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Research Article

# Will future wind power development in Scandinavia have an impact on wolves?

**Cecilia Miltz[1], Ane Eriksen[1], Camilla Wikenros[2], Petter Wabakken[1], Håkan Sand[2] and Barbara Zimmermann[1]**

[1]Department of Forestry and Wildlife Management, Inland Norway University of Applied Sciences, Campus Evenstad, Koppang, Norway
[2]Department of Ecology, Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, Riddarhyttan, Sweden

**Correspondence: Cecilia Miltz (cecilia.miltz@gmail.com)**

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The global energy demand is growing, and the world is shifting towards using more renewable energy, like increased onshore wind power development. We used Global Positioning System (GPS) and Very High Frequency (VHF) location data from adult, territorial wolves *Canis lupus* in Scandinavia (Sweden and Norway; 1999–2021), to examine the potential for wind power development to affect wolf behavioural ecology. We examined the spatial overlap of areas proposed for wind power development with wolf territory activity centres prior to construction, to test to what extent overlap varies with season, time of day and social status (breeding versus non-breeding wolves). Measures of overlap were the distance between wolf activity centre points and nearest proposed wind turbine, the probability of proposed wind turbines being within the activity centre, and the density of proposed wind turbines within the activity centre. The wolf activity centre points were closer to sites of proposed turbines in early summer than in late winter and the density of proposed turbines in the activity centre was higher in early summer than in late winter. These findings probably result from an altitudinal shift in wolf area use between summer and winter. We also found that the probability for proposed turbines to be within the activity centre was higher for non-breeding than for breeding wolves during early summer, whereas it was higher for breeding compared to non-breeding wolves during late winter. This difference might be an effect of that breeding wolves have a restricted area use during the early summer season (denning period), resulting in a lower probability of turbines being inside their activity centre as compared to late winter. There was no clear pattern for other seasonal and social status differences. The results should be viewed as a starting point for further research and supplemented with before-after studies.

Keywords: environmental impact, GPS collars, renewable energy, space use, wind turbines, wolf

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## Introduction

The global demand for renewable and non-renewable energy from human activities is on the rise with a 20% increase from 2009 to 2021 (REN21 2021). In the light of climate change, many countries around the world are shifting towards using renewable energy (United Nations 2021). In fact, wind power development has increased nearly 53% from 2019 to 2020, and onshore wind power made up 36% of new power capacity installations (Global Wind Energy Council 2021, REN21 2021).

Onshore wind turbines are built in wind-exposed places (Ryberg et al. 2020), often in areas of relatively high elevation in the landscape. Development sites for wind turbines are constrained by several criteria, such as steep slopes and short distances to water bodies, settlements, roads and monuments (Ryberg et al. 2020). Wind power constructions also come with alterations to the habitat including cleared vegetation, intense and loud installation activity, and the construction of roads, buildings, and power lines (Kuvlesky et al. 2007, Helldin et al. 2012).

Wildlife can be affected by wind power development in diverse ways. Direct disturbances by wind turbines include noise, visual disturbance, or direct mortality (Arnett et al. 2007, Kuvlesky et al. 2007, Helldin et al. 2012, Lovich and Ennen 2013). Such direct disturbances can, for example, lead to a disruption of acoustic communication of animals, habitat fragmentation, and barrier effects (Helldin et al. 2012). Indirect impacts of wind power development include increased human activity due to improved access for hunters and recreationists (Helldin et al. 2012). Other direct and indirect effects of wind power development on wildlife relate to the alteration and loss of habitat (Arnett et al. 2007, Lovich and Ennen 2013). Most studies on the effects of onshore wind power development on wildlife have been focusing on avian species and bats (Kuvlesky et al. 2007). Consequences for those species can be both direct effects, such as mortality due to collisions, or effects due to, for example, habitat changes (Rydell et al. 2012). There are some studies on large terrestrial mammals investigating the response to wind power development. For example, Skarin et al. (2018) investigated the effects of wind power development on semi-domesticated reindeer *Rangifer tarandus* and found that they shifted their home ranges out of sight from wind power plants and that they were more disturbed during the operational compared to construction phase. Another study, which investigated effects on black bears *Ursus americanus* found avoidance of wind power development sites during the construction phase (Wallin 1998, as cited in Ferrão da Costa et al. 2018). There are as well studies on effects of wind power development on wolves *Canis lupus*. So far, research on the effects of wind power development on wolves has mainly focused on reproduction and choice of denning sites, indicating home range shifts away from wind power plants, a decrease in reproductive success, changes in den site selection, and relocation of rendezvous sites (Álvares et al. 2011, 2017). However, these changes are often only temporary and dependent on the distance of the breeding site in relation to the wind power plant (Ferrão da Costa et al. 2018). In another study, Passoni et al. (2017) found that wind power plants are often built in high quality areas for wolf reproduction in Croatia.

The wolf is a generalist species with regards to habitat requirements and is highly adaptable (Mech and Boitani 2003). This is reflected in its widespread distribution across a variety of different habitat types. Wolves usually avoid areas with high human activity connected to, e.g. roads and human settlements (Hebblewhite et al. 2005, Kaartinen et al. 2005, Karlsson et al. 2007, Ordiz et al. 2015, Carricondo-Sanchez et al. 2020). However, the strength of the effects depends on season and time of day, and it seems likely that wolves are the most vulnerable to disturbance during the denning and rendezvous season (Houle et al. 2010), when movements of breeding wolves and their pack members are concentrated to the denning area due to the restricted mobility of the pups (Jedrzejewski et al. 2001, Packard 2003). A study on wolf area use during summer in Scandinavia showed that wolves chose daytime resting sites at intermediate distances to gravel roads and human settlements, at large distances to main roads, and that they avoided open areas (Zimmermann et al. 2014). During the night, distance to gravel road did not affect their choice of resting sites, they still avoided main roads, but not as strongly, and they avoided open areas (Zimmermann et al. 2014). Furthermore, it was found that wolves use gravel roads for travelling likely because it maximises travel speed, may ease their travel and probably minimise energy expenditure (Eriksen et al. 2009, Zimmermann et al. 2014). During winter, wolves in Scandinavia were shown to prefer areas of low elevations within their territories, particularly during the last part of the winter, when the accumulated snow cover increases with increasing elevation (Ordiz et al. 2020). In some areas, this is most likely a response to the seasonal and elevational changes in snow depths, and thereby in the spatial distribution of moose *Alces alces* (Allen and Singh 2016), the main prey species in this region (Sand et al. 2008, 2012).

