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Abstract

Renewable energy sources like wind energy are rapidly expanding in order to meet challenges of climate change. Wind energy is leaving a significant negative impact on wildlife through collision of birds and bats with operating wind turbines. Raptors are one of the many species exposed to this threat. Golden eagle (*Aquila chrysaetos*) is a long-lived raptor with slow reproduction rate. The species is listed as Near Threatened in Sweden and faces several threats, such as illegal persecution and collisions with trains and wind turbines. Knowledge of movement ecology and flight behaviour of Golden eagles is therefore essential for a successful management and conservation of the species, if we are to identify the causes of collisions and the spatio-temporal distribution of threats. Topography, wind, habitats and elevation have been suggested to impact on flight behavior for Golden eagles. I studied the movement ecology of Golden eagles by using data from 31 GPS transmitter equipped Golden eagles. Topographic and life history variables were used to explain the patterns of flight height using Generalized Linear Mixed Models (GLMMs). A combination of these factors including, wind speed and the habitat variables significantly affected the flight height, but overall model predictability was low. This calls for getting a deeper understanding on-site wind conditions and local weather. The flight height of marked birds within wind farm areas was higher than flight height further away from wind turbines. Home range analyses revealed that 60 % of the home range areas (95 % contour) contained operating wind turbines and 85 % of the home ranges contained proposed wind turbines, not constructed yet. Movement ecology in Golden eagles is likely to be affected by wind farms and it needs to be taken into account while planning construction of new wind farms.

Introduction

One of the greatest challenges we meet today is of climate change and the resulting consequences on biodiversity ecosystems. Renewable energy sources are quickly expanding as a mitigation measure to reduce emissions and wind energy is one form of energy used as a strategy. However, wind energy also comes at a cost, through its impact on wildlife. Collisions of birds and bats with wind turbines are one of the most important negative impacts of wind farms. (Smallwood and Karas, 2009). Knowledge of how and why wind farms impact on birds is urgent since this problem is intensifying worldwide, as the installed capacity of wind energy is expanding rapidly (Renewable energy, 2014). The total installed wind power in Sweden was 3607 MW in 2012 (Energimyndigheten, 2013) and Sweden has plans to increase it to 30 TWh until 2020 (Regeringens prop. 2008/09:163).

Raptors are among the bird species most affected by wind turbines. Raptors are shown to be more vulnerable to collision since they fly closer to wind farms compared to other bird species (Osborn et al., 1998, Thelander., 2003). The reasons for this behavior are yet unknown. Golden eagle is one of five large carnivores in Sweden. It is categorized as Near Threatened in the Swedish Redlist (Swedish Species Information Centre, 2014) meaning, it is protected by, and is a species requiring special habitat conservation measures according to EU Bird Directive and EU Habitat Directive (European Commission, 1992 and 2009). Sweden holds a population of about 1200 individuals, with an estimation of 500 breeding pairs (Hjernquist, 2011). Annual reproduction rate was 0,45 offspring/pair for the years 2005-2010 (Hjernquist, 2011) and 2013 had an estimation of 125 successful breeding attempts (Viltskadecenter, 2013). Golden eagles inhabit the boreal zone and are distributed over all Sweden, but 90% of the Swedish population resides in the northern part of Sweden. In the southern part, only a few breeding pairs occurs, which are scattered over a large area (Hjernquist, 2011, Moss et al., 2012). Golden eagles are long-lived and have a low reproductive rate since they normally mature during the 4th or 5th year (Steenhof et al., 1983). Often, successful reproduction is not achieved until a few years after maturation (Tjernberg**,** 2010). In Sweden, about 65% of adult pairs breed and out of these, only 40% have a successful breeding with a high year to year variation (Hjernquist, 2011).

It is well established from several countries that Golden eagles collide with wind turbines (Smallwood and Karas, 2009, Martínez et al., 2010, Loss et al., 2013). Reasons for these collisions are not yet fully understood but species-specific flight behavior is known to affect the vulnerability to collision (Thelander et al., 2003, Barrios and Rodriguez, 2004, Drewitt and Langston, 2006, Smallwood et al., 2009). Other factors which are thought to influence on mortality is age of individual and season. Subadults (individuals one to three years old) and floaters (adult individuals without any territory) among Golden eagles had higher mortality rates, 20% and 14.8% respectively (California Energy Commission, 2002) at Altamont Pass Wind Resource Area, U.S.A compared to juveniles (individuals up to one year old) and breeding individuals. This is attributed to a greater tendency to hunt live prey within the wind farm area and to a higher occurrence of individuals in these age classes within the wind farm area. Other consequences of wind turbines on raptor include disturbance, displacement and habitat loss (Drewitt and Langston, 2006, Winder et al., 2014). Together with, a low first-year survival, (McIntyre et al., 2006), and additive mortality from poisoning (Fisher et al., 2006), illegal persecution (Whitfield et al., 2004) and collisions with trains (Tjernberg, 2010, Stone et al., 2001), power lines (Tjernberg, 2010, Lopéz-Lopéz et al., 2011) and wind turbines (Smallwood and Thelander, 2008) this large raptor is vulnerable and at large risk of declining in case of additive mortality from collisions with wind turbines.

Several factors are known to influence the flight behavior of Golden eagles and other raptors. Availability of favorable wind conditions, is an important factor determining flight altitude in soaring birds (Shamoun-Baranes et al., 2003, Lanzone et al., 2012), and this factor is highly connected to topography since steep areas (e.g slopes) in the landscape produce orographic winds (Bohrer et al., 2011). Golden eagles are known to use orographic updraft winds during flight in order to minimize energy costs, and Katzner et al. (2012) showed how topography can influence Golden eagles flight altitude in North America. Over cliffs and steep slopes they flew at a lower altitude compared to flat ground and gentle slopes. Other factors influencing flight altitude is type of habitat, temperature (Niles et al., 1996, Johnston et al., 2013) and elevation (Hoover and Morrison, 2005). As Golden eagles lower flight altitude they also decrease the altitudinal variation in flight (Spaar and Bruderer, 1996, Lanzone et al., 2012). A decrease in the altitudinal variation can also be seen with an increasing wind speed for Golden eagles (Lanzone et al., 2012).

To be able to successfully conserve a species that moves over large scales, knowledge on movement and dispersal is vital. Animals move in order to enhance benefits from better feeding opportunities, avoid predation, escape harsh climate or in search for resources (Alerstam et al., 2003). With new and improved tracking technique the possibility to follow individual's movement patterns have increased and thereby increasing our knowledge in movement patterns and its drivers for Golden eagles. To be able to determine the vulnerability of Golden eagles to risk of collisions with wind turbines, movement and flight behavior of these birds need to be understood.

Aim of the study

This work focuses on studying Golden eagles movement behaviour in Sweden in order to assess possible impact of wind turbines. Specifically, I aim to answer the following questions:

(i) What are the characteristics of wind conditions and topography used by Golden eagles in Sweden?
(ii) What are the patterns of flight behavior of Golden eagles and the factor affecting it?
(iii) What are the effects of wind turbines on flight behaviour of Golden eagles?

I also aim to study the likely overlap between space use by Golden eagles and existing and proposed wind farms in Sweden.

Material and methods

Study area

Marking of Golden eagles were conducted in boreal landscapes in northern Sweden, in the two counties of Västerbotten and Västernorrland during 2010 and 2011. The landscape comprises of coniferous forests, lakes and mires. Forests are dominated by Scots Pine (*Pinus sylvestris*) and Norway Spruce (*Picea abies*) with some elements of deciduous trees like Birch (*Betula* spp.), Aspen (*Populus tremula*) and Goat Willow (*Salix caprea*).

Forestry is the dominant land use practice and landscape consists of large, even-aged stands of Scots Pine or Norway Spruce and clear-cuts (Engelmark and Hytteborn, 1999). Elevation ranges between 100-650 m.a.s.l.

Movement data

14 juveniles and 29 adult Golden eagles from 16 different sites were equipped with GPS-transmitters during 2010 and 2011. Both eagles from territories close to wind farms and eagles with territories further away from wind farms were marked. Two types of transmitters were used, a 70 g Solar Argos/GPS PTT-100 manufactured by Microwave Telemetry, Inc. USA (hereby referred to as MTI) and a 135 g GPS PLUS Bird manufactured by Vectronic Aerospace GmbH, Germany (hereby referred to as VAS). Both of the transmitter types are partly driven by solar cells to extend life-span of the battery. Positions from MTI transmitters were sent by Argos- and GPS-satellites with a horizontal precision of ±18 meters and a vertical precision of ±22 meters (Hipkiss et al., 2013). Positions from VAS transmitters were sent by GSM-net and had a vertical and horizontal precision of ±2 meters (Hipkiss et al., 2013). Positions from both transmitters were sent to the database Wireless Animal Remote Monitoring (WRAM 2011) at the Swedish University of Agricultural Science (SLU). Transmitters were programmed to send positions with different intervals during the different seasons according to the schedule in table 1. In order to minimize battery use VAS transmitters were also equipped with an activity sensor which recorded locations only when the unit was within 30° of the horizontal plane, i.e when the bird was moving or changing position while perching. GPS-transmitters recorded altitude (above sea level), latitude and longitude for each position (Hipkiss et al., 2013).

Table 1. Registration intervals for Vectronic Aerospace (VAS) and Microwave Telemetry (MTI) GPS transmitters. Starting and stopping times are scheduled for MTI transmitters.

