



Factors driving landscape level variation in breeding ecology of Golden Eagle (*Aquila chrysaetos*) on Gotland.

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Abstract

The Golden Eagle (*Aquila chrysaetos*) is an iconic bird of prey, widely distributed across the Northern Hemisphere. The versatility of the golden eagle has allowed them to inhabit a wide range of habitats, where adult eagles establish territories with their partner. Of the near 500 breeding pairs in Sweden, the majority inhabit the mountainous boreal landscapes of the north. However, the highest density of breeding pairs is concentrated on the island of Gotland in the Baltic Sea southeast of mainland Sweden. The island contains atypical habitats for golden eagles, characterized by flat landscapes, limited boreal forest, and widespread human presence. This study explored the underlying factors driving breeding ecology for golden eagles on Gotland. Temporal and spatial patterns of reproductive success were tested for correlation with habitat type, food supply, human disturbance, wind turbines, and con- and interspecific density dependency. A strong correlation was detected between temporal roe deer (*Capreolus capreolus*) abundance and number of occupied golden eagle territories. Territories with many nearby territories were correlated with higher reproductive success. Furthermore, reproductive success displayed weak but insignificant positive trends with coniferous forest, wind turbines and white-tailed eagle (*Haliaeetus albicilla*) presence, and weak negative trends with human disturbance and roe deer related traffic accidents. However, further studies are required to draw conclusions. To further increase our knowledge of this extraordinary sub-population, future research would benefit from exploring accurate movement patterns and habitat use of individual eagles, detailed dietary habits, and relative disturbance of human activities during different parts of the year.

Keywords: Golden Eagle, *Aquila chrysaetos*, population ecology, Gotland, breeding

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Abbreviations

AIC	Akaike Information Criterion
CABG	County Administrative Board of Gotland
GE	Golden Eagle
GIS	Geographical Information System
NMD	Nationella MarktäckeData
NWAC	National Wildlife Accident Council
SEPA	Swedish Environmental Protection Agency
SGU	Geological Survey of Sweden
SLU	Swedish University of Agricultural Sciences
WTE	White-Tailed Eagle

1. Introduction

The golden eagle (GE) is one of the largest and most iconic birds of prey in the world (Watson 2010). As large carnivores continue to experience worldwide decline, it is important to preserve the apex predators like golden eagle for maintaining, sustaining, and restoring ecosystems (Ripple et al. 2014). It is listed in Annex 1 of the EU Birds Directive, which includes species needing special habitat measures (European Union 2009). In Sweden, golden eagle is red-listed as near-threatened (Eide 2020) and protected under the Swedish law, forbidding killing, illegal capture, and general disturbance to the species (Artskyddsförordningen 2007:845). Globally, golden eagles are not threatened, with a rough estimate of c. 85 000 to 160 000 mature individuals (BirdLife International 2021). In Europe, the number of breeding pairs is estimated between 9 600 and 12 800 pairs. The number of breeding pairs in Sweden was estimated to be 500 in 2023 (Åsbrink & Källman 2023). The majority are located in the typical golden eagle habitats of the north, comprised by vast boreal landscapes, mountains, and minimal human disturbance. However, a significant sub-population, comprising about 80 breeding pairs, are concentrated on the island of Gotland in the Baltic Sea southeast of mainland Sweden. Although the island contains atypical habitats for golden eagle, characterized by flat landscapes, limited boreal forest, and widespread human presence, it supports the highest density of golden eagle breeding pairs in Sweden with a remarkable margin. This study aims to explore the population ecology of this extraordinary sub-population of golden eagle.

1.1 Study area

The study area encompasses the whole islands of Gotland and Fårö (henceforth referred to simply as Gotland), an island group located almost 100 km outside mainland Sweden in the Baltic Sea (56.9 – 58.0°N, 18.0 – 19.3°E) (Figure 1). Gotland is the biggest island of Sweden, and the entire island system has an area of 3184 km² (Regionfakta 2023). Approximately 61 000 people inhabit Gotland, with 41 % living in rural and agricultural areas (Holm 2015). Gotland's only city, Visby, got listed as a UNESCO World Heritage site in 1995 (UNESCO n.d.). During summers, Gotland is a popular tourist location that hosts approximately 900 000 tourists yearly (Holm 2015). Additionally, with over 12 500 privately owned

holiday homes, mostly owned by people outside Gotland (SCB 2023), Gotland experiences high peaks of human activity during the summers (Holm 2015).