The Scandinavian wolf population has its main distribution in an area where wind power development has been ongoing since the 1990s (Pettersson et al. 2010). This gave us the opportunity to use existing Global Positioning System (GPS) and Very High Frequency (VHF) location data from collared adult, territorial wolves, to test whether an overlap of (at that time) proposed wind power development sites and wolf area use occurs on the landscape. Specifically, we wanted to quantify the potential for wind power development to affect wolf behavioural ecology. To do so, we estimated the overlap between wolf territory activity centres prior to construction of wind power plants with the spatial distribution of the (at that time) proposed wind turbine development. We did not have access to wolf location data over the entire time period before, during and after construction of wind turbines, so overlap was only assessed on the spatial scale. This method does not investigate the actual effect of wind power development on wolf area use but is a first attempt to investigate if there is the potential for wind power development to influence wolves in Scandinavia.

We predicted the overlap between proposed wind turbine sites and wolf area use to be greater during early and late summer compared to early and late winter, because wolves prefer more remote areas with less human disturbance during summer but follow their main prey in winter migrating to lower elevations (Carricondo-Sanchez et al. 2020). As wind turbine placement is affected by wind speed (Ryberg et al. 2020) and wind speed is usually highest on the top of mountains (Valsaraj et al. 2020), wind turbines are generally not built in lower elevations. We also predicted a higher overlap during daytime, when wolves select bed sites farther from human activity, than during night, when wolves usually hunt and feed (Sand et al. 2005). Lastly, we predicted a greater overlap for breeding than for non-breeding wolves, specifically in early and late summer (i.e. denning and rendezvous seasons). Breeding wolves may be more selective for more remote areas with low human disturbances when choosing homesites (i.e. denning and rendezvous sites) (Kaartinen et al. 2010, Iliopoulos et al. 2014, Sazatornil et al. 2016). In the Scandinavian wolf population range, remoteness is closely related to elevation, because human activity and buildings usually are situated at lower elevations. This could result in breeding wolves using areas in higher elevations in the summer seasons whereas non-breeding pairs without pups are less restricted by that.

## Material and methods

### Study area

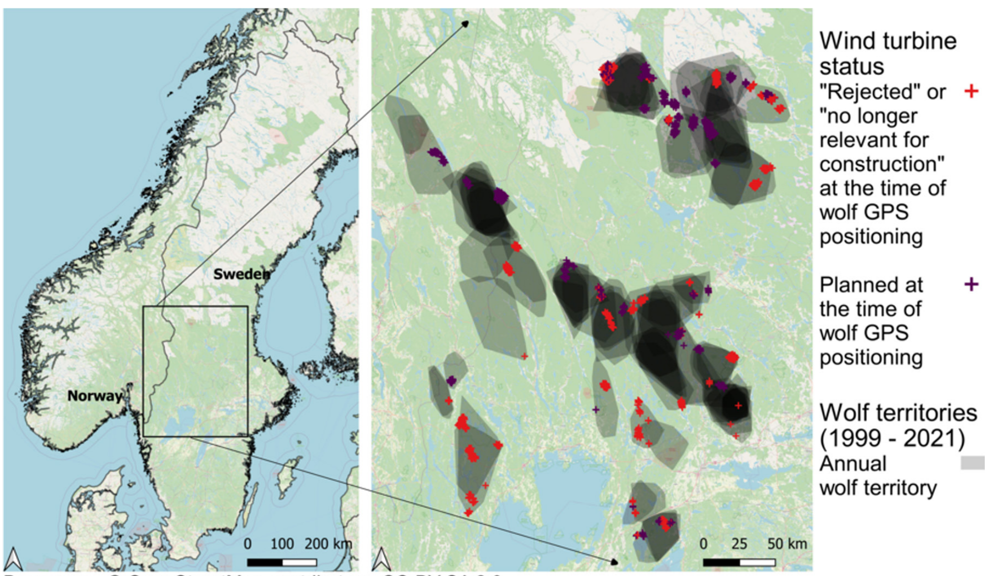
The study area has an approximate size of 77 000 km$^2$ and is located crossborder in Sweden and Norway (Fig. 1). The study area has a mean elevation of 298 m a.s.l. (range: 0–1000 m). It is dominated by boreal coniferous forest with Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* mixed with deciduous trees, mostly birch *Betula spp.* and aspen *Populus tremula* (Esseen et al. 1997). The mean density of secondary roads is 0.88 km km$^{-2}$, whereas primary road density is lower with a mean of 0.19 km km$^{-2}$ (Zimmermann et al. 2014). The climate is continental in most of the study area, with snow cover between November/December and March/April (Norwegian Centre for climate services 2022, SeNorge 2023, The Swedish Meteorological and Hydrological Institute 2023).

The wolf was functionally extinct in Scandinavia in 1966 (Wabakken et al. 2001). Today's Scandinavian wolf population was founded by two wolves from the Finnish–Russian source population in 1983 (Wabakken et al. 2001). The population started increasing from 1991, and in winter 2021/2022, the Scandinavian wolf population was estimated to 540 (95% CI = 427–702) individuals in 55 breeding pairs (i.e. territorial packs) and 28 non-breeding scent-marking pairs (Wabakken et al. 2022).