	VAS	**MTI**		
Month	**Interval**	**Start**	**Stop**	**Interval**
mar-apr	30 min	08:00	16:00	1 h
may-aug	10 min	03:00	19:00	1 h
sep-oct	30 min	08:00	16:00	1 h
nov-feb	2 h	10:00	16:00	2 h

Transmitters were attached to the birds using a teflon backpack harness (figure 1). Harnesses used on juveniles were attached on the bird with weakening points in order to fall off after about a year. Juveniles were tagged in their nests, before fledgling. Marking was conducted in known territories with help of the Swedish Golden Eagle Society (Kungsörnsgruppen). Adult individuals were caught in September to November in bow nets and tagged by a group of specialist trappers during 2010 and 2011. Weakening points was not used on adult birds. 14 adult females, 12 adult males, 6 juvenile males and 4 juvenile females were marked. In 4 juveniles sex was unknown. Sex was determined through blood samples after method by Fridolfsson and Ellegren (1999). For birds used in data analyse and marked with VAS transmitters the equipment had a mean weight of 3.4% (± 0.6%, n=24) of the birds body mass and for MTI transmitters mean weight was 1.7% (± 0.3%, n=7) of birds body mass.

Figure 1. Photo of a Golden eagle with an attached GPS transmitter. Photo: Navinder Singh

Maps

Elevation, slope values, vegetation type and wind speed values for each GPS position was determined by extracting values from raster maps. For elevation data map with a 2*2 m (x,y) resolution from Lantmäteriet (Lantmäteriet, 2014) was used. A 2*2 m grid cell was reported for each scanning point of the elevation. Density of scanning points varied between 0 points/m² (for reflecting surfaces such as water and concrete) and >0,5 points/m² for open areas. For flat, hard ground surfaces the error was 0.1 m but at steep and richly vegetated areas the error was much higher.

The vegetation raster map was also imported from Lantmäteriet (Lantmäteriet, 2014) and had a resolution of 25*25m with a total of 60 different vegetation classes. I merged these classes into nine different habitat types considered important for Golden eagles (Sandgren, 2012).

Wind speeds at 135 meter for each GPS position were extracted using a raster map with a resolution of 228*522m (x,y) (Uppsala University, 2014). Wind maps for other heights are available but mean flight heights of Golden eagles in this study were close to 135 meters (144 m ± 0.6 m n= 31) and a high correlation (0.91) between wind speeds at 49 m and 135 m were seen. Rotor swept zones of wind turbines extend up to 150 m which also motivated the choice of using wind speeds at 135 m

Slope values were extracted from the elevation map into a raster map using function “terrain” in R package “raster” (Hijmans, 2014). Aspect (cardinal) of slopes was extracted but since this is a circular variable ranging in value from 0-360°, this variable was transformed into two variables, eastness and northness for each slope with values from -1 to 1 in order to be able to use them in analyses (Hijmans, 2014). Northness will take values close to 1 if aspect is facing north and value of -1 if aspect faces south. If aspect is east or west it will take a value of 0. Eastness behaves similarly expect that a value of 1 means aspect of east and -1 aspect for west.

For location of wind turbines I used available coordinates from the Swedish webpage "www.vindlov.se" and their service "Vindbrukskollen". I used coordinates for 1 401 existing ("uppförda" in Swedish) and for 4 349 proposed ("behandlas", "beslut", "beviljat" and "handläggs" in Swedish) wind turbines and I extracted the distance from each location for the eagles to the closest wind turbine for both existing and proposed wind turbines.

Projection used for all maps was RT 90 and all analyses and extracting values from maps was performed in program R (R Core Team, 2013).

Data preparation

Between the years 2010-2014 a total of 118 195 locations of Golden eagles were recorded for 47 different individuals equipped with GPS transmitters. Individuals with fewer than 200 locations in total and with less than 20 locations per year were removed from the data. 31 individuals with a total of 94 797 locations remained to be used in data analyses. Locations from these 31 individuals were used in all statistical analyses except the analyses for home range areas. Since individuals were marked in 2010 and 2011 and some transmitters stopped sending positions during the study period I had different number of individuals sending data in each year (Table S1). Number of individuals within age category and sex can also be seen in table S1. Net squared displacement for each individual was estimated using package "adehabitatLT" in R (Calenge, 2006) and individuals were divided in either "Long distance movers" (squared net displacement of > 150 kilometers) or "Short distance movers" (squared net displacement of < 150 kilometers).

Seasons

Aerial activity and flight behaviour, e.g. undulating display flight, differ between seasons and therefore all positions was divided into either "breeding" or "nonbreeding" to calculate for possible impact in flight behaviour (Bergo, 1987, Watson, 1997). Breeding was considered between March to July and nonbreeding between August to October.
Since battery in transmitters was partly solar driven the transmitters reported very few positions from November to February and to avoid a skewed result, positions within these months were removed.

Movement data around wind turbines

Wind turbines highly affect wind speed and turbulence intensity up to a distance of two- to three rotor diameters downwind from the turbine and changes in wind conditions can be seen up to a distance of 2000 m from larger wind turbines (Zhang et al., 2012, Smith et al., 2013). For a150 meter rotor swept zone two rotor diameters are 300 meters downwind from the turbine. I categorized all locations of Golden eagles into distance classes from existing and proposed wind turbines in order to analyse differences in flight behaviour. 94 797 Locations of eagles were categorized into three distance classes, "long", "medium" and "short" in terms of their distance from nearest wind farm. "Long" included positions exceeding a distance of >2000 meters from nearest wind turbine, "medium" included positions between 301-2000 meters and "short" included positions within < 300 meters from closest wind turbine (Table 2).

Flight height (hereon referred to as AGL) for each location of eagles was determined by subtracting elevation from above sea level for each location. Mean AGL for individuals with territories within wind farm areas were calculated. Only two individuals, a breeding pair (ID 12 and 13), had territory within a wind farm area (figure 2) and therefor any statistical tests for comparing AGL within and outside wind farm areas could not be calculated. Instead I randomly sampled four individuals from the dataset and calculated mean AGL for all their positions. For wind farm eagles, I also extracted AGL for those locations within a distance of 300 meters to the existing wind turbines and compared those with all locations from them in order to determine potential differences in AGL for locations close to wind turbines.

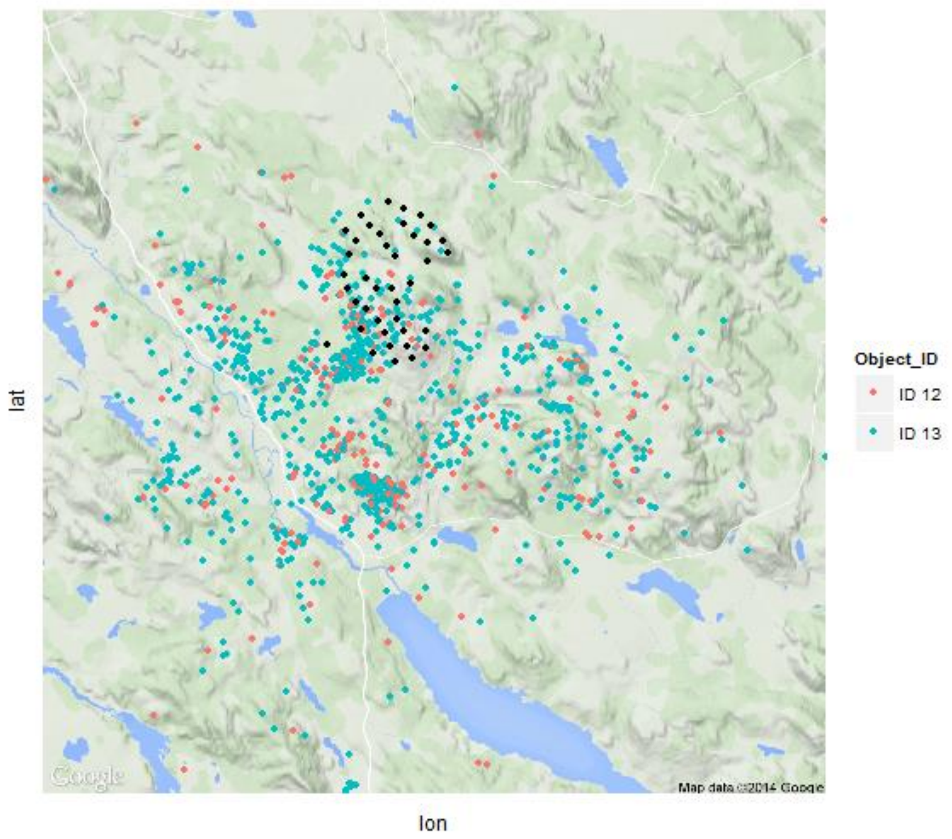

Figure 2. Recorded locations as blue and red points for a breeding Golden eagle pair with territory within a wind farm area. Operating wind turbines are represented by black points.

Statistical analyses

Correlation between variables was tested and none exceeded 0.5, resulting in including all of them. To analyse which variables affects flight height of Golden eagles a generalized linear mixed effects model was run using package "lme4" in R (Bates et al., 2014). Variables "habitat", "slope", "elevation", "wind speed", "season", "sex" and "class" (adult or juvenile) and "eastness" or "northness" of slope and "distance class" (from existing wind turbines) were put in the model as fixed effects and ID of bird as random effect to account for repeated measurements. To select the best fitting model, the model weights and importance of variables were calculated using an AIC (Akaike's Infomation Criterion) based model selection using package MuMIn in R (Barton, 2014) (Table S2).

To test for a difference in flight height between locations within 300 meters from existing wind turbines compared to locations within 300 meters from a proposed wind turbine a Wilcoxon rank sum test was run. Several studies has pointed out how sites of wind turbines and Golden eagles to some extent select for same, favourable wind conditions and environments which creates these wind conditions (Lanzone et al., 2012, Johnston et al., 2013, Miller et al., 2014). Favourable features of topography for both eagles and wind turbine sitings have been proposed to be steep slopes and high elevation (Miller et al., 2014). Areas with wind speeds higher than 7.2 m/s are in Sweden considered as of national interest for exploration of wind energy (Energimyndigheten, 2013).