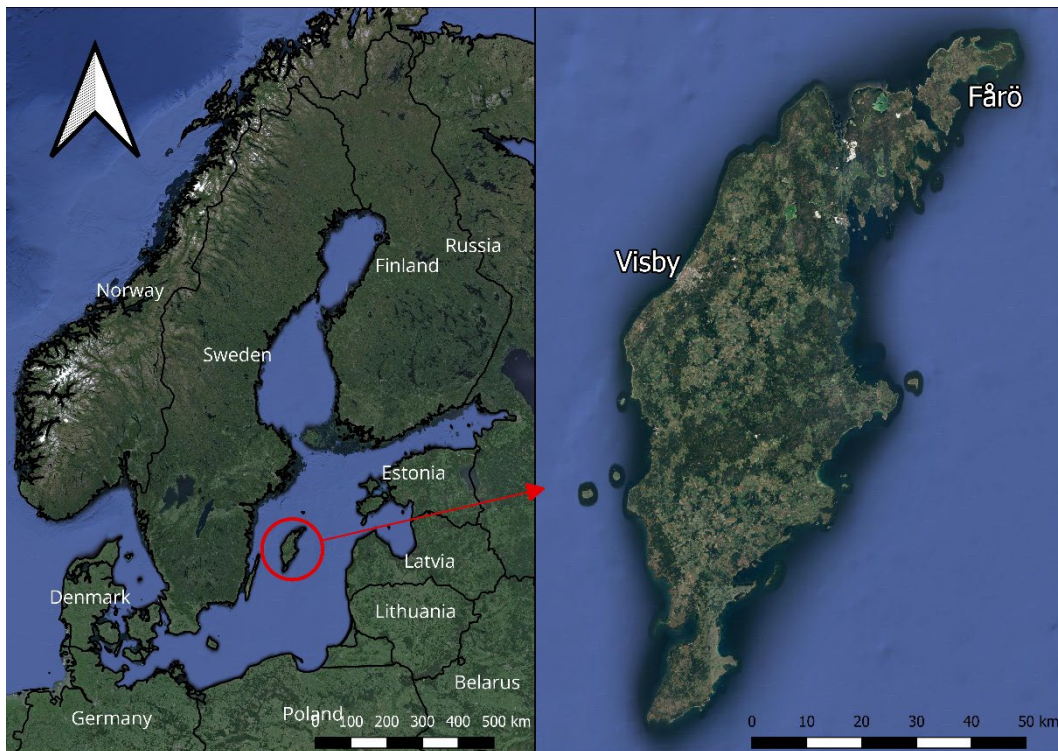


Figure 1. The location and extent of study area, which includes the islands of Gotland and Fårö. Visby is the only city in the study area. Reference system is SWEREF99 TM.

The landscape and habitat composition on Gotland differs from mainland Sweden. The landscape, rich in sedimentary rocks such as sandstone and limestone, comprises barren and rocky landscapes in the north, and deciduous-rich meadow landscapes in the south (Holm 2015). The landscape is largely influenced by agriculture, with sheep breeding being particularly ingrained in the culture. Gotland's location and shallow coastlines provides breeding locales, foraging sites, and resting sites for many migratory birds (Larsson 2022), and excellent feeding grounds for wintering waterbirds (Nilsson & Hermansson 2021). However, many terrestrial mammals are absent, compared to mainland Sweden. For several thousand years, mountain hare (*Lepus timidus*) and red fox (*Vulpes vulpes*) represented the largest terrestrial wildlife on Gotland, introduced by early human settlers (Andersson 2016). Red fox remains the largest terrestrial predator on Gotland to this day. In 1907, the European rabbit (*Oryctolagus cuniculus*) got introduced to Gotland and has since expanded across all of Gotland (Notini et al. 1952). Rabbits on Gotland depend on easily dug soils with low groundwater level for burrowing, and rocks and bushes for predator protection. These conditions exist in patches on Gotland, making the rabbit population clustered. Except in the far south, European rabbit is largely absent on mainland Sweden (SLU Artdatabanken

2024a). Almost 40 years ago, roe deer (*Capreolus capreolus*) were introduced to Gotland (Tärnström 2011). The abundance of food and lack of natural predators led to a rapid increase in roe deer, which are now abundant all over Gotland (Pettersson et al. 2019; Jägareförbundet Mitt 2020). Subsequently, traffic accidents involving roe deer has increased greatly, according to the National Wildlife Accident Council (NWAC) in Sweden. However, according to bag statistics, the population is stabilizing (Andersson 2023). The most recent addition to the Gotland fauna is the fallow deer (*Dama dama*). Since several individuals escaped captivity around 15 years ago, a small population of approximately 35 individuals has been established in the northwestern parts of Gotland (SLU Artdatabanken 2024b).