Besides wolves, three other large and medium-sized carnivores are present in the study area, i.e. brown bear *Ursus arctos*, Eurasian lynx *Lynx lynx* and wolverine *Gulo gulo*. The wolves' main prey year round in the study area is moose (Sand et al. 2008, 2012), secondary prey is roe deer (Sand et al. 2016).

### Wind power development sites

The wind turbine placements for Sweden were retrieved from the County Administrative Boards' website 'Vindbrukskollen'




Base map - © OpenStreetMap contributors, CC-BY-SA 2.0
European country outlines: @EuroGeographics and UN-FAO
Sources for data for wind turbine placements - Norway: NVE Norge, Norwegian Licence for Open Government Data (NLOD); Sweden: Vindbrukskollen, Länsstyrelserna, CC0 1.0

Figure 1. The study area in Sweden and Norway, showing proposed wind power development sites (2022) that overlap with annual territories of wolves monitored with Very High Frequency (VHF) or Global Positioning System (GPS) collars during 1999–2021. The annual territories of wolves were determined using the 100% minimum convex polygon (MCP). The wind turbines in the different status categories are displayed – wind turbines that are planned at the time of wolf GPS positioning and wind turbines that are 'rejected' or 'no longer relevant for construction' at the time of wolf GPS positioning.

(County Administrative Board and Swedish Energy Agency 2022). Wind turbine placements for Norway were retrieved from the Norwegian Water Resources and Energy Directorates' geographical thematic data website (The Norwegian Water Resources and Energy Directorate 2022). We included wind turbines of all status categories because we assumed that all these wind turbine sites corresponded to places of high interest for wind power development. Therefore, we call them all 'proposed wind turbines' throughout the paper, regardless of whether they were ever constructed. To make sure that including the categories 'rejected' and 'no longer relevant for construction' at the time of wolf GPS positioning did not bias our results, we performed the same analysis without wind turbines of these categories and present the results in the Supporting information.

A wind power plant is defined as a group of wind turbines that are used for electricity production. The placement of individual turbines within a wind power plant is dependent on various conditions, such as the terrain, wind speed and direction, turbine size, but there are strategies on how to place individual wind turbines in an optimised way (Emami and Noghreh 2010).

### Study animals and location data

Wolves on snow-covered ground were darted and immobilised from a helicopter, and equipped with a VHF (Telonics Inc, Mesa, Arizona, USA) or GPS collar (Tellus by Followit Sweden AB, and GPS/Vertex Plus by VECTRONIC Aerospace GmbH, Germany) following the methods described by Arnemo and Evans (2017). All captures were evaluated and approved by the Swedish Animal Welfare Agency (no.: 5.8.18-18473/2020, C 150/15, 407/12), and by the Norwegian Environment Agency and the Norwegian Food Safety Authority (i.e. FOTS ID 7224, 15370, and 26561). A detailed description with wolf capture procedures can be found in Sand et al. (2006). For this study, we considered wolf location data from 166 adult territorial wolves collared from 1999 to 2021. GPS collars were programmed to collect 2 or 6 locations per day, depending on wolf territory and year of study. The VHF collars were typically tracked at intervals of 1 to 3 days. For limited time periods, collars took locations or were tracked at a more intensive schedule. To obtain comparable data from all territories and seasons, we down-sampled all GPS and VHF locations to an interval of ≥ 4 hours.

We split the location data into four, 3-month seasons, approximately representing the different stages of a typical wolf year: early summer (1 May – 31 July), late summer (1 August –31 October), early winter (1 November – 31 January), and late winter (1 February –30 April). The early summer season includes the birth of pups and denning period for breeding pairs. In the study area the median time of birth is 1 May (Nordli et al. 2023). The rendezvous period is included in the late summer season for breeding pairs. During late winter, mating takes place with a median of 27 February (Nordli et al. 2023). To have enough locations for home range and area use analyses for each territory-year-season, we only included seasons with a minimum of 60 days of locations. When data of both the adult male and female were available for a given time stamp, we picked the individual for which the location was acquired first. We categorised the location data by time of day, where daytime was defined as 08:00 to 19:59 and night was defined as 20:00 to 07:59. The purpose of this categorisation was to reflect human activity periods rather than bright and dark hours.

We obtained the information on social status (breeding and non-breeding) for each season from the annual wolf monitoring reports (Wabakken et al. 1999, 2022). Non-breeding pairs are two scent-marking (i.e. resident, territorial) adult wolves without pups, whereas breeding pairs consist of one or two adult wolves with offspring (i.e. resident packs), mostly pups (Wabakken et al. 1999, 2022). Wolf monitoring in Scandinavia takes place during October to March. Therefore, the social status during early and late winter corresponded to that of the concurrent monitoring season. Status during the early summer and late summer seasons was dependent on whether reproduction was confirmed during the summer or during monitoring the following winter.

### Data exploration

The data exploration, spatial analyses and modelling were carried out in R ver. 4.3.1 (www.r-project.org) in 'RStudio' (RStudio Team 2022) and in QGIS Desktop ver. 3.16.15 (QGIS Development Team 2022). We followed the protocol established by Zuur et al. (2010) for general data exploration. During data exploration, we detected outliers for the distance from wolf territory activity centres to the nearest proposed wind turbine, but these outliers represented true values. We therefore concluded not to exclude them.

### Wolf area use

We defined seasonal home ranges using the 100% minimum convex polygon (MCP) method for each wolf pair using the packages 'adehabitatHR' (Calenge 2006) and 'sp' (Pebesma and Bivand 2005, Bivand et al. 2013). Preference of this method versus probabilistic methods is because resident wolves are highly territorial and patrol territory borders frequently for scent-marking. Kernel methods often include unused areas outside of the territory because they are based on a point density function that predicts presence also in areas of absences, particularly if an animal spends a lot of time close to the territory border. However, we used the kernel method with reference bandwidth and a grid size of 50 m to define the activity centres (50% kernel utilisation distribution) during the different years, seasons and time of days of the wolves, using the 'adehabitatHR' package (Calenge 2006). We then clipped the 50% kernel volume contour, which represents the activity centre, with the seasonal home ranges (100% MCP) in cases where the kernel estimation extended the activity centre to outside of the wolf territory (Supporting information).