It has been proposed that Golden eagles decrease AGL as wind speeds increases (Lanzone et al., 2012). In order to determine if slopes, elevation and wind speeds for locations of Golden eagles were different in areas were wind turbines were present I choose to use a general linear mixed model. Three models were calculated, each had either slope, elevation or wind speed as response variable, and the three distance classes from existing wind turbines as fixed effects. ID of eagle was used as random effect in all three models to account for repeated measurements.

Home ranges

To study the potential overlap between wind farm areas and the home ranges of golden eagles, I created 50% and 95% contour Minimum Convex Polygon (MCP) based home ranges (with function "mcp" from package "adehabitatHR" in R, Calenge, 2006) and extracted number of existing and proposed wind turbines within these areas. By using all the 43 individuals from the original dataset and removing those individuals with recorded positions for less than 200 days a new data set was created. It is important to include a minimum of one year to be able to analyse home range areas for Golden eagles since this species alter use of home range depending on season (Haworth et al., 2006). A limit of 200 days responds to about a year since transmitters didn´t record locations every day during winter period. 20 individuals remained to be used in the home range analyses and data was checked manually to ensure all individuals had recorded locations for at least a year. Of the 20 individuals, 15 were adults and 5 were juveniles. 12 of the individuals were male, 6 females and 2 juveniles with unknown sex.

A Minimum Convex Polygon creates a home range area for an individual by taking the most outlying positions and encloses those, considering the area within those positions as the home range area (Burgman and Fox, 2003). For migrating eagles a Minimum Convex Polygon will not show the actual home range area since they migrate long distances. Therefor I created minimum convex polygon for 95% and 50% which means that the function excludes outer positions by 100 minus the percent value to get a more "true" home range. Because mcp´s smaller than 100 % were calculated it was important to include all recorded locations for every individual in order to get a more reliable result for the actual home ranges. Winter positions were included even if an individual lacked positions during some months. During December, 11 individuals lacked locations and during January another 11 individuals lacked locations. Eight of these individuals lacked locations in both months. One individual lacked locations for November. For all other months locations were recorded for all individuals. Within each home range I extracted number of existing and proposed wind turbines using function "intersect" from package "raster" in R (Hijmans, 2014).

Brownian Bridge has been proposed to be a better method to analyse home range areas for animals (Horne et al., 2007). Locations of Golden eagles in this study have been recorded with varying time intervals plus some of these individuals migrate to large distances, which makes it difficult to establish grid sizes for analyses that can be set for all individuals together, when there is a large variation in space use across individuals. An alterative would be to undertake the analyses of each individual at a time. Winter locations are too few and these errors make Brownian Bridge an unreliable method for this dataset (Horne et al., 2007).

Results

Distance classes

I used distance to wind turbine as a fixed effect in my statistical analyses. To determine the reliability of the glmm tests it was important to know how many individuals that locations were recorded for within the three different distance classes. Most of locations recorded close to wind turbines (within distance classes “short” and “medium”) came from a breeding pair (n=364 for “short” and n=1338 for “medium”), which have a territory within a wind farm area. A total of six individuals had recorded locations close to wind turbines. Four of these individuals had a territory within, or close to a wind farm area. Ten individuals had recorded locations within a medium distance to turbines of which six of them also had recorded locations within closer wind turbines (Table 2). All 31 individuals had recorded locations for a distance larger than 2000 meters from a wind turbine. 18 individuals had recorded locations at shorter distances from proposed wind turbines, 23 individuals in “medium” distance and all 31 individuals further away (table 3). Locations for each distance class category were used in all data analyses comparing variables with respect to distance to nearest existing or proposed wind turbine.

Table 2. Schedule for number of locations of Golden eagles extracted within three distance classes and number of individual that locations are recorded for. Distance is calculated from existing wind turbines.

Distance class	**Distance to wind turbine (m)**	**Number of individuals**	**Number of Locations**
Short	< 300	6	381
Medium	301-2000	10	1 525
Long	> 2000	31	92 891

Table 3. Schedule for number of locations of Golden eagles extracted within three distance classes and number of individual that locations are recorded from. Distance is calculated from proposed wind turbines.

Distance class	**Distance to wind turbine (m)**	**Number of individuals**	**Number of locations**
Short	< 300	18	638
Medium	301-2000	23	1 847
Long	> 2000	31	92 312

Wind speed

Mean wind speed (at 135m) at observed eagle locations was 6.0 m/s (SE= <0.1, n=94 797) with a range of 0-10 m/s and a median of 6.1 m/s (for distribution see figure 3). For locations within a 300 meter distance of wind turbines both mean and median wind speed was 7.4 m/s with a range of 6.2 to 8 m/s. For locations within 301-2000 meters to existing wind turbine mean and median wind speed was 6.9 m/s with a range of 5.1 to 8 m/s (figure 4).

Wind speeds extracted at locations close to wind turbines were on average higher compared to wind speeds further away from wind turbines. Average wind speed at locations close to wind turbines were 7.2 m/s. As distance to wind turbine increased wind speed decreased (p <0.001, table 4).

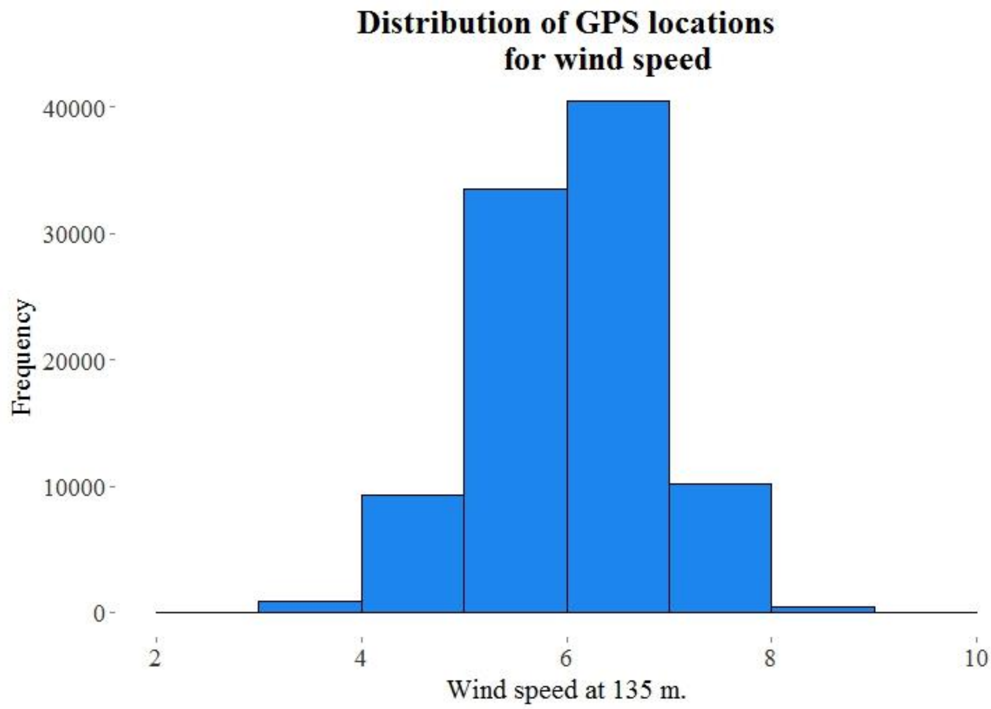

Figure 3. Distribution of locations recorded for Golden eagles (n=31) for wind speed at 135 meter.

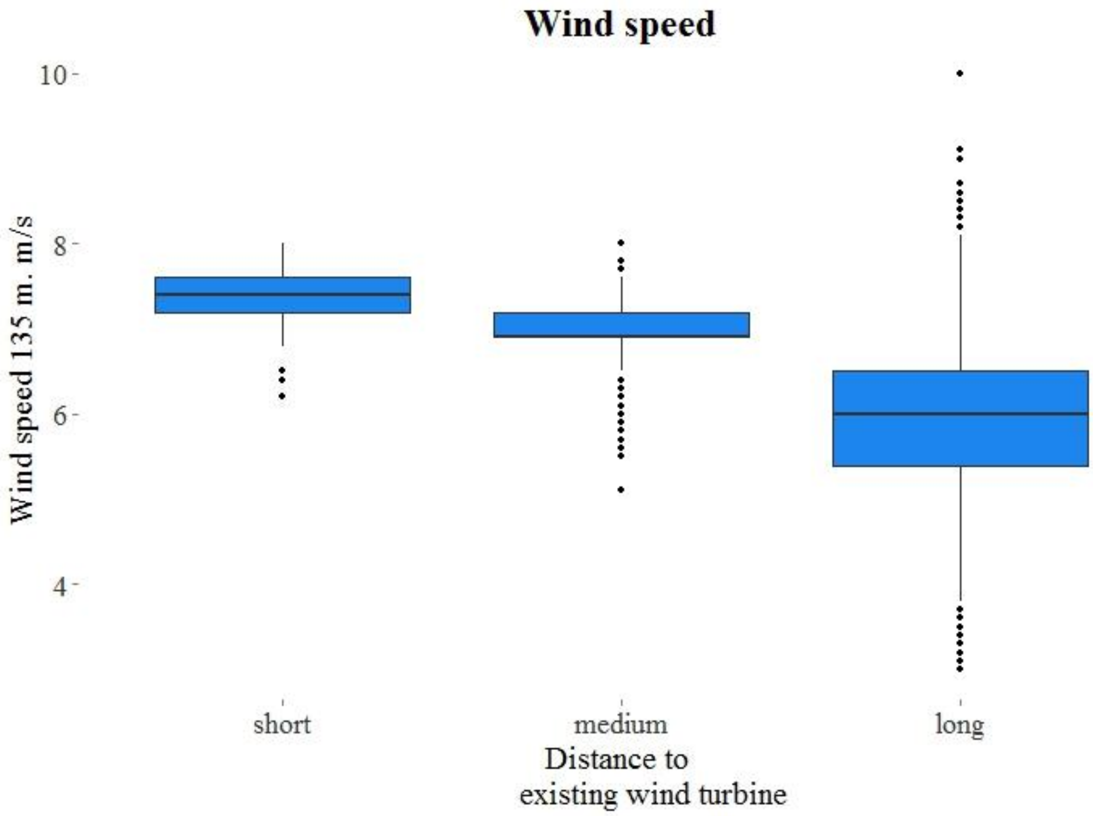

Figure 4. Boxplot for wind speeds (m/s at 135 m) at recorded locations for Golden eagles. Boxes from left to right corresponds to distance class “short” (< 300m), “medium” (301- 2000m) and “large” (> 2000 m) from existing wind turbine.

