8	0.051
% conifers in forest	1	0.4	0.516	6.4	**0.012**	1.7	0.199
vertical vegetation structure	1	3.5	0.062	5.3	**0.021**	1.7	0.199
rotor diameter	1	1.4	0.243	0.1	0.833	2.3	0.132
canopy height	1	0.3	0.619	12.1	**< 0.001**	3.5	0.061
forest edge distance	1	0.0	0.979	0.1	0.758	4.9	**0.027**
sampling period	3	21.0	**< 0.001**	26.5	**< 0.001**	90.1	**< 0.001**
turbine distance x sampling period	3	6.0	0.114	2.4	0.497	14.6	**0.002**
turbine distance x rotor diameter	1	0.1	0.803	0.1	0.736	6.7	**0.010**

Table S3: *Results of subset analysis only for sampling points at 250 m and 450 m distance from wind turbines. Estimates and p-values of the effects on call activity of three foraging guilds. Significant effects (p-value < 0.05) are shown in bold.*

		Open-space foragers		Edge-space foragers		Narrow-space foragers	
Variables	Df	Chi^2	p-value	Chi^2	p-value	Chi^2	p-value
turbine distance	1	0.4	0.515	0.1	0.761	6.0	**0.015**
recording level 'canopy'	1	9.0	**0.003**	16.2	**< 0.001**	0.7	0.390
% conifers in forest	1	5.0	**0.026**	1.5	0.216	1.3	0.249
vertical vegetation structure	1	1.3	0.247	6.5	**0.011**	1.6	0.211
rotor diameter	1	1.0	0.311	0.0	0.973	2.6	0.114
canopy height	1	0.1	0.730	9.4	**0.002**	0.6	0.435
forest edge distance	1	0.0	0.945	2.5	0.113	1.2	0.270
sampling period	3	42.1	**< 0.001**	19.1	**< 0.001**	27.4	**< 0.001**
turbine distance x sampling period	3	6.9	0.076	0.9	0.821	6.4	0.096
turbine distance x rotor diameter	1	0.0	0.835	0.2	0.668	0.02	0.880

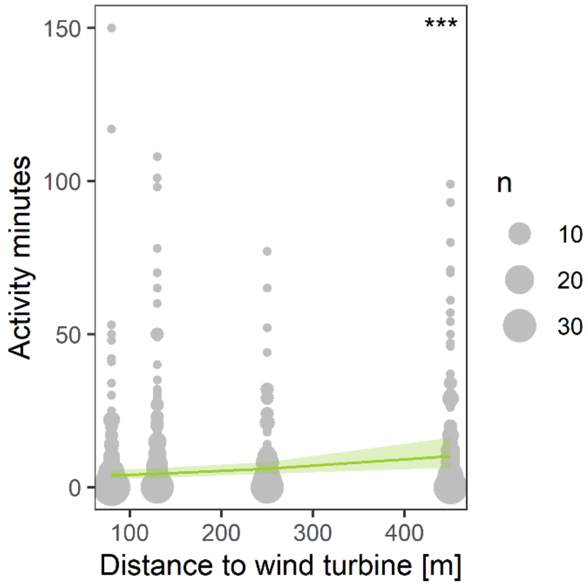


Figure S1: *Effect (line) and 95%-confidence interval (shade) of wind turbine distance on activity of narrow-space foragers. Raw data is shown in grey and asterisks denote the significance level of effects (*** <0.001 < ** <0.01 < * <0.05 <n.s.).*

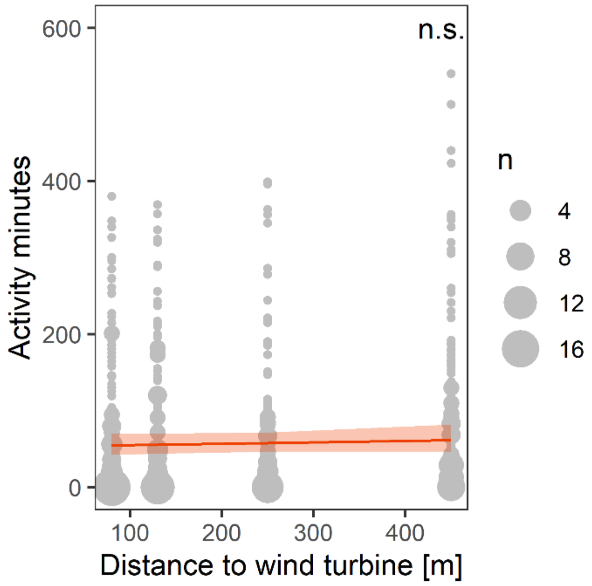


Figure S2: *Effect (line) and 95%-confidence interval (shade) of wind turbine distance on activity of edge-space foragers. Raw data is shown in grey and asterisks denote the significance level of effects (*** <0.001 < ** <0.01 < * <0.05 <n.s.).*

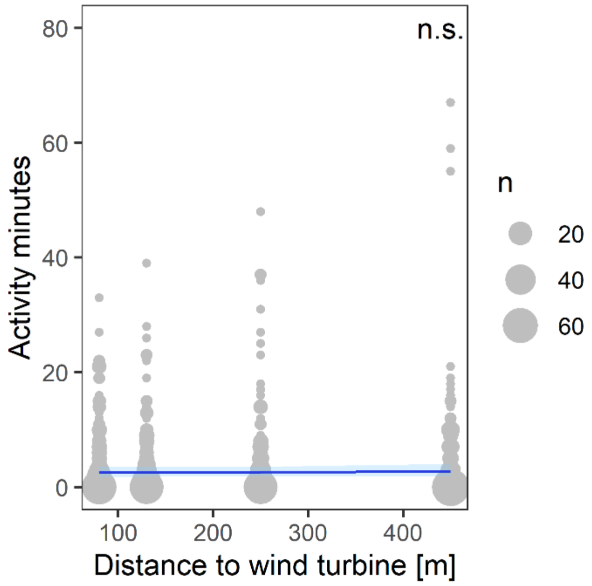


Figure S3: *Effect (line) and 95%-confidence interval (shade) of wind turbine distance on activity of open-space foragers. Raw data is shown in grey and asterisks denote the significance level of effects (*** <0.001 < ** <0.01 < * <0.05 <n.s.).*

