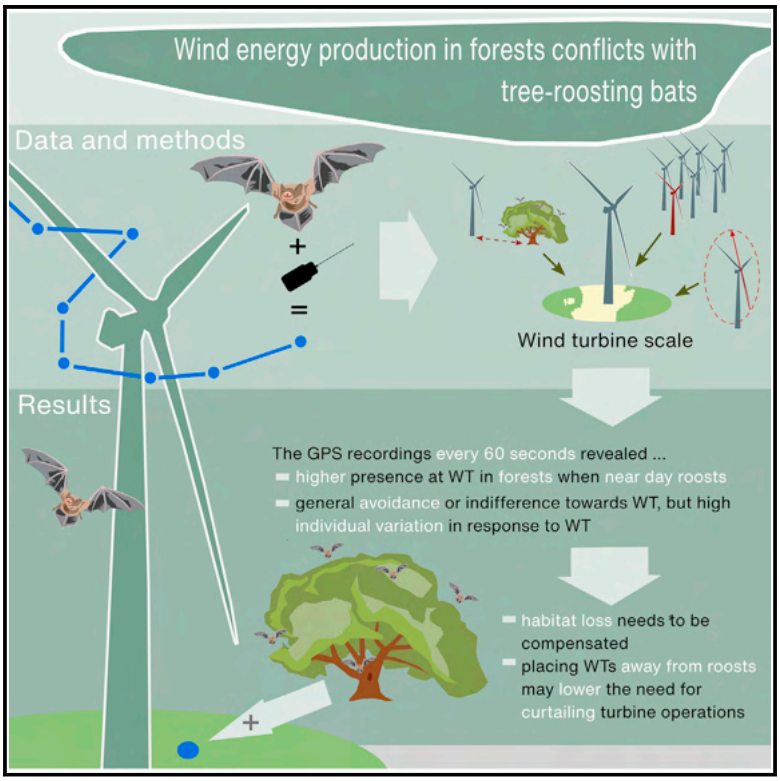
Report

Current Biology

Wind energy production in forests conflicts with tree-roosting bats

Graphical abstract



Highlights

- In forests, bats were more often present at wind turbines (WTs) near roosts
- Beyond roosts, bats avoided WTs, but individual responses varied
- Placing WTs near roosts may increase the casualty risk and the need for curtailments
- Habitat loss due to WT operation must be compensated

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In brief

Using high-resolution GPS tracking from common noctules in Germany, Reusch et al. reveal that bats were most active at wind turbines (WTs) in forests when WTs were placed close to daytime roosts, yet that bats avoided WTs over several km distances beyond roosts, indicating that WTs at forest sites may lead to high numbers of casualties and habitat loss.

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Report

Wind energy production in forests conflicts with tree-roosting bats

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SUMMARY

Many countries are investing heavily in wind power generation,[1] triggering a high demand for suitable land. As a result, wind energy facilities are increasingly being installed in forests,[2,3] despite the fact that forests are crucial for the protection of terrestrial biodiversity.[4] This green-green dilemma is particularly evident for bats, as most species at risk of colliding with wind turbines roost in trees.[2] With some of these species reported to be declining,[5–8] we see an urgent need to understand how bats respond to wind turbines in forested areas, especially in Europe where all bat species are legally protected. We used miniaturized global positioning system (GPS) units to study how European common noctule bats (*Nyctalus noctula*), a species that is highly vulnerable at turbines,[9] respond to wind turbines in forests. Data from 60 tagged common noctules yielded a total of 8,129 positions, of which 2.3% were recorded at distances <100 m from the nearest turbine. Bats were particularly active at turbines <500 m near roosts, which may require such turbines to be shut down more frequently at times of high bat activity to reduce collision risk. Beyond roosts, bats avoided turbines over several kilometers, supporting earlier findings on habitat loss for forest-associated bats.[10] This habitat loss should be compensated by developing parts of the forest as refugia for bats. Our study highlights that it can be particularly challenging to generate wind energy in forested areas in an ecologically sustainable manner with minimal impact on forests and the wildlife that inhabit them.

RESULTS AND DISCUSSION

We used high-resolution biologging to investigate the response of common noctule bats (*Nyctalus noctula*) to wind turbines at a predominantly forested site in late spring and late summer, which is the time when most casualties occur at turbines in Central Europe.[9] We hypothesized that the movement activity of bats would depend on the distance to turbines and roosts. We predicted that common noctules would be most likely active at wind turbines next to daytime roosts and that beyond the vicinity of daytime roosts common noctules avoid wind turbines.[10,11] Specifically, bats were expected to avoid central wind turbines more than peripheral wind turbines and particularly those with large rotors.[10]

We retrieved global positioning system (GPS) tags from 60 of 80 tagged common noctule bats, yielding 8,129 spatial positions (Figure 1). After emerging from roosts at around 12 min after sunset (median), bats traveled over distances of 16 km (median) per night, thereby covering areas of 11 ± 34 km^2 (median ± one SD; kernel density area, KDE 95) (Table S1). The assignment of movement modes to spatial positions by hidden Markov models revealed that about 40% belonged to commuting (COM), 51% to area-restricted movement (ARM) indicating insect hunting, and 9% to undefined movements. ARM was observed mostly over forests and COM over farmland and meadows (Figure S1). The estimates on flight height confirm that common noctule bats were flying in the range of the rotor-swept area of turbines (median 60 m; range 0–614 m; after neglecting negative values; Figure 2). Overall, 2.3% of observed spatial positions were recorded at distances <100 m from the nearest wind turbine (for comparison, 1.4% of the created random positions). A resource selection analysis (Table S3) revealed a higher presence probability of bats at wind turbines sited in forests when these turbines were placed next to daytime roosts of bats (Figure 3A1). This effect was absent for wind turbines placed outside forests, although roosts were also present there, for example, at avenue trees. However, ~79% of documented roosts were in the forest.