Gotland's central location in the Baltic Sea provides windy conditions favorable for wind power (Region Gotland 2010). In 2020, the wind power industry on Gotland included 145 wind turbines (SCB 2020). This makes Gotland the county with the second most wind turbines per surface unit in Sweden (SCB 2020; SCB 2024).

1.2 Golden eagle (*Aquila chrysaetos*)

1.2.1 Morphological attributes and distribution

Their body is covered by a variable dark-brown plumage with brighter, almost golden colored neck feathers. Their body mass varies between regions and sex, with males ranging between 2.3 and 5 kg and females between 3 and 6.5 kg (Watson 2010; Lish et al. 2016). Golden eagles are long-winged raptors, with wingspans ranging between 1.8 and 2.2 m. Their main distribution includes North America and Northern Eurasia, as well as certain areas in Northern Africa (Watson 2010). Currently, there are six recognized subspecies of golden eagle globally, with the nominate *Aquila chrysaetos chrysaetos* breeding in northwestern Europe. Depending on the harshness of winters and availability of food, some golden eagle populations are migratory, while some are not (Watson 2010). The mild climate of Gotland allows golden eagles to remain stationary across the island. Golden eagles establish lifelong partnerships, usually referred to as breeding pairs, but can replace deceased partners if necessary (SLU Artdatabanken 2024c).

1.2.2 Ecology

Eagles entering the breeding population establish a home range, incorporating their nesting area and their hunting range (Watson 2010). They usually prefer undisturbed areas with suitable nest sites, patches of open landscape with high prey detectability and foraging opportunities, and rugged terrain features for efficient movement in thermals and updrafts (Watson 2010; Bohrer et al. 2012). Globally,

home ranges sizes vary considerably, but usually ranges between 20 and 200 km² (McGrady 1997). Home ranges of adults in Sweden usually ranges between 30 and 70 km² (Singh et al. 2016) but varies depending on studies (Moss et al. 2014). Within the home range, a breeding territory exclusive to the breeding pair is established which is actively defended against intruding eagles (Watson 2010). For the remainder of this report, “occupied breeding territories”, “territories”, or “breeding pairs”, are used interchangeably. The number of breeding pairs in Sweden fluctuates among years (Figure 2), partly in relation to varying food supply. However, both Sweden and Gotland have experienced a slight population increase during the last two decades. In a 40 year scope, the Gotland population has increased greatly, from 10 breeding pairs in 1983 to 77 in 2023 (Tjernberg 1983; Åsbrink & Källman 2023).