There was no difference in the wind speeds used by sexes (6.0 m/s ± 0.01 for both sexes, n= 16 for females and n= 15 for males, neither between seasons (6.0 m/s ± 0.01 for both seasons, n= 22 for breeding season and n= 31 for nonbreeding season). The use of wind conditions was similar between months with a range of 5.9- 6.4 m/s. Adults had a mean of 6.2 m/s (s.e = <0.01, n=20) and juveniles had a mean of 5.8 m/s (s.e= <0.01, n= 11).

Table 4. Model results for differences in wind speeds (m/s) for locations of Golden eagles (n= 31) between distance classes from existing wind turbines. Distance class short used as base. Asterisk (*) indicates significant p-values (< 0.001).

fixed effect	estimate	s.e	t value	random effect	variance	s.d
intercept*	7.20	0.06	124.56	eagle ID	0.14	0.37
medium*	-0.43	0.04	-10.27			
long*	-1.03	0.04	-26.60			

Slope

Mean value of slope used by eagles was 2.8 ° (s.e=0.01º, n=94 797) with a range between 0 to 23.5 °. A statistical analysis with generalized linear mixed model with slope as response variable and distance class as explanatory variable showed significance results for all three distance classes ($p < 0.001$). Slope degrees increased as distance to wind turbine increased but difference in average slope degrees between the three distance classes was low (table 5). Juveniles used marginally steeper slopes than adults, 3.5° for juveniles (s.e =0.01°, n= 11 and 2.0° for adults (s.e = <0.01°, n= 20). Eagles used rather gentle slopes, both during the breeding (2.9º ± <0.01, n= 22) and nonbreeding season (2.7º ± 0.02, n= 31).

Table 5. Model results for differences in slope (°) for locations of Golden eagles (n= 31) between distance classes from existing wind turbines. Distance class short used as base. Asterisk (*) indicates significant p-values (< 0.001).

fixed effect	estimate	s.e	t value	random effect	variance	s.d
intercept*	1.96	0.17	11.74	eagle ID	0.96	0.98
medium*	0.74	0.13	5.78			
long	0.15	0.12	1.25			

Aspect of slope

Mean values of aspect of slopes for recorded locations were all close to zero (facing east or west; mean= <0.01, s.e = <0.01, n=31 facing north or south; mean= 0.07, s.e = <0.01, n=31). This means slopes were facing neither east, west, north or south.

Elevation

Mean ground elevation used by eagles was 524.7 (m.a.s.l) (s.e =0.7 m, n=31) for all locations recorded. Females (538.4 m ±1.0, n=16) used slightly higher elevations than males (512.5 m ± 0.9, n=15). Juveniles on an average used significantly higher ground elevation than adults (juveniles= 616.2 m ± 0.9, n= 11, adults= 425.8 m ± 0.8, n=20, W= 764323495, p= <0.001) (figure 5).

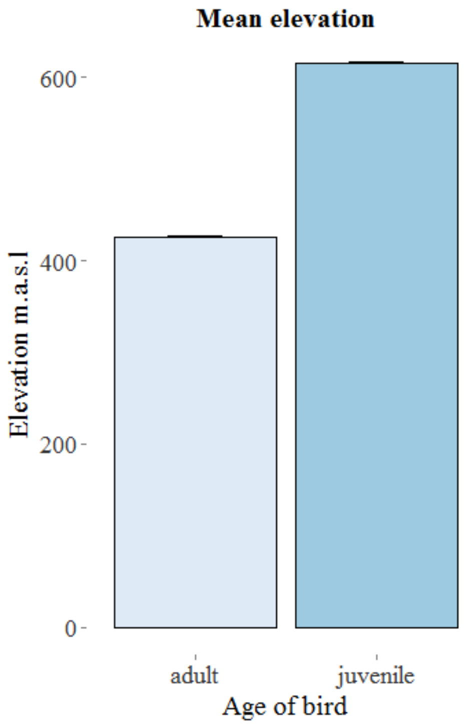

Figure 5. Mean elevation (m.a.s.l.) for locations recorded from adult (n= 20) and juvenile (n= 11) Golden eagles. Black error bars indicates s.e. values.

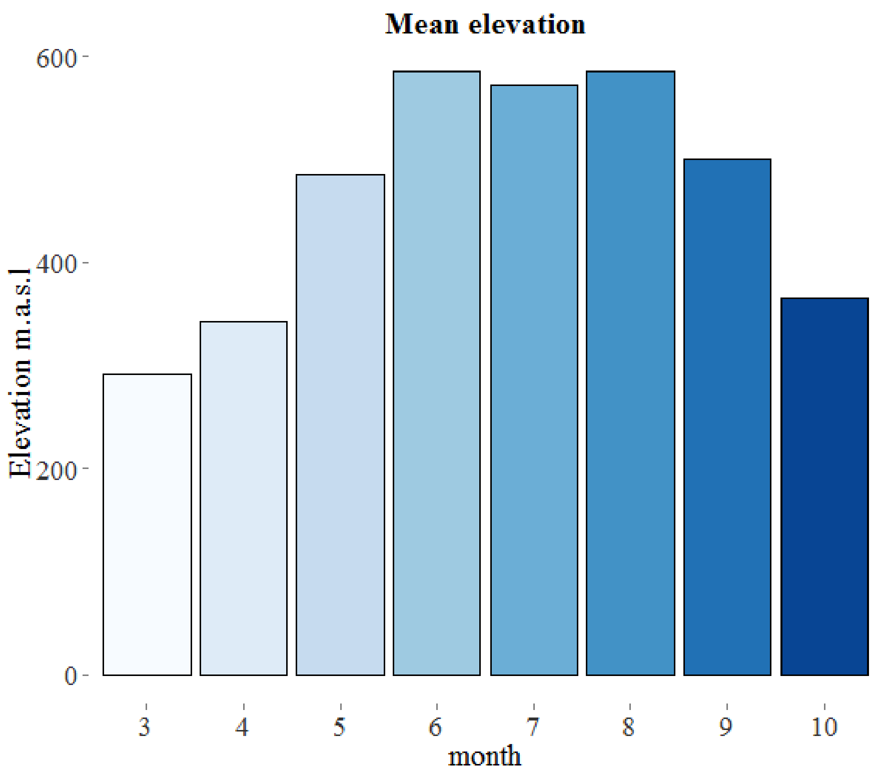

Figure 6. Mean elevation levels (m.a.s.l) per month for locations recorded from Golden eagles (n=31). Number corresponds to month of year, i.e 3 for March. Black error bars indicates s.e for each month.

Eagles used higher elevations in summer as compared to other times of the year (figure 6). Locations closer to wind turbines were at higher mean ground elevation (523.8 m ± 2.3, n= 6) than those in a distance of 301- 2000m (427.9 m ± 2.2, n= 10) from existing wind turbines. Mean elevation levels for locations within distance class “long” (526.3 m ± 0.7, n= 31) was close to mean elevation for the shorter distance to wind turbines (figure 7). There was a significant difference between the three distance class (p= <0.001) and ground elevation decreased with an increasing distance from wind turbine (Table 6).

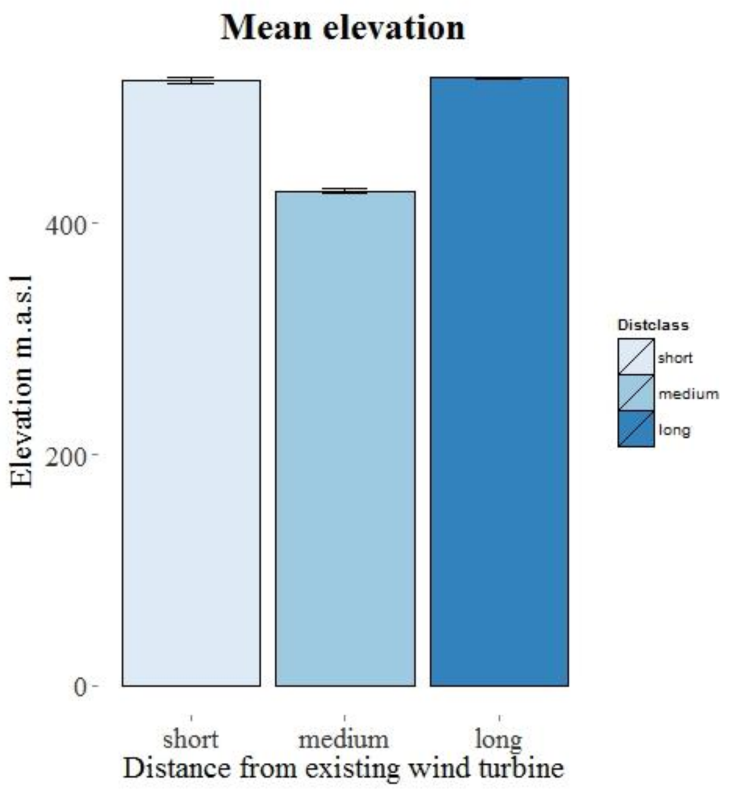

Figure 7. Mean elevation levels (m.a.s.l) per distance class from existing wind turbine for locations recorded from Golden eagles (n= 31). Black error bars indicates s.e for each distance class.