Our study highlights that it is key for the permitting process to search intensively for bat roosts in forests designated for wind turbine deployments and to inform stakeholders about suitable and unsuitable sites for wind turbines. We recommend that wind turbines are not installed near daytime roosts because of

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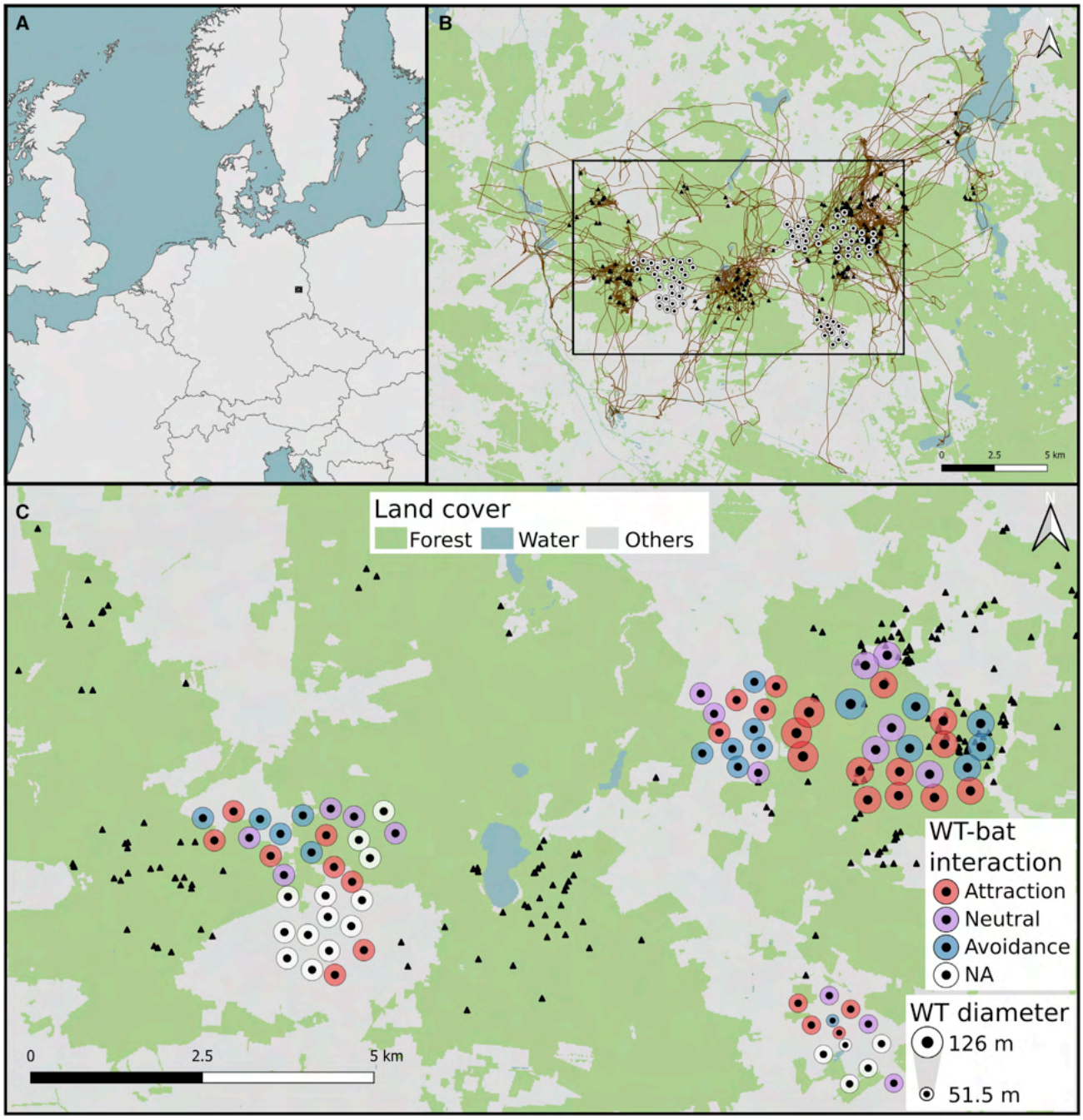

Figure 1. Flight paths of 60 common noctule bats

(A) Study area (black box) in Europe drawn with "rworldmap."[12]

(B) Flight paths, tree roosts (black triangles), wind turbines (WTs; circles with a black center; n = 80),[13] and forest (green), as well as water (blue) (Corine: GeoBasis-DE/BKG 2018).

(C) WT symbol size correlates to the rotor diameter. Colors indicate avoidance (blue), preference (red), or indifferent (purple) behavior of bats toward WTs given as the relationship between random versus observed locations within a 100 m radius around wind turbines. White: no locations.

See also Figure S1 and Table S1.

the following two reasons: (1) a high activity of bats at wind turbines close to roosts may lead to high numbers of casualties. Many aerial insectivores such as common noctule bats use tree hollows for maternity colonies (late spring and early summer) and for mating (late summer and early fall), which may lead to an increased abundance of individuals in the vicinity of roosts during these periods. After weaning, juveniles may use the area around maternity roosts for their first flights, starting around

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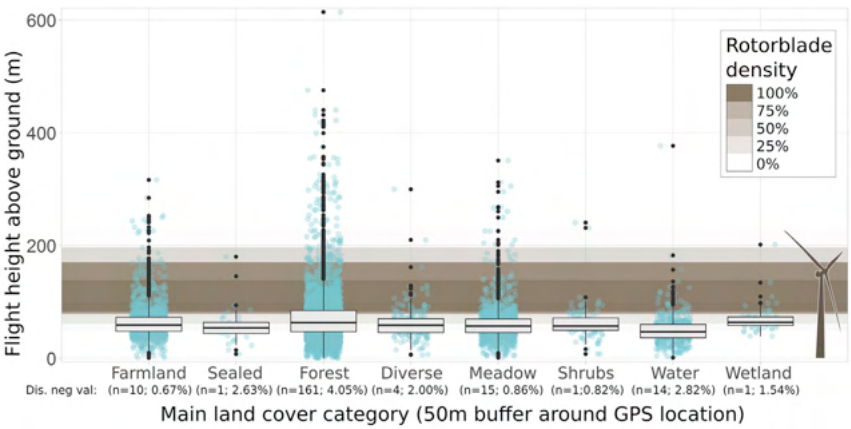

Figure 2. Estimated flight height above ground (m) in relation to main land cover and rotor blade density

Background color intensity depicts the rotor blade density in the study area at the respective heights. The x axis shows the different main land cover categories (50 m radius around the GPS location): farmland, meadow, shrubs and herbaceous vegetation (shrubs), forest, sealed surface (sealed), water, and wetland. "Diverse" describes GPS locations covering several land cover categories with no category exceeding 50% within the 50 m buffer. Negative flight height estimations were disregarded (Dis. neg val, number of disregarded values, and percentage per main land cover in parenthesis). See also Table S1.

July in the case of temperate zone bats of the Northern hemisphere. Apparently, juvenile bats are particularly vulnerable at wind turbines.[14] In late summer, bats may swarm around mating roosts, which may also cause an increased abundance of bats around such roosts. Frequent bat casualties at wind turbines next to daytime roosts may deplete local populations and cause local or regional extinction of species.[5,6] It should be noted that the availability of natural roosts may change during the operation period of wind turbines owing to the natural decay of trees and the activity of woodpeckers. Therefore, even when avoiding bat roosts at the time of turbine erection, it cannot be ruled out that roosts establish during the later operation period of turbines, particularly in case of cavities created by woodpeckers, which seems to be preferred by common noctules.[15] (2) If permitting authorities grant companies to set up wind turbines in forests, it seems necessary to curtail the operation of wind turbines during times of high bat activity.[2] In Germany, acoustic surveys are conducted to identify ambient conditions when bats are most active in the rotor-swept area. These data can then be used to formulate criteria for stopping temporarily the operation of wind turbines when bats are active.[2] Such curtailment schemes may reduce the number of casualties by more than 80% at low revenue losses for the company; however, this has only been shown for turbines sited in open landscapes.[16] We argue that it is likely that such curtailments are stricter for wind turbines operating in than outside forests. This will lower the potential for wind power generation at forested sites, leading to lowered contributions to the reduction of greenhouse gas emissions and lowered monetary revenues for companies. However, how do bats respond to wind turbines in forests at some distance to bat roosts?