The proportion of the home range that is covered by the activity centre is expected to differ between seasons, e.g.

during early summer, which includes denning, the activity centre area was expected to be much smaller than during other seasons. To correct for this variation, we calculated the 'relative activity centre area' as a value between 0 and 1 by dividing the area of the activity centre with the total area of the individual seasonal home ranges for each combination of wolf pair, year, season, and time of day. A higher value would represent an activity centre covering more of the home range, whereas a lower value would represent an activity centre covering a smaller proportion of the home range.

### Response variables

We measured the Euclidean distance, using the planar method, between wolf activity centre point (geometric centre point of activity centre) and the nearest proposed wind turbine location using the package 'rgeos' (Bivand and Rundel 2021). The probability of proposed wind turbines being within the activity centre of wolves was determined by categorising the presence/absence (i.e. 1 or 0) of turbines in the activity centres using the package 'sf' (Pebesma 2018, Pebesma and Bivand 2023).

To account for the evidence that wolves respond to wind turbine construction within 3 km of den sites (e.g. moved dens, decreased reproductive success; Ferrão da Costa et al. 2018), we added a 3 km buffer around wind turbines as part of our estimates of wind turbine density (per $km^2$). We used the point density tool in ArcGIS Pro ver. 3.02 (Esri 2024) to estimate the wind turbine point density in the activity centres with a cell size of 10 m using the tool Point Density (Spatial Analyst). We then extracted the mean wind turbine density per $km^2$ in the activity centre using the tool Zonal Statistics (Spatial Analyst).

### Modelling procedures

To identify proposed wind turbines that overlap with individual wolf home ranges, we conducted an overlay analysis at the landscape level (i.e. in the entire wolf range for which we had available data). We generated home ranges using the 100% MCP method for each wolf territory, year, and season using the packages 'adehabitatHR' (Calenge 2006) and 'sp' (Pebesma and Bivand 2005, Bivand et al. 2013). We then conducted a simple spatial overlay analysis to choose only the wolves that overlapped with proposed wind turbine sites for the further analysis in QGIS Desktop ver. 3.16.15 (QGIS Development Team 2022).

For the analysis we only used wolf locations from before any wind power construction took place. This allowed us to examine naïve wolf use of areas, free of potential response to wind power development. We did not have sufficient data to compare overlap before, during and after the construction of wind turbines, and we were therefore not able to add the temporal overlap to our analysis. When wind turbines lacked an exact construction start date, we only used wolf location data until two years before the operational start. When a wolf territory overlapped with wind turbines in operation, and there were several wind turbines within a wolf territory, we only used wolf locations from before the start of construction of the first wind turbine.

We used generalised linear mixed models (GLMM) with a random error structure for territory ID, to assess seasonal variation in use based on, 1) relative activity centre area as a function of season and social status, and 2) mean elevation as a function of season. We did this using the package 'glmmTMB' (Brooks et al. 2017). We did this to test if our assumption that wolves used areas in higher elevations during summer and that the relative activity centre varies across seasons is correct.

To model factors that might influence the variation in the distance between activity centre point and nearest proposed wind turbine, we used GLMMs with a gamma distribution and log link function. For the probability of proposed wind turbines being within the activity centre we used GLMMs with a binomial distribution and logit link function. For the wind turbine density in the activity centre, we used GLMMs with a Tweedie distribution and a log link function. All three model approaches included season, time of day and social status as well as their interactions as explanatory variables (Table 1; see more details in the Supporting information). Furthermore, we included the territory ID as a random error structure to account for wolf territory differences. For the probability of proposed wind turbine sites in the activity centre, we additionally included the relative activity centre area as an offset to account for the territory size differences throughout the different seasons (Table 1; see more details in the Supporting information).

We ran a total of 15 models for each response variable (Supporting information). All models were run with the function *glmmTMB* from the package 'glmmTMB' (Brooks et al. 2017). We used the Akaike's information criterion corrected for small sample size ($AIC_C$; Sugiura 1978, Hurvich and Tsai 1991) to compare models, considering models with the lowest $AIC_C$ the best ones and with a $\Delta AIC_C < 2$ as competitive. We assessed the model fit using tools provided in the 'DHARMa' package (Hartig 2022). Tools to assess the model fit were plotting the residuals, plotting a Q–Q plot, and testing for distribution, dispersion, and outliers. To generate predictions based on the best model, we used the package 'ggeffects' (Lüdecke 2018). We report the 95% confidence interval (CI) throughout the manuscript.

## Results

### Data overview

We used 55 371 locations from 31 wolf territories between 1999 to 2021 for this study, which included 44 wolves from 30 individual breeding pairs (i.e. packs) and 36 wolves from 25 individual non-breeding pairs. The number of recorded GPS and VHF locations varied among wolf pairs and seasons (average: 296 locations, range: 60–550 locations, Supporting information).