Table 6. Model results for differences in elevation (m.a.s.l) for locations of Golden eagles (n=31) between distance classes from existing wind turbines. Distance class short used as base. Asterisk (*) indicates significant p-values (< 0.001).

fixed effect	estimate	s.e	t value	random effect	variance	s.d
intercept*	495.5	18.1	27.4	eagle ID	20963	144.8
medium*	-105.5	7.3	-14.4			
long*	-109.8	6.8	-16.0			

Habitat

46.4% of the locations from all eagles occurred within *closed canopy forest*. *Open mires and wetlands* (24.5%) and *young forest* (16.5%) were the next most used habitats (Table 7 and figure 8). Pattern of use of habitat types is similar over the two seasons with *closed canopy forest* being the most used habitat type. Across months, a similar pattern is seen with only the difference in the use of *young forest* in March. Both *clear-cuts* and *young forest* are less used during May to August compared to other months (Table 10 and figure 9).

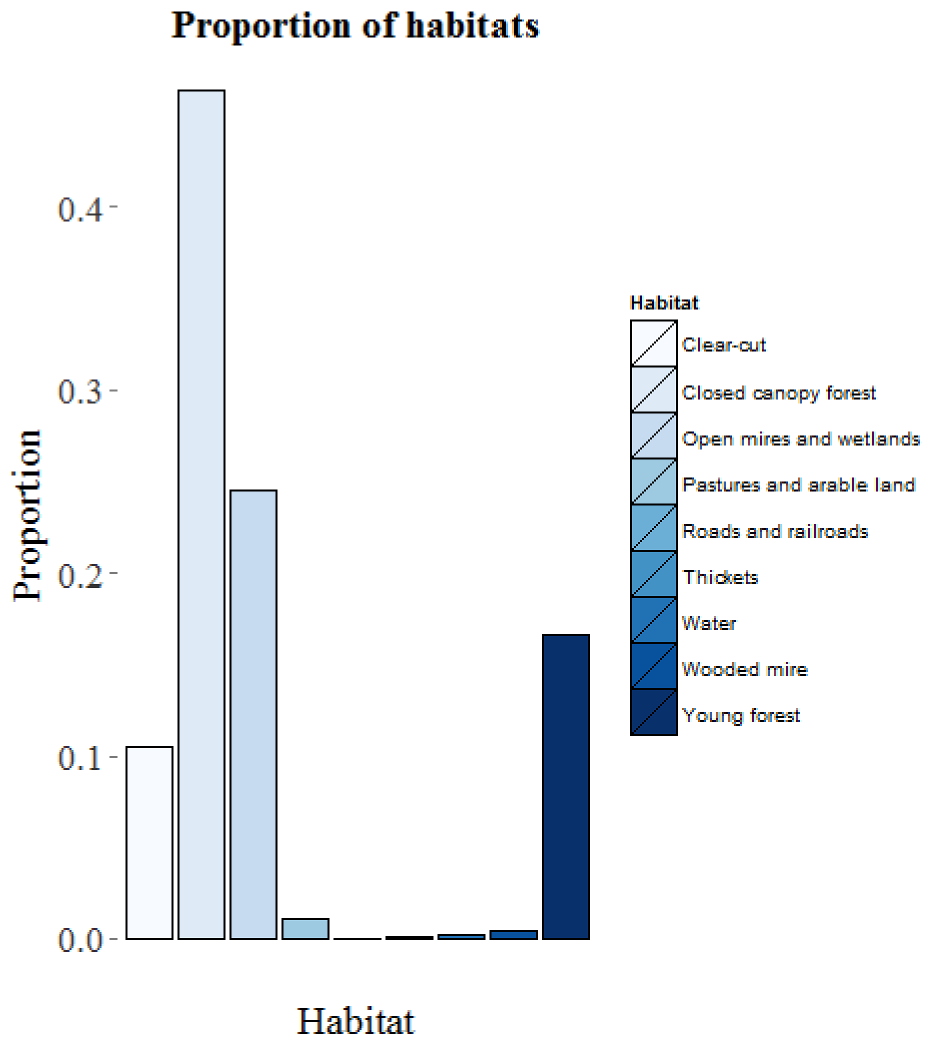

Figure 8. Proportion of habitats for locations recorded from 31 Golden eagles.

Table 7. Proportion of locations recorded from Golden eagles (n=31) within different habitat types. Locations are shown for the full study period (2010- 2014), per season and per month. *Roads and railroads* is not included since only one location was recorded within that habitat.

Proportion of GPS position extracted (%)								
Period	**Habitat**							
	Clear-cut	*Closed canopy forest*	*Open mires and wetlands*	*Pastures and arable land*	*Water*	*Thickets*	*Wooded mire*	*Young forest*
2010-2014	10.5	46.4	24.5	1.1	0.2	0.2	0.5	16.5
Breeding	10.3	47.9	21.8	1.4	0.3	0.2	0.5	17.7
Nonbreeding	12.8	49.5	36.5	0.4	0.1	0.2	0.5	16.0
March	19.5	32.7	0.3	6.9	0.2	0.0	0.3	40.1
April	24.6	60.1	2.7	10.3	0.4	0.0	1.9	47.1
May	11.3	50.0	16.8	0.1	0.2	0.1	0.4	21.1
June	8.6	47.4	30.0	0.5	0.1	0.2	0.4	12.8
July	7.7	50.9	27.7	1.2	0.5	0.2	0.4	11.5
Aug	6.9	44.9	38.4	0.2	0.1	0.2	0.2	9.1
Sep	13.4	41.6	25.7	0.0	0.1	0.1	1.0	18.1
Oct	28.6	33.3	4.0	1.4	0.0	0.0	0.9	31.4

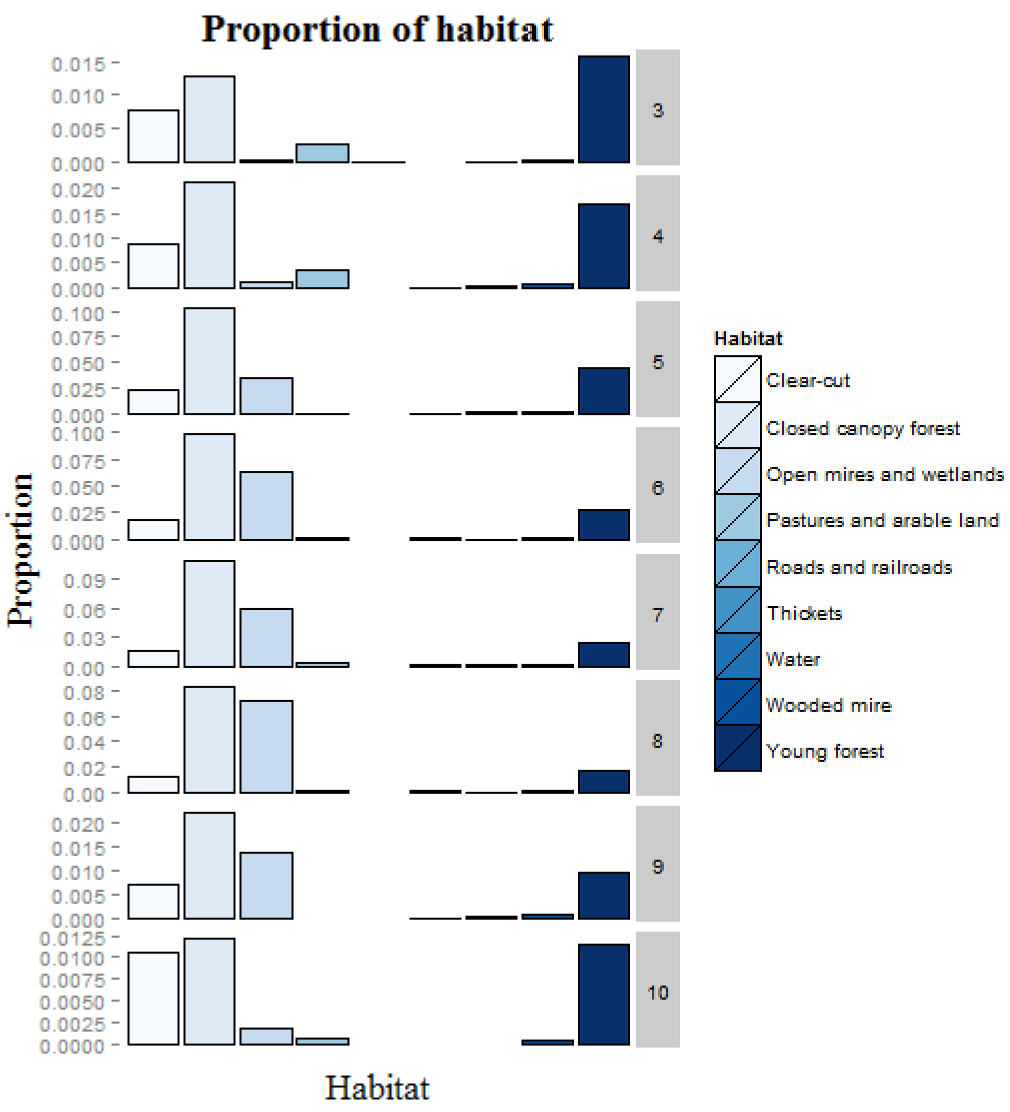

Figure 9. Proportion of habitats per month for locations recorded for Golden eagles (n= 31). Numbers at right hand y axis indicate month of year, i.e 3= March.