To account for the roost effect at forested sites, we excluded all spatial positions of bats at distances <500 m from the nearest roost based on the median of the spatial position in relation to the wind turbines rounded up to the nearest hundredth digit (removing 25,949 spatial positions [53.2%] of the total dataset and 18,203 [55.2%] for the male subset). Removing this effect, we observed the avoidance of bats toward wind turbines inside and outside forests (Figures 3A2, S2A2, S2A4, and S2A6). The rotor diameter of wind turbines had no effect on the avoidance response of common noctule bats (Figures 3B4 and 3B6). However, we observed that bats tend to be less active at central than at peripheral wind turbines at forest sites, whereas bats selected central wind turbines more than peripheral wind turbines outside forests (Figures 3C2, 3C4, and 3C6). The avoidance behavior of bats at the population level was most apparent for males in late summer (Figures S2F2, S2F4, and S2F6). Avoidance responses of common noctule bats over several km distances have already been observed in a study conducted at a coastal migration corridor, which suggested that bats lose habitats in landscapes with high densities of wind turbines.[11] Acoustic surveys at farmland sites also confirm that the acoustic activity of bats decreases over 1 km distance toward wind turbines.[17,18] Recently, it was shown that forest specialist bats, which belong to the guild of narrow-space foragers,[19] halved their acoustic activity along a transect from 450 m distance to 80 m distance from wind turbines at forested site.[10] Accordingly, avoidance behavior toward wind turbines may be a general phenomenon observed over larger spatial scales in various bat species across different functional guilds. This avoidance behavior may be driven by turbine noises, which may startle bats or interfere with their acoustic orientation—possibly also with the network foraging style of open-space foraging bats like common noctules that depend on eavesdropping on conspecifics.[20,21] However, do all individuals respond in a similar way to wind turbines?

To elucidate individual responses of common noctule bats to wind turbines, we analyzed the data using resource selection functions (distance to closest wind turbine; integrated as individual random slopes in models). This analysis confirmed that on the population level (fixed effects) common noctule bats avoided wind turbines over several km distances; however, responses varied largely between individuals (Figure 4; Table S3). Across all seasons and sexes, only 14% of the individuals differed from the observed general avoidance response toward wind turbines, and this difference was not explained by habitat. In addition, we conducted a seasonal comparison of individual responses toward wind turbines to elucidate whether the response differs between early and late summer. This analysis was only performed with data from male bats since we were not allowed to work with pregnant or lactating females in early summer. Based on the data of males, we observed indifferent responses of males toward wind turbines in early summer, but avoidance of wind turbines in late summer (Figures 4B and 4C; Table S3). We were not able to identify specific factors that explained the inter-individual variation of the response behavior of bats toward wind turbines (Figure S3).[22]

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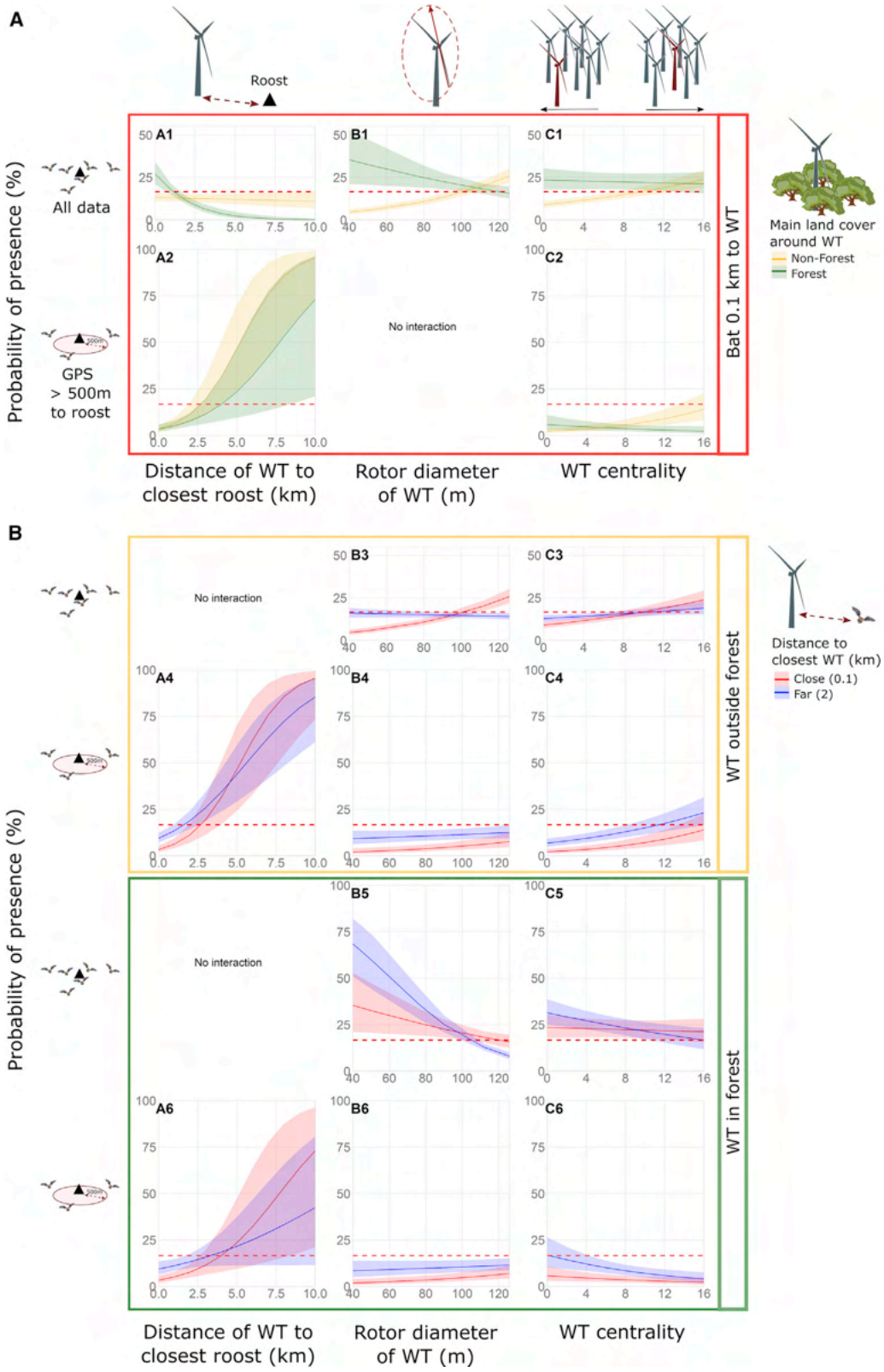

