

# WILDLIFE BIOLOGY

## Research article

## Wind energy development can lead to guild-specific habitat loss in boreal forest bats

Reed April McKay<sup>1</sup>✉, Sarah Elizabeth Johns<sup>1</sup>, Richard Bischof<sup>1</sup>, Fiona Mathews<sup>2</sup>, Jeroen van der Kooij<sup>3</sup>, Natalie Yoh<sup>4,5</sup> and Katrine Eldegard<sup>1</sup>

<sup>1</sup>Norwegian University of Life Sciences, Environmental Sciences and Natural Resource Management, Ås, Norway

<sup>2</sup>School of Life Sciences, University of Sussex, Falmer, Brighton, UK

<sup>3</sup>Nature Education, Research and Consultancy van der Kooij, Slattum, Norway

<sup>4</sup>The Nelson Institute for Environmental Studies, University of Wisconsin-Madison, Madison, WI, USA

<sup>5</sup>Durrell Institute of Conservation and Ecology (DICE), School of Anthropology and Conservation, Canterbury, UK

Correspondence: Reed April McKay ([reed.april.mckay@nmbu.no](mailto:reed.april.mckay@nmbu.no))

### Wildlife Biology

2024: e01168

doi: [10.1002/wlb3.01168](https://doi.org/10.1002/wlb3.01168)

Subject Editor: Patrick J. C. White

Editor-in-Chief: Ilse Storch

Accepted 27 October 2023



Forest management rarely considers protecting bats in Fennoscandian regions although all species rely on forest habitat at some point in their annual cycle. This issue is especially evident as wind parks have increasingly been developed inside Fennoscandian forests, against the advice of international bat conservation guidelines. In this study, we aimed to describe and explain bat community dynamics at a Norwegian wind park located in a boreal forest, especially to understand potential avoidance or attraction effects. The bat community was sampled acoustically and described using foraging guilds (short, medium, and long-range echolocators; SRE, MRE, LRE) as well as behavior (commuting, feeding and social calls). Sampling was undertaken at two locations per turbine: 1) the turbine pad and 2) a paired natural habitat at ground level, as well as from a meteorological tower. We used a recently developed method for camera trapping nocturnal flying insects synchronously with bat acoustic activity. Our results reveal trends in feeding and general bat activity across foraging guilds in relation to insect availability, habitat type, wind, temperature, and seasonality. We show how seasonal patterns in behavior across guilds were affected by habitat type, temperature, and wind. We found that SRE commuting and especially feeding activity was highest in natural habitats, whereas LRE overall activity at habitats more season dependent. We found that nocturnal insect availability was positively correlated with total bat feeding activity throughout the night. Our results provide evidence for both direct and indirect risks to bat communities by wind parks: SRE bat habitat is lost to wind energy infrastructure and LRE bat may have an increased risk of fatality. Our findings provide important insights on seasonal and spatial variability in bat activity, which can inform standardizing monitoring of bats acoustically in boreal forests, at wind parks, and in combination with non-invasive insect monitoring.

Keywords: acoustic monitoring, avoidance effect, bat - insect monitoring, boreal forest, foraging guilds, wind turbine



[www.wildlifebiology.org](http://www.wildlifebiology.org)

## Introduction

As Fennoscandian countries strive to meet zero-emission goals, there are high demands to use forests for renewable energy (Enevoldsen 2016, Searchinger et al. 2018, Neumann et al. 2022). Boreal forests play a vital role in supporting global biodiversity (Bradshaw and Warkentin 2015) and sequestering carbon (Pan et al. 2011). In Europe, most of the boreal forest is in Fennoscandian countries where it dominates the landscape, covering 38–68% of the land area (Nordic Co-operation | Nordic Council and Nordic Council of Ministers. 2008, Framstad et al. 2013). Boreal forests are some of the most heavily exploited types of land-cover in these countries (Zhou et al. 2021). The rapid expansion of onshore wind energy infrastructure in Nordic countries in the Fennoscandian region (Norway, Sweden, Finland) is expected include substantial installation in forests (Högbom et al. 2021). Rehbein et al. (2020) found that large wind parks already overlap with key biodiversity areas such as forests, and will continue to be developed in such areas, in Fennoscandia. Wind energy development in the Nordic region has increased by 14% between 2005–2019 (Nordic Energy Research 2021) and, as of 2020, makes up 15% of total energy production (Nordic Energy Research 2021, Wråke et al. 2021). The Nordic Clean Energy Scenarios project (NCES) predicts that Nordic wind energy, will increase to as high as 65% of total energy production by 2050 (Wråke et al. 2021). The balance between managing forests for economic productivity, biodiversity and with consideration to carbon stocks requires a synergistic strategy to effectively balance the needs to industrial productivity and safeguarding ecological stability (Dinesen et al. 2021).

Wind energy infrastructure has the potential for direct, indirect, as well as cumulative adverse impacts on wildlife, especially bats (Laranjeiro et al. 2018). Both local populations and transient/migratory populations can be at risk from wind turbine development and operations (Kunz et al. 2007, Roscioni et al. 2013, Arnett et al. 2016). Wind energy may also affect predator–prey interactions (Rydell et al. 2010b, Voigt 2021). In spring and summer, the local movements of migratory bats may correspond with activity of high-flying insects (Reynolds et al. 2017), both of which can suffer mortality when colliding with or flying near turbines. Rydell et al. (2010b) and Jansson et al. (2020) provide arguments along with some evidence for the theory that a portion of the bat fatalities at wind turbines in Europe are caused by migrating bats feeding on insects during late summer and autumn migration. Residential populations of insects and bats at the ground level will have their habitat radically changed by the development of turbines, especially in forest. In some cases, the development of turbines may improve the habitat suitability for species that thrive in open or edge environments (Kirkpatrick et al. 2017). Such development can also displace species that require forest cover and/or are sensitive to the sounds and presence of turbines by degrading the habitat, resulting in broad cascading effects (Barré et al. 2018, Roemer et al. 2019). Ellerbrok et al. (2022) and Gaultier et al.

(2023) both recently found that bats, especially those adapted to flying in cluttered habitat, were deterred by the presence of wind turbines in northern Europe. These studies emphasize the importance of acknowledging habitat loss from wind turbines as a risk to bats. However, neither study evaluated how bat behavior i.e. feeding activity, may be influenced by the presence of wind turbines differently from overall activity. Furthermore, the studies were not designed to distinguish if the observed effects were from sound/noise disturbance or habitat degradation. Understanding the specific drivers of wind turbine effects on bats is essential for making informed decisions regarding mitigation as well as the placement and development of energy infrastructure.

Norway, Sweden, and Finland are all member states of EUROBATs, an extension of the Convention on the Conservation of Migratory Species of Wild Animals (Bonn Convention; CMS), and The Agreement on the Conservation of Populations of European Bats. EUROBATs has provided a series of publications informing best practices in bat monitoring, management, and conservation for party states to follow as guidelines. Rodrigues et al. (2015) describes the most recent EUROBATs guidelines for monitoring bats for wind energy projects which include recommendations for pre- as well as post-construction monitoring and mitigation measures at wind parks. Unfortunately, there are many examples of party states failing to follow these guidelines (Barré et al. 2022). A resolution to the EUROBATs guidelines for managing bats in relation to wind parks has since been published which urges parties to implement national bat monitoring programs at wind parks in accordance with the existing guidelines, and that the guidelines will be updated to reflect advances in research and conservation practices since 2015 (EUROBATs 2022). Bat species associated with boreal regions are expected to be the most impacted by climate change (Jones and Rebelo 2013) and many European migratory bat species ranges are predicted to move northward in response to climate change (Rebelo et al. 2010). The Fennoscandian and Baltic countries are especially limited in this capacity with little to no monitoring of bats at wind parks (Gaultier et al. 2020), in part due to knowledge gaps in general bat ecology and how to implement broadscale monitoring programs in this region. Addressing such knowledge gaps through developing international bat conservation strategies in Fennoscandian boreal regions is critically important for conserving European mammalian biodiversity.

There are national bat monitoring guidelines for most EUROBATs party states (Battersby 2010, Barova and Streit 2018). Effective monitoring to evaluate bat populations on a large scale require a variety of surveys but increasingly acoustic monitoring is becoming an integral tool. Acoustic monitoring of bats has rapidly advanced in the last few decades, as the technology available for collecting and analyzing bat calls becomes more sophisticated, affordable, and accessible (Sugai et al. 2019). Passive acoustic monitoring provides a non-invasive and standardizable means of monitoring wildlife over broad time and spatial scales and is expected to continue to expand in playing a vital role in how bats are monitored in

the future (Browning et al. 2021). Echolocating bats have a wide range of call types that can also be flexible in structure, such that the effectiveness of identifying bat species acoustically varies across taxa and is heavily influenced by recording conditions (Kershenbaum et al. 2016). An alternative to species level analysis of bat acoustic data is to categorize the passes into sonotype defined foraging guilds that group bat species based on similarities in their echolocation which tend to reflect morphological, taxonomic, and ecological traits (Aldridge and Rautenbach 1987, Denzinger and Schnitzler 2013, Frey-Ehrenbold et al. 2013, Müller et al. 2013, Froidevaux et al. 2016, Erasmy et al. 2021). We have combined manual acoustic analysis to species level with foraging guild categorizations and evaluated for behavior to capture complexity in the bat community while acknowledging the limitations of species level analysis.

We address knowledge gaps in the seasonal activity patterns and habitat use of bats in Fennoscandian boreal forest using acoustic monitoring and camera trapping to investigate differences in bat activity and behavior at a wind park located in a boreal forest. This study aims to 1) describe seasonal patterns in bat acoustic activity including response to

wind and temperature 2) compare bat acoustic activity (guild and behavior) between undeveloped ‘natural’ forest habitats and habitat modified by wind energy infrastructure (‘turbine pads’), and 3) test if prey availability was related to bat feeding activity. Our results are discussed in the context of future management and monitoring strategies for bats in boreal forests as well as at forested wind parks.

## Materials and methods

### Study area

Data were collected between 1 July and 29 September 2020 at BKW/Scanergy AS Marker wind park located in Ørje, Norway within Viken (Østfold) county (turbine 5 (North): 59°30'58.1"N, 11°43'12.1"E, turbine 12 (South): 59°27'52.7"N 11°45'15.8"E, Fig. 1). This period was selected because late summer and early autumn have been identified as peak period for bat fatalities at wind parks in northern Europe by several studies (Rydell et al. 2010a). We could only collect data over one field season due to a change in

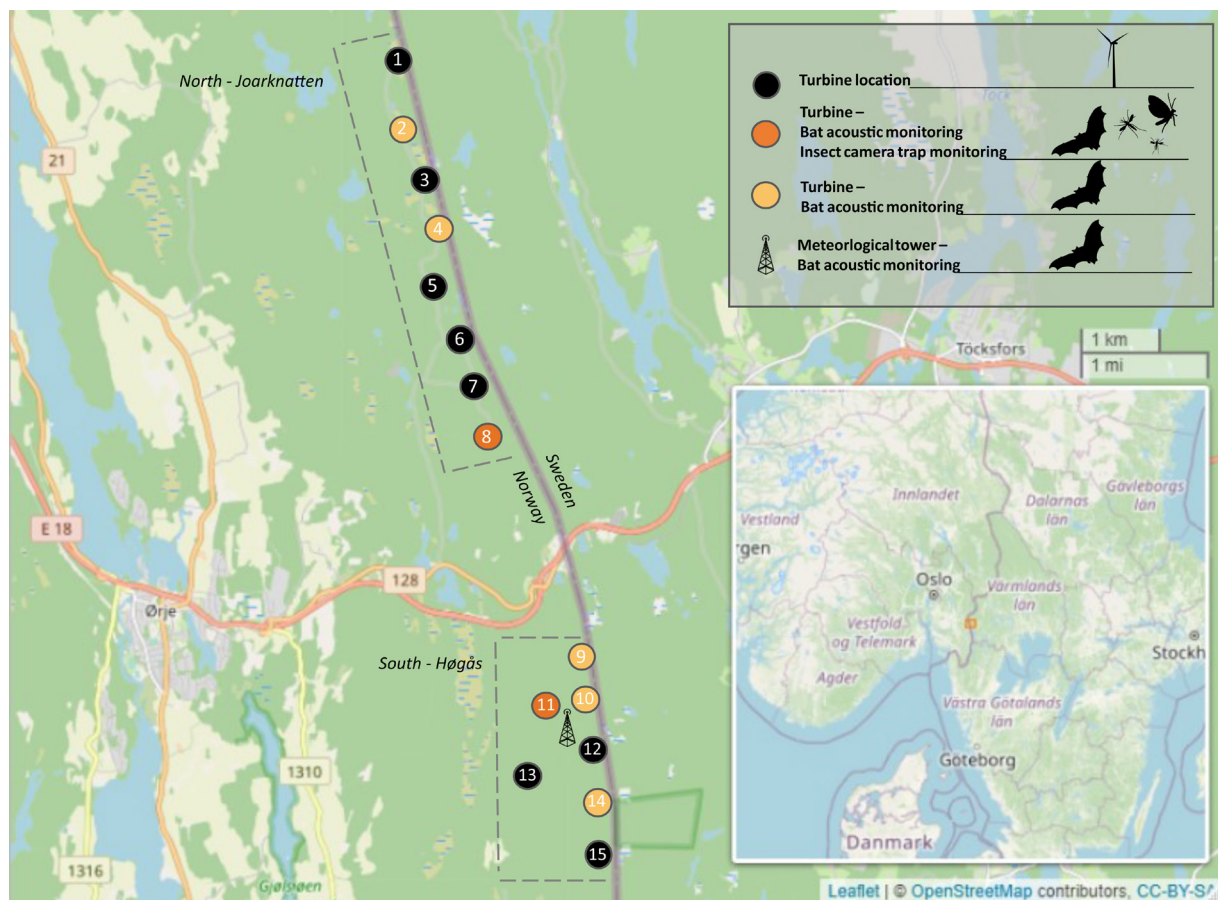


Figure 1. Map of Marker wind park in southeast Norway and the sampling locations. Internal map of the wind park in relation to Oslo, the capital of Norway. The thick gray line east of the wind turbines is the Norwegian – Swedish border. Thin, gray dashed line indicates the North (Joarknatten) and South (Høgås) facilities. The location of the meteorological tower is indicated in the south facility. Data collection was in the summer and autumn of 2020. Meteorological tower image: <https://www.pngwing.com/en/free-png-tacee>.