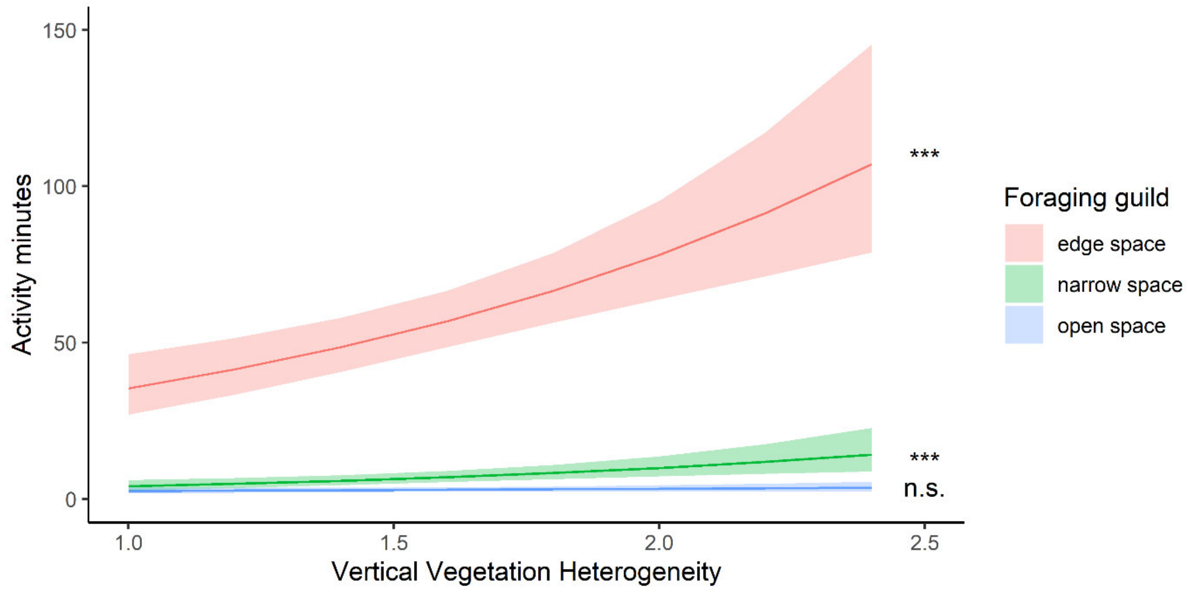


Figure S4: *Effects (lines) and 95%-confidence intervals (shades) of vertical vegetation heterogeneity on activity of three foraging guilds. Asterisks denote the significance level of effects (*** <0.001 < ** <0.01 < * <0.05 <n.s.).*

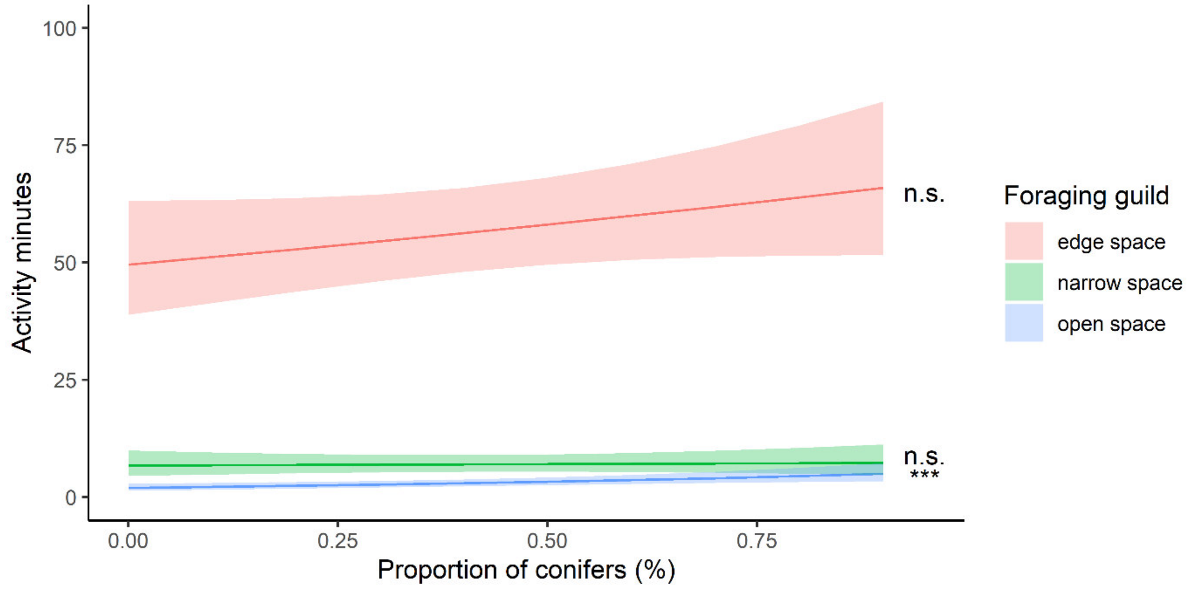


Figure S5: *Effects (lines) and 95%-confidence intervals (shades) of tree composition on activity of three foraging guilds. Asterisks denote the significance level of effects (*** <0.001 < ** <0.01 < * <0.05 <n.s.).*