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It is possible that unaccounted intrinsic or extrinsic factors might cause bats to respond differently. For example, bats could engage in exploratory behavior and mistake wind turbines for large trees.[23] The observation of a less pronounced avoidance behavior toward wind turbines in late compared with early summer is consistent with this idea. Juvenile bats might explore turbine structures; however, we could not test age as a factor since fully grown juvenile and adult bats looked similar. Bats may also respond to wind turbines depending on whether or not wind turbines operate under a curtailment scheme. Unfortunately, we had no access to the operation schemes of local turbines, which prevents us from conducting a more detailed analysis.

Conclusion

Forests are preferred habitats for many bat species worldwide. Building wind turbines in forests goes along with fragmentation when maintenance roads are built and with habitat loss when clearings are created for wind turbines.[2] In Europe, monitoring schemes are usually required to assess the potential of wind turbines to impact forest-associated bat species. Accordingly, habitat loss caused by clearings has to be compensated by setting aside other forest patches for bats. Based on our GPS study, we now reveal that common noctule bats are most likely active at turbines within a 500 m distance to daytime roosts. Therefore, we recommend maintaining a minimum distance of 500 m between bat roosts and wind turbines. Further, strict curtailments should be put into practice to avoid high numbers of casualties at wind turbines in forested areas. In addition, we observed that—beyond 500 m distance to roosts—common noctule bats avoid wind turbines. This avoidance behavior toward wind turbines is consistent with recent observations in the same species and also in bats of other functional guilds.[10,11,17,18] Avoidance of bats toward wind turbines might have remained unnoticed until recently because previous surveys have focused primarily on the rotor-swept area of turbines using either ultrasonic detectors or thermal imagery.[2,23] However, the detection ranges of these techniques for monitoring bats are limited to a few tens of meters.[24] In summary, wind turbines at forested sites impact bats in several negative ways. If wind turbines have to be built in forests, i.e., in the absence of alternative sites or alternative sources of renewable energy, we call for engaging in detailed pre-construction surveys that involve searching for potential roosts in the vicinity of prospected sites. The observation of bats avoiding wind turbines over several hundred meters[10] or even several km suggests that wind turbine operation in forests leads to habitat loss for bats over a larger spatial scale than currently considered during the permitting process. We therefore request that this habitat loss be considered in the planning of wind energy facilities. If wind turbines are planned to be located in forests, we suggest that forest areas larger than the cumulative area of turbine clearings and maintenance roads be provided to compensate for the habitat degradation associated with wind turbine operation. The selected forest areas should be at a sufficient distance from wind turbines to avoid any disturbances caused by wind turbines over long distances. Further, the set-aside forests should be of similar structure if not even of higher quality.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2022.12.050.

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AUTHOR CONTRIBUTIONS

C.C.V. and S.K.-S. conceptualized the study. C.R., A.A.P., and M.F. carried out the fieldwork. C.R. conducted the analyses with the support of A.A.P. and S.K.-S. C.C.V. and C.R. drafted the original manuscript. S.K.-S. reviewed and edited the manuscript. All authors commented on the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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Figure 3. Presence probability (95% CI) of common noctule bats in relation to WT characteristics

(A1–A6) Distance to roost (km), (B1–B6) rotor diameter (m), and (C1–C6) centrality (number of WTs within 1 km radius). The response was estimated for (A) bats close to WTs in different main land covers around turbines (red box), as well as (B) turbines in open areas (yellow) and in forests (green) regarding distance to WTs (near [0.1 km]; far [2 km]). The remaining fixed effects were set to the median. The red dashed line describes the 16.7% threshold (observed:random positions = 1:5) separating habitat avoidance (below) from preference (above).
See also Figures S2–S4 and Tables S2 and S3.

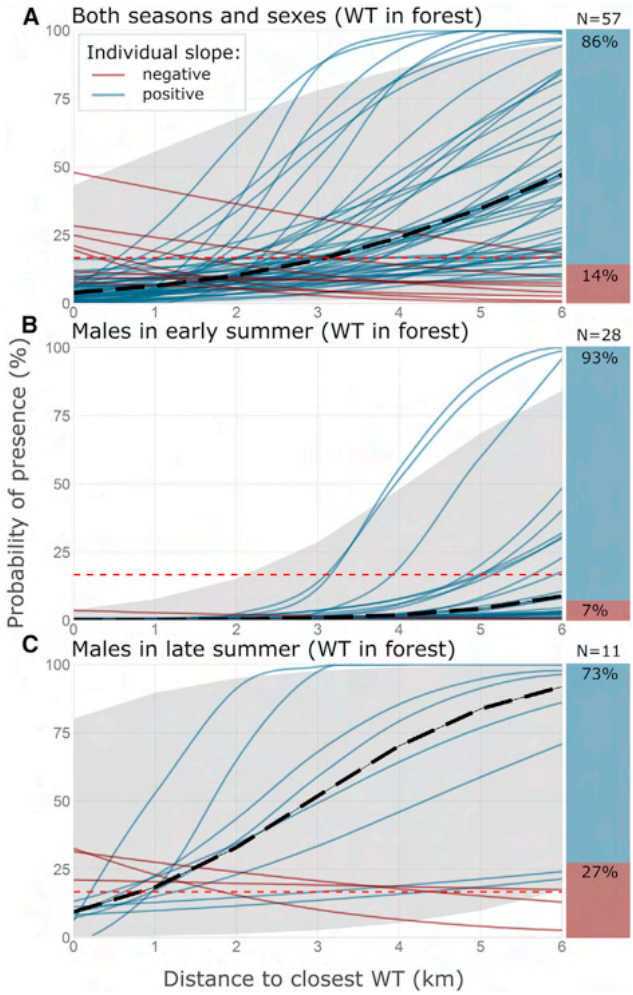

Figure 4. Individual responses of common noctule bats toward wind turbines (WTs) excluding positions <500 m near roosts

Presence probability in relation to wind turbines for both sexes and seasons (A), and males only in early (B) and late summer (C). Solid lines represent individuals (dark red, negative slope; blue, positive slope), and dashed lines represent population levels (gray polygon, prediction interval). The red dashed line separates avoidance (below) from preference (above). Stacked boxplots next to the figures show the percentage of negative and positive slopes and the total sample size on top.