Table 1. $AIC_C$ table showing the five best ranking models for the distance (m) from the wolf territory activity centre point to the nearest proposed wind turbine (Distance), the probability of proposed wind turbines being within the activity centre (Probability) and the wind turbine density per km² in the activity centre (Density) in Scandinavia (Sweden and Norway; 1999–2021). The activity centres were estimated with Global Positioning System (GPS) and Very High Frequency (VHF) location data of adult, territorial wolves. A complete overview of the $AIC_C$ table can be found in the Supporting information.

| Candidate models | K | $\Delta AIC_c$ | $AIC_cWt$ | Cum. Wt | LL |
|---|---|---|---|---|---|
| **Distance** | | | | | |
| Season | 6 | 0.00 | 0.49 | 0.49 | -3450.16 |
| Season + Social status | 7 | 1.94 | 0.18 | 0.67 | -3450.09 |
| Season + Time of day | 7 | 2.08 | 0.17 | 0.84 | -3450.16 |
| Season + Time of day + Social status | 8 | 4.03 | 0.06 | 0.91 | -3450.09 |
| Social status × Time of day + Season | 9 | 6.01 | 0.02 | 0.93 | -3450.03 |
| **Probability** | | | | | |
| Season × Social status + offset | 9 | 0.00 | 0.73 | 0.73 | -181.48 |
| Season × Social status + Time of day + offset | 10 | 1.98 | 0.27 | 1.00 | -181.40 |
| Season + offset | 5 | 13.19 | 0.00 | 1.00 | -192.27 |
| Season + Social status + offset | 6 | 13.42 | 0.00 | 1.00 | -191.35 |
| Season + Time of day + offset | 6 | 15.11 | 0.00 | 1.00 | -192.19 |
| **Density** | | | | | |
| Season + Social status | 8 | 0.00 | 0.31 | 0.31 | 420.62 |
| Season | 7 | 0.85 | 0.20 | 0.51 | 419.15 |
| Season × Social status | 11 | 1.16 | 0.17 | 0.68 | 423.22 |
| Season + Time of day + Social status | 9 | 1.97 | 0.11 | 0.79 | 420.69 |
| Season + Time of day | 8 | 2.78 | 0.08 | 0.87 | 419.23 |

The table shows the candidate model structure (all models had a random error structure of the territory ID included), with the explanatory variables season (early summer (1 May –31 July, including the birth of pups and breeding pairs), late summer (1 August – 31 October, including the rendezvous period for breeding pairs), early winter (1 November –31 January), and late winter (1 February – 30 April, including mating)), time of day (day and night), and the social status (non-breeding (i.e. resident, territorial) and breeding pairs (i.e. packs)). The probability models included an offset of the relative activity centre area (activity centre area / home range). Furthermore, it shows the number of estimated parameters (K), difference in Akaike information criterion (corrected) ($AIC_c$) between model and best model ($\Delta AIC_c$), Akaike weights ($AIC_cWt$), cumulative Akaike weight (Cum. Wt.), negative likelihood (LL).

We found variable spatial overlap between 1222 proposed wind turbines and previously established territories of collared adult wolves. The wolves' relative activity centre area varied between seasons and with social status (marginal $R^2$/conditional $R^2$: 0.580/0.671; Fig. 2a, Supporting information). The relative activity centre area was 4.50 and 1.45 times larger for non-breeding than for breeding pairs during early summer (non-breeding pair: 0.36, 95% CI: [0.32; 0.40]); breeding pair: 0.08, 95% CI: [0.06; 0.11]) and late summer (non-breeding pair: 0.39, 95% CI: [0.34; 0.43]; breeding pair: 0.27, 95% CI: [0.25; 0.30]), respectively (Fig. 2a, Supporting information). In contrast, in early winter (non-breeding pair: 0.34, 95% CI: [0.30; 0.38]; breeding pair: 0.39, 95% CI: [0.36; 0.42]) and late winter (non-breeding pair: 0.30, 95% CI: [0.27; 0.33]; breeding pair: 0.34, 95% CI: [0.32; 0.37]), the relative activity centre areas was 1.15 and 1.12 times larger for breeding than for non-breeding wolves, respectively (Fig. 2a, Supporting information).

There was very strong evidence for that area use of wolves occurred at slightly higher (1.103 times) elevations during early summer (290 m, 95% CI: [252; 327]) compared to late winter (263 m, 95% CI: [226; 301]), whereas there was strong evidence that the elevation was 1.047 times higher during early summer compared to early winter (277 m, 95% CI: [239; 315]). There was no difference in mean elevation between late (293 m, 95% CI: [255; 331]) and early summer (marginal $R^2$/conditional $R^2$: 0.012/0.948; Fig. 2b, Supporting information).

## Distance to nearest proposed wind turbine

The distance from the wolf territory activity centre point (n = 355) to the nearest proposed wind turbine was on average 8657 m (range: 139–32 962 m; 95% CI: [8103; 9211]). The top-ranking model to explain the observed variation in the distance included only season (Table 1). The second-best ranking model which had an $AIC_C < 2$ additionally included the social status (Table 1). There was strong evidence for that the activity centre point was around 1.27 times closer during early summer (7141 m, 95% CI: [5737; 8890]) than during late winter (9101 m, 95% CI: [7346; 11 276]) (Fig. 3a, Table 2). There was no clear pattern for other seasonal differences (Fig. 3a, Table 2). The model had a marginal $R^2$ of 0.022 and a conditional $R^2$ of 0.498, indicating that a large extent of the variance is explained by the random error structure, i.e. the territory ID. Time of day and social status of the wolves were not included in the top-ranking model.

## Probability of proposed wind turbines being within activity centres

Out of 323 combinations of wolf pair, year, season, and time of day, 47% (n = 153) of all seasonal home ranges did not have proposed wind turbines within their activity centre whereas 53% (n = 170) did have proposed wind turbines within their activity centre. The top-ranking model that best explained the observed variation in the probability of proposed wind turbines being within the activity centre included