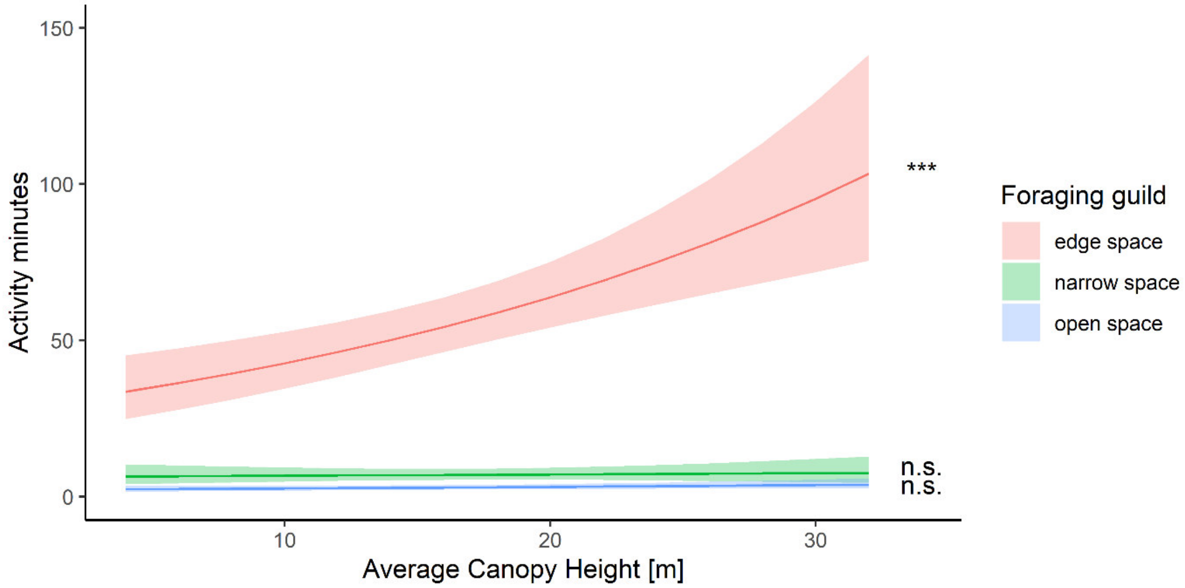


Figure S6: *Effects (lines) and 95%-confidence intervals (shades) of tree height on activity of three foraging guilds. Asterisks denote the significance level of effects (*** <0.001 < ** <0.01 < * <0.05 <n.s.).*

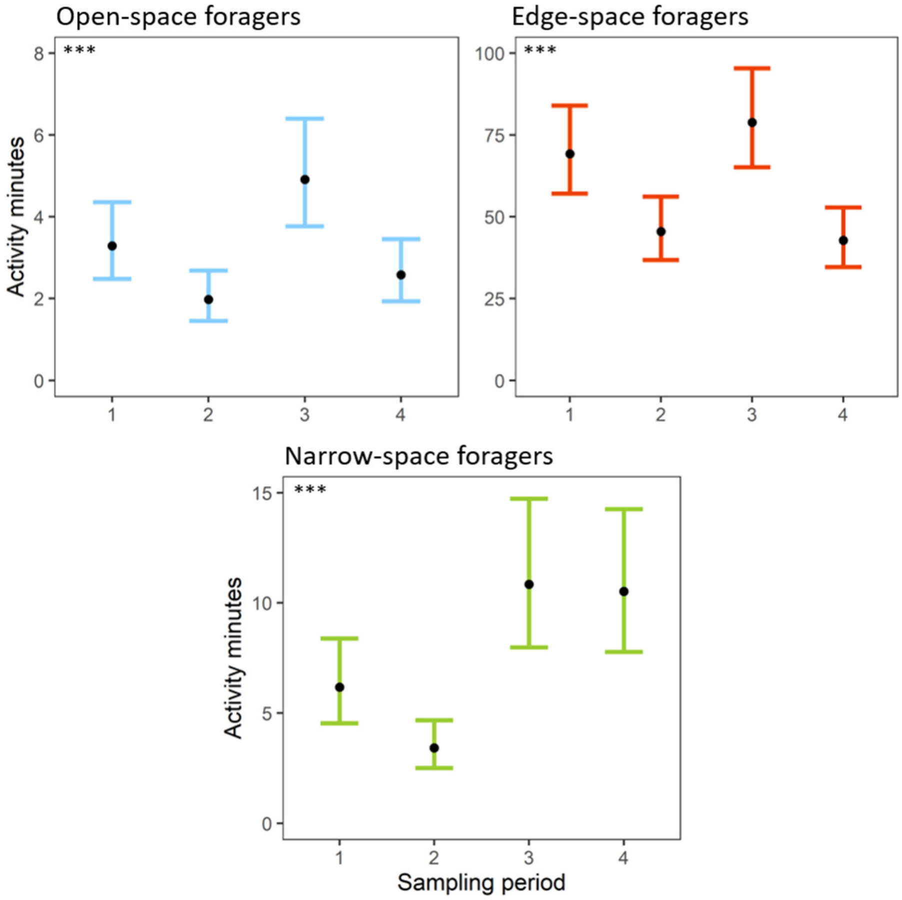


Figure S7: *Effects (points) and 95%-confidence intervals (lines) of sampling period (1=May/June, 2=June/July, 3=July/August, 4=August/September) on activity of three foraging guilds. Asterisks denote the significance level of effects (*** <0.001 < ** <0.01 < * <0.05 <n.s.).*