See also Figures S2–S4 and Tables S2 and S3.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Annotated GPS locations	This study	https://doi.org/10.5281/zenodo.7535030
Experimental models: Organisms/strains		
Common noctule bat *Nyctalus noctula*	Northeastern Germany; n atural tree roosts	N/A
Software and algorithms		
R 3.6.2[25]	The R Project for Statistical computing[25]	https://cran.r-project.org/mirrors.html
R Studio 1.1.383	R Studio[26]	https://www.rstudio.com/products/rstudio/download/
QGIS 3.10.3	QGIS Geographic Information System, QGIS Association	https://www.qgis.org
Inkscape	Inkscape Project, 2020	https://inkscape.org
Other		
GPS nanoFix GEO-MINI	Pathtrack, Otley, United Kingdom	https://www.pathtrack.co.uk/
Corine land cover map ("Digitales L andbedeckungsmodell für Deutschland", 2018 (LBM-DE2018))	GeoBasis-DE/ Federal Agency f or Cartography and Geodesy (BKG)[27]	https://gdz.bkg.bund.de
Digital terrain model ("Digitales Geländemodell Gitterweite 200m für Deutschland", 2015 (DGM 200))	GeoBasis-DE/ Federal Agency for Cartography and Geodesy (BKG)[28]	https://gdz.bkg.bund.de
Wind turbine data ("Windkraftanlagen d es Landes Brandenburg"; last update 10.01.2020)	Landesamt für Umwelt Brandenburg[13]	https://mlul.brandenburg.de/lua/gis/wka.zip

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Christian C. Voigt (voigt@izw-berlin.de).

Materials availability

This study did not generate new unique reagents.

Data and code availability

The datasets used generated in this study are available at https://doi.org/10.5281/zenodo.7535030. R code used in analysis is available from the lead contact.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Experimental bats and site

Our work was conducted during late spring (May and June) and late summer (August and September) in 2019 and 2020 in Brandenburg (Germany) under the animal welfare license #2347-5-2019 and conservation license #4543/131+3#27171/2019. Our study site was dominated by forests (43 % of local land cover) and farmland (28 %), where wind turbines were placed both either in pine silvicultures (~30 % of wind turbines) or farmland (~50 %). The study area included three wind parks with a total of 80 wind turbines (on average 27 per wind park).

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METHOD DETAILS

GPS Attachment and Data Collection

During late spring, we focused on males to avoid disturbance of maternity roosts. At daytime, we monitored bat boxes in the vicinity of wind parks for the presence of common noctule bats. We selected bats for our study from these boxes. In case we observed bats in natural roosts, we captured emerging bats with mistnets (8-10m length, 10 mm mesh size, Solida, Steinbach, Germany; 6-9m length, 16mm mesh size, Ecotone, Gdynia, Poland) set up at various heights (2-18 m) in front of the roost. We noted the sex and the age (based on epiphyseal closure) in each captured bat. In addition, we measured the forearm length (0.1mm, digital caliper, Ecotone, Gdynia, Poland) and body mass (precision 0.1 g, electronic pocket scale, Ecotone, Gdynia, Poland). The GPS-VHF unit was protected from the elements by a light-weight rubber bag, which was glued to the back of bats with skin glue (Torbot bonding cement, Torbot, Cranston, USA). By attaching the unit to the fur (and not the skin), we ensured that the GPS-VHF unit would fall off the bat within about 5 days. For retrieving the tagged bats or the GPS-VHF unit, we located the VHF signal of the radio-transmitter by homing in using a receiver and an antenna (ICOM IC-R30, ICOM, Japan; Australis 26K Receiver, Titley Scientific, Australia). The complete unit made up on average 7.9 % of the bat's body mass, which we considered acceptable given the shortness of our experiment, and since past studies could not detect negative effects on bats equipped with these or heavier tags.[14,20–22,29–31] In total, we equipped 80 common noctules with GPS logger units (nanoFix GEO-MINI. Pathtrack, Otley, United Kingdom), of which we retrieved 60. Each tag was also equipped with a radiotransmitter (Telemetrie-Dessau, Dessau, Germany) for retrieving either the tagged bat or the separated GPS unit. Units weighed about 2.3 g, which made up 7.9 ± 0.9 % (mean ± one standard deviation) of the bats' body masses (29.1 ± 3.1 g; range 24.1-39.7 g). GPS units were programmed to start recordings at the day when tags were employed if the individual was caught during the day or in the subsequent night when bats were captured while emerging from the roost. This ensured that caught individuals habituated to the attached GPS logger. For recording nights, GPS units sampled spatial positions every minute, starting at 20:00 or 21:00 hours (CET; depending on sunset) and lasting until 02:00 hours (CET), the presumed latest return time of common noctules.[22,31]

Data preparation and environmental predictor variables

For all data processing and analysis we used the software R[25] and R Studio.[26] We described flight paths by using basic parameters such as total distance traveled, duration (Table S1; Figure S1), step length (distance between subsequent spatial positions of a track), turning angles (angle between three subsequent spatial positions of a track) and speed (step length divided by time elapsed between the corresponding spatial positions). We determined the flight height above the ground (m) (see results and discussion, as well as, Figure 2) by subtracting the height of the Earth's surface[28] from the height above the geoid estimated by our GPS devices. Negative values were disregarded (Figure 2). Due to the high level of imprecision of altitude measured by GPS devices,[32] we did not use the flight height above ground estimates in further analyses. We used Hidden Markov models to assign one of two movement modes, namely Area Restricted Movement behavior (ARM) or COMmuting behavior (COM), to each GPS location based on step length and turning angles. We set mean step lengths to starting values of 40 m (± 40 m standard deviation SD; state one/ ARM) and 200 m (± 200 m SD; state two/ COM). Furthermore, turning angle means were set to π (state one/ ARM) and 0° (state two/ COM). We fitted the Hidden Markov model with a gamma distribution for step length and von Mises distribution for turning angles (fitHMM function, R package 'moveHMM').[33] A threshold of 0.75 was set to correctly assign one of the states to a GPS location. We characterized GPS locations below this certainty level as undefined. The two resulting states were later used for separating foraging from search behavior. Specifically, short step lengths and larger turning angles were used to identify foraging behavior (indicated by ARM). Straight trajectories defined by small turning angles and rapid flights defined by large step lengths were used to identify search behavior (indicated by COM). Based on a 20 m raster of the Corine land cover map (LBM-DE2018; see key resources table), we assigned the main underlying land cover type within a buffer of 50 m to each GPS location. The land cover types were summarized into nine categories: sealed surface, city green, farmland, meadows, shrubs and herbaceous vegetation, forest, open natural areas, wetland and water. After estimating the proportion of each land cover category within the 50 m buffer, we selected the category with the highest proportion inside the buffer. If the main category represented >50 % of the 50 m buffer, the GPS location was assigned to this land cover type, otherwise it was characterized as "diverse". Furthermore, we calculated the distances of the GPS locations to the closest WT.[11,27]