ownership of the wind park which entailed uncertainty and challenges around access to the wind park and weather data. Additionally, due to the COVID-19 pandemic, travel within Norway was made challenging and limited the ability to do field work.

The entire wind park in 2020 included 15 Vestas V136 3.6 MW turbines that are 142 m tall at the nacelle with 68 m long blades. The turbines are installed at two facilities, Joarknatten and Høgås, which we refer to as the north and south facility respectively (Fig. 1) and collectively as the wind park. Each turbine, within each facility, were between 500 m and 1 km apart. The distance between the two closest turbines from the north and south facility is approximately 3 km. The wind park and supporting infrastructure covers an area of approximately 8.6 km<sup>2</sup> of cleared land (Wiersdalen Karlsen 2017), located in a boreal production forest dominated by *Picea abies* and *Pinus sylvestris*, containing several small lakes and wetlands. The weather for this area during the summer and autumn is warm and mild, with average daily temperatures ranging between 7 and 20°C, with average monthly rainfall between 76–81 mm (<http://weatherspark.com>). Temperature and wind speed data were collected approximately once every 10 min from the nacelles of the turbines at the wind park throughout the study period and were made available for analysis.

### Bat acoustic monitoring

Bat acoustic monitoring took place from 1 July to 29 September 2020 at seven wind turbines (three in the northern facility and four in the southern facility; turbines 2, 4, 8, 9, 10, 11 and 14). Wildlife Acoustics Song-Meter4-BATFS detectors (hereafter detectors) combined with either SMM-U2 or SMM-U1 microphones (hereafter U2 or U1 microphones) were deployed at ground-level in pairs at 7 turbines (14 detectors in total) and two detectors were deployed a meteorological tower ‘at height’, above the forest canopy and within the rotor sweep zone.

At each turbine locality where bat acoustic monitoring took place (Fig. 1), two different habitat types were sampled: a turbine pad site and a natural habitat site. The turbine pad sites were located on crane auxiliary pads, between 45–110 m from the base of the nearest turbine. Each turbine was surrounded by a large, flat gravel pad that had been developed for installing and maintaining the turbine. Crane auxiliary pads, the location of turbine pad sites, were within or directly adjacent to the gravel pad surrounding turbines. Natural sites were closer to forest edge and sampled habitat that had not been physically altered by development and were located between 80 and 115 m from the base of the turbine. This design ensured that disturbance from light or sound produced by the turbines were as similar as possible between the two different habitat types. The design enabled us to quantify how changes in physical habitat due to development, regardless of light and sound disturbance, impacted the activity patterns and behavior of bats. At ground level detector sites, detectors were affixed to wooden poles approximately 2 m

high, with either U2 or U1 microphones. Turbine pads and natural sites at each turbine locality were monitored simultaneously. Ground level detector sites were monitored for 20 days out of every 30. The 7 turbines localities were split into two monitoring groups which had a 10 day overlap (turbines 2, 8 and 10 in one group, turbines 4, 9, 11 and 14 in the other) such that at least one turbine from both the northern and southern facility were actively being monitored.

Two detectors were deployed at height continuously between 16 July and 23 September on a meteorological tower (met tower detectors) located in the southern facility (Fig. 1). Both met tower detectors were deployed with U1 microphones oriented slightly upward and stationed at approximately 45 (sampling above the forest canopy, hereafter referred to as Met 45) and 95 (sampling within the turbine rotor sweep zone, Met 95) m high, directed toward north and east, respectively.

Detectors collected 16-bit resolution full spectrum .wav files, programmed to become active from one hour before sunset to one hour after sunrise, triggered to ultrasonic activity, with a 256 kHz sampling rate, 12 kHz minimum trigger frequency and maximum recording length of 15 seconds. Detectors were checked approximately once a week while deployed for regular maintenance checks and to collect data.

### Bat acoustic analysis

Bat acoustic data were processed using Kaleidoscope Pro (ver. 5.1.9i, Wildlife Acoustics). We defined a bat pass in the study as a recording which contained at least two pulses, with less than 1 second of separation between them (Fenton et al. 1973), otherwise files were classified as noise and not included in further analysis. All passes identified as ‘NoID’ by the classifier were treated as bat passes and manually analyzed. Bat pass duration varied between 2–15 seconds long. These recordings were then classified using the Bats of Europe Classifier (ver. 5.2.1) auto ID function. The species list was specified as only those species found in Norway according to the 2015 Norwegian Red List (Henriksen and Hilmo 2015), excluding *Eptesicus serotinus* (conservation status Not Applicable). In 2021, *Pipistrellus pipistrellus* was designated as ‘Not Applicable’ on the Norwegian Red List (Eldegard et al. 2021) and thus this species was reclassified as unknown pipistrelle species due to similarities in call structure with other *Pipistrellus* spp. (Montauban et al. 2021).

All bat passes were manually analyzed by one analyst (Author1, n=19 438). Forty-five passes were found to be noise files and were subsequently removed. During manual verification, bat passes were classified to two-tiers: 1) subguild or species level, following parameters from Russ 2021 and 2) guild-level. For guild-level analysis, we used three foraging guilds to describe the bat community: short range (SRE; grouping *Myotis* species, *Plecotus auritus*, *Barbastella barbastellus*), medium range (MRE, grouping *Pipistrellus* species), and long range echolocators (LRE; grouping *Eptesicus nilssonii*, *Vespertilio murinus*, *Nyctalus noctula*). Grouping species in this way provided a robust method for comparing trends

within foraging guilds which may encompass rarer species or species with overlapping call structures (Denzinger and Schnitzler 2013). We chose to identify bat passes to sub-guild, genus, or species to provide more detailed taxonomic data for forest management. Where a bat pass could not be assigned to species with confidence, these were classified into sub-guilds: *E. nilssonii* or *V. murinus* (LR1) and *V. murinus* or *N. noctula* (LR2), *Myotis* species (SR1), *Pipistrellus* species (MR1). Bat passes that were not feasible to classify confidently to any of these categories were classified as 'NoID'. Comparisons between the results of the manual acoustic analysis and the automatic acoustic analysis can be found in the Supporting information. Behavior was also recorded for each pass: commuting, feeding (feeding buzz), or social (Middleton et al. 2014, Russ 2021). Feeding buzzes were prioritized over social calls where both occurred such that a pass containing both would be categorized as a feeding pass but otherwise passes with social calls were classified as social passes.

### Insect camera trapping

Insect camera traps were deployed in pairs (combined with the bat acoustic natural and turbine pad sites) at one turbine locality in the north and one in the southern facility (turbines 8 and 11, respectively, Fig. 1) to monitor the abundance of flying insects. The camera trap survey period was paired with bat acoustic detectors between 16 July 2020–28 September 2020 however, due to equipment failures, sampling effort was uneven across sites (Supporting information). The camera traps were designed to closely follow the methods described in Ruczyński et al. (2020) and consisted of a digital camera (Ricoh WG-6 Waterproof 20 m / 65.6 ft; Model R02050 2019) oriented skyward, in protective water-resistant housing, attached to an external battery power source and programmed to take images (JPG, 5184 × 3888 pixels) every 10 min with flash. Only photographs taken between 2 h (accounting for differences in how the bat acoustic detectors calculated sunset and calculations in R) before sunset and 1 h after sunrise were included in the analyses such that the dataset was comparable with bat acoustic recordings. Photographs were manually annotated using VGG annotator (Dutta and Zisserman 2019) to identify the number of flying insects as well as to describe the quality of the photo (viable = high quality image or unviable = poor quality image). Insect abundance was quantified as the sum of insects identified in each image per night.

### Data preparation

We prepared seven datasets (Supporting information): 1) unaggregated bat passes for each site, 2) ground level nightly aggregated total summed bat activity per site 3) ground level nightly aggregated SRE bat feeding activity per site, 4) ground level nightly aggregated SRE bat commuting activity per site, 5) ground level nightly aggregated LRE bat feeding activity per site, 6) ground level nightly aggregated LRE

bat commuting activity per site, 7) insect abundance and total (all guilds) bat feeding (social and commuting passes excluded) activity combined aggregated to hour per site (only turbines 8 and 11, when both cameras and acoustic detectors were active) combined with weather data and, 8) insect counts and bat feeding passes per site per hour for turbines 8 and 11 when both cameras and acoustic detectors were active. Additional variables per detector location were included in all datasets such as detector site (14 ground level detector sites and 2 met tower detector sites, n = 16) and locality (7 turbines and one met tower locality, n = 8) as well as habitat type (turbine pad, natural or meteorological tower). Data from the meteorological tower was only included in dataset 1. The variable 'hours since sunset' was calculated for hourly aggregated data. The variable 'night' was created by adjusting the true date and time by 12 h centered at noon to conceptualize bat activity on a nightly scale. The variable Julian night was also included, which is the Julian day (the sequential number of the day in the year) applied to night rather than day.

For datasets 2–6 (nightly aggregated datasets), relevant bat activity was represented as the sum of bat passes per night per site. The nightly mean wind speed as well as temperature averaged across the whole wind park was included. Weather data were collected from the turbine nacelles approximately every 10 min, but there were missing hours or nights for some turbines, so weather data were aggregated, and the mean was taken across the whole wind park. For hourly and nightly aggregated datasets (2–8), zeroes values were inserted for nights when a detector or camera trap was present and functioning but did not record any bat or insect activity.

### Statistical analysis

We applied negative binomial generalized additive models (GAMs) with restricted ML (REML) using the R package 'mgcv' ver. 1.8-41 (www.r-project.org, Wood 2011) to model bat acoustic activity in response to habitat, temporal, and environmental variables. This model approach was selected to account for the non-linear patterns in seasonality that were detected in exploratory analyses, and which were too complex to be adequately captured by including second-order polynomials as predictors. A set of five different model groups were explored to explain patterns of total bat acoustic activity, SRE feeding, SRE commuting, LRE feeding and LRE commuting activity separately (Table 1). We analyzed these subsets of the data separately rather than fitting one complex model with several interaction terms, to make it easier to interpret model outputs, but also to improve model fit. The predictor variables for these models were: locality, habitat, the interaction between Julian night and habitat (allowed for separate shapes of relationships with Julian night for each habitat), mean nightly wind speed, and mean nightly temperature. Locality was treated as a random effect using a smooth ('re'). A Gaussian process smooth was applied to the interaction between Julian night and habitat to address temporal autocorrelation, and a thin plate regression spline smooth was applied to average nightly wind speed. Temperature was treated as a

Table 1. Model specifications for the generalized additive models of bat acoustic activity for total bat activity and four subsets of guild (short range and long range echolocators) – behavior (feeding and commuting) specific acoustic activity. The % zeroes (Z%) of the datasets, the total number of bat passes and insect counts for the datasets used in each model is also reported. For models Insect and Bats–Insects, % zeroes refer to the number of hourly detector hours for bat feeding passes and insect counts, respectively. Outputs for bat data models available in the Supporting information, insect model outputs in The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020.