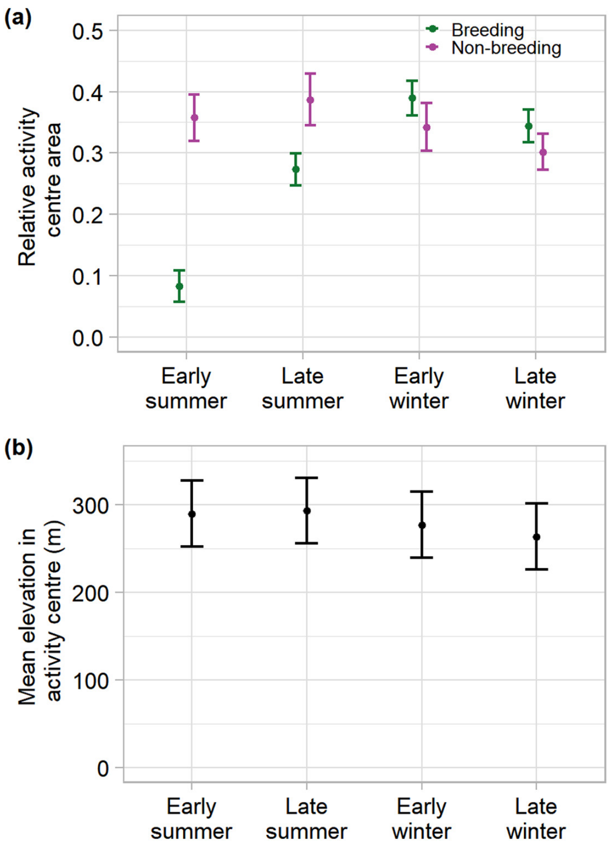



Figure 2. (a) Relative activity centre area of wolves, estimated based on Global Positioning System (GPS) and Very High Frequency (VHF) location data, which is the area of the activity centre (estimated with the kernel density area) divided by the total area of the home range (estimated with the 100% minimum convex polygon (MCP)) for seasonal home ranges that overlap with proposed wind power development sites in Scandinavia (Sweden and Norway) during the years 1999-2021. The different seasons (early summer (1 May – 31 July, including the birth of pups for breeding pairs), late summer (1 August – 31 October, including the rendezvous period for breeding pairs), early winter (1 November – 31 January), and late winter (1 February – 30 April, including mating)) for wolves of different social statuses (non-breeding (i.e. resident, territorial) and breeding pairs (i.e. packs)) are displayed. (b) Mean elevation (m) of the activity centres across the different seasons.

the interaction between season and social status (Table 1). The second-best ranking model which had an $AIC_C < 2$ additionally included time of day (Table 1). There was very strong evidence for that the probability was 3.90 times higher for non-breeding pairs (0.70, 95% CI: [0.37; 0.90]) (Fig. 3b, Table 2) during early summer as compared to breeding pairs (0.18, 95% CI: [0.07; 0.40]). Whereas a 2.04 times higher probability for having proposed wind turbines within the activity centre during late winter was found for breeding pairs (0.53, 95% CI: [0.28; 0.76]) as compared to non-breeding pairs (0.26, 95% CI: [0.11; 0.51]) (Fig. 3b, Table 2). There was no clear pattern for other combinations of season and social status (Fig. 3b, Table 2). The model had a marginal $R^2$ of 0.127 and a conditional $R^2$ of 0.590, indicating that a large extent of the variance is explained by the random error structure, the territory ID.

### Wind turbine density in activity centre

The wind turbine density within the wolves' activity centres (n = 355) was on average 0.036 wind turbines $km^{-2}$ (range: 0.000–0.853 wind turbines $km^{-2}$; 95% CI: [0.027; 0.044]). The top-ranking model that best explained the observed variation in the wind turbine density of the wolf activity centre included the season and social status (Table 1). The second-best ranking model which had an $AIC_C < 2$ included only the season, whereas the third-best ranking model included the interaction between the season and social status (Table 1). The fourth-best ranking model included the season, social status, and time of day (Table 1). There was moderate evidence that the wind turbine density was 1.75 times higher during early summer (0.014 wind turbines $km^{-2}$, 95% CI: [0.007;0.031]) compared to late winter (0.008 wind turbines $km^{-2}$, 95% CI: [0.004;0.018]) (Fig. 3c.1, Table 2). There was no clear difference between the other seasons and the social statuses (Fig. 3c.1, 3c.2, Table 2). The model had a marginal $R^2$ of 0.029 and a conditional $R^2$ of 0.740, indicating that a large extent of the variance is explained by the random error structure, the territory ID.

## Discussion

Our study confirmed that established wolf territories do overlap with sites chosen for wind power development at the landscape level. As predicted, proposed sites for wind turbines were closer to the wolves' activity centre point during summer, and farthest in late winter. We also found that the probability of proposed wind turbines being within the activity centre, was higher for breeding compared to non-breeding pairs during late winter whereas in the early summer, the opposite was found. The wind turbine density was higher during early summer compared to late winter. There was no clear pattern for other seasonal and social status differences. There are several features of wolf behavioural ecology that might have influenced these results.

During the denning and rendezvous seasons, movements of breeding wolves are concentrated near the sites where pups are located (Jedrzejewski et al. 2001, Packard 2003), with a successive increase in area use over time as the pups become more mobile. As a result, breeding pairs typically have smaller activity centres, relative to their annual home ranges, than non-breeding pairs. Our results were consistent with this aspect of wolf behaviour. Smaller activity centres also result in a lower probability for proposed wind turbines to be inside the activity centre. This behavioural effect might explain why breeding pairs had lower overlap between activity centres and proposed sites for wind turbines as compared to non-breeding pairs during early summer, but could also be a result of different selection of habitat for den and rendezvous sites.