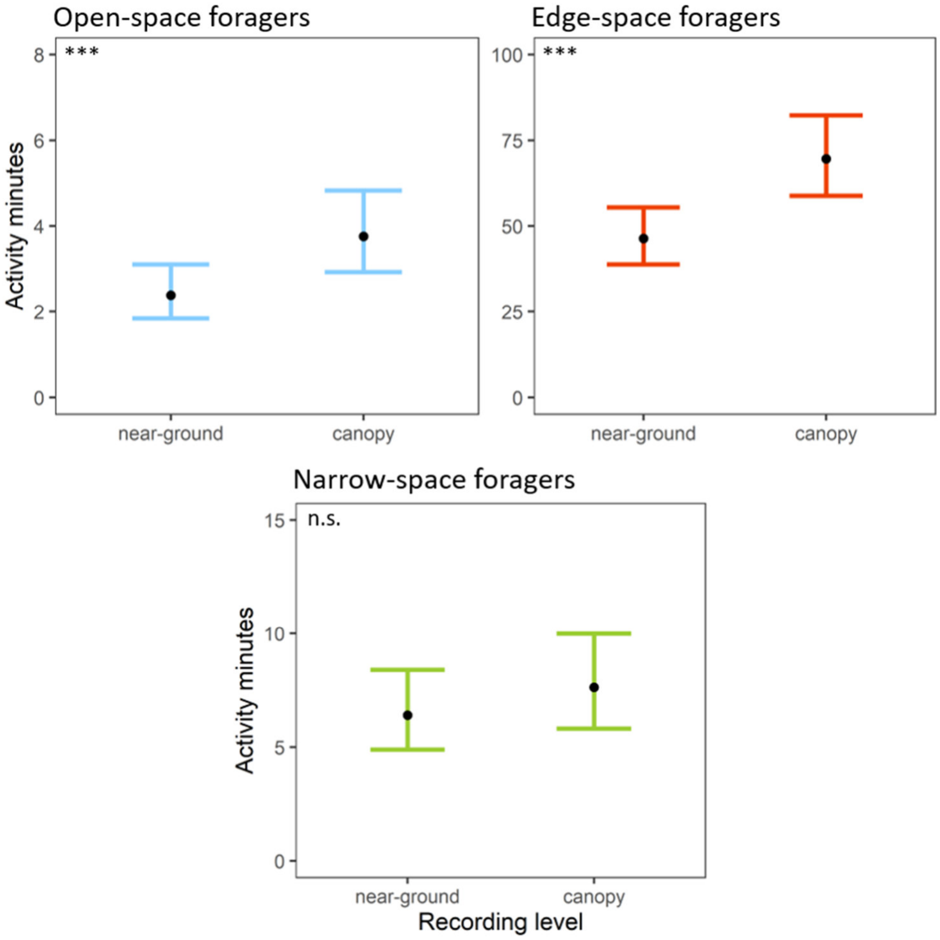


Figure S8: *Effects (points) and 95%-confidence intervals (lines) of recording level on activity of three foraging guilds. Asterisks denote the significance level of effects (*** <0.001 < ** <0.01 < * <0.05 <n.s.).*

Appendix Chapter 3

Supporting information A

Here, we present a detailed and reproducible description of our methodology.

1. Study area

Our study was conducted in Hesse, the federal state of Germany with the highest proportion of forests (42%; BMEL, 2016) and a total number of 472 of wind turbines within forests (Quentin & Tucci, 2022). The studied turbines were set up between year 2006 and 2018 (age at the time of field work: 6.3 ± 2.8 years, mean ± one standard deviation, hereafter) in forest of sizes ranging between 184 and 5,193 ha (median: 957 ha). We selected forests far from settlements or industrial areas and with low fragmentation by forest roads to minimize anthropogenic disturbances other than those caused by the turbines. Study sites were at least 3.5 km apart to avoid spatial autocorrelation of sampling points.

2. Sampling of bat calls and covariates

For recording of bat calls, ultrasonic recorders were set to a pre-trigger time of 500 ms, post-trigger time of 1,000 ms and recording intersection time of 20 s. We chose the CrestAdvanced trigger algorithm to enhance the recording probability of quiet calls and minimize sensitivity towards disturbing noise (Elekon AG, 2020). For recordings at the clearing, the microphone was attached at a height of 1.5 - 2 m to a vertical structure such as shrub, fence post or similar that was located as central as possible in the clear-cut area. Distance of clearing sampling points to wind turbines varied between 13 and 70 m (33 ± 15 m). For recordings at the forest edge, we chose a tree of representative height in the first row. We attached recorders just below the canopy at a height between 2.6 and 17.6 m (10.5 ± 4.2 m) to a tall vertical branch facing the forest clearing. The distance of forest edge sampling points from the wind turbine varied between 22 and 79 m (40 ± 15 m). For recordings above the closed forest, we attached the recorders to a branch at canopy height which ranged from 5 to 29 m (15.9 ± 6.9 m). We recorded four times at each sampling site, with a minimum of 19 and a maximum of 61 days (36 ± 13 days) between each recording.

Bat echolocation call activity could be influenced by wind turbine characteristics and environmental parameters. Therefore, we collected data on tower height, rotor diameter, and age of wind turbines (HLNUG, 2019) and measured the size of the clearcut area at wind turbines using aerial imagery (Google Ireland Limited, Dublin, Ireland).

3. Call analysis

Please consult main text.