Flight height (AGL)

Mean flight height above ground level (AGL) for all eagles was 144.0 meters (s.e=0.6 m, range= 0.01- 1744.5 m, n=31). Mean AGL differed between breeding and nonbreeding season with a mean of 148.6 m for breeding season (s.e= 0.8 m, n= 22) and 131.9 m (s.e= 1.1 m, n= 31) for nonbreeding season. Mean AGL for females (131.9 m ± 0.9 m, n= 16) was lower than that of males (154.7 m ± 0.9 m, n= 15) (figure 9). Adults flew higher as compared to juveniles (170.1 m for adults, s.e= 1.1 m, n=20; and 119.7 for juveniles, s.e=0.7m, n= 11) (figure 9). Mean AGL was the highest over habitat types *water* and *wooded mires* and the lowest over *clear-cuts* and *young forest* (table 8). AGL varied between distance classes from existing wind turbines with higher values for closer distances to wind turbines (figure 10).

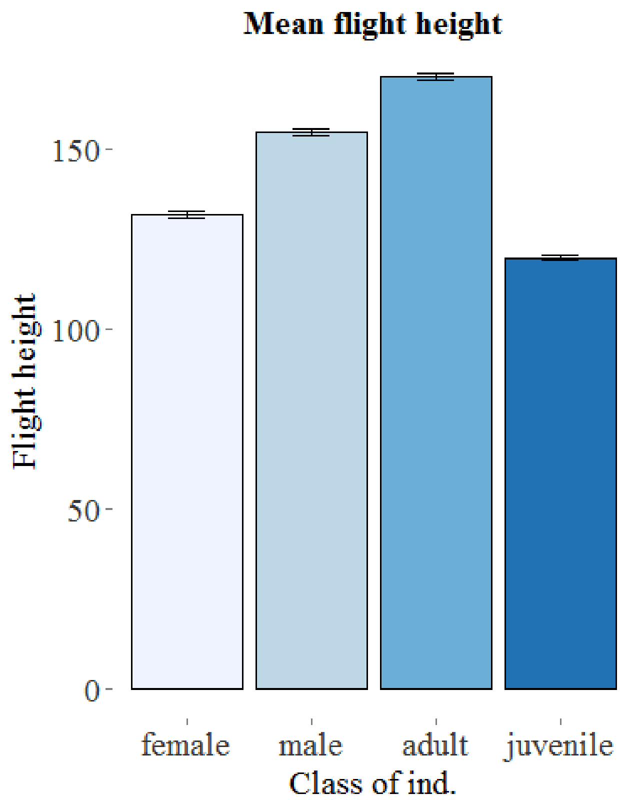

Figure 9. Mean flight height for locations recorded from Golden eagles (n= 31) divided by class of bird. Black error bars indicates s.e value.

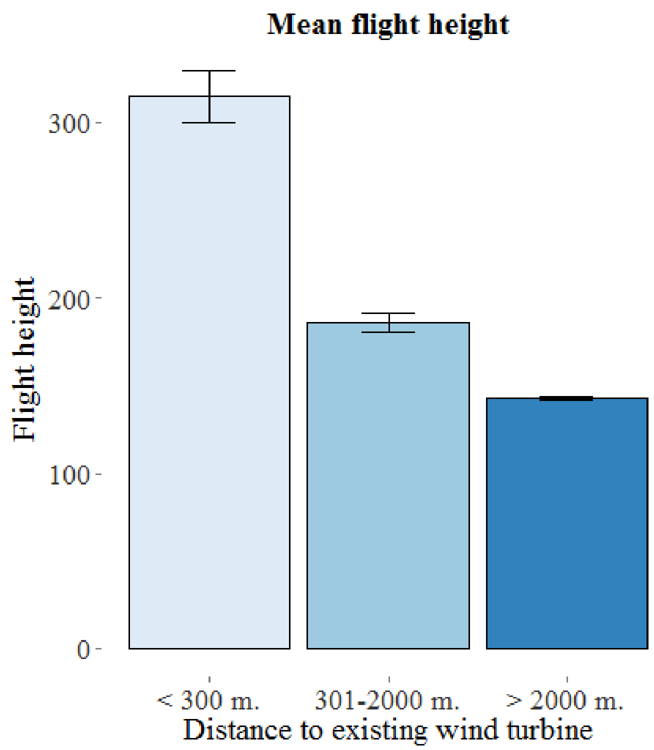

Figure 10. Mean flight height for locations recorded from 31 Golden eagles between different distances to existing wind turbines. Black error bars indicates s.e for each distance class.

Table 8. Mean flight height (AGL) for locations recorded from Golden eagles (n=31) in different habitat types.

Habitat	**Mean**	**SE**	**Number of locations**
Clear-cut	114.5	1.8	9 945
Closed canopy forest	144.6	0.9	44 028
Open mires and wetlands	138.5	1.1	23 238
Other open areas	NA	NA	NA
Pastures and arable land	190.0	7.7	1 064
Roads and railroads	NA	NA	1
Settlements and urban areas	NA	NA	NA
Thickets	153.6	16.1	148
Water	272.4	24.8	210
Wooded mire	248.4	15.9	429
Young forest	161.2	1.8	15 734

Mean AGL for all locations from two eagles (ID 12 and 13) with territory within a wind farm area was 219.0 meters (s.e =3.8 m, n=4902) (table 9 and figure 11). Mean AGL for locations from ID 12 and 13 within 300 meters from wind turbines was 324.5 meters (s.e =16.1 m, n=364) (table 9). Mean flight height for four randomly sampled individuals was 162.0 meters (s.e =1.2 m, n=24 535) (table 9 and figure 11).

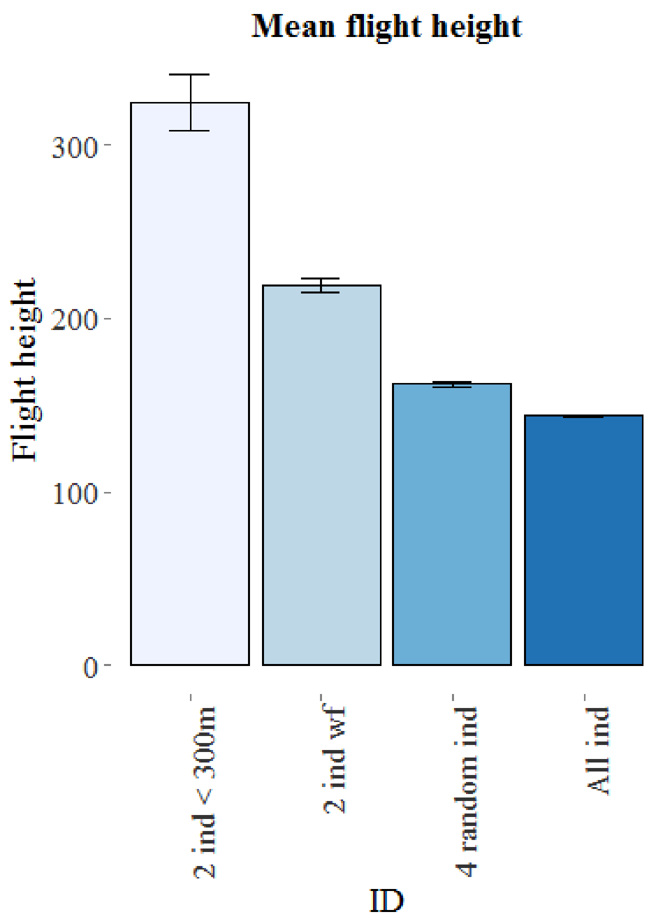

Figure 11. Mean flight height (AGL) for locations recorded from Golden eagles. Blue bars are mean AGL for 2 eagles with territory within a wind farm area. Bars from left to right, 1st bar: mean AGL for locations within 300 meters from existing wind turbine, 2nd bar: mean AGL for all positions from these two individuals. 3rd bar is mean AGL for four randomly sampled individuals and 4th bar is mean AGL for all eagles (n= 31) in the dataset.

Table 9. Flight height (AGL) for all eagles (n= 31) in the dataset, two individuals with territory within a wind farm area and for four individuals randomly sampled from the dataset. For the two individuals results are also reported for positions recorded within a 150 m buffer zone from existing wind turbines and also for positions further away than 150 m from existing wind turbines.

ID	mean AGL (m)	s.e (m)	Number of locations
All eagles (n= 31)	144.0	0.6	94 797
Id 12 and 13	219.0	3.8	4 902
Id 12 and 13 ≤ 300 m windturbine	324.5	16.1	364
4 randomly sampled individuals	162.0	1.2	24 535

From the model selection for the glmm model I chose to exclude variable "northness" since this did not have a statistically significant effect in the generalized linear mixed model. I also excluded variable "eastness" because all the models from the model selection were very equal in weight when including this variable. When I excluded both these variables the strongest model had a weight of 0.929 which was much higher than the other models in that selection (table S2).

Golden eagles flew higher closer to wind turbines as opposed to when they were located away from wind turbines ("short"; 206.19 m ± 19.25 m, t-value= 10.70, p= <0.001, "medium"; -147,9 m ±10,8 m, t-value= -13,8, p=<0,001, "long"; -111,2 m ±10,0 m, t-vale= -11,1, p=< 0,001) (table S3).