QUANTIFICATION AND STATISTICAL ANALYSIS

The statistical analysis was also done with the software R[25] and R Studio.[26] We tested whether avoidance of or attraction to wind turbines, expressed as the probability of bat presence, depended on features (rotor diameter) and site characteristics of wind turbines (WT; distance to potential bat roosts and density of wind turbines, i.e. central or peripheral location of WT in relation to others in a radius of 1 km around wind turbines, hereafter 'centrality'). We set the rotor diameter, distance to roosts and WT centrality in statistical interactions with the surrounding main land cover of the WT (forest and non-forest areas) and distance of bat spatial positions to wind turbines (Table S3). Thus, the full model formula was: Presence ~ (rotor diameter + distance to potential bat roosts + centrality) * forest and non-forest + (rotor diameter + distance to potential bat roosts + centrality) * distance bat-WT + (distance bat-WT | bat ID). A subset of data from only males was used to test for seasonal differences by including three-way-interactions with field season in the model selection. This leads to the following full model formula for the male data subset: Presence ~ ((rotor diameter +

distance to potential bat roosts + centrality) * forest and non-forest) * season + ((rotor diameter + distance to potential bat roosts + centrality) * distance bat-WT) * season + (distance bat-WT | bat ID). The analyses were based on resource selection functions (RSF), in which we analyzed preference for certain WT characteristics against randomized spatial positions within the 100% minimum convex polygon of individual flight paths (RSF-MCP100$_{flightpath}$) in a use-vs.-availability design (see Figure S4), based on the protocol of Reusch et al.[11] We placed five random positions per observed GPS location randomly anywhere within the 100% MCP of the according individual flight path and fitted generalized linear mixed effect models with Template Model Builder (glmmTMB function from R package 'glmmTMB')[34] with binomial error distribution (see Tables S2 and S3). The resulting ratio of observed to random positions of 1:5 leads to a 16.7 % threshold (calculation: (1/(1+5))*100 = (1/6)*100 = 16.7 %) separating habitat avoidance (below) from preference (above) (e.g. see Figures 3 and S3). We included individuals as random effects in the RSF to test for differences in the response of individuals toward WT (see Figures 4 and S4; Table S3). Specifically, individuals were included as random intercept and the distance to closest wind turbine was integrated as individual random slopes in the models (see Tables S2 and S3). Model selection was based on the Akaike information criterion corrected for small sample sizes (AICc) and we selected simpler models whenever dAICci < 2, for dAICci = AICci – AICcmin (see Table S2).[35,36] We, additionally, performed model averaging for the candidate models with a dAICc < 2 to confirm our results (see Table S3). Numeric variables included as fixed effects in the model selection were tested for multicollinearity and only one of the compared variables was included in the model if |Kendall's tau| > 0.7.[37] This was the case for rotor diameter and hub height of WT in the study area (Kendall's tau = 0.97, $N_{observations}$=48774). We chose rotor diameter for the further analyses based on it indicating the actual risk area for bats. To assess model quality we determined the area under the curve (AUC) (see Table S3). For better visualization 0.1 km (close) and 2 km (far) were chosen as representative values for distance to WT in figures based on observations in the field.

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Supplemental Information

Wind energy production in forests conflicts with tree-roosting bats

Christine Reusch, Ana Ailin Paul, Marcus Fritze, Stephanie Kramer-Schadt, and Christian C. Voigt

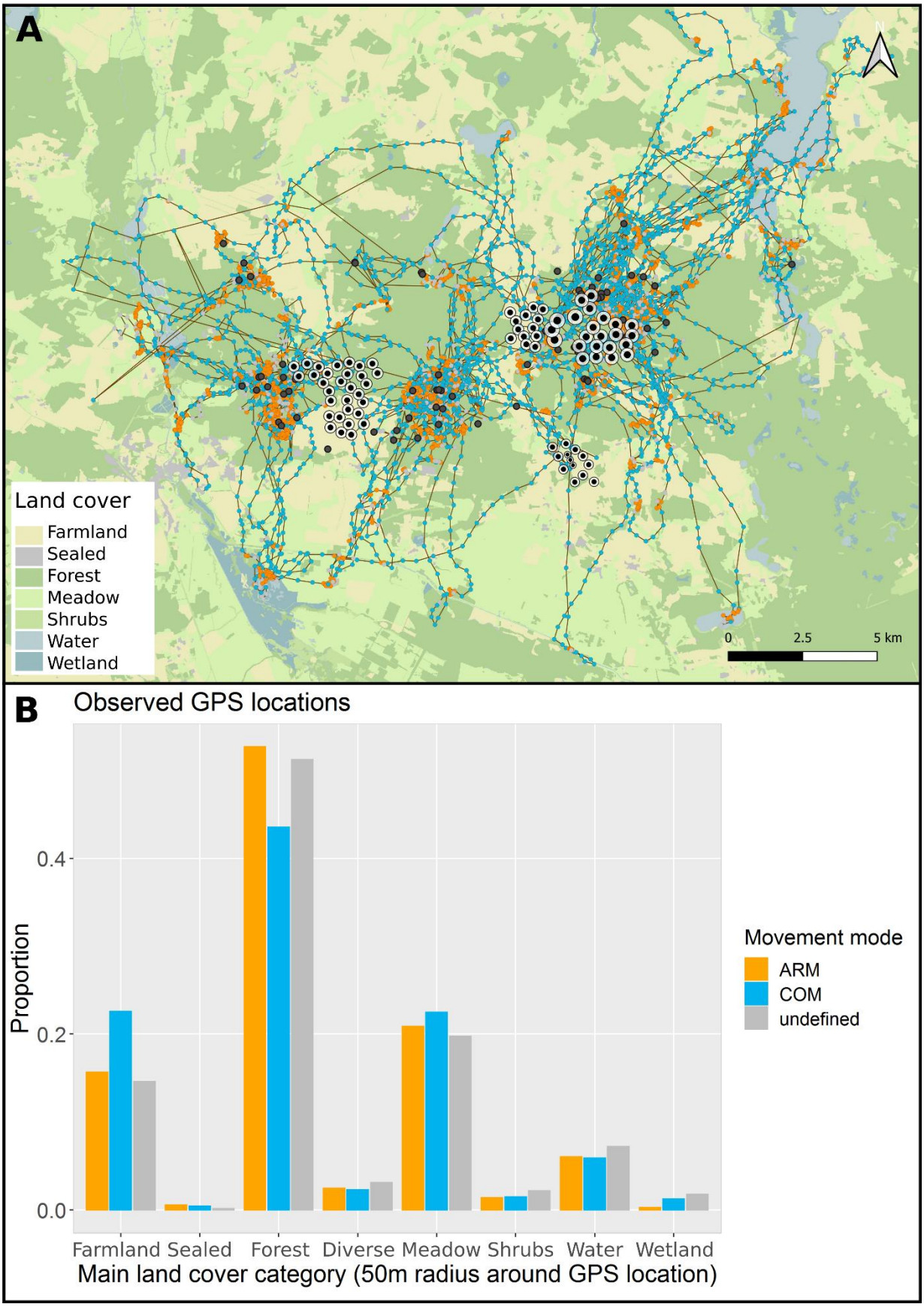

Figure S1 Distribution of movement modes with regard to main land cover. Related to figure 1, table S1 and STAR methods. A) Flight paths of common noctule bats (*Nyctalus noctula*; N=60) under consideration of movement mode in Germany (Brandenburg). Each GPS