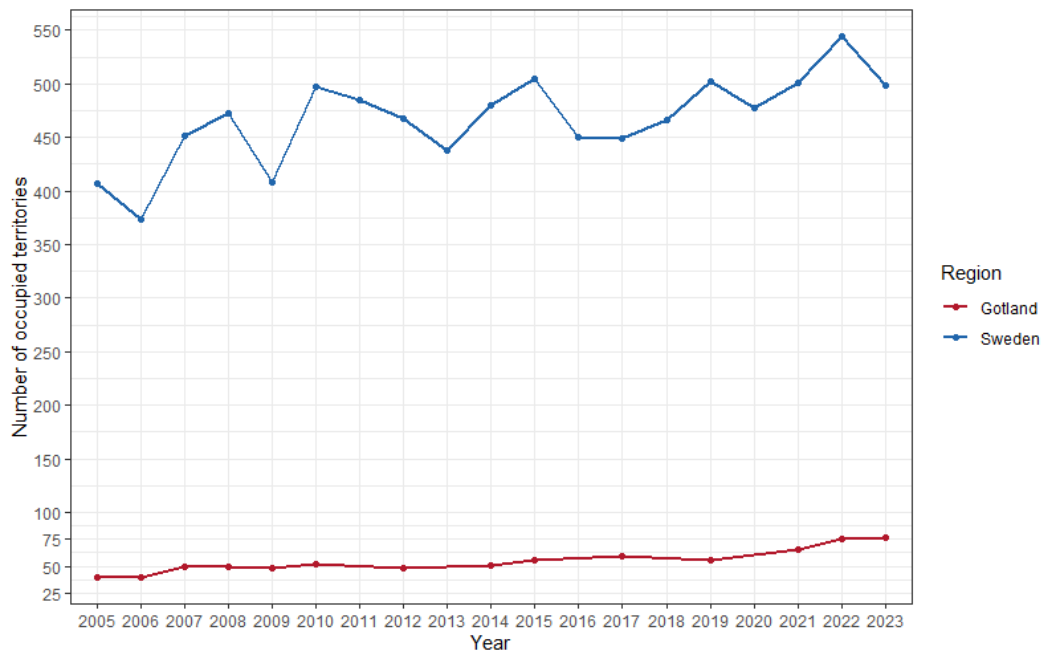


Figure 2. Number of occupied territories in Sweden and Gotland. Data is gathered by NGOs administered by Kungsörn Sverige, and the County Administrative Boards of Sweden. For 2020, no data was collected for Gotland.

1.2.3 Interactions with conspecifics

Territory boundaries usually align with geographical features affecting wind conditions and updrafts, such as mountain ridges and water bodies (Watson 2010). Breeding pairs mark territory boundaries by performing undulating display flights to neighboring pairs near the territory boundary (Harmata 1982). Interactions with the mate, especially during the breeding period, might also trigger display flight behavior (Watson 2010). In Sweden, the breeding period lasts between March or April when the eggs are laid, until August when nestlings have left the nest (Watson

2010; Tjernberg 1981). Aggressive attacks on intruding eagles do occur, although more commonly on non-breeding intruders than neighboring breeding eagles. In northern Sweden, average distance between nearest neighboring territories varies between 10 km for mountain regions and 17 for boreal regions (Tjernberg 1985). On Gotland, the distance is presumably less, due to the high number of territories on a relatively small surface (Figure 3). Currently, there are over 24 breeding territories per 1000 km² on Gotland, making this sub-population one of the densest golden eagle populations in the world (Watson 2010).