They flew higher during nonbreeding season with an average of 16.2 m higher (±1.5 m, t-value= 10.5, p=< 0.001) (table S3).

Both ground elevation and slope had a significant impact on AGL for Golden eagles (p=< 0,001 for both variables). Flight height increased with steeper slopes (3.51° ± 0.28), and decreased with increasing ground elevation (-0.15 m ± 0.006). AGL also increased with increasing wind speed (4.60 m/s ± 0.89). All habitat types had a significant impact on AGL (p=<0.001). AGL was lowest over *clear-cuts* (table S3, *clear-cut* used as base) and highest over *water* (157.86 m ± 13.10). There were no significant differences in the flight height across sex or age groups (Table S3). R square was 0.19 for the glmm model.

Flight height (AGL) within wind turbine areas

Golden eagles flew higher over existing wind turbines compared to over proposed wind turbines (existing; 314.9 m ± 14.9 m proposed; 260.1 m ± 10.8 m W=136689, p=0,0008). Number of locations and number of individuals within each distance class from proposed and existing wind turbines are shown in table 2 and 3.

Minimum Convex Polygon areas (mcp)

I calculated the MCP home ranges for 20 individuals. The core (50 % contour) areas ranged in size between 22 km^2 to 82 387 km^2. For the extended (95 % contour) area the range was between 477 km^2 and 253 823 km^2 for all eagles. Two eagles were classified as "short distance movers" according to the NSD-value and 18 as "long distance movers". The two short distance movers had a 95 % contour area of 661 km^2 and 1 116 km^2 respectively. The long distance movers had a range between 477 km^2 and 253 823 km^2 for the 95 % contour area.

Overlap between eagle home ranges and existing wind farms

Within the extended range (95 % contour), 60 % (n= 12) of the home ranges contained existing wind turbines. The number of wind turbines within home range area ranged between 41 and 455 existing wind turbines. 45 % (n= 9) of the core home ranges (50 % contour) contained existing wind farms (range 31- 185) (figure 12).

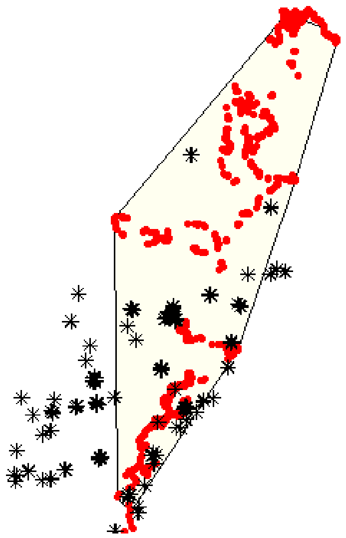

Figure 12. A 193 591 km^2 home range area (90 % contour) of a juvenile Golden eagle with GPS tracked locations as red points and 265 existing wind turbines (within the home range) as black stars (*).

Overlap between eagle home ranges and proposed wind farms

85 % (n= 17) of the extended range (95 % contour) of the mcp´s contained proposed wind turbines. The range for number of proposed wind turbines within home range areas was between 9- 2 554 proposed wind turbines. 70 % (n= 14) of the core home ranges (50 % contour) contained proposed wind turbine with a range between 10- 450 number of proposed wind turbines (figure 13).

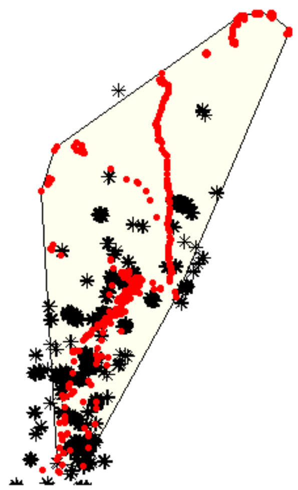

Figure 13. A 216 051 km^2 home range area (90 % contour) of an adult Golden eagle with GPS tracked locations as red points and 2 554 proposed wind turbines (within the home range) as black stars (*).

Discussion

This work aimed to determine how wind speed, topography and life history variables impact on flight height of Golden eagles in Sweden. Another aim was also to assess possible impact of wind turbines on movement ecology of this raptor. My results showed that eagles used wind speeds within 6-7 m/s more frequently than other wind speeds and wind speeds were higher at locations recorded closer to wind turbines compared to further away. Slopes and aspect of slopes does not seem to be of high importance for eagles in Sweden since used values for these variables were rather low. Juveniles used higher ground elevations than adult eagles and frequency of higher elevations used increased during summer months. Most used habitat types in terms of frequency of use were *closed canopy forest*, *open mires and wetlands*, *young forest* and *clear-cuts*. AGL was lowest over *clear-cuts* and highest over *water*. I found that topography, wind speed and distance to wind turbine had a significant effect on AGL of Golden eagles in Sweden. Age and sex of eagle did not seem to affect AGL. However, a low R square of the statistical model for variables impacting on AGL of Golden eagles indicates there are more possible variables that may significantly affect flights heights, but are not included in this study, for e.g. actual wind conditions or weather.. More than half of the eagles in this study had a home range (95 % contour) which overlapped with existing wind turbines and 85 % of the home ranges overlapped with proposed wind turbines.

Mean wind speeds within age groups and sex reported in my study are all very similar with mean values around 6-7 m/s and frequency of use was much higher within these values for all eagles. Especially ranges of wind speed within shorter distances (distance classes “short” and “medium”) to existing wind turbines were narrow (5.1 – 8 m/s). In this study wind speed is the only variable measured for wind but Bohrer et al. (2011) results suggest how Golden eagles have a preference for orographic winds in North America. Also Miller et al. (2014) found how migrating Golden eagles in different regions in North America always selected for areas with potential of orographic updraft winds. Golden eagles seem to use more orographic winds in increasing wind speeds (Lanzone et al., 2012).

It has been suggested that topography drives AGL of Golden eagles in North America (Katzner et al., 2012), however, it doesn't seem to be the case in Sweden which is confirmed by the fact that the average slope used by eagles was rather low. The topography in Sweden, in general is not as dramatic as in the study areas of Katzner et al. (2012). Sandgren et al. (2014) found that juvenile Golden eagles in Sweden selected for steep slopes over 5 ° during post-fledging period with an increase in preference with increasing incline of slopes. Eagles select for nesting areas with cliffs or old trees that often are located on steep slopes (Watson, 1997). Therefore, eagles might be found to use steeper slopes during fledging and post fledging period. During later periods in life this may not be the case and this could be an explanation to the variation between my study and Sandgren et al. (2014) study where they only included slopes within home ranges. Researchers has pointed out how eagles prefer slopes and cliffs in a south-facing direction, both during migration and as nesting positions (Watson, 1997, Miller et al., 2014) whereas a study in Spain didn´t find any selection for south- facing slopes in nesting areas (Lòpez-Lòpez et al., 2007). In Sweden, there seem to be a preference for south-facing slopes as nesting areas since 54 % of the areas around nesting in the study by Sandgren et al. (2014) included south-facing slopes. However, this doesn´t seem to be the case for movement behavior outside nesting areas in Sweden since eagles in my study used gentle slopes and zero values for cardinals (indicating lack of cardinal).

Golden eagles select for higher ground elevation levels where wind conditions often are favourable (Miller et al., 2014) and results from my study shows how eagles lower flight altitude as elevation increases in Sweden. Mean elevation levels used are higher in a distance less than 300 meters from existing wind turbines which is not surprising since wind turbines often are built at higher elevations where wind conditions are favourable. Mean elevation levels used were higher during summer months. Most individuals in the used dataset spent summer months in northern Sweden (own, unpublished data) where elevations are often higher compared to southern Sweden. This might have contributed to the difference in used elevation levels between months.

Eagles in Sweden inhabit the boreal zone influencing habitat selection towards clear-cuts as open hunting areas (Sandgren, 2014, Moss et al., 2014). In this study most locations from eagles were extracted within habitat *closed canopy forest*. This is expected because large areas of Sweden are covered with forest due to forestry being the dominant land use practice in several regions. *Open mires and wetlands, young forest* and *clear-cuts* are among the habitat types more used which is consistent with results from other populations globally; in Idaho golden eagles selected for shrub habitats and avoided open and disturbed areas like grasslands and agricultural areas (Marzluff et al., 1997) and in Spain the amount of open, disturbed areas within eagle territory was low (Lòpez-Lòpez et al., 2007). *Clear-cuts* and *young forest* are used as hunting areas in Sweden (Sandgren et al., 2014, Moss et al., 2014), which is shown in this work by the fact that mean AGL was lower in these two habitats, probably due to hunting behavior. No locations were recorded within habitats *other open areas* and *settlements and urban areas* so these habitats weren´t included in analyses.

Mean AGL for eagles in this study was 144.0 m. Adults flew higher than juveniles on average and males flew higher than females. Age class of eagle was not shown to impact on AGL with a significant result in the glmm model. However, difference between mean AGL for adults and juveniles was large (170.1 m ± 1.1 for adults, 119.7 m ± 0.7 for juveniles) and p- value for age class was low (p= 0.191) which indicates how age of bird might affect AGL. Differences in flight behavior depending on age of eagle have been suggested before (California Energy Commission, 2002, Johnston et al., 2013). The reason for differences in AGL between sexes could be because males perform undulating display flights, mostly during breeding season (Bergo, 1987, Watson, 1997). Glmm model didn´t show any significant result that sex effects AGL but result revealed how eagles flew lower during breeding season compared to nonbreeding season. Eagles flew higher over habitats *water*, *wooded mire* and *pastures and arable land*, probably because these habitats are not used by eagles (Marzluff et al., 1997). Mean AGL for eagles was higher when they flew close to wind turbines compared to further away and mean AGL within a 300 m distance to wind turbine was well above the larger rotor swept zones. Same pattern was seen for the two wind farm eagles (ID 12 and 13) which also increased AGL closer to wind turbines. Mean AGL for wind farm eagles was higher than mean AGL for all eagles in the dataset and reason for this is unknown. Eagles also flew higher over existing wind turbines than over areas where wind turbines are proposed. Wind turbines are known to displace eagles both in space (Garvin et al., 2011) and at a ranging level (Walker et al., 2005). However, no study has yet reported a vertical displacement of eagles due to wind farms. This is one of the strongest result from this study.