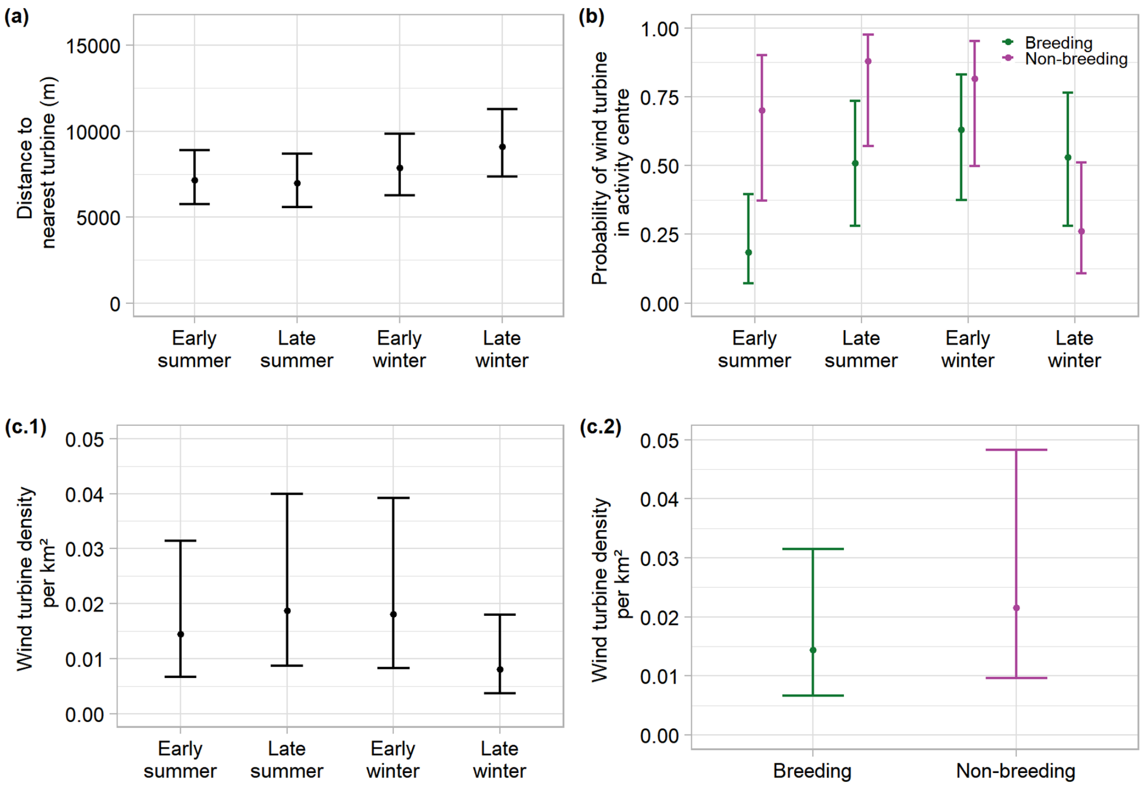



Figure 3. Prediction plots generated from the top-ranking generalised linear mixed models (GLMM) for the activity centre overlap with proposed wind turbines in Scandinavia (Sweden, Norway; 1999–2021). The activity centre was determined based on Global Positioning System (GPS) and Very High Frequency (VHF) location data. (a) The distance (m) from the wolf territory activity centre point to the nearest proposed wind turbine with a 95% confidence interval (CI) during the different seasons (early summer (1 May – 31 July, including the birth of pups for breeding pairs), late summer (1 August – 31 October, including the rendezvous period for breeding pairs), early winter (1 November – 31 January), and late winter (1 February – 30 April, including mating)). (b) The probability of proposed wind turbines being within the activity centre with a 95% CI during the different seasons and social statuses (non-breeding (i.e. resident, territorial) and breeding pairs (i.e. packs)). (c) The wind turbine density (per km$^2$) in the activity centre with a 95% CI (c.1) during the different seasons and (c.2) for the social statuses.

Contrary to our predictions, we observed a higher probability of proposed wind turbines inside the activity centre for non-breeding pairs compared to breeding pairs, during early summer. Breeding wolves select dens and rendezvous sites in more remote areas with relatively lower human disturbance (Kaartinen et al. 2010, Iliopoulos et al. 2014, Sazatornil et al. 2016). Remoteness in the distribution range of the Scandinavian wolf population is closely related to elevation, because human activity and buildings usually are situated at lower elevations. Since wind turbines are usually proposed at the highest elevations in the landscape, we expected that activity centres of breeding pairs would overlap more with proposed wind turbine sites than those of non-breeding pairs. However, the more restricted area use of breeding pairs described above might have been a much stronger factor for our measures of overlap than the expected effect of habitat selection, and therefore our predictions regarding breeding versus non-breeding pairs were not met for the probability of proposed wind turbines to be placed inside activity centres.

In our study area, wolves prey mainly on moose (Sand et al. 2008, Zimmermann et al. 2015). When snow accumulates in mid-winter, moose in the north-western parts of our study area tend to migrate or concentrate their activity to lower elevations within their home ranges, where there is less snow and higher availability of browse (Allen and Singh 2016). Similarly, wolves appear also to concentrate their area use during winter to these lower elevations (Allen and Singh 2016, Ordiz et al. 2020), likely because they follow their preys' habitat selection, and because deep snow at higher elevations make wolf movement more difficult and increase energy costs of locomotion (Houle et al. 2010). Our results also showed that the mean elevation in the wolves' activity centre is lower during the early and late winter as compared to the summer. As wind turbine placement is affected by wind speed (Ryberg et al. 2020) and wind speed is usually highest on the top of mountains (Valsaraj et al. 2020), wind turbines are generally built at higher elevations. This may explain why we generally found the lowest overlap between proposed wind turbine sites and wolf area use during late winter, i.e. the farthest distance from the activity centre point to the closest wind turbine and the lowest density of wind turbines per km$^2$.