4. Data analysis

We performed generalized linear mixed models (GLMMs) to assess influence of habitat and measured covariates on echolocation and foraging activity of bats. We analysed the data of each of the three foraging guilds separately, because contrasting activity levels prevented us from fitting all data in one model. We checked for multicollinearity between predictors and discarded wind turbine tower height and age as it was strongly correlated with rotor size. Furthermore, we discarded size of clearing around wind turbines as predictors, because GLMMs would identify a significant effect on bat activity which was, however, only driven by two plots with exceptionally large clearings. All continuous fixed factors were standardized with a z-transformation to enable comparability of estimates (Schielzeth, 2010). For each foraging guild, we then constructed binomial GLMMs (glmmTMB package; Brooks et al., 2017) with either number of activity minutes or presence-absence of feeding buzzes as dependent variable, with habitat and forest category as well as rotor diameter and its interaction with habitat as predictors (fixed factors) and with recording point nested in study site (random effect). Additionally, we added the month in which the recording took place as fixed factors to account for temporal autocorrelation. For every model we checked the model fit with help of the DHARMa package for residual diagnostics (Hartig, 2020) and, if necessary, added parameters to allow for varying dispersion within a predictor and specified data family. Predictor estimates and p-values were calculated with Wald-$\chi 2$-tests (car package; Fox & Weisberg, 2019). We used estimated marginal means (emmeans package, Lenth, 2021) to calculate p-values for the single levels of categorical predictors.

Supporting information B

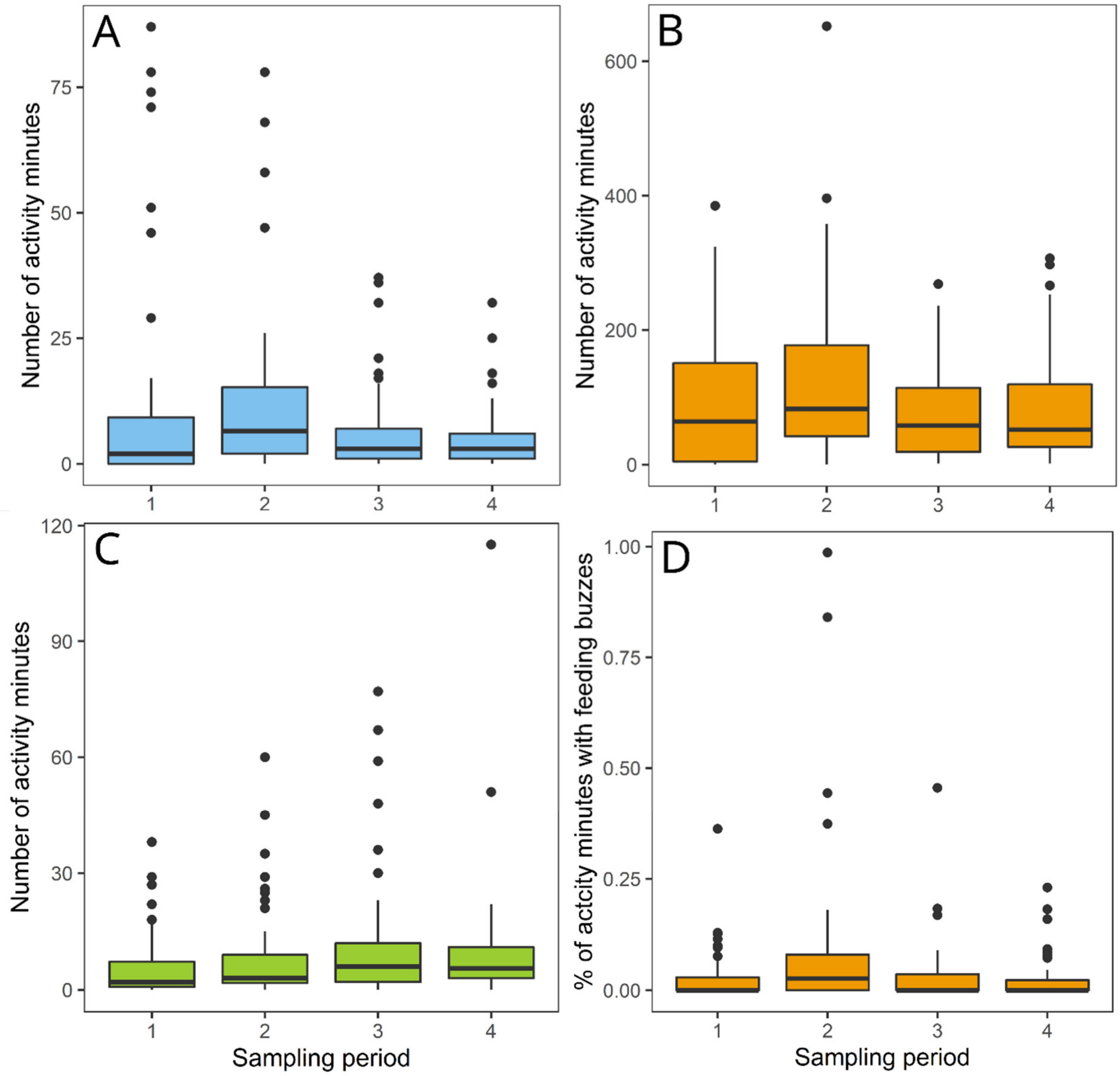


Fig. S1: *Temporal variation in the raw data of bat activity between foraging guilds. Panels A-C show bat echolocation activity for the (A) open-space, (B) edge-space and (C) narrow-space foraging guild. Panel D shows the foraging activity of edge-space foraging bats. Data for foraging activity of open-space and edge-space foraging bats was not sufficient to depict temporal variation. Sampling periods: 1 = May/June, 2 = June/July, 3 = July/August, 4 = August/September.*