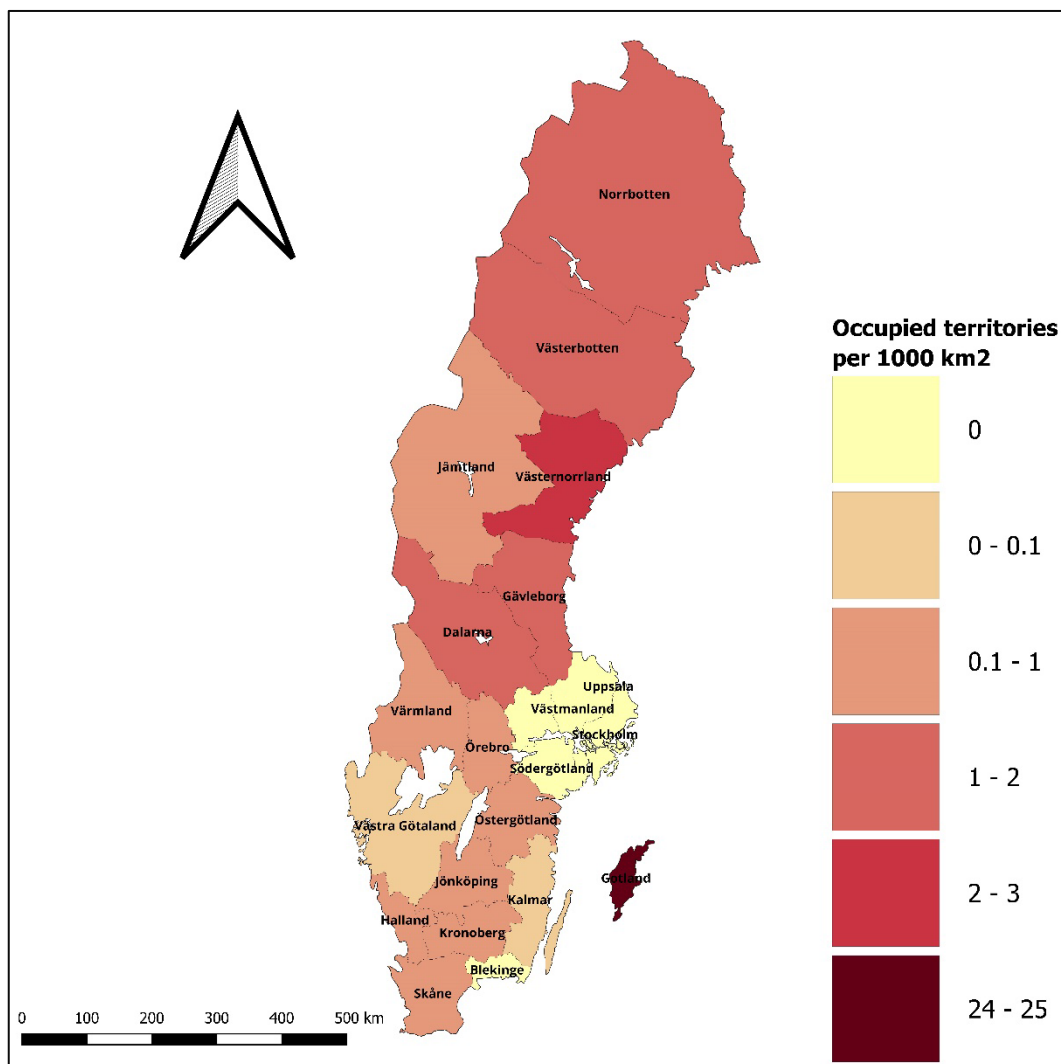


Figure 3. Density of golden eagle territories occupied by a breeding pair in different counties of Sweden 2023 (Åsbrink & Källman 2023). Differences in sampling effort among counties are not accounted for.

1.2.4 Nest characteristics

Centrally located within the territory, a core area is established where eagles spend more than 50 % of their time and build their nests (McLeod et al. 2002). Depending on habitat and availability, nest substrates vary between trees (Wiss 2008), cliffs (Kochert & Steenhof 2012), artificial structures (Kochert & Steenhof 2012), and, on rare occasions, earth mounds (Boeker & Ray 1971). Location and orientation of nests might vary depending on weather conditions, as extreme weather might lead to death of eggs or nestlings (Steenhof et al. 1997; Watson 2010; Kochert et al. 2019). Throughout large parts of south and central Europe, as well as Norway (Dunker 2023), cliff nests dominate (Watson 2010). In Sweden (Tjernberg 1983), as well as Finland, Slovakia, and the Czech Republic, tree nests dominate (Watson 2010). In Estonia, Belarus, and Gotland, golden eagles nest exclusively in trees, even though the landscape in Gotland provides several suitable cliff areas for nesting (Randla & Tammur 1996; Wiss 2008). The most common tree nesting sites in Sweden are pure pine stands, where >70 % of the basal area consists of pine trees (*Pinus sylvestris*) (Tjernberg 1983a). The remaining tree nests are distributed among spruce stands, deciduous stands, and mixed stands. On Gotland, eagles display great adaptability for tree nesting characteristics, ranging between tall coniferous forest, mixed forest, and lone trees on clearcuts (Wiss 2008). Usually, breeding pairs maintain and choose between several nests in their territory, seemingly prioritizing nests far away from neighboring pairs (Watson 2010). As nests usually are well-concealed, the number of alternative nests for each pair is difficult to assess. However, Tjernberg (1983a) estimated the mean number of nests per pair in Sweden to 2.4, ranging from one to six, usually located within 1000 meters from clearcuts.

1.2.5 Dietary habits

The diet for golden eagles varies among habitats. In some areas, golden eagles are specialists, preying heavily on just one or two prey families (Watson 2010). In other areas, golden eagles are generalists, feeding on more than 10 prey families relatively evenly. Diet can also vary heavily between seasons. In continental Europe, the main diet is usually represented by four small- to medium sized prey families, namely Leporidae, Sciuridae, Tetraonidae, and Phasianidae. Golden eagles are also capable of killing large ungulates up to 30 kg (Bruns 1970). In Sweden, parts of roe deer and reindeer (*Rangifer tarandus*) has been found in nests (Tjernberg 1981). However, as golden eagles also scavenge, especially during the winter, body parts of large ungulates parts are likely to originate from carrion (Watson et al. 1992). Watson et al. (1992) argues that the high densities of golden eagle in western Scotland stems from the abundance of deer and sheep carrion in the area. Across Sweden, Leporidae constitutes an important prey family (Tjernberg