Model	Response	Zeroes (%)	Bat passes	Feeding passes	Social passes	Insect counts	Dataset
Bats total	Sum bat passes per site per night (ground level only)	13	19 206	4034	547	NA	2
SRE feeding	Sum SRE feeding passes per site per night	84	327	32	0	NA	3
SRE commuting	Sum SRE commuting passes per site per night	31	3787	0	0	NA	4
LRE feeding	Sum LRE feeding passes per site per night	62	3703	3703	0	NA	5
LRE commuting	Sum LRE commuting passes per site per night	24	10 584	0	NA	NA	6
Insects	Sum feeding bat passes and insect count per site per night for each hour with weather data	94 and 87	372	372	NA	4546	7
Bats–Insects	Sum feeding bat passes per insect count per site per hour	94 and 87	373	373	NA	4563	8

linear fixed effect because it consistently had a positive linear effect on all bat activity. We used a tensor product interaction between temperature and wind speed for all model groups but this term either had little effect and contributed toward overdispersion in most models, so it was dropped.

To evaluate the relationship between insect counts per hour and weather throughout the season, we applied a negative binomial GAM with REML predicting the number of insect counts per hour in response to average hourly wind speeds and temperature, the night in the season, and locality as a random effect (Table 2, Insects). A thin plate regression spline was applied to wind, temperature, and a Gaussian process smooth to night in season (Julian night). There were hours when camera traps and acoustic detectors were active, but no weather data were available so seventeen insect counts and one bat feeding pass were excluded in this model. To predict the number of bat feeding passes per hour in response to insect availability, another negative binomial GAM with REML was fitted in response to a categorical binary insect count variable

(0 insects counted per site per hour = ‘No insects’, 1 or more insects counted per site per hour = ‘Insects active’), locality as a random effect and hour (hours since sunset) with thin plate regression spline smooth (Table 2, Bats–Insects).

We carried out model validation with the `gam.check` function to confirm that we had selected appropriate  $k$ -values and that the model fitted our data, inspecting standard graphical model validation plots. All data analysis was carried out in R ([www.r-project.org](http://www.r-project.org)).

## Results

### Bat pass classification

Bat acoustic data were collected over 950 detector nights across 91 nights and 16 detector site locations. A total of 19 438 passes across 56.5 h (mean bat pass length 10.8, SD 4.0 seconds) of recordings were manually verified. The LRE represented 76% of the total bat activity, of which *E. nilssonii*

Table 2. The relationship between insect activity, environmental conditions, and bat feeding activity. The Insects model expresses the relationship between the sum number of insects (per image per hour) and environmental variables throughout the season. The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020. Temperature and wind speed were nightly averages (mean). The Bats–Insects model explains the relationship between insect presence (0/1) and the number of bat passes (per hour per site) where hour is the hours since sunset. Confidence intervals (95%), both the upper (UCL) and lower (LCL) are reported for parametric terms.

Model	Variable	Estimate	SE	z	p	LCL	UCL
Insects	<i>Parametric terms</i>						
	(Intercept)	−0.372	0.668	−0.557	0.578	−1.68	0.937
	<i>Smooth terms</i>	Estimate	edf	X <sup>2</sup>	p		
	Wind speed	10.823	59	89.03	0.010		
	Locality	1.722	9	4.91	0.037		
	Temperature	5.248	9	62.50	< 0.001		
	Julian night	0.955	1	21.07	< 0.001		
Deviance explained: 25%							
Bats–Insects	<i>Parametric terms</i>						
	(Intercept)	4.50	0.746	−6.03	< 0.001	5.960	−3.04
	Insects active (binary)	1.61	0.393	4.09	< 0.001	0.838	2.38
	<i>Smooth terms</i>	Estimate	edf	X <sup>2</sup>	p		
	Hour (since sunset)	7.821	14	65.5	< 0.001		
	Locality	0.902	1	8.67	< 0.001		
	Deviance explained: 40.7%						

passes contributed 95%. Therefore, *E. nilssonii* represented 72% of total acoustic activity. SRE passes made up 21% of all bat passes, of which 86% were SR1 (*Myotis* species) passes. Only 0.5% of the passes were classified as MRE, with the remaining 2.5% classified as NoID bat passes. Therefore, MRE and NoID passes were excluded from guild specific analyses. Several species classified as threatened or near threatened on the Regional Red List for Norway were detected, including *B. barbastellus* (n = 10 passes), *Pipistrellus nathusii* (n = 9 passes), *N. noctula* (n = 182 passes) and *V. murinus* (n = 168 passes), LR2 (n = 221 passes). Passes of *B. barbastellus* and *P. nathusii* were validated by at least two external bat acoustic experts. Commuting, feeding, and social passes made up 76%, 21%, and 3% of the activity recorded, respectively (Fig. 2).

### Spatial and temporal patterns in bat activity

Bat activity varied across the season and across the different detector sites. Collectively both detectors at turbine 9 contributed approximately 41% of all bat activity recorded (Fig. 2). Bat activity increased from July and peaked between August and September for nearly all sites, then steadily declined for the rest of the season (Fig. 3). Across the study period, ground level detectors recorded a mean of 20 bat passes per night while the met tower sites collected an average 12 passes per night. The met tower sites collected only 232 bat passes in total: 197 passes from Met45 and 35 passes from Met95. Of these, 223 passes belonged to bats in the LRE guild, with one MRE pass, seven SRE passes, and one NoID pass also being recorded. The behavior most often recorded at the met tower was commuting activity (n = 217 passes), however there were feeding (n = 12), and social (n = 3) passes recorded from both

detectors (Fig. 3). Average nightly temperature and wind speeds had a strong influence on total bat activity at ground level sites (Supporting information). Ninety-two percent of bat activity recorded occurred when nightly average wind speeds were less than 12 m s<sup>-1</sup> and when temperatures were greater 10°C. We found that temperature had a strong positive linear effect on bat activity in all models tested but the effect of wind was more varied (Supporting information). Bat activity began to decline as wind speeds increased over 10 m/s but warmer average temperatures, bats were still active at higher wind speeds (Fig. 4).

When all bat activity was aggregated by night, we found no significant difference in average bat acoustic activity between natural and turbine pad habitats during the study period, but the shapes of relationships with Julian night differed between the habitats (Supporting information). However, when the bat activity was subset by guild and behavior, it was possible to see average differences in habitat use. SRE bat activity was higher at natural sites compared to turbine sites throughout the season and feeding activity was substantially higher at natural sites than at turbine pad sites (Fig. 5a–b). LRE bat commuting and feeding activity was dominant in both natural and turbine pad habitat types, though we found some evidence that LRE bats are more active at turbine pads than natural sites later into the season but were recorded more often at natural sites in early July (Fig. 5c–d).

### Relationship between bat activity and insect availability

We collected concurrent bat and insect activity data for 2041 h across 176 nights at the natural and turbine pad sites at



Figure 2. (a) Proportions of bat activity for behavior (dark gray=commuting, medium gray=feeding, light gray=social) for all detector sites, for the entire sampling period pooled. (b) An overview of total bat passes recorded for the entire study period by guild for each site. Foraging guilds: Short range echolocators (SRE, blue), medium range echolocators (MRE, yellow), long range echolocators (LRE, red) and unidentified bat (NoID, gray). The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020..



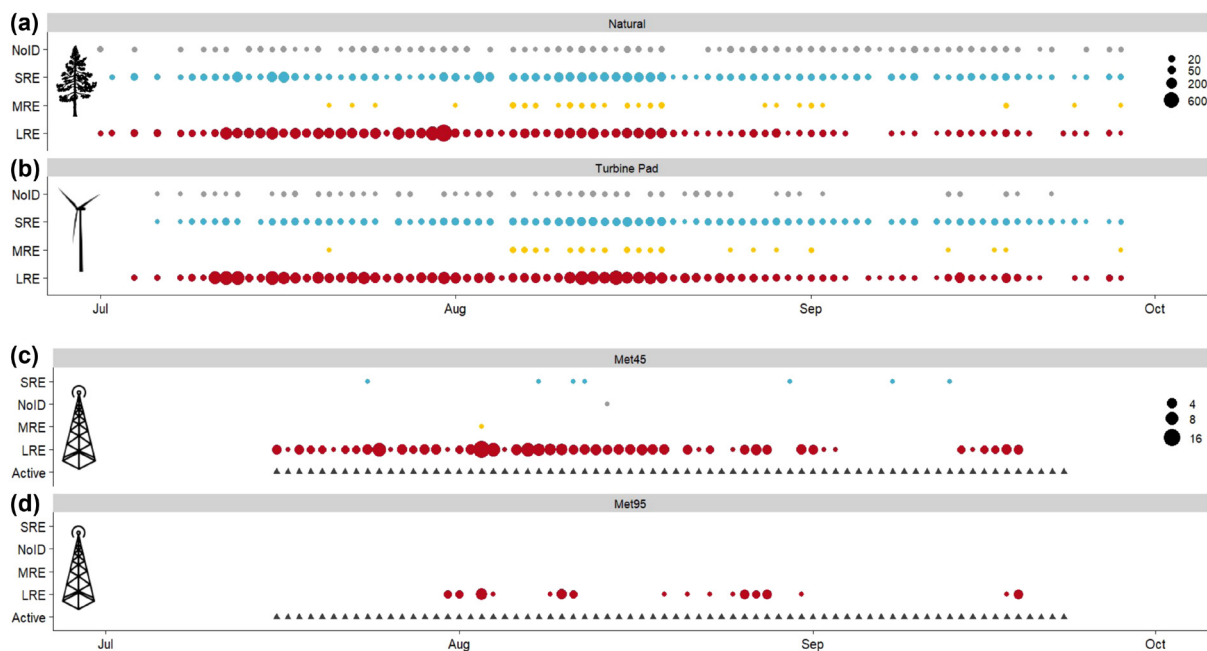


Figure 3. Seasonal activity for each foraging guild (NoID (unidentified bat) = gray, SRE (short range echolocator) = blue, MRE (medium range echolocator) = yellow, LRE (long range echolocator) = red) across the ground level sites, (a) at natural and, (b) turbine habitats and for the meteorological tower sites; microphone deployed 45m (c) and 90 m (d) heights). The size of the dots corresponds to the number of bat passes per night. Black triangles indicate nights when the met tower detectors were actively recording data. A more detailed overview of when detectors were active at each site is found in the supporting information. The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020.

turbines 8 (N08,  $n=442$  h; P08,  $n=454$ ) and 11 (N11,  $n=544$ ; P11,  $n=603$ ). There were 10 642 viable photos across all sites, of which 578 photos contained at least one insect which equated to 4563 insects present overall. Bat activity was recorded in 94% of recording hours (Table 1). Of the 104 detector – camera trap hours that included bat feeding passes, there were a total of 373 bat passes counted within those hours.

We found that temperature had a strong positive influence on the number of insects counted in an image per hour, as did the night in the season. The difference in localities had a clear strong influence on insect counts. We also found strong evidence that hourly average wind speeds were associated with the number of insects, but the effect was much weaker than temperature (Table 2, Insects). The results of the Bats – Insects model suggest that if insects were observed, this increased the likelihood of observing bat feeding passes at the same site. We observed a bimodal trend in insect activity as well as in bat feeding activity, with peaks occurring at sunset and sunrise (Fig. 6).

## Discussion

Nightly bat activity peaked between July and early August, with another smaller peak in late August, with mean nightly temperature explaining activity better than wind speeds. We show how assessing total bat activity without evaluating behavior can mask guild-specific responses. Species adapted

to flying in and near cluttered vegetation (SRE: short range echolocators) were recorded significantly less at turbine pad sites than at paired natural sites. Feeding activity of SRE bats was almost exclusively recorded at natural sites, suggesting that the developed areas around the turbine pads remove or degrade foraging habitat for these species. Bat species adapted for flying in open spaces (LRE: long range echolocators) were most frequently observed across the study period and area, regardless of habitat or behavior type. The high activity of LRE bats across the wind park raises conservation concern for species in this foraging guild which are amongst the most at risk for direct mortality with turbines. Ground-level acoustic monitoring was more effective at sampling the bat community and seasonal activity patterns than monitoring at heights above the forest canopy and within the rotor sweep zone. However, data collected from detectors deployed at a met tower in the wind park revealed that LRE bats were active at 45 m and 95 m heights between August and September, during the same period when most turbine fatalities are observed for LRE bat species in northern Europe (Rydell et al. 2010a, Rydell et al. 2017, Apoznański et al. 2018, Gaultier et al. 2020). We found support for our hypothesis that prey availability was linked to bat feeding activity using a relatively novel insect camera trap method paired with bat acoustic detectors. There was a positive relationship between insect presence and bat feeding activity, especially during warmer night hours, regardless of habitat. The wind park hosted a bat community of at least 8 out of 11 of Norway's known bat species, including the critically endangered *B. barbastellus*.