Supporting information C

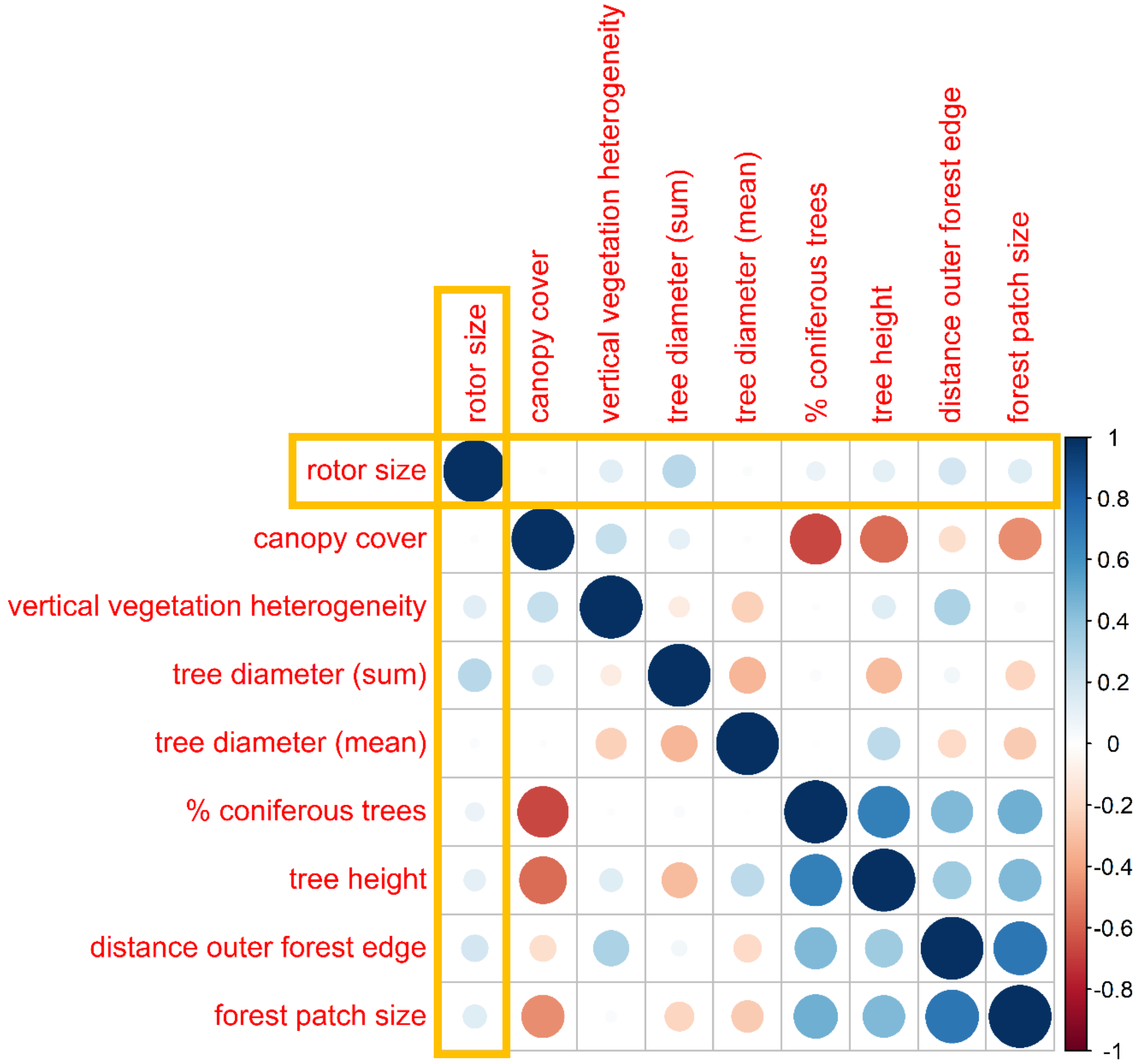
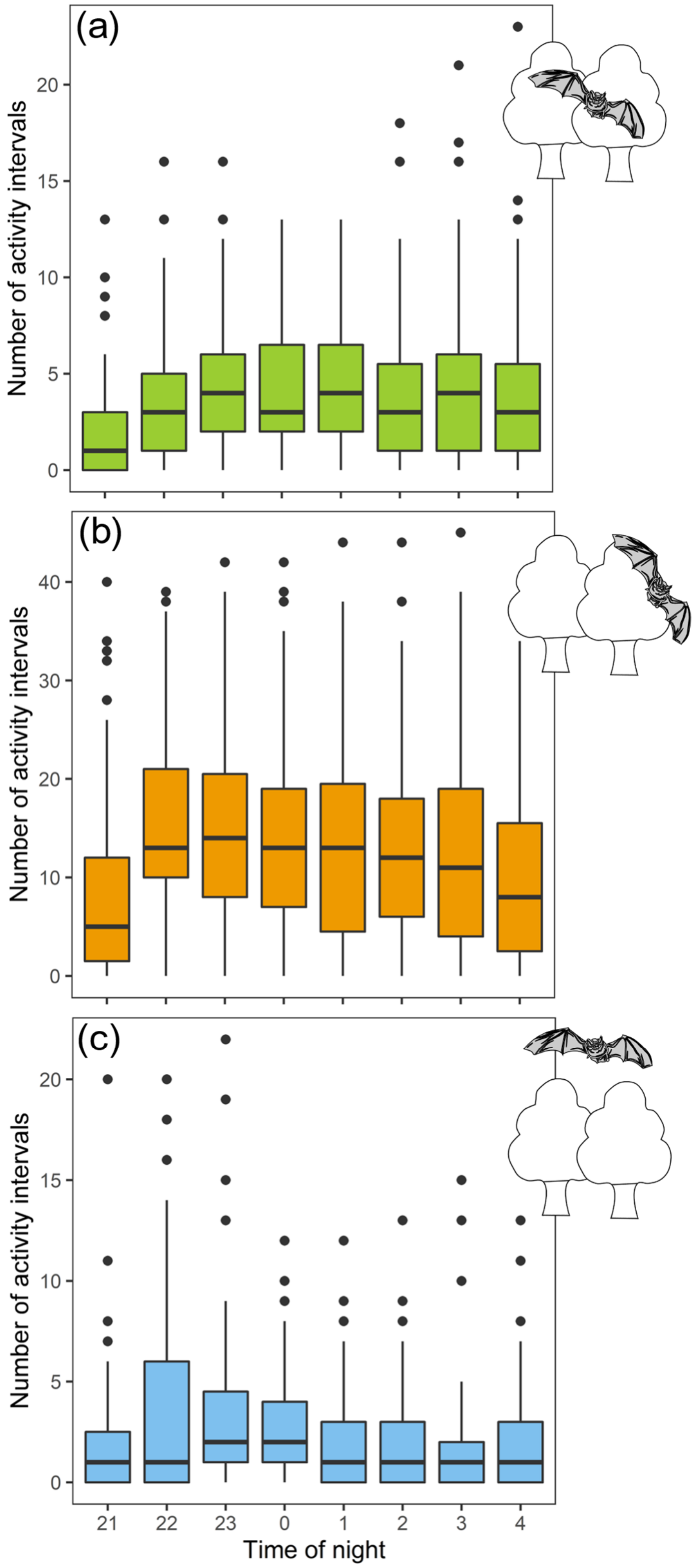
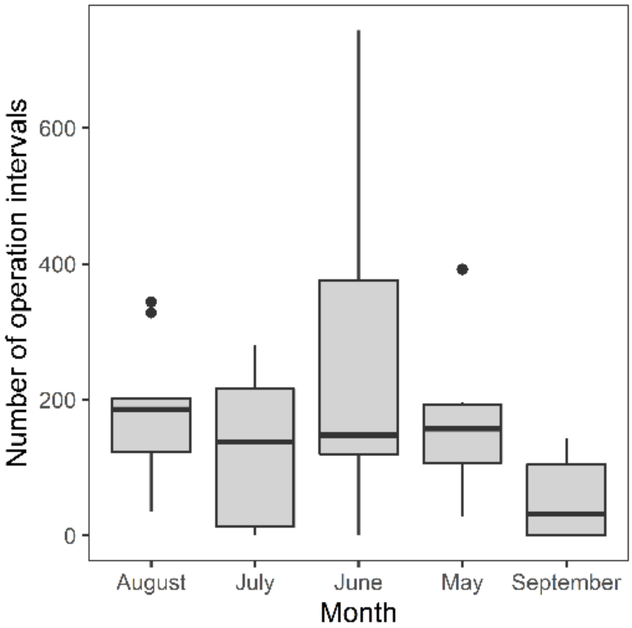