1981). In the mountains of northern Sweden, diet mainly comprises mountain hare (*Lepus timidus*), willow grouse (*Lagopus lagopus*), and rock ptarmigan (*Lagopus muta*) (Nyström et al. 2006). Dietary preferences are broader in the boreal regions of Sweden, with higher proportions of black grouse (*Tetrao tetrix*), western capercaillie (*Tetrao urogallus*), and common crane (*Grus grus*) (Tjernberg 1981). The golden eagle diet on Gotland contrasts mainland Sweden, as western capercaillie and ptarmigans are absent, and black grouse are rare (Tjernberg 1981; Högström & Wiss 1992). Instead, eagles consume European rabbits, hedgehogs (*Erinaceus europaeus*), and members of Anatidae, particularly ducks, to a larger degree than mainland Sweden (Högström & Wiss 1992). However, since the study of Högström & Wiss (1992) was published, the number of roe deer has increased exponentially (Pettersson et al. 2019). Waterbirds, as well as other birds, remain abundant on Gotland, especially across the coastlines (Larsson 2022).

1.2.6 Threats and density modifying factors

The longevity and low reproductive rates of golden eagle make them susceptible to small changes to mortality rates (Watson 2018). Therefore, to conserve the species, threats must be identified early. Golden eagles rely on open areas in order to hunt prey (Watson 2010). Clearcuts derived from Swedish forestry practices open the boreal landscape, providing suitable hunting grounds for golden eagle (Moss et al. 2014; Sandgren et al. 2014). However, in the process of deforestation, suitable nesting sites might be removed as well (Tjernberg 1983), possibly affecting territory occupancy and reproductive success (Whitfield et al. 2006). On Gotland, where golden eagles nest exclusively in trees (Wiss 2008), suitable nesting trees may be a valuable resource.

Food supply is a limiting resource for golden eagle (Newton 1979 see Whitfield 2013). Abundance and distribution of prey species might correlate to golden eagle reproductive parameters and habitat usage (Steenhof et al. 1997; Whitfield et al. 2009). Furthermore, golden eagle density correlates positively with abundant sheep and deer carrion (Watson 1992 see Watson 2010). The correlation between food supply and breeding success has been observed in several other raptor species (Gargett 1975; Newton et al. 1986; Katzner 2005).

As with many large predator species, golden eagles suffer from human disturbance and persecution (Woodgerd 1952; Whitfield 2004; Watson 2010). Historically, culling golden eagles was legal, and even compensated for in some areas (Woodgerd 1952). However, even after receiving protection, illegal culling remains prevalent to this day, usually in relation to livestock and wildlife management such as red grouse (*Lagopus lagopus scotica*) management in Scotland (Whitfield 2004). Unintentional disturbances by humans also remains a problem for golden eagles (Watson 2010). Common sources of disturbance include forest management, construction, and recreational activities. Additionally, as

ecotourism continues to grow as a source of revenue, so does the risk of human disturbance (Whitfield 2008). According to an expert survey, human disturbance may even occur a kilometer away from the nest (Whitfield 2008), although the distance varies depending on nest location and topography of the surrounding (Camp et al. 2007). Nest disturbance might keep parental eagles away from eggs or young, temporarily or permanently, potentially resulting in offspring death by starvation, predation, overheating, dehydration or freezing (Suter & Joness 1981). On Gotland, where human activity peaks during the breeding season, human disturbance might be a prevalent factor for golden eagle breeding success.

Human infrastructure, particularly wind farms, is an increasing threat to golden eagles (Hunt 2002). Large raptors, among many bird species, are vulnerable to mortal collisions with turbine blades (Hunt 2002; Smallwood & Thelander 2008; Watson et al. 2018). When eagles detect and avoid wind turbines, the avoidance behavior causes functional habitat loss (Fielding et al. 2021), potentially affecting territory occupancy and reproductive success (Whitfield et al. 2006).