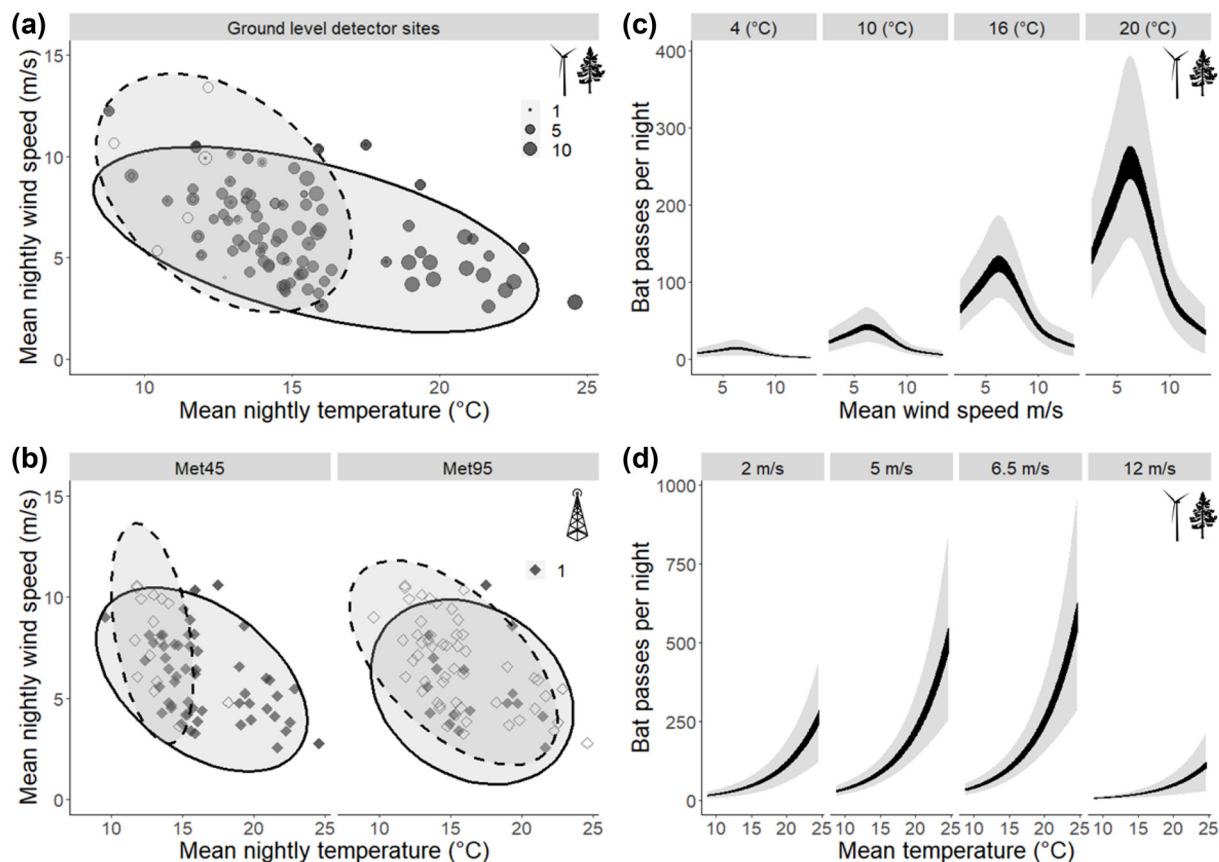


Figure 4. The relationship between average nightly temperature and wind speed and bat activity at ground-level (a, c, d) and the meteorological tower (b). For panels (a) ( $n = 811$  detector nights) and (b) ( $n = 140$  detector nights), filled points represent nights where bats were active and empty points represent nights with no bat activity. The size of the point is relative to the number of nights with the same temperature and wind conditions. The ellipses represent the 95% bivariate confidence interval for detector nights when bats were active (solid line) and inactive (dashed line). Panels (c) and (d) use predictions from the bats total model to show the relationship between temperature and predicted bat activity (bat passes per night) at ground level based on data from turbine 9, predicted for 31 July for both turbine pads and natural sites (black line, thickness corresponds to increased variance between habitats at different temperatures; gray shaded area = 95% confidence interval). The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020.

Our findings provide further evidence for the critical need to enforce bat monitoring at wind parks and develop mitigation efforts towards bat-friendlier wind energy operations, especially in boreal forests.

This study is based on empirical data from only one season. Repeating the study in another year, or in several years, could disentangle weather and seasonal effects. However, we would argue that our main finding, i.e. guild-specific responses to habitat change, would likely be similar in another year, unless the study was done in a year with poor weather conditions throughout most of the season. Furthermore, the lack of between-year variation was partly compensated for by carrying out continuous monitoring throughout the season. We expect the impacts of weather and season to be similar from year to year, although effect sizes could vary with between-year variation in bat activity and environmental conditions.

Our study is one of very few studies that draw attention to the risks of bats at wind parks in this region. It can be used to draw insights on how to develop bat monitoring techniques in similar wind parks in boreal forests. Unfortunately, so long

as there are no regulations that enforce pre- or post-construction monitoring of bats at wind parks on a national level, it may be challenging to gain access to wind parks to conduct studies for multiple years. Future research and bat monitoring efforts will benefit from multiple year studies that can better account for between-year variations in bat activity.

### Bat activity response to weather and seasonal patterns

We found that bat activity responded to mean nightly temperature more so than wind speed. There were 43 detector nights with more than 100 total bat passes (Supporting information) when mean nightly temperatures were greater than  $12^{\circ}\text{C}$  but wind speeds were between  $2.5$  and  $9\text{ m s}^{-1}$ . These high activity nights illustrate how temperature is a stronger driver than wind speeds during certain periods in the year for bats in this region. Our findings lend further support to the findings of Rydell (1989) that temperature was the main driving weather predictor of bats as well as insect abundance

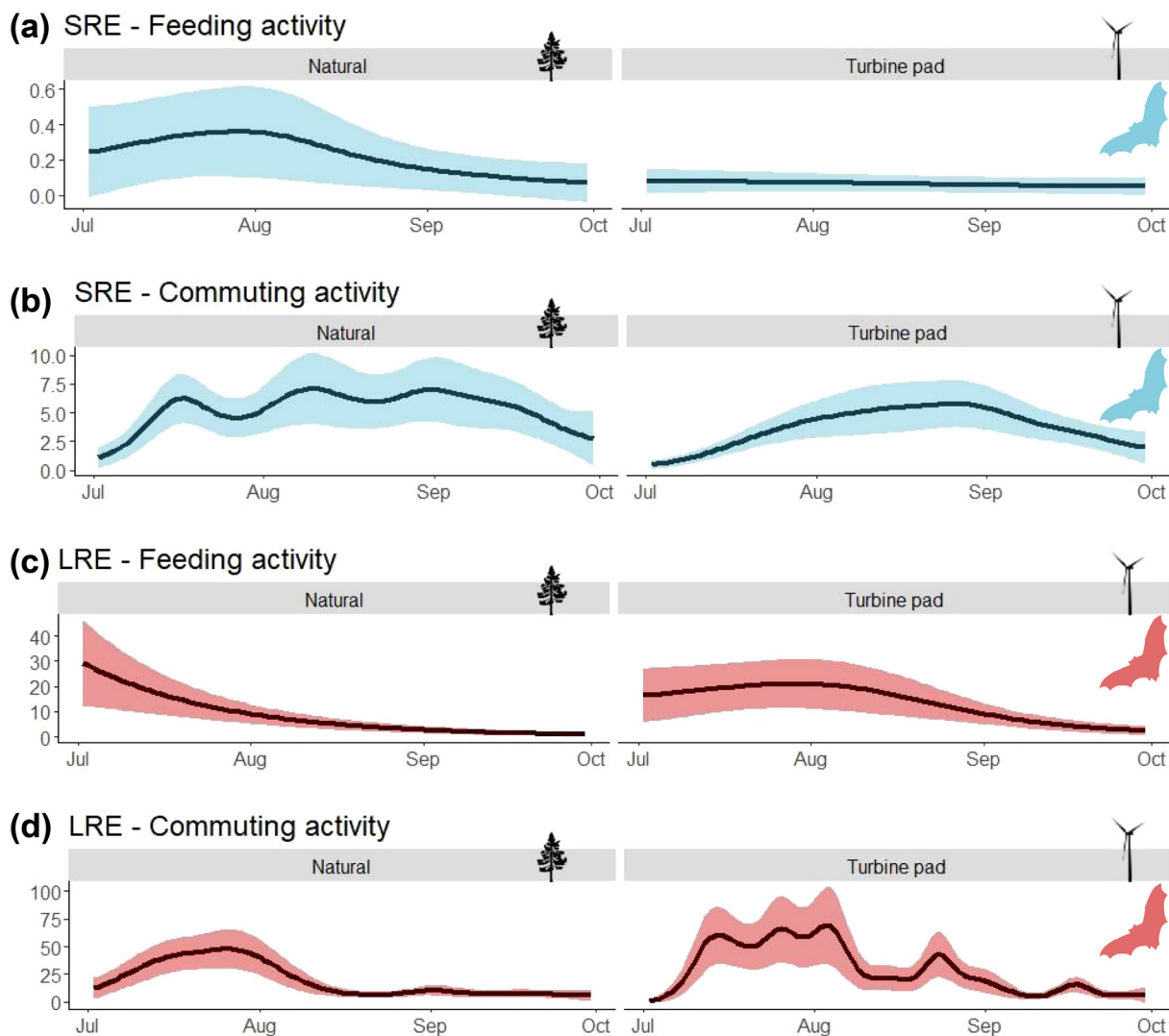


Figure 5. Predictions from models summarized in the supporting information of the guild-behavior specific GAMs of bat passes per night. These predictions are based on data for turbine 9, predicted across the season for both turbine pads and natural sites together (black line, thickness corresponds to increased variance between habitats at different temperatures, shaded area = 95% confidence interval). SRE (blue) = short range echolocators, LRE (red) = long range echolocators. The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020.

in southern Sweden. The stronger influence of temperatures than of wind speeds on bat activity may be especially true in forested areas where bats as well as insects can use the vegetation as a wind break to remain active on warmer nights, as suggested by Verboom and Spoelstra (1999). Perks and Goodenough (2020) found a positive relationship between wind speeds and bat activity across most of the bat community and suggested that the effect that increased wind speeds have on bat activity is likely influenced by multiple factors.

Studies from wind parks in Europe and the US have found that bat activity dropped off after 5–6  $\text{m s}^{-1}$  (Horn et al. 2008, Rydell et al. 2010a, Amorim et al. 2012) or 8  $\text{m s}^{-1}$  (Cryan et al. 2014). In temperate regions, such as in the UK and in the US, bat survey guidelines do not suggest monitoring bats on nights where temperatures drop below 10°C and

or wind speeds are consistently above 8  $\text{m s}^{-1}$  (Richardson et al. 2021) or even 4  $\text{m s}^{-1}$  (US Fish and Wildlife, 2022). Studies in boreal regions (Baerwald and Barclay 2009, Snively et al. 2021), including within Norway (Michaelsen 2017, Frafjord 2021), have reported trends in bat activity like those in temperate regions.