position was assigned to the estimated movement mode (orange – area restricted movement (ARM), light blue – commuting (COM), grey – undefined). The background map was obtained from Corine landcover map.[S1] Information on wind turbines (white circle with black dot in the center; N=80 within our study site) was obtained from LfU (2020).[S2] Dark grey points indicate tree roosts. B) Proportion of main land cover categories on population level in dependence of movement mode. On the x axis the different main land cover categories within a 50m radius around the GPS location are shown: Farmland, meadow, shrubs and herbaceous vegetation (Shrubs), forest, sealed surface (Sealed), water and wetland. 'Diverse' describes GPS locations covering several land cover categories with no category exceeding 50% of the 50m buffer. The movement modes ARM, COM and undefined each sum up to 1. Only the observed data are included in this figure.

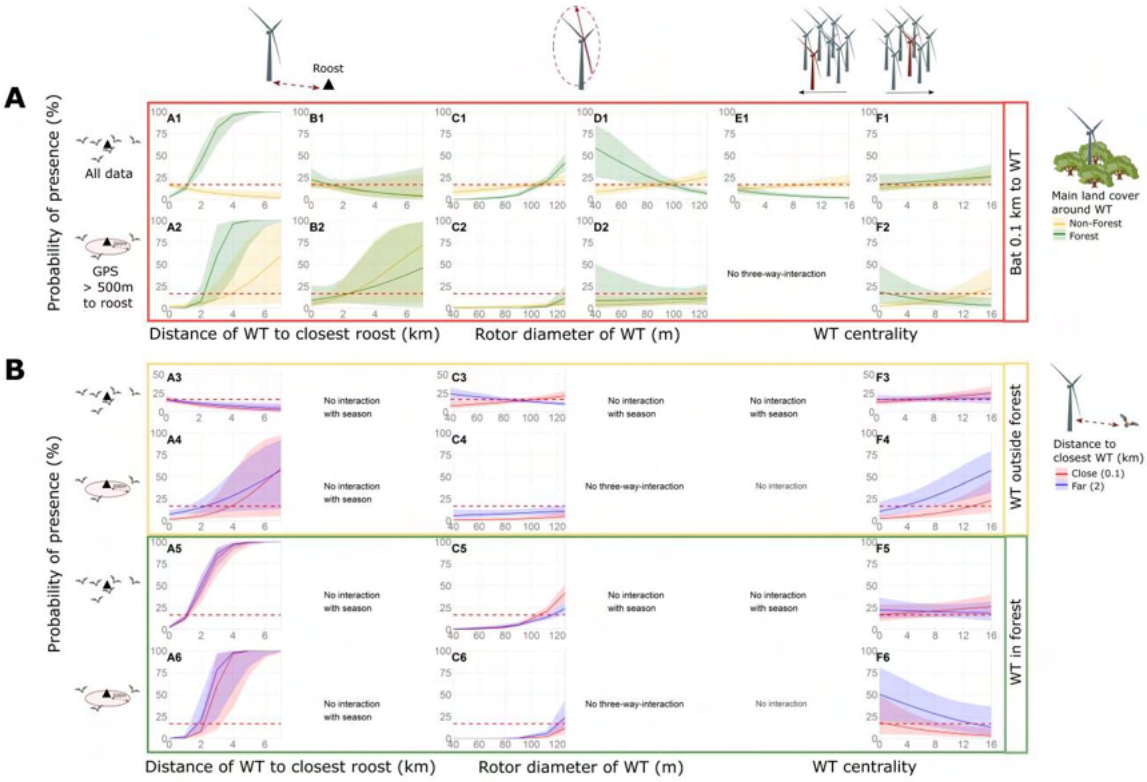

Figure S2 Estimated probability of presence of male common noctules (*Nyctalus noctula*) in relation to wind turbine (WT) characteristics and field season. Related to figures 3-4, figures S3-S4, and tables S2-S3. The columns show the probability of presence with regard to A1-A6 & B1-B6) the distance between WT to closest roost (km), C1-C6 & D1-D6) diameter of rotor blades (m) and E1-E6 & F1-F6) centrality (number of WT within 1 km radius). For each characteristic early summer is shown on the left and late summer on the right side. The response was estimated for A) bats close to WT in different main land covers around WT (red box), as well as B) WT in open areas (yellow) and in forests (green) with respect to distance to WT (near (0.1 km); far (2 km)). The associated polygons show the respective 95% confidence interval. The remaining fixed effects of the models were set to the median (rotor diameter = 90 m, number of neighboring WTs = 6, distance of WT to closest roost = 0.44 km, distance of GPS to WT = 0.1 km (blue frame), and main land cover around WT = non-forest (rows 3-4; yellow frame) or forest (rows 5-6; green frame)). The red dashed line describes the 16.7 % threshold (observed:random points = 1:5) separating habitat avoidance (below) from preference (above). The analysis is based on the complete male dataset of the local RSF (rows 1, 3 and 5) as well as a male data subset with GPS positions at >500 m distance from a potential daytime roost (rows 2, 4 and 6).