Fig. S2: *Correlation matrix showing dependencies of variables of the forest sites and the size of wind turbines, represented by rotor size (diameter).*

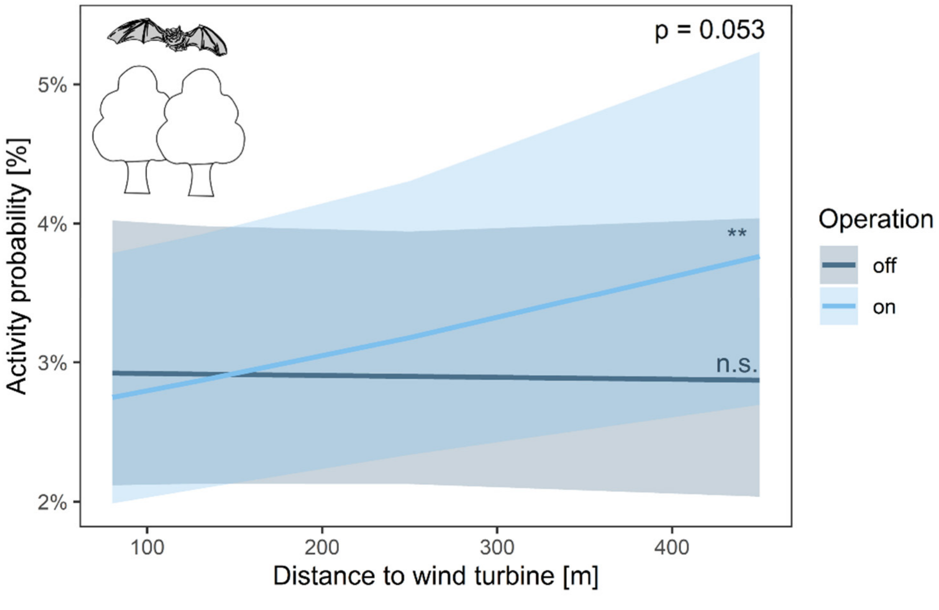
Appendix Chapter 4



Appendix S1: Recorded activity bats from three foraging guilds throughout the night. *Mean number (bars) and interquartile range (shades) of 10-min intervals with recorded activity of (a) narrow-space, (b) edge-space and (c) open-space foraging bats.*



Appendix S2: Recorded operation of wind turbines across sampling points throughout the year. *Mean number (bars) and interquartile range (shades) of recorded 10-min intervals with wind turbine operation.*



Appendix S3: Bat activity at increasing distance to operating and non-operating wind turbines. *Mean estimates (lines) and 95%-confidence intervals (shades) of activity probability in open-space foraging bats depending on distance to wind turbines at times of wind turbine operation ('on') and standstill ('off') in 10-min intervals of the night. Asterisks denote the significance level of the effect for different turbine operation modes (*** < 0.001 < ** < 0.01 < * < 0.05 < n.s.).*