In our study, wind speeds of 5 or 6.5  $\text{m s}^{-1}$  had higher predicted rates of bat activity than lower wind speeds (Fig. 3) on nights when temperatures were greater than 10°C. On 90% of the nights when bats were active at the met tower, mean nightly weather conditions were when winds were less than 10  $\text{m s}^{-1}$  and temperatures greater than 13°C. In comparison, studies from Sweden have found similar but varied effects of how temperature and wind influence bat activity. Rydell et al. (2017) reported that 90% of bat activity recorded at turbines

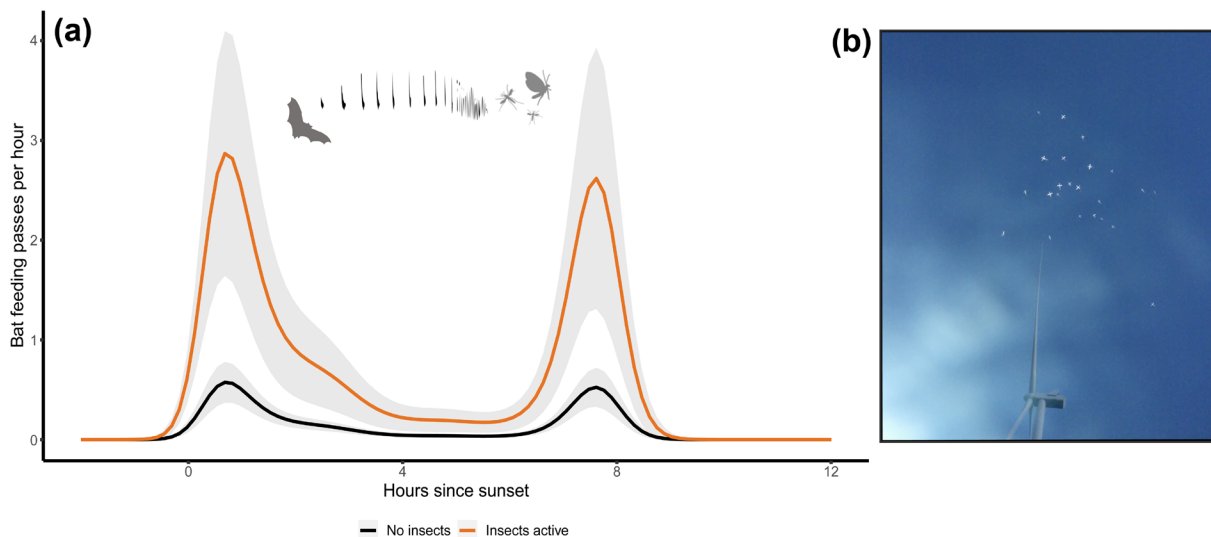


Figure 6. (a) Predictions from the GAM model “Bats – Insects” (Table 2) of bat feeding passes per hour (orange line = bat activity when insects were present, black line = bat feeding activity when insects were not recorded, shaded area = 1 SD) for the locality turbine 11 throughout the night. Time is expressed in hours since sunset. The illustration is of a bat emitting a feeding buzz at flying insects. (b) Image that contains insects collected from a camera trap during this research. The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020.

(~ 100 m high, averaged over 10 min, several wind parks between 2012–2015) occurred when winds were less than  $5.8 \text{ m s}^{-1}$  and temperatures were greater than  $14.6^\circ\text{C}$ . [de Jong et al. \(2021\)](#) also measured average nightly bat activity in response to weather conditions recorded at the turbine nacelle at 3 turbines for two seasons and found that 90% of bat activity occurred when temperatures were greater than  $9^\circ\text{C}$  and wind speeds were less than  $8.2 \text{ m s}^{-1}$ . Even if temperature is a stronger driver of bat activity than wind speeds, wind speed in relation to turbine rotation speeds should be considered when trying to predict bat activity near active turbines as well as potential collision risks. [Cryan and Barclay \(2009\)](#) observed that bats will more frequently approach wind turbines at lower wind speeds ( $< 10 \text{ m s}^{-1}$ ) and when blades are spinning.

The weather data for this study was collected from the turbine nacelles, approximately 140 m higher than the ground level bat acoustic detector microphones. Collecting weather data from nacelle height is a method that is used in several published studies and is common in environmental assessments ([Mathews et al. 2016](#), [de Jong et al. 2021](#), [NatureScot et al. 2021](#), [Peterson et al. 2021](#)) and provides – relevant weather data for determining which turbine operational wind speeds relate to bat activity. Ground-level monitoring stations may have provided a clearer indication of how bats were responding to the more local environment. However, we found average daily temperatures to be highly correlated ( $r^2 = 0.95$ ) with weather conditions recorded at nearby (~10 km) weather station, though temperatures collected from wind turbine nacelles were consistently slightly higher (mean average difference of  $0.82^\circ\text{C}$ ) than measurements recorded from the weather station (2 m high). No measurements of wind speed from nearby weather stations

were available. Bat acoustic activity is known to vary within an area and between years. While we do not have multiple years to compare in this study, we found rapid changes in bat activity across sites and within the season. Recently there have been several exciting studies published on the ecology of bats in the Fennoscandian region using broadscale acoustic monitoring ([Vasko et al. 2020](#), [Blomberg et al. 2021](#), [Gaultier et al. 2023](#), [Kotila et al. 2023](#)) which reported similar seasonal bat activity patterns to our findings. [Kotila et al. \(2023\)](#) reported seasonal activity patterns of *E. nilssonii* (LRE foraging guild) and *Myotis* spp. (SRE foraging guild), from project that spanned 8 different localities stretching from latitudes approximately  $60\text{--}66^\circ$  North in Finland between 2015–2021. The patterns [Kotila et al. \(2013\)](#) reported for lower latitudes, resembled the seasonal patterns observed at Marker wind park ( $59^\circ$  North) in 2020 with a steady increase throughout the summer leading to a peak in August followed by drop off in activity in September. While site specific considerations are important, it may be possible to apply latitudinal defined bat monitoring regions across Fennoscandia for international, broadscale monitoring programs.

Bats living in Fennoscandia are already living at some of the most far northern extents of their ranges and must operate under environmental constraints unique from conspecifics living at lower latitudes. Even in the southern extents of the Fennoscandia, summers are considerably colder and wetter than the European mainland. Night length radically shifts throughout the summer at northern latitudes. The summer nights remain light such that this period more closely resembles an extended twilight rather than true night. The nights in our study area are approx. 5 h and 20 min long at the summer solstice in late June and will nearly double in length by the start of September (Steffen Thorsen, Time

and Date AS 1995–2023). The shortest nights in the year correspond with a critical period of the bat maternity season when most adult females are in the third trimester of pregnancy or lactating in southern Norway (Dietz and Kiefer 2016, Eldegard et al. 2021). The short and light nights in late June – early July exacerbates already extreme energy demands on Fennoscandian bats. This is especially true for reproductive females and for species that are not adapted to fly in open or well-lit spaces, such as SRE bats. Bats at northern latitudes have a shorter reproductive and weaning period, are inclined to rely on more ephemeral and/or energy rich prey (Boyles et al. 2016), can require smaller, more connected foraging habitats (Frafjord 2013), and may continue to forage during weather conditions that would otherwise be inclement for conspecifics at lower latitudes (Rydell 1989, 1991). Monitoring bats in Fennoscandia cannot be directly mirrored from methods used in temperate Europe. However international monitoring standards can be adapted and implemented to learn which best practices are most effective in Fennoscandian regions.

### Monitoring at height

Only 1.2% of all bat passes were collected from the two met tower detectors. However, the seasonal peaks in LRE bat activity observed at 45 and 95 m high reflected similar patterns recorded from the ground level detectors (Fig. 3). Temperature and wind speeds had a similar effect on bat activity, regardless of height (Fig. 4) with slightly less activity at taller heights when temperatures were below 10°C. At height monitoring is challenging and often records less bat activity than at ground level detectors. The recording environment on turbines and similar structures tends to be poorer than typical ground-level deployments and can be expensive to deploy and maintain suggesting it may not always be an effective monitoring tool (Voigt et al. 2021). Studies which have paired ground-level and at height bat acoustic monitoring frequently find that the patterns observed between the two types of detectors are similar, even if the volume of data collected is contrasting, but make it possible to detect some high-flying species more effectively (Collins and Jones 2009) and predict fatalities at wind turbines (Roemer et al. 2019, Barré et al. 2023). de Jong et al. (2021) found that the bat activity at nacelle height was more varied than from ground-level detectors, within and between years. The low number of bat passes recorded in our study may be because bats in the study area were less drawn to the meteorological tower than an active turbine or simply reflect truly low activity at the heights measured.

Although there was little data collected from the two met tower detectors, we found it informative to have some representation of bat activity above the forest canopy and within the turbine rotor sweep zone. Many open space foraging bats i.e. LRE bats which are more vulnerable to turbine collisions are highly associated with foraging above the forest canopy and may ascend to 300 m in height (O'Mara et al. 2019) or higher for scouting, migrating or foraging insects

(Gillam et al. 2009). We recorded only 7 SRE bat passes from the met tower detectors collectively. However, the boreal forest canopy is lower relative to temperate forests (Vankat 2002) and may be an important foraging area for SRE bats when navigating in densely planted plantation forests and during the short, light summer nights. We recorded 12 bat feeding passes from the met tower, both heights combined, which did not provide enough information to draw conclusions about bat foraging behavior. Given the limited knowledge of bat ecology in Fennoscandian region, we still recommend implementing some form of at height bat monitoring at wind parks to describe bat activity more likely to reflect collision risks and to explore how this may be related to insect foraging.

### Avoidance effects and fatal attractions

We found that SRE bats (86% *Myotis* spp.) are less likely to hunt prey at turbine pads than in nearby natural environments, suggesting that bats in this guild are impacted by loss of foraging habitat from wind park infrastructure. SRE bats, including *Myotis* species, are mostly considered 'narrow space' foragers which are associated with interior forests (Norberg and Rayner 1987, Denzinger and Schnitzler 2013, Frey-Ehrenbold et al. 2013, Froidevaux et al. 2016). Turbine pad habitat in this study was further from vegetation and tree lines than natural sites, so it is not surprising SRE bats were less likely to commute there. However, we were surprised by how little feeding activity was observed relative to commuting activity at turbine pads. Wind turbine development can have indirect negative impacts on bats by creating an avoidance effect. The exact drivers of this avoidance effect have been debated in different regions. There is some evidence to suggest that anthropogenic noise (Finch et al. 2020, Allen et al. 2021) or lights (Bennett and Hale 2014) can be disturbing for bats at wind parks. Habitat fragmentation and degradation could also explain avoidance effects (Lesiński 2007, Barré et al. 2018), especially if turbine development causes insect declines and subsequently reduces foraging habitat (Rydell et al. 2010b, Millon et al. 2015).

Gaultier et al. (2023) and Ellerbrok et al. (2022) both monitored bats at wind parks in European forested landscapes in the same period as this study and found similar avoidance effects; *Myotis* spp. activity was more likely to be recorded further from turbines. However, these studies did not evaluate feeding behavior, so it is not possible to compare commuting vs foraging habitat use. Furthermore, both studies were more focused on studying how bats responded with increasing distance from turbines whereas all sites in our study were within 200 m of the turbine base and instead sampled developed (turbine pads) vs undeveloped (natural) habitat. Therefore, the potential avoidance effects observed for SRE bats at the wind park in this study are not likely to be linked to sound or light disturbance but rather the removal of vegetation, the ground substrate, and perhaps also subsequent reduction in prey abundance.

Without pre- and post-construction data to compare, it is not possible to quantify the impact that Marker wind park



may have had in displacing SRE bats, but our findings suggest that the park infrastructure creates less desirable foraging habitat for SRE bats than natural, undisturbed habitat. All the species included in the SRE guild in this study area are highly associated with forest habitat and include the *B. barbastellus* (found in our study) and *Myotis nattereri* (not found in our study) which are critically endangered species in Norway (Eldegard et al. 2021). While *B. barbastellus* and similar SRE are rarely found as fatalities at wind parks, the removal of forest and other landscape features such as wetlands and freshwater bodies can remove roost sites, reduce feeding opportunities, or fragment habitat connectivity (Apoznański et al. 2018).

The LRE bats were found to occupy the open habitat provided by the turbine pads more often than in the natural sites, regardless of the behavior recorded. This would be expected as the species in this guild are most associated with open foraging habitats (Schnitzler et al. 2003). While LRE bats may not be at high risk of losing foraging habitat from wind energy infrastructure (Roemer et al. 2019), the risk that the turbines themselves pose to these species is a critical concern. All the species within the LRE guild for our study area are considered medium-high risk for wind turbine mortality in Europe and are representative of carcasses found at wind parks in Norway and Sweden (Follestad et al. 2007, Rydell et al. 2017, Apoznański et al. 2018). There is some evidence that high flying bat species such as LRE bats are fatally attracted toward wind turbines though the reason for this attraction is debated and is species specific. Theories include that bats approach turbines out of sheer curiosity, due to migratory activity, because tall structures can be attractive social/breeding sites, or because turbines may be hotspots for insect prey (Cryan and Barclay 2009, Voigt et al. 2018, Richardson et al. 2021). However, Gaultier et al. (2023) found some evidence to suggest that *E. nilssonii* (LRE) avoid turbines in forests in Finland.

*Eptesicus nilssonii*, contributed to 70% of the bat passes recorded in all habitats and throughout the survey season. *Eptesicus nilssonii* has historically been one of the most common bat species in Fennoscandia (Rydell 1993, Tidenberg et al. 2019, Suominen et al. 2022) but recently sharp population declines have been observed (Rydell et al. 2018, Rydell et al. 2020, Eldegard et al. 2021) resulting in its national conservation status shifting from 'Least Concern' to 'Near Threatened' and 'Vulnerable' in Sweden and Norway, respectively (Eide et al. 2020, Eldegard et al. 2021). *Eptesicus nilssonii* is a species that has been reported as fatalities at wind parks in Norway and Sweden (Follestad et al. 2007, Rydell et al. 2017) and so wind parks – such as the one in this study – where their activity is high, should be aware of the potential risk to this species which is already experiencing population declines.