This study shows how 60 % of the calculated mcp areas (95 % contour) for 20 eagles had existing wind turbines in their home ranges. For the long distance movers a 95 % contour home range mainly represents maximum observed displacement, which may vary across years. Therefore the number of wind farms within this area may vary year by year. However the mcp area (95 % contour) with the largest number of proposed wind turbines included 2 554 wind turbines which is substantial. The 50 % contour area gives a more reliable picture of the actually home range and 70 % of home ranges had proposed wind turbines within that area. The maximum number of proposed wind turbines within the 50 % contour area was 450 wind turbines. Construction of wind turbines decreased raptor abundance with 47 % at a wind farm area in U.S.A compared to the pre-construction period (Garvin et al. 2011). Golden eagles are territorial and displacement by wind turbines constructed within a home range will not always lead to an abandonment of the home range (Lie Dahl et al. 2012). Instead it might lead to a shift in use of the home range, which could cause a home range area of poorer quality. Construction of wind turbines within white-tailed eagle (*Haliaeetus albicilla*) territory caused a decrease of reproductive success, due to displacement of eagles and /or habitat loss around nests (Lie Dahl et al. 2012). Whitfield et al. (2007) pointed out how an alteration or abandonment of a home range is a complex issue. For example, a shift of use of the home range might not be possible if the home range is constrained by neighbouring eagles since they are territorial animals, defending the territory against introducers.

Reproductive success of Golden eagles in Sweden is low (Hjernquist, 2011) and a decrease of that quote could cause a decline of the population. Not only can an operational wind turbine displace eagles but the period during construction and the footprints this period leaves can also cause habitat disturbance. Construction of wind turbines causes alteration of habitat, both permanent alterations like construction of roads and power lines, and temporary alterations like an alteration of vegetation type (Kuvlesky et al., 2007). Eagles are known to be sensitive to human disturbance and low food supply, which have negative impacts on reproduction success (Richardson and Miller, 1997, Steidl and Anthony, 2000, Moss et al., 2012). Power lines pose a collision risk for eagles and at least one of the marked eagles in this study has been killed through this course of action (unpublished data). With a population that is already listed as Near Threatened, the results of 70 % of home ranges (50 % contour) containing proposed wind turbines are concerning. The Swedish parliament aims for a population of minimum 150 breeding pairs per year (Regeringens proposition 2012/13:191, Riksdagens protokoll 2013/14:43). An increase of wind turbines proposed within the areas used by Golden eagles poses a significant threat for their successful breeding (Garvin et al., 2011, Lie Dahl et al., 2012). A threat which may jeopardize the national goal of maintaining a viable golden eagle population in Sweden (Regeringens proposition 2012/13:191, Riksdagens protokoll 2013/14:43).

Limitations

There were several caveats in this study, which are important to note. Wind speed was extracted at 135 m for all locations in the data irrespective of at which height location was measured for. This means that there is a possibility that eagles flew within other wind speeds than those measured in this study. Since Golden eagles seem to select for orographic winds (Bohrer et al., 2011, Lanzone et al., 2012, Miller et al., 2014) analysing these kinds of winds instead of wind speed might have given a higher R square in my study. Several juveniles have recorded locations for only a year or less (own, unpublished data). All juveniles in this study where hatched in northern Sweden and because elevation levels are higher there results for elevation could be skewed. Sample size in distance class “short” for existing wind turbines is low with only six individuals with recorded locations and most locations recorded from two individuals. Results from distance class “short” for existing wind turbines are therefor unreliable. A calculation of both a 95 % contour and a 50 % contour area gave a good overview of the extent of home ranges in this study. However, Brownian Bridge has been proposed to be a better method to analyse home ranges for animals (Horne et al., 2007) and software for performing the analyse has been introduced (Calenge, 2006). When calculating a Brownian Bridge the amount of uncertainty is dependent on intervals between locations, location errors and mobility of the animal, where longer time intervals and larger mobility of the animal will increase level of uncertainty (Horne et al., 2007). GPS transmitters on Golden eagles in this study has all sent locations with varying time interval and some have reported locations underneath sea level. Locations from winter period are few and lacking in several individuals. Golden eagles are highly mobile, able to travel long distances in a short matter of time making Brownian Bridge an unreliable method for this dataset. Golden eagles suited with more developed GPS transmitters will probably make this method more suitable in the future, hopefully giving us more detailed and reliable results of movements and home ranges. Golden eagles are known from before to use different areas within their home range to different extend, they are also known to shift use of areas depending on season (Marzluff et al., 1997, Lòpez-López et al., 2007, Sandgren et al., 2014). Calculating Brownian Bridge will also enable us to see with which frequency Golden eagles use areas within their home range, an important parameter to include when planning construction of wind turbine sites.

Conclusion

A number of important factors seem to affect habitat use and flight height of Golden eagles in Sweden. Topography does not appear to be as important for Golden Eagles in Sweden as in North America. Eagles flew much higher in a wind farm area in contrast to areas away from wind farms or in the areas where wind farms are absent. Wind farms may vertically displace eagles and force them to fly higher in areas with windmills. There is a great potential of overlap between the golden eagles' movements and proposed wind farms in Sweden, which needs immediate attention, if we are to meet the goals of the Ecosystem based Management of Golden eagles in Sweden.

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Appendix I

Table S1. Schedule for number of locations recorded from Golden eagles (n= 31) and for number of individuals in each category.

	Number of individuals	Number of locations
Year		
2010	10	3 395
2011	28	33 368
2012	22	50 098
2013	13	7 906
2014	2	30
2010-2014	31	94 797
Month		
March	23	3 747
April	21	4 981
May	21	19 652
June	19	19 758
July	23	20 395
Aug	23	17 718
Sep	24	5 063
Oct	28	3 483
Season		
Breeding	22	68 533
Nonbreeding	31	26 264
Sex		
Female	16	44 471
Male	15	50 326
Class		
Adult	20	45 556
Juvenile	11	49 241

Table S2. Model selection table for a generalized linear mixed model with eight variables as fixed effects and flight height (AGL) as response variable. Random effect for all models was ID of eagle. Plus means that the fixed effect was included in the model. Locations from 31 Golden eagles were used in the model.

Model selection table													
Intercept	class	distance class	elevation	habitat	season	sex	slope	wind speed	df	logLik	AICc	delta	weight
206.2	+	+	-0.1564	+	+	+	3.515	4.609	19	-630184.7	1260407	0.00	0.929
209.5	+	+	-0.1564	+	+		3.514	4.607	18	-630188.6	1260413	5.88	0.049
197.7		+	-0.1565	+	+	+	3.513	4.617	18	-630189.5	1260415	7.58	0.021
200.6		+	-0.1565	+	+		3.513	4.615	17	-630193.4	1260421	13.43	0.001
236.8	+	+	-0.1485	+	+	+	3.344		18	-630198.9	1260434	26.42	0.000
240.0	+	+	-0.1485	+	+		3.344		17	-630202.8	1260440	32.29	0.000
228.2		+	-0.1486	+	+	+	3.342		17	-630203.7	1260442	34.09	0.000
230.9		+	-0.1485	+	+		3.342		16	-630207.7	1260447	39.93	0.000
215.7	+	+	-0.1519	+		+	3.275	4.434	18	-630245.0	1260526	118.66	0.000
217.8	+	+	-0.1519	+			3.275	4.433	17	-630248.9	1260532	124.37	0.000
Random terms (all models): 'Eagle ID'													

Table S3. Model results with flight height (AGL) as response variable and eight variables as fixed effects. For distance class; distance short is used as base. For season; breeding is used as base. For class; adult is used as base. Habitat types are written with first letter as capital and clear-cuts are used as base. Asterisk (*) indicate significanr p- values (p= <0.001). Locations from 31 Golden eagles were used in the model.

fixed effects	**estimate**	**s.e**	**t value**	**p value**	**random effect**	**variance**	**s.d**
*intercept**	206.19	19.25	10.70	< 0.001	eagle ID	6682	81.74
*dist.class Medium**	-146.57	10.75	-13.62	< 0.001			
*dist.class Long**	-108.52	10.04	-10.80	< 0.001			
*season nonbreeding**	16.78	1.542	10.88	< 0.001			
class juvenile	-26.73	20.44	-1.31	0.191			
sex male	6.825	19.35	0.35	0.724			
*slope**	3.51	0.28	12.19	< 0.001			
*elevation**	-0.15	0.006	-24.62	< 0.001			
*wind speed**	4.60	0.89	5.17	< 0.001			
*Closed canopy forest**	62.27	2.51	24.76	< 0.001			
*Open mires and wetlands**	55.57	3.16	17.55	< 0.001			
*Pastures and arable land**	65.86	6.61	9.96	< 0.001			
*Roads and railroads**	304.66	186.7	1.63	0.103			
*Thickets**	80.18	15.57	5.14	< 0.001			
*Water**	157.86	13.10	12.04	< 0.001			
*Wooded mire**	120.20	9.25	12.98	< 0.001			
*Young forest**	48.70	2.43	20.03	< 0.001			

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