Table 2. Top-ranking model estimates of fixed effects with the 95% confidence interval. The random error structure of the wolf territory ID was included in all models. The model of the probability additionally had the offset of the relative activity centre area (activity centre area / home range) included. The estimates are displayed for the distance (m) from the wolf activity centre point to the nearest proposed wind turbine (Distance), the probability of proposed wind turbines being within the activity centre (Probability), and the wind turbine density per km$^2$ in the activity centre (Density) in Scandinavia (Sweden, Norway; 1999–2021). Activity centres were estimated with Global Positioning System (GPS) and Very High Frequency (VHF) location data from adult, territorial wolves. The different seasons included were early summer (1 May –31 July, including the birth of pups and breeding pairs), late summer (1 August –31 October, including the rendezvous period for breeding pairs), early winter (1 November –31 January), and late winter (1 February –30 April, including mating). The two social statuses are non-breeding (i.e. resident, territorial) and breeding pairs (i.e. packs). An α-level of 0.05 was used to determine evidence of effect.

| | | | Confidence interval | | | |
|---|---|---|---|---|---|---|
| Response variable | Explanatory variable (with levels) | Estimate | Lower | Upper | z value | p-value |
| **Distance** | (Intercept) | 8.87 | 8.65 | 9.09 | 79.42 | < 0.001 |
| | Season [early winter] | 0.10 | -0.08 | 0.27 | 1.10 | 0.27 |
| | Season [late winter] | 0.24 | 0.09 | 0.40 | 3.08 | < 0.01 |
| | Season [late summer] | -0.02 | -0.18 | 0.14 | -0.30 | 0.77 |
| **Probability** | (Intercept) | -1.78 | -2.84 | -0.72 | -3.28 | < 0.01 |
| | Social [non-breeding pair] | 2.34 | 0.87 | 3.80 | 3.12 | < 0.01 |
| | Season [early winter] | 2.02 | 0.93 | 3.11 | 3.64 | < 0.001 |
| | Season [late winter] | 1.60 | 0.56 | 2.64 | 3.02 | < 0.01 |
| | Season [late summer] | 1.52 | 0.58 | 2.47 | 3.17 | < 0.01 |
| | Social [non-breeding pair]:Season [early winter] | -1.38 | -3.36 | 0.59 | -1.38 | 0.17 |
| | Social [non-breeding pair]:Season [late winter] | -3.49 | -5.27 | -1.71 | -3.84 | < 0.001 |
| | Social [non-breeding pair]:Season [late summer] | -0.38 | -2.36 | 1.61 | -0.37 | 0.71 |
| **Density** | (Intercept) | -4.24 | -5.02 | -3.46 | -10.67 | < 0.001 |
| | Season [early winter] | 0.22 | -0.27 | 0.71 | 0.89 | 0.37 |
| | Season [late winter] | -0.58 | -1.04 | -0.12 | -2.48 | < 0.05 |
| | Season [late summer] | 0.26 | -0.17 | 0.68 | 1.19 | 0.23 |
| | Social [non-breeding] | 0.40 | -0.06 | 0.86 | 1.71 | 0.09 |

Time of day was not related to any of the three measures of overlap between proposed wind turbine sites and wolf area use in our study. This was likely because wolf activity centres were similar in size and shape at day and night for a given wolf and season, despite wolves being more active during night (Eriksen et al. 2009). In contrast, the seasonal activity centres are formed by processes at a much wider spatio-temporal scale than the diel activity patterns of wolves. Breeding behaviour (Jedrzejewski et al. 2001, Packard 2003) and seasonally changing weather conditions, which can lead to a change in prey distribution and therefore change of wolf movement patterns (Fuller 1991), could be drivers of such processes.

A study in Portugal found that wolves avoid wind power development sites during the construction phase (Álvares et al. 2011, 2017, Ferrão da Costa et al. 2018). This behaviour during the construction phase has also been shown for other species such as black bears (Wallin 1998, as cited in Ferrão da Costa et al. 2018). In our study, proposed areas for wind turbines were closest to the wolf activity centre during the early and late summer seasons. However, we could not find any difference in distance for breeding versus non-breeding pairs. In our study system, wolves use much larger home ranges (~ 1000 km$^2$, Mattisson et al. 2013) than in Portugal (~ 170 km$^2$, Pimenta et al. 2005, as cited in Ferrão da Costa et al. 2018), and we therefore expect a much larger variation in nearest distances between activity centre points and proposed wind turbine sites in our as compared to the Portuguese study area.

Our results need to be interpreted with care, because of the limitation of our study to not being able to perform a before-after comparison. Therefore, we cannot make any conclusion as of the effect wind turbines will have on wolves, but only on the potential for wind power development to influence wolves. Furthermore, residual diagnostics for the best-ranking model for the distance to the closest wind turbines revealed a deviation from the expected distribution and detected outliers. Since these outliers represented true values, we decided not to remove them. For the wind turbine density, the test for homogeneity of variance and the within-group deviations from uniformity were significant. A lot of the variance was explained by the random error structure (i.e. distance: 0.022/0.498 (marginal/conditional $R^2$); probability: 0.127/0.590; density: 0.029/0.740), which also limits the reliability of our results. Furthermore, there were several models for the density that were equally good. Therefore, to make a more precise conclusion on the potential effect of wind turbine development on wolf behaviour, further research with a before-after study design is needed. Such data is however difficult and expensive to obtain and requires long-term telemetry studies of wolves in areas with wind power development.

Considering the rapid expansion of wind power plants in remote areas and their potential for long-lasting effects on wildlife and ecosystem services, environmental impact assessments should include species at all levels of the food web including top predators, because these species can play an important role in ecosystem functioning (Hairston et al. 1960, Estes et al. 2011). Our study highlights the potential for wind power development to impact wolf area use, with the greatest potential impact likely to occur in summer.

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## Author contributions

**Cecilia Miltz**: Conceptualization (equal); Formal analysis (lead); Methodology (equal); Writing – original draft (lead); Writing – review & editing (equal). **Ane Eriksen**: Conceptualization (equal); Methodology (equal); Supervision (supporting); Writing – review & editing (equal). **Camilla Wikenros**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (supporting); Writing – review & editing (equal). **Petter Wabakken**: Funding acquisition (equal); Writing – review & editing (equal). **Håkan Sand**: Funding acquisition (equal); Writing – review & editing (equal). **Barbara Zimmermann**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (equal); Methodology (equal); Supervision (lead); Writing – review and editing (equal).

## Data availability statement

Data are available from the DataverseNO: https://doi.org/10.18710/4DLXE3 (Miltz et al. 2024).

## Supporting information

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

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