### Monitoring insect–insectivorous bat relationships

We found a positive relationship between insect presence and bat feeding activity by deploying bat acoustic detectors paired

with insect camera traps. Bats and flying nocturnal insects are both taxa that are difficult to monitor for population declines and are often of special conservation concern (Frick et al. 2020, van Klink et al. 2022). Høye et al. (2021) identified non-invasive camera trapping such as the method used in our study, in combination with automatic identification tools, as focally important methods for revolutionizing the utility of entomological research. Scholz and Voigt (2022) as well as Voigt (2021) have drawn attention to how the phenomena of feeding bats being killed at turbines in combination with insect fatalities at turbines can be creating a biodiversity sink. Certain prey species, such as soft-bodied nocturnal Diptera and Lepidoptera species, are also dependent on forest and densely vegetated areas (Pettersson et al. 1995) such that wind parks in forests likely exacerbate the risk to foraging bats. Several studies in Sweden have found evidence to suggest insects swarming at wind turbines could be linked to bat activity (Rydell et al. 2016, Jansson et al. 2020, de Jong et al. 2021). Specifically, Rydell et al. (2016) found evidence that LRE species may be eating diurnal flies resting on the turbines themselves. It is known certain bat species will hunt for insects near turbines (Horn et al. 2008, Valdez and Cryan 2013, Roeleke et al. 2016, Foo et al. 2017) and we observed LRE feeding at turbine pads. Feeding near turbines is likely to increase the risk of collisions which creates an opportunity to identify conditions for swarming insects and feeding bats, then mitigating the risks of fatalities. However, more research is needed to test the 'feeding-attraction hypothesis' (Kunz et al. 2007, Reimer et al. 2018) and determine whether insect abundance predicts bat collisions.

Equipment failures led to gaps in the dataset such that it was not possible to account for insect abundance in this study. However, to our knowledge no existing published studies have used this camera trapping method to document the relationship between flying nocturnal arthropod availability and bat acoustic activity. The original design of the camera trapping method used in our study was prone to power source failures which led to sparse data collection of data. More information regarding the camera trap design and equipment failures are described in Johns (2021). We recommend employing similar methods during periods when weather conditions are optimal (warm nights, no rain, low winds) to make the most of the battery life and because image quality during rain or fog is extremely poor. We agree with the original developers of the method that deploying the camera trap toward an open sky produces the best quality images for identifying insects (Ruczyński et al. 2020). Another drawback of this camera trapping method is that manual analysis of images is very time consuming. Choiński et al. (2023) has developed an automated tool for identifying insects from photos collected using this method which would radically increase the efficiency of using this method. Designing a camera trap with reliable power sources, solid weatherproof housing and automated processes for insect identification would lead to more complete datasets with more exciting potential for relating insect abundance to bat acoustic data. Future studies should consider applying a combined insect camera trapping and

acoustic monitoring sampling design stratified at different heights at active wind parks to study these dynamics. This camera trapping method is not designed for identifying taxa but could also be combined with genetic non-invasive methods such as eDNA for account for the insect community assemblages (Valentin et al. 2020).

### Management recommendations

Our findings provide evidence that wind parks in forest remove foraging habitat for short range echolocating bats. We therefore recommend that environmental impact assessments for wind farm development in forest should assess potential loss of foraging habitat for resident bat species. We document high levels of activity throughout the summer and autumn across the wind park for bat species that are most vulnerable to fatally colliding with turbines, highlighting the need for post-construction monitoring to evaluate how bats are directly impacted by wind turbines. By manually identifying all bat passes, we were able to identify differences between commuting and feeding habitat across guilds. This demonstrates the value of evaluating behavior as well as taxa from bat acoustic monitoring data. We observed peaks in flying nocturnal insect activity as well as bat feeding activity at approx. 1 and 7 h after sunset. If further evidence arises for the feeding-attraction hypothesis, camera traps could be used to better inform wind turbine curtailment and blade feathering strategies.

There was no mention of bats in the two environmental impact assessments we are aware of which evaluated the potential costs to biodiversity for building the wind park where this study was located (Fiskevold et al. 2012, Marker Vindpark et al. 2017). If pre-construction bat monitoring surveys had implemented, it is likely that the presence of the critically endangered *B. barbastellus* would have been observed much earlier and steps could have been taken to reduce habitat loss for this rare forest specialist. This is a species for which there is only one other known location of a few individuals in Norway. Carcass searches that took place in the same season found two *V. murinus* carcasses under turbines at this wind park (unpubl.) in late August, suggesting there are direct negative impacts on high flying bats at this wind park.

Ours is one of few studies that brings attention to the risks to bats at wind parks in the Fennoscandian region, and it can be used to draw insights on how to develop bat monitoring techniques in similar forested wind parks. Building wind parks in forests is common in the Fennoscandian region (Gaultier et al. 2020, 2023) and development is predicted to increase (Enevoldsen 2016, Enevoldsen and Permien 2018). The 'green-on-green' dilemma (Straka et al. 2020) posed by expanding wind energies at the cost of biodiversity requires interdisciplinary, open science and international collaborations. This study included resident as well as migratory bat species and was also located directly on the Norwegian–Swedish border such that even residential bat populations are expected to move across international borders. Fennoscandian countries have an important role to play in developing strong

bat monitoring programs at wind farms as wind energy development expands rapidly and climate change is expected to cause European bat species ranges to shift northwards.

### Conclusion

We found evidence of reduced activity and a particularly strong reduction in feeding behavior in short range echolocating bats near wind turbines. Long-range echolocating bats, which are at risk of fatally colliding with wind turbines, remained highly active throughout the wind farm. By combining insect camera trapping with bat acoustic monitoring, we observed a positive correlation between bat feeding activity and insect presence. Further exploring this method may give future studies more mechanistic access to the impact of wind energy infrastructure on bats and their feeding ecology. This in turn could facilitate better-informed mitigation strategies. Our findings suggest that wind energy developments in boreal forests may produce guild-specific habitat loss.

*Acknowledgements* – We express deep gratitude to BKW/Scanergy AS Marker Vindpark and Huy Hong (previously with Proxima Scandinavia AS) for facilitating this research, as well as to all landowners that granted us access to deploy our equipment on their properties. Thank you to Alexander Rambøl and Tommy Rambøl with his associates for their diligent and creative collaboration in deploying our equipment safely and securely. Thank you to Anna Cieka and Larisa Bishop-Boros of WEST Inc., as well as Goniela Iskali of Apex Clean Energy, who provided valuable insights and advice regarding study design. Thank you to Roar Økseter and Tommy Traagstad who lent support in the field. Thank you to Ronny Steen for creating the bat image and to Pierre Dupont for creating the wind turbine and insect images. Thank you to Jon Russ, Julie Dahl Møller, Hans J. Baagøe, Kjell Isaksen, and Tore Christian Micahelsen for providing their feedback and validation of *Pipistrellus nathusii* and *Barbastella barbastellus* acoustic recordings. *Funding* – Funding for this research was provided by the Norwegian Environmental Agency and the Norwegian University of Life Sciences.

### Author contributions

**Reed April McKay:** Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (supporting); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Sarah Elizabeth Johns:** Investigation (supporting); Writing – review and editing (supporting). **Richard Bischof:** Formal analysis (supporting); Methodology (supporting); Supervision (supporting); Writing – review and editing (supporting). **Fiona Mathews:** Formal analysis (supporting); Methodology (supporting); Supervision (supporting); Writing – review and editing (supporting). **Jeroen van der Kooij:** Investigation (supporting); Writing – review and editing (supporting). **Natalie Yoh:** Formal analysis (supporting); Methodology (supporting); Writing – review and editing (supporting). **Katrine**

**Eldegard:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Methodology (supporting); Supervision (lead); Writing – review and editing (supporting).

### Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1002/wlb3.01168>.

### Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.x0k6djhrp> (McKay et al. 2023).

### Supporting information

The Supporting information associated with this article is available with the online version.

## References

- Aldridge, H. D. J. N. and Rautenbach, I. L. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. – *J. Anim. Ecol.* 56: 763–778.
- Allen, L. C., Hristov, N. I., Rubin, J. J., Lightsey, J. T. and Barber, J. R. 2021. Noise distracts foraging bats. – *Proc. R. Soc. B* 288: 20202689.
- Amorim, F., Rebelo, H. and Rodrigues, L. 2012. Factors influencing bat activity and mortality at a wind farm in the Mediterranean region. – *Acta Chiropterol.* 14: 439–457.
- Apoznański, G., Sánchez-Navarro, S., Kokurewicz, T., Pettersson, S. and Rydell, J. 2018. Barbastelle bats in a wind farm: are they at risk? – *Eur. J. Wildl. Res.* 64: 1–10.
- Arnett, E. B., Baerwald, E. F., Mathews, F., Rodrigues, L., Rodríguez-Durán, A., Rydell, J., Villegas-Patracá, R. and Voigt, C. C. 2016. Impacts of wind energy development on bats: a global perspective. – In: Voigt, C. C. and Kingston, T. (eds), *Bats in the Anthropocene: conservation of Bats in a changing world*. Springer International Publishing, pp. 295–323.
- Baerwald, E. F. and Barclay, R. M. R. 2009. Geographic variation in activity and fatality of migratory bats at wind energy facilities. – *J. Mammal.* 90: 1341–1349.
- Barova, S. and Streit, A. 2018. Action plan for the conservation of all bat species in the European Union 2019–2024. – <http://iene.se/wp-content/uploads/EU-Bats-Action-Plan-Final.pdf?fbclid=IwAR2h3JnxYx-xeznPOAhHOZtAhGzNXZarsFf-8skR0QcJyBpoPARVwm4zjLE>.
- Barré, K., Le Viol, I., Bas, Y., Julliard, R. and Kerbiriou, C. 2018. Estimating habitat loss due to wind turbine avoidance by bats: implications for European siting guidance. – *Biol. Conserv.* 226: 205–214.
- Barré, K., Froidevaux, J. S. P., Leroux, C., Mariton, L., Fritze, M., Kerbiriou, C., Le Viol, I., Bas, Y. and Roemer, C. 2022. Over a decade of failure to implement UNEP/EUROBATS guidelines in wind energy planning: a call for action. – *Conserv. Sci. Pract.* 4: e12805.
- Barré, K., Froidevaux, J. S. P., Sotillo, A., Roemer, C. and Kerbiriou, C. 2023. Drivers of bat activity at wind turbines advocate for mitigating bat exposure using multicriteria algorithm-based curtailment. – *Sci. Total Environ.* 866: 161404.
- Battersby, J. 2010. Guidelines for surveillance and monitoring of European bats. EUROBATS publication series No. 5. UNEP / EUROBATS. – Secretariat, p. 95.
- Bennett, V. J. and Hale, A. M. 2014. Red aviation lights on wind turbines do not increase bat–turbine collisions. – *Anim. Conserv.* 17: 354–358.
- Blomberg, A. S., Vasko, V., Salonen, S., Pétersons, G. and Lilley, T. M. 2021. First record of a Nathusius’ pipistrelle (*Pipistrellus nathusii*) overwintering at a latitude above 60°N. – *Mammalia* 85: 74–78.
- Boyles, J. G., McGuire, L. P., Boyles, E., Reimer, J. P., Brooks, C. A. C., Rutherford, R. W., Rutherford, T. A., Whitaker, J. O. and McCracken, G. F. 2016. Physiological and behavioral adaptations in bats living at high latitudes – *Physiol. Behav.* 165: 322–327. <https://doi.org/10.1016/j.physbeh.2016.08.016>.
- Bradshaw, C. J. A. and Warkentin, I. G. 2015. Global estimates of boreal forest carbon stocks and flux. – *Global Planet. Change* 128: 24–30.
- Browning, E., Barlow, K. E., Burns, F., Hawkins, C. and Boughey, K. 2021. Drivers of European bat population change: a review reveals evidence gaps. – *Mamm. Rev.* 51: 353–368.
- Choiński, M., Zegarek, M., Hałat, Z., Borowik, T., Kohles, J., Dietzer, M., Eldegard, K., McKay, R. A., Johns, S. E. and Ruczyński, I. 2023. Insect detection on high-resolution images using deep learning. – In: Saeed, K., Dvorský, J., Nishiuchi, N., Fukumoto, M. (eds), *Computer information systems and industrial management*. Cham: Springer Nature Switzerland (lecture notes in computer science), pp. 225–239.
- Collins, J. and Jones, G. 2009. Differences in bat activity in relation to bat detector height: implications for bat surveys at proposed Windfarm sites. – *Acta Chiropterol.* 11: 343–350.
- Cryan, P. M. and Barclay, R. M. R. 2009. Causes of bat fatalities at wind turbines: hypotheses and predictions. – *J. Mammal.* 90: 1330–1340.
- Cryan, P. M., Gorresen, P. M., Hein, C. D., Schirmacher, M. R., Diehl, R. H., Huso, M. M., Hayman, D. T. S., Fricker, P. D., Bonaccorso, F. J., Johnson, D. H., Heist, K. and Dalton, D. C. 2014. Behavior of bats at wind turbines. – *Proc. Natl Acad. Sci. USA* 111: 15126–15131.
- de Jong, J., Millon, L., Håstad, O. and Victorsson, J. 2021. Activity pattern and correlation between bat and insect abundance at wind turbines in south Sweden. – *Animals* 11: 3269.
- Denzinger, A. and Schnitzler, H. U. 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. – *Front. Physiol.* 4: 164.
- Dietz, C. and Kiefer, A. 2016. *Bats of Britain and Europe*. – Bloomsbury Publishing.
- Dinesen, L., Højgård Petersen, A. and Rahbek, C. 2021. Synergy in conservation of biodiversity and climate change mitigation: Nordic peatlands and forests. – *Nordisk Ministerråd*.
- Dutta, A. and Zisserman, A. 2019. The via annotation software for images, audio and video. – In: *Proceedings of the 27th ACM international conference on multimedia*. New York, NY, USA. Association for Computing Machinery (MM 2019), pp. 2276–2279.
- Eggertsson, O., Nygaard, P. and Skovsgaard, J. P. 2008. History of afforestation in the Nordic countries.
- Eide, W., Ahrné, K., Bjelke, U., Nordström, S., Ottosson, J. and Sundberg, S. 2020. Tillstånd och trender för arter och deras livsmiljöer rödlistade arter i Sverige 2020. – SLU Artdatabanken.