The number and distribution of golden eagles on Gotland may also depend on golden eagle density. Breeding pairs compete with other pairs for suitable nest sites and food supply (Newton 1979 see Whitfield 2013). Less resources per eagle increases the risk for conflicts and may force eagles to inhabit less suitable habitats. They may also compete for nest sites and food supply against other eagle species, such as Bonelli's eagle (*Aquila fasciata*) in Israel (Bahat 1989 see Watson 2010). On Gotland, the only other eagle species present is the white-tailed eagle (WTE) (*Haliaeetus albicilla*). Whitfield (2002) and (2013) found no evidence for diet-related competitive effects between sympatric golden eagle and WTE in Scotland. The dietary overlap between golden eagle and WTE in Scandinavia is limited, since golden eagles generally prioritize actively hunting small and medium sized mammals and grouse (Tjernberg 1981), while WTE prefers fish, seabirds and shorebirds (Halley 1998). As both species are scavengers (Tjernberg 1981; Halley 1998), the risk of food related competition increases when carrion is a significant food source for both species, such as western Scotland or in mainland Sweden (Singh et al. 2024). If sheep and roe deer carrion are important food sources on Gotland, interspecific competition may exist directly, through interference or in food limited periods, indirectly. However, as the golden eagle is the superior competitor around carrion (Halley & Gjershaug 1998), WTE is more likely to suffer from interactions. As of nest site competition, golden eagle traditionally prioritizes cliff nests in high elevations while WTE prefer tree nests at lower elevations near the coast in Scottish conditions (Evans et al. 2010). However, the seemingly large overlap in nest sites preferences on Gotland, where golden eagles nest exclusively in trees, might be a source of competition (Wiss 2008). Nevertheless, as it currently stands, there is no evidence for significant nest site-related competitive effects

between golden eagle and WTE. On the contrary, Whitfield (2002) found higher breeding success in golden eagle ranges when WTE activity increased.

1.3 Purpose

Although the golden eagle sub-population on Gotland has gone through a remarkable increase in breeding pairs in the last 40 years (Tjernberg 1983; Åsbrink & Källman 2023), the underlying reasons for this development and its dynamics remain largely unexplored. The conditions for golden eagles on Gotland are unique, which is reflected in the variation in feeding habits (Högström & Wiss 1992) and nest site selection (Wiss 2008) compared to mainland Sweden. This study serves as a first step in understanding temporal and spatial patterns for the population ecology on Gotland. This includes summarizing historical and recent reproduction data for golden eagles on Gotland and Sweden, in relation to weather parameters and roe deer abundance. Furthermore, the correlation between reproductive success and spatial variance of several territory environment parameters will be analyzed. Environmental parameters comprising habitat composition, food supply, human disturbance, prevalence of wind power, and con- and interspecific density dependent effects are explored. Ultimately, this study aims to characterize the most influential predictors for golden eagle breeding dynamics on Gotland, providing foundation and direction for future studies of this remarkable sub-population.

2. Material and Methods

2.1 Reproductive success

There are many methods for describing and measuring reproductive success of raptor populations (Steenhof et al. 2017). Productivity is the most widely used measure of reproductive rate of golden eagle populations and refers to the number of young produced (to fledging stage) per number of territorial pairs or occupied nesting territories in a particular year (Steenhof & Newton 2007), originally defined in Postupalsky (1974). Most golden eagle chicks fledge between the age of 51 and 75 days (Steenhof & Newton 2007; Steenhof et al. 2017). Golden eagles, among other large raptor species, skip breeding during certain years. Failure to lay eggs despite breeding attempts may be the result of difficult environmental conditions in regard to egg-laying and reproduction. The breeding parameters for Gotland are determined on a per-territory basis according to the standardized golden eagle survey methodology suggested by the Swedish Environmental Protection Agency (SEPA) (SEPA 2022). For this study, temporal variation of golden eagle population productivity was defined as number of young produced per occupied breeding territory (henceforth referred to as territories) per year. Variation in productivity among territories (territory productivity) was defined as total number of young produced per total number of breeding attempts per territory between 2021 and 2023. The reason behind using number of breeding attempts instead of years occupied for territory productivity was to distinguish variation among territories with a limited dataset.

2.2 Temporal population trends

Population productivity between 2005 and 2023 was calculated for the Gotland population, and the Swedish population as a whole, using breeding data published by SEPA in collaboration with Kungsörn Sverige (Kungsörn Sverige 2023; SEPA 2024a; SEPA 2024b). Breeding parameters were not complete for all years. A detailed summary of breeding parameters on Gotland was calculated for the years 2021 to 2023, as extensive data was collected by the County Administrative Board

of Gotland (CABG) for this period. The average temperature during the golden eagle breeding period on Gotland between 2021 and 2023 was calculated using historical climate data collected and compiled by the Swedish Meteorological and Hydrological Institute (SMHI) (SMHI 2024). Unusually hot and cold days were calculated using the standard outlier formula. Summary statistics was carried out in Microsoft Excel.