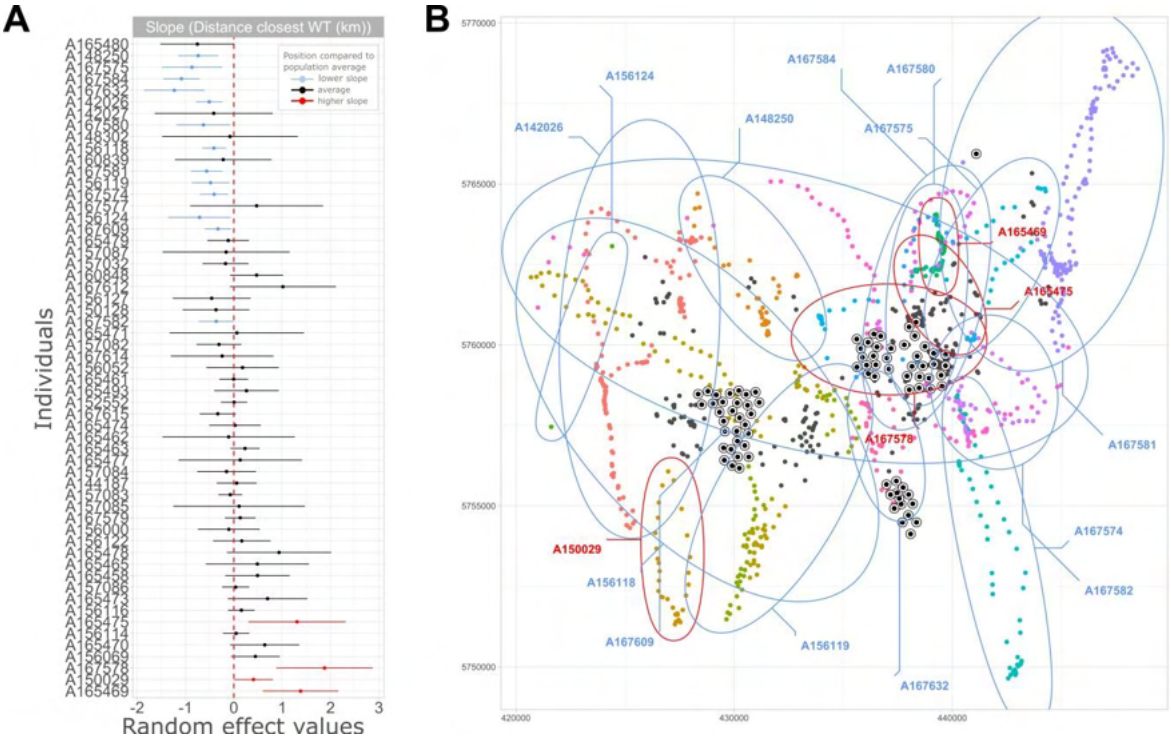

Figure S3 Individual variation in behavior towards wind turbines (WT) and the spatial context excluding roost near behavior. Related to figures 3 and 4, figures S1-2, S4, as well as, tables S2-S3. A) Forest plot of the random slope values per individual grouped by their behavior with regard to the distance to the closest WT (km) in comparison to the population. The model included both seasons and sexes, but locations ≤500 m closest roost were removed. The horizontal lines show the 95% confidence interval. B) GPS locations of those individuals that show a higher or lower slope than given in the population level (colors representing individuals). Ellipses, values and individual labels are colored according to the legend in A). Dark grey points characterize tree roosts and white circles with black dots in the center are WT[S2].

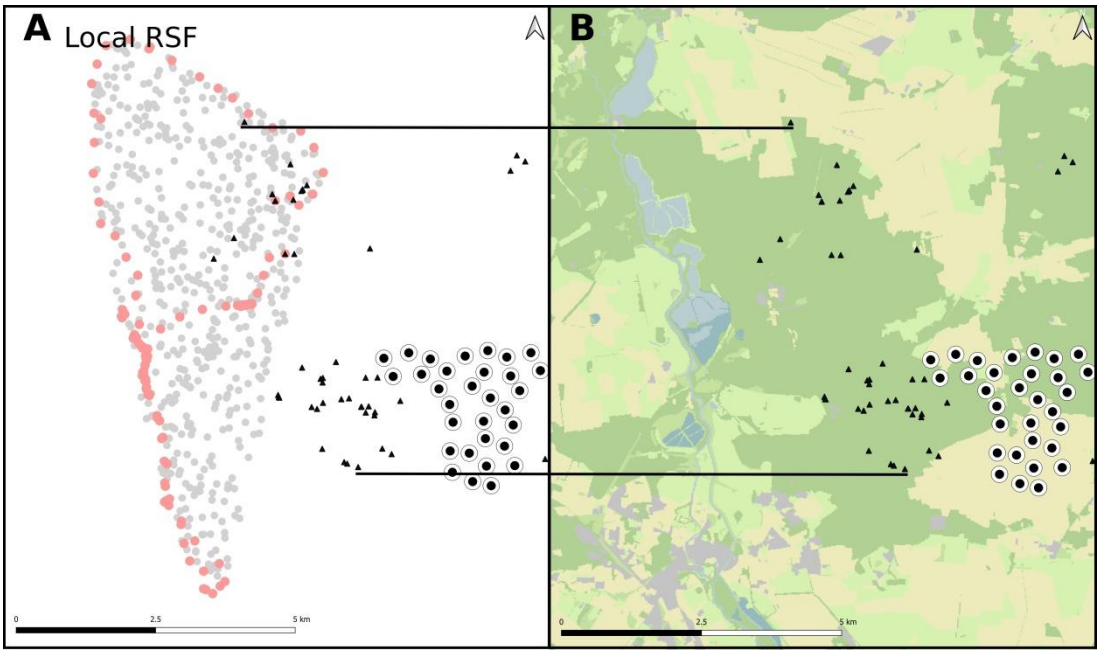

Figure S4 Overview of the methodological approach. Related to figures 3-4, figures S2-S3, tables S2-S3 and STAR methods. A) The data are shown for an exemplary flight path ("21529_19617_A142026") at a local scale (RSF with regard to an individual MCP100 per flight path; RSF $_{MCP100/flight\ path}$). Random points are grey, while the observed GPS locations are given in pink. B) shows the covered area where random points have been generated. The background map was obtained from Corine landcover map.[S1] Information on WT (symbol: white circle with black dot in the center) was obtained from LfU (2020).[S2] Tree symbols characterize tree roosts used by the individuals.

Movement parameter	Median (minimum and maximum)
Flight path per individual:	2 (1 - 3)
Total flight distance per flight path (km):	16 (3 - 46)
Maximal distance to start per flight path (km):	4 (0 - 18)
Flight duration (min):	124 (21 - 314)
Minimal distance to closest WT (m):	157 (6 - 4009)

Table S1 Description of flight paths of common noctule bats (*Nyctalus noctula*). Related to figures 1-2 and figure S1. The described flight paths belong to 60 individuals (42 males, 18 females) in Brandenburg in early and late summer of 2019 and 2020. Movement parameters (median and range values) were calculated across all 107 flight paths. These data were filtered for the subsequent use versus availability analyses ($N_{individuals}$ = 60, $N_{flight\ paths}$ = 107, $N_{GPS\ locations}$ = 8129).

Supplemental references

[S1] GeoBasis-DE/BKG (Federal Agency for Cartography and Geodesy). 2018. Digitales Landbedeckungsmodell für Deutschland (LBM-DE2018). https://gdz.bkg.bund.de.

[S2] LfU (Landesamt für Umwelt Brandenburg). 2020. Windkraftanlagen des Landes Brandenburg. https://mlul.brandenburg.de/lua/gis/wka.zip. Last update 10 January 2020.