- Eldegard, K., Syvertsen, P., Bjørge, A., Kovacs, K., Støen, O.-G. and van der Kooij, J. 2021. Pattedyr: vurdering av arter for Norge. Rødlista for arter 2021. – Artsdatabanken.
- Ellerbrok, J. S., Delius, A., Peter, F., Farwig, N. and Voigt, C. C. 2022. Activity of forest specialist bats decreases towards wind turbines at forest sites. – *J. Appl. Ecol.* 59: 2497–2506.
- Enevoldsen, P. 2016. Onshore wind energy in northern European forests: reviewing the risks. – *Renew. Sustain. Energy Rev.* 60: 1251–1262.
- Enevoldsen, P. and Permien, F.-H. 2018. Mapping the wind energy potential of Sweden: a sociotechnical wind atlas. – *J. Renew. Energy* 2018: e1650794.
- Erasmus, M., Leuschner, C., Balkenhol, N. and Dietz, M. 2021. Shed light in the dark – how do natural canopy gaps influence temperate bat diversity and activity? – *Forest Ecol. Manage.* 497: 119509.
- EUROBATs 2022. 9 th Session of the Meeting of the Parties. Resolution 9.4: Wind Turbines and Bat Populations. – [https://www.eurobats.org/sites/default/files/documents/pdf/Meeting\\_of\\_Parties/Resolution%209.4%20Wind%20Turbines%20and%20Bat%20Populations.pdf](https://www.eurobats.org/sites/default/files/documents/pdf/Meeting_of_Parties/Resolution%209.4%20Wind%20Turbines%20and%20Bat%20Populations.pdf).
- Fenton, M. B., Jacobson, S. L. and Stone, R. N. 1973. An automatic ultrasonic sensing system for monitoring the activity of some bats. – *Can. J. Zool.* 51: 291–299.
- Finch, D., Schofield, H. and Mathews, F. 2020. Traffic noise playback reduces the activity and feeding behaviour of free-living bats. – *Environ. Pollut.* 263: 114405.
- Fiskevold, M., Mortensen, M., Myrmæl, A., Heimstad, R., Sandbakk, T., Molin, P., Seirestad, D. T. and Løset, F. 2012. Høgås, Elgåsen og Joarknatten vindkraftverkkonsekvensutredning. 170822–1/2012. – SWECO, p. 117. [https://www.statsforvalteren.no/siteassets/fm-oslo-og-viken/miljo-og-klima/rapporter/miljo\\_overnavdelingen-i-ostfolds-rapportserie-1985-2018/2014\\_05-naturfaglige-undersokelser-i-ostfold-xiv-del2.pdf](https://www.statsforvalteren.no/siteassets/fm-oslo-og-viken/miljo-og-klima/rapporter/miljo_overnavdelingen-i-ostfolds-rapportserie-1985-2018/2014_05-naturfaglige-undersokelser-i-ostfold-xiv-del2.pdf).
- Follestad, A., Flagstad, Ø., Nygard, T., Reitan, O. and Schulze, J. 2007. Vindkraft og fugl på Smøla 2003–2006. – NINA Rapport 248, p. 78, <https://brage.nina.no/nina-xmlui/handle/11250/2443870>.
- Foo, C. F., Bennett, V. J., Hale, A. M., Korstian, J. M., Schildt, A. J. and Williams, D. A. 2017. Increasing evidence that bats actively forage at wind turbines. – *PeerJ* 5: e3985.
- Frafjord, K. 2013. Influence of night length on home range size in the northern bat *Eptesicus nilssonii*. – *Mamm. Biol.* 78: 205–211.
- Frafjord, K. 2021. The influence of night length: activity of the northern bat *Eptesicus nilssonii* under conditions of continuous light in midnight sun compared to a southern population. – *BMC Zool.* 6: 34.
- Framstad, E., de Wit, H., Mäkipää, R., Larjavaara, M., Vesterdal, L. and Karlton, E. 2013. Biodivers. Carbon Storage Dyn. Old North. Forests, vol. 507. – Nordic Council of Ministers (TemaNord, 2013: 507).
- Frey-Ehrenbold, A., Bontadina, F., Arlettaz, R. and Obrist, M. K. 2013. Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. – *J. Appl. Ecol.* 50: 252–261.
- Frick, W. F., Kingston, T. and Flanders, J. 2020. A review of the major threats and challenges to global bat conservation. – *Ann. N. Y. Acad. Sci.* 1469: 5–25.
- Froidevaux, J. S. P., Zellweger, F., Bollmann, K., Jones, G. and Obrist, M. K. 2016. From field surveys to LiDAR: shining a light on how bats respond to forest structure. – *Remote Sens. Environ.* 175: 242–250.
- Gaultier, S. P., Blomberg, A. S., Ijäs, A., Vasko, V., Vesterinen, E. J., Brommer, J. E. and Lilley, T. M. 2020. Bats and wind farms: the role and importance of the Baltic Sea countries in the European context of power transition and biodiversity conservation. – *Environ. Sci. Technol.* 54: 10385–10398.
- Gaultier, S. P., Lilley, T. M., Vesterinen, E. J. and Brommer, J. E. 2023. The presence of wind turbines repels bats in boreal forests. – *Landsc. Urban Plan.* 231: 104636.
- Gillam, E. H., McCracken, G. F., Westbrook, J. K., Lee, Y. F., Jensen, M. L. and Balsley, B. B. 2009. Bats aloft: variability in echolocation call structure at high altitudes. – *Behav. Ecol. Sociobiol.* 64: 69–79.
- Henriksen, S. and Hilmo, O. 2015. Norsk rødliste for arter 2015, <https://doi.org/10.13140/RG.2.1.2130.0083>.
- Högbom, L., Abbas, D., Armolaitis, K., Baders, E., Futter, M., Jansons, A., Jögeste, K., Lazdins, A., Lukminė, D., Mustonen, M., Øistad, K., Poska, A., Rautio, P., Svensson, J., Vodde, F., Varnagirytė-Kabašinskienė, I., Weslien, J., Wilhelmsson, L. and Zute, D. 2021. Trilemma of Nordic–Baltic forestry – how to implement UN sustainable development goals. – *Sustainability* 13: 5643.
- Horn, J. W., Arnett, E. B. and Kunz, T. H. 2008. Behavioral responses of bats to operating wind turbines. – *J. Wildl. Manage.* 72: 123–132.
- Høy, T. T., Loboda, S., Koltz, A. M., Gillespie, M. A. K., Bowden, J. J. and Schmidt, N. M. 2021. Nonlinear trends in abundance and diversity and complex responses to climate change in Arctic arthropods. – *Proc. Natl Acad. Sci. USA* 118: e2002557117.
- Jansson, S., Malmqvist, E., Brydegaard, M., Åkesson, S. and Rydell, J. 2020. A Scheimpflug lidar used to observe insect swarming at a wind turbine. – *Ecol. Indic.* 117: 106578.
- Johns, S. E. 2021. Bats, insects and weather: spatial – temporal trends on a boreal forest wind facility in Norway. MSc thesis, Norwegian Univ. of Life Sciences. – [https://nmbu.brage.unit.no/nmbu-xmlui/bitstream/handle/11250/2823341/M60\\_Johns\\_MScEcology\\_2021\\_Official.pdf?sequence=1&isAllowed=y](https://nmbu.brage.unit.no/nmbu-xmlui/bitstream/handle/11250/2823341/M60_Johns_MScEcology_2021_Official.pdf?sequence=1&isAllowed=y).
- Jones, G. and Rebelo, H. 2013. Responses of bats to climate change: learning from the past and predicting the future. – In: Adams, R. A. and Pedersen, S. C. (eds), *Bat evolution, ecology, and conservation*. Springer, pp. 457–478.
- Kershenbaum, A. et al. 2016. Acoustic sequences in non-human animals: a tutorial review and prospectus. – *Biol. Rev.* 91: 13–52.
- Kirkpatrick, L., Oldfield, I. F. and Park, K. 2017. Responses of bats to clear fell harvesting in Sitka spruce plantations, and implications for wind turbine installation. – *Forest Ecol. Manage.* 395: 1–8.
- Kotila, M. et al. 2023. Large-scale long-term passive-acoustic monitoring reveals spatio-temporal activity patterns of boreal bats. – *Ecography* 2023: e06617.
- Kunz, T. H., Arnett, E. B., Erickson, W. P., Hoar, A. R., Johnson, G. D., Larkin, R. P., Strickland, M. D., Thresher, R. W. and Tuttle, M. D. 2007. Ecological impacts of wind energy development on bats: questions, research needs, and hypotheses. – *Front. Ecol. Environ.* 5: 315–324.
- Laranjeiro, T., May, R. and Verones, F. 2018. Impacts of onshore wind energy production on birds and bats: recommendations for future life cycle impact assessment developments. – *Int. J. Life Cycle Assess.* 23: 2007–2023.
- Lesiński, G. 2007. Bat road casualties and factors determining their number. – *Mammalia* 71: 138–142.