2.3 Golden eagle breeding parameters and spatial distribution

The CABG estimated a variety of breeding parameters for each breeding territory on Gotland between 2021 and 2023. Data was collected using a standardized method developed by the SEPA (SEPA 2022). Breeding data was collected each year between 1 February and 15 September. Definitions of breeding parameters are defined by SEPA (2022), and essential definitions are compiled in Appendix 1. Data included coordinates of the estimated core area of each territory. In the dataset provided by the CABG, spatial information was available for 71 out of 77 occupied territories on Gotland for 2023. 62 territories had complete data for the number of breeding attempts and nestlings between 2021 and 2023 and were used for further analysis. Due to the sensitive nature of golden eagle nesting sites in Sweden, exact locations of territories will remain discrete in this report. The extent of each territory used for analysis was calculated in QGIS by adding a 2.5 km buffer to each core area coordinate, creating a spheric 20 km² area encompassing the core area. The size of simulated territories was based on estimated core home range sizes for golden eagle calculated by Singh et al. (2016), which ranged between 5 and 30 km². Due to the dense distribution of breeding pairs on Gotland, larger core home range sizes than 20 km² was deemed unlikely. It's important to note that the shape and configuration of golden eagle core home ranges is much more complex in reality. However, the current information on golden eagle movement patterns in Gotland is limited, justifying this simple approach of simulating spheric 20 km² territories. Nevertheless, this approach will provide insight into environmental spatial trends among territories. Average territory productivity was calculated for each territory with confirmed occupancy for all years between 2021 and 2023, which excluded 9 territories from the analysis. Distance to nearest neighboring territory was calculated in QGIS by constructing a distance matrix of core area coordinates for each territory. For this study, territories were considered neighbors if the central point of territories were located within six km of each other. Using WTE survey data provided by CABG, each territory was classified as either with or without WTE presence. WTE presence is defined as WTE being observed in the golden eagle territory during the study period.

2.3.1 Habitat types, soil types, and human disturbance

Using the estimated radius of each territory, and the nationwide environmental mapping of Sweden, Nationella marktäckedata (NMD), the amount and proportion of different habitat types in each territory was calculated in QGIS. NMD is maintained by the Swedish Environmental Protection Agency (SEPA) as well as other Swedish governmental agencies and organizations (SEPA 2023). Data was delivered in raster format GeoTiff (.tif), with Sweden's surface layer divided into 25 different classes with 10 m resolution, in the reference system SWEREF99 TM (EPSG: 3006). Mapping was carried out between 2017 and 2019 using a combination of satellite data, LiDAR, and physical maps (SEPA 2023). In QGIS, the 25 classes were combined into eight different habitat types (coniferous forest, arable land, other open land, deciduous and mixed forest, clearcut, wetland, inland water, and marine water) and three types of artificial surfaces (buildings, roads, and all artificial surfaces). Other open land includes dry vegetated or non-vegetated open surfaces like bedrock. The definition of each calculated habitat type is compiled in Appendix 2.

As European rabbit is dependent on suitable substrates for burrowing, the proportion of certain soil types was calculated for each territory as a potential proxy for prey supply. Using the estimated radius of each territory, and the nationwide mapping soil types in Sweden provided by the Geological Survey of Sweden (SGU), proportion of different soil types in each territory was calculated in QGIS (SGU 2018). The proportion of moraine, sand, and bedrock in each territory was calculated in a similar fashion as habitat types. Mapping for Gotland was done by interpreting aerial images and manual field controls along the road network and the estimated positional error is estimated to be between 100 and 200 m.

Artificial surface coverage was used as proxy for human activity in the analysis. As marine water was absent more than 50 % of territories, each territory was classified as either being coastal or non-coastal territories for analysis purposes. Coastal territories were defined as territories with proportion of marine water being higher than zero.

2.3.2 Field work estimating golden eagle food supply

Presence and density of crepuscular mammalian prey species, particularly European rabbit, was calculated using spotlight transects, a supported method for estimating relative abundance of Lagomorphs (