Appendix S4: Comparison of AICc values and predictors of null, full and selected time series models for each foraging guild. *WT operation = wind turbine operation mode, WT distance = distance to focal wind turbine, wind speed = linear effect of wind speed, wind speed*^{2} *= quadratic effect of wind speed, temperature = air temperature, rotor size = diameter of wind turbine rotor, vegetation = vertical vegetation heterogeneity, time = time of night, wind direction = direction of wind in relation to orientation of recording transect.*

Bat foraging guild	Model	AICc	Variables
Narrow-space	Null	10109.77	*(1|night/plot) + ar1(time+0|night/plot)*
	Full	9988.796	*WT operation + WT distance + wind speed + wind speed*^{2} *+ temperature + rotor size + vegetation + wind direction + time + WT operation * WT distance + WT operation * wind direction + WT operation * wind speed + (1|night/plot) + ar1(time+0|night/plot)*
	Selected	9978.524	*WT operation + WT distance + wind speed + rotor size + vegetation + time + WT operation * wind speed + (1|night/plot) + ar1(time+0|night/plot)*
Edge-space	Null	46173.04	*(1|night/plot) + ar1(time+0|night/plot)*
	Full	46159.98	*WT operation + WT distance + wind speed + wind speed*^{2} *+ temperature + rotor size + vegetation + wind direction + time + WT operation * WT distance + WT operation * wind direction + WT operation * wind speed + (1|night/plot) + ar1(time+0|night/plot)*
	Selected	46150.73	*WT operation + WT distance + wind speed + rotor size + vegetation + time + (1|night/plot) + ar1(time+0|night/plot)*
Open-space	Null	7189.784	*(1|night/plot) + ar1(time+0|night/plot)*
	Full	7100.305	*WT operation + WT distance + wind speed + wind speed*^{2} *+ temperature + rotor size + vegetation + wind direction + time + WT operation * WT distance + WT operation * wind direction + WT operation * wind speed + (1|night/plot) + ar1(time+0|night/plot)*
	Selected	7094.697	*WT operation + WT distance + wind speed + temperature + rotor size + vegetation + WT operation * WT distance + (1|night/plot) + ar1(time+0|night/plot)*

Appendix S5: Results of full GLMMs at 10-min and nightly resolution. Estimates and p-values of the effects on call activity of three bat foraging guilds. *Significant effects (p-value < 0.05) are shown in bold. P-values of factors that were significant in the full model but not in the selected model or reversed are marked with red. Time of night and wind direction could not be assessed in the models for full nights (shaded).*

			Temporal resolution			
			10 min intervals		full nights	
Bat foraging guild	predictors	Df	Chisq	p-value	Chisq	p-value
Narrow -space	turbine operation	1	1.234	0.267	1.955	0.162
	turbine distance	1	104.647	**< 0.001**	16.349	**< 0.001**
	wind speed - linear	1	0.484	0.487	4.860	**0.027**
	wind speed - quadratic	1	0.000	0.989	0.082	0.774
	air temperature	1	0.012	0.912	6.564	**0.010**
	rotor diameter	1	10.722	**0.001**	8.901	**0.003**
	vertical vegetation heterogeneity	1	40.652	**< 0.001**	1.359	0.244
	wind direction	2	1.727	0.422		
	time of night	1	2.118	0.146		
	turbine operation x turbine distance	1	0.030	0.863	1.404	0.236
	turbine operation x wind direction	4	1.941	0.379		
	turbine operation x wind speed - linear	1	3.475	0.062	0.294	0.588
Edge-space	turbine operation	1	1.562	0.211	0.271	0.603
	turbine distance	1	13.665	**< 0.001**	1.957	0.162
	wind speed - linear	1	0.140	0.708	3.163	0.075
	wind speed - quadratic	1	0.076	0.783	0.001	0.974
	air temperature	1	0.439	0.507	4.963	**0.026**
	rotor diameter	1	3.616	0.057	2.752	0.097
	vertical vegetation heterogeneity	1	4.848	**0.028**	9.736	**0.002**
	wind direction	2	4.264	0.119		
	time of night	1	2.674	0.102		
	turbine operation x turbine distance	1	0.191	0.662	0.041	0.839
	turbine operation x wind direction	4	1.695	0.429		
	turbine operation x wind speed - linear	1	0.455	0.500	0.304	0.581

			Temporal resolution			
			10 min intervals		full nights	
Bat foraging guild	predictors	Df	Chisq	p-value	Chisq	p-value
Open-space	turbine operation	1	0.229	0.632	0.039	0.843
	turbine distance	1	3.217	0.073	1.758	0.185
	wind speed - linear	1	0.984	0.321	2.968	0.085
	wind speed - quadratic	1	0.074	0.785	0.000	0.999
	air temperature	1	17.579	**< 0.001**	20.024	**< 0.001**
	rotor diameter	1	3.938	**0.047**	1.361	0.243
	vertical vegetation heterogeneity	1	81.502	**< 0.001**	24.789	**< 0.001**
	wind direction	2	3.540	0.170		
	time of night	1	0.174	0.677		
	turbine operation x turbine distance	1	3.711	0.054	1.391	0.238
	turbine operation x wind direction	4	3.704	0.157		
	turbine operation x wind speed - linear	1	1.426	0.232	0.498	0.480

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Declaration/ Erklärung

Ich versichere, dass ich meine Dissertation mit dem Titel „Acoustic bat activity at wind turbines in temperate forests - Avoidance patterns and potential causes“ selbstständig ohne unerlaubte Hilfe angefertigt und mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfsmittel bedient habe.

Diese Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Marburg, den 16.06.2023

Julia Sophie Ellerbrok