- Marker Vindpark, A. S., Christophersen, E. B., Westin, M. and Heggøy, A. 2017. MTA OG Detaljplan høgås OG joarknatten vindkraftverk. revision 1. – Rambøll.
- Mathews, F.; Richardson, S.; Lintott, P.; Hosken, D. 2016. Understanding the risk of European protected species (bats) at onshore wind turbine sites to inform risk management. – Report by Univ. of Exeter. Report for RenewableUK.
- Michaelsen, T. C. 2017. Spatial distribution of bats (Chiroptera) in valleys at northern latitudes in Europe. – *Folia Zool.* 66: 196–202.
- McKay, R. A., Johns, S. E., Bischof, R., Matthews, F., van der Kooij, J., Yoh, N. and Eldegard, K.. 2023. Data from: Wind energy development can lead to guild-specific habitat loss in boreal forest bats. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.x0k6djhpr>.
- Middleton, N., Froud, A. and French, K. 2014. Social calls of the bats of Britain and Ireland. – Pelagic Publishing Ltd.
- Millon, L., Julien, J.-F., Julliard, R. and Kerbiriou, C. 2015. Bat activity in intensively farmed landscapes with wind turbines and offset measures. – *Ecol. Eng.* 75: 250–257.
- Montauban, C., Mas, M., Tuneu-Corral, C., Wangenstein, O. S., Budinski, I., Martí-Carreras, J., Flaquer, C., Puig-Montserrat, X. and López-Baucells, A. 2021. Bat echolocation plasticity in allopatry: a call for caution in acoustic identification of *Pipistrellus* sp. – *Behav. Ecol. Sociobiol.* 75: 70.
- Müller, J., Brandl, R., Buchner, J., Pretzsch, H., Seifert, S., Strätz, C., Veith, M. and Fenton, B. 2013. From ground to above canopy – bat activity in mature forests is driven by vegetation density and height. – *Forest Ecol. Manage.* 306: 179–184.
- Neumann, W., Bjärstig, T., Thellbro, C. and Svensson, J. 2022. Footprint of large scale expansion of wind power in productive boreal forests – forests under a zero-emission strategy. – In: EGU general assembly 2022, Vienna, Austria (EGU22-8685), <https://doi.org/10.5194/egusphere-egu22-8685>.
- Norberg, U. and Rayner, J. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. – *R. Soc. Lond. Philos. B* 316.
- Nordic Co-operation | Nordic Council & Nordic Council of Ministers, 2008. History of afforestation in the Nordic countries. In Norden. Denmark. – <https://policycommons.net/artifacts/1138169/history-of-afforestation-in-the-nordic-countries/> on 23 Nov 2023. CID: 20.500.12592/vqnfvc.
- Nordic Energy Research 2021. Renewable energy in the Nordics 2021. – <https://pub.norden.org/nordicenergyresearch2021-03/>.
- O'Mara, M. T., Wikelski, M., Kranstauber, B. and Dechmann, D. K. N. 2019. Common noctules exploit low levels of the atmosphere. – *R. Soc. Open Sci.* 6: 181942.
- Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S. and Hayes, D. 2011. A large and persistent carbon sink in the World's forests. – *Science* 333: 988–993.
- Perks, S. J. and Goodenough, A. E. 2020. Abiotic and spatiotemporal factors affect activity of European bat species and have implications for detectability for acoustic surveys. – *Wildl. Biol.* 2020, wlb.00659.
- Peterson, T. S., McGill, B., Hein, C. D. and Rusk, A. 2021. Acoustic exposure to turbine operation quantifies risk to bats at commercial wind energy facilities. – *Wildl. Soc. Bull.* 45: 552–565.
- Pettersson, R. B., Ball, J. P., Renhorn, K.-E., Esseen, P.-A. and Sjöberg, K. 1995. Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. – *Biol. Conserv.* 74: 57–63.
- Rebelo, H., Tarroso, P. and Jones, G. 2010. Predicted impact of climate change on European bats in relation to their biogeographic patterns. – *Global Change Biol.* 16: 561–576.
- Rehbein, J. A., Watson, J. E. M., Lane, J. L., Sonter, L. J., Venter, O., Atkinson, S. C. and Allan, J. R. 2020 Renewable energy development threatens many globally important biodiversity areas. – *Global Change Biol.* 26: 3040–3051. <https://doi.org/10.1111/gcb.15067>.
- Reimer, J. P., Baerwald, E. F. and Barclay, R. M. R. 2018. Echolocation activity of migratory bats at a wind energy facility: testing the feeding-attraction hypothesis to explain fatalities. – *J. Mammal.* 99: 1472–1477.
- Reynolds, D. R., Chapman, J. W. and Drake, V. A. 2017. Riders on the wind: the aerocology of insect migrants. – In: Chilson, P. B., Frick, W. F., Kelly, J. F. and Liechti, F. (eds), *Aerocology*. Springer International Publishing, pp. 145–178.
- Richardson, S. M., Lintott, P. R., Hosken, D. J., Economou, T. and Mathews, F. 2021. Peaks in bat activity at turbines and the implications for mitigating the impact of wind energy developments on bats. – *Sci. Rep.* 11: 3636.
- Rodrigues, L., Bach, L., Dubourg-Savage, M.-J., Karapandža, B., Rnjak, D., Kervyn, T., Dekker, J., Kepel, A., Bach, P., Collins, J., Harbusch, C., Park, K., Micevski, B. and Minderman, J. 2015. Guidelines for consideration of bats in wind farm projects. – In: Eurobats Publication Series. Vol. 3, pp. 1–51.
- Roeleke, M., Blohm, T., Kramer-Schadt, S., Yovel, Y. and Voigt, C. C. 2016. Habitat use of bats in relation to wind turbines revealed by GPS tracking. – *Sci. Rep.* 6: 28961.
- Roemer, C., Bas, Y., Disca, T. and Coulon, A. 2019. Influence of landscape and time of year on bat-wind turbines collision risks. – *Landscape Ecol.* 34: 2869–2881.
- Roscioni, F., Russo, D., Di Febbraro, M., Frate, L., Carranza, M. L. and Loy, A. 2013. Regional-scale modelling of the cumulative impact of wind farms on bats. – *Biodivers. Conserv.* 22: 1821–1835.
- Ruczyński, I., Hałat, Z., Zegarek, M., Borowik, T. and Dechmann, D. K. N. 2020. Camera transects as a method to monitor high temporal and spatial ephemerality of flying nocturnal insects. – *Methods Ecol. Evol.* 11: 294–302.
- Russ, J. (ed.) 2021. Bat calls of Britain and Europe: a guide to species identification. – Pelagic Publishing.
- Rydell, J. 1989. Feeding activity of the northern bat *Eptesicus nilsoni* during pregnancy and lactation. – *Oecologia* 80: 562–565.
- Rydell, J. 1991. Seasonal use of illuminated areas by foraging northern bats *Eptesicus nilsoni*. – *Holarc. Ecol.* 14: 203–207.
- Rydell, J. 1993. *Eptesicus nilsonii*. – *Mamm. Species* 430: 1–7.
- Rydell, J., Bach, L., Dubourg-Savage, M.-J., Green, M., Rodrigues, L. and Hedenström, A. 2010a. Bat mortality at wind turbines in northwestern Europe. – *Acta Chiropterol.* 12: 261–274.
- Rydell, J., Bach, L., Dubourg-Savage, M.-J., Green, M., Rodrigues, L. and Hedenström, A. 2010b. Mortality of bats at wind turbines links to nocturnal insect migration? – *Eur. J. Wildl. Res.* 56: 823–827.
- Rydell, J., Bogdanowicz, W., Boonman, A., Pettersson, S., Suchecka, E. and Pomorski, J. J. 2016. Bats may eat diurnal flies that rest on wind turbines. *Mamm. Biol.* 81: 331–339. <https://doi.org/10.1016/j.mambio.2016.01.005>.

- Rydell, J., Ottvall, R., Pettersson, S. and Green, M. 2017. The effects of wind power on birds and bats – <http://www.diva-portal.org/smash/get/diva2:1382564/FULLTEXT01.pdf>.
- Rydell, J., Eklöf, J., Fransson, H. and Lind, S. 2018. Long-term increase in hibernating bats in Swedish Mines - effect of global warming? – *Acta Chiropterol.* 20: 421–426.
- Rydell, J., Elfström, M., Eklöf, J. and Sánchez-Navarro, S. 2020. Dramatic decline of northern bat *Eptesicus nilssonii* in Sweden over 30 years. – *R. Soc. Open Sci.* 7: 191754.
- Schnitzler, H.-U., Moss, C. F. and Denzinger, A. 2003. From spatial orientation to food acquisition in echolocating bats. – *Trends Ecol. Evol.* 18: 386–394. [https://doi.org/10.1016/S0169-5347\(03\)00185-X](https://doi.org/10.1016/S0169-5347(03)00185-X).
- Scholz, C. and Voigt, C. C. 2022. Diet analysis of bats killed at wind turbines suggests large-scale losses of trophic interactions. – *Conserv. Sci. Pract.* 4: e12744.
- Scottish Natural Heritage (NatureScot); Natural England, N. R. W. R. S. P. R. E. L., the University of Exeter; the Bat Conservation Trust (BCT) 2021 Bats and onshore wind turbines - survey, assessment and mitigation. – <https://www.nature.scot/doc/bats-and-onshore-wind-turbines-survey-assessment-and-mitigation>.
- Searchinger, T. D., Beringer, T., Holtsmark, B., Kammen, D. M., Lambin, E. F., Lucht, W., Raven, P. and van Ypersele, J. P. 2018. Europe's renewable energy directive poised to harm global forests. – *Nat. Commun.* 9: 3741.
- Snively, M. L., Pendleton, G. W., Christie, K. S. and Blejwas, K. M. 2021. Little brown myotis activity patterns in south-Central Alaska. – *Northwest. Nat.* 102: 216–231.
- Straka, T. M., Fritze, M. and Voigt, C. C. 2020. The human dimensions of a green-green-dilemma: lessons learned from the wind energy – wildlife conflict in Germany. – *Energy Rep.* 6: 1768–1777.
- Sugai, L. S. M., Silva, T. S. F., Ribeiro, J. W., Jr and Llusia, D. 2019. Terrestrial passive acoustic monitoring: review and perspectives. – *BioScience* 69: 15–25.
- Suominen, K. M., Kotila, M., Blomberg, A. S., Pihlström, H., Ilyukha, V. and Lilley, T. M. 2022. Northern bat *Eptesicus nilssonii* (Keyserling and Blasius, 1839). – In: Hackländer, K., Zachos, F. E., (eds), *Handbook of the mammals of Europe*. Springer, pp. 1–27. [https://doi.org/10.1007/978-3-319-65038-8\\_45-1](https://doi.org/10.1007/978-3-319-65038-8_45-1).
- Tidenberg, E.-M., Liukko, U.-M. and Stjernberg, T. 2019. Atlas of Finnish bats. – <http://hdl.handle.net/10138/309134>.
- US Fish and Wildlife 2022. Range-wide Indiana bat & northern long-eared bat survey guidelines. – <https://www.fws.gov/media/range-wide-indiana-bat-and-northern-long-eared-bat-survey-guidelines>.
- Valdez, E. W. and Cryan, P. M. 2013. Insect prey eaten by hoary bats (*Lasiurus cinereus*) prior to fatal collisions with wind turbines. – *West. North Am. Nat.* 73: 516–524.
- Valentin, R. E., Fonseca, D. M., Gable, S., Kyle, K. E., Hamilton, G. C., Nielsen, A. L. and Lockwood, J. L. 2020. Moving eDNA surveys onto land: strategies for active eDNA aggregation to detect invasive forest insects. – *Mol. Ecol. Resour.* 20: 746–755.
- van Klink, R. et al. 2022. Emerging technologies revolutionise insect ecology and monitoring. – *Trends Ecol. Evol.* 37: 872–885.
- Vankat, J. L. 2002. Boreal and temperate forests. – In: *Encyclopedia of Life Sciences*. John Wiley & Sons, Ltd, <https://doi.org/10.1038/npg.els.0003738>.
- Vasko, V., Blomberg, A. S., Vesterinen, E. J., Suominen, K. M., Ruokolainen, L., Brommer, J. E., Norrdahl, K., Niemelä, P., Laine, V. N., Selonen, V., Santangeli, A. and Lilley, T. M. 2020. Within-season changes in habitat use of forest-dwelling boreal bats. – *Ecol. Evol.* 10: 4164–4174.
- Verboom, B. and Spoelstra, K. 1999. Effects of food abundance and wind on the use of tree lines by an insectivorous bat, *Pipistrellus pipistrellus*. – *Can. J. Zool.* 77: 1393–1401.
- Voigt, C. C. 2021. Insect fatalities at wind turbines as biodiversity sinks. – *Conserv. Sci. Pract.* 3: e366.
- Voigt, C. C., Rehnig, K., Lindecke, O. and Petersons, G. 2018. Migratory bats are attracted by red light but not by warm-white light: implications for the protection of nocturnal migrants. – *Ecol. Evol.* 8: 9353–9361.
- Voigt, C. C., Russo, D., Runkel, V. and Goerlitz, H. R. 2021. Limitations of acoustic monitoring at wind turbines to evaluate fatality risk of bats. – *Mamm. Rev.* 51: 559–570.
- Wiersdalen Karlsen, T. 2017. Klagebehandling vindkraftverk i Marker Kommune, <https://webfileservice.nve.no/API/PublishedFiles/Download/201200476/1974700>.
- Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. – *J. R. Stat. Soc. B* 73: 3–36.
- Wråke, M., Karlsson, K., Kofoed-Wiuff, A., Folsland Bolkesjø, T., Lindroos, T. J., Hagberg, M., Bosack Simonsen, M., Unger, T., Tennback, B., Ogner Jåstad, E., Lehtilä, A., Putkonen, N. and Koljonen, T. 2021. Nordic clean energy scenarios: solutions for carbon neutrality. – *Nordic Energy Research*.
- Zhou, N., Hu, X., Byskov, I., Næss, J. S., Wu, Q., Zhao, W. and Cherubini, F. 2021. Overview of recent land cover changes, forest harvest areas, and soil erosion trends in Nordic countries. – *Geogr. Sustain.* 2: 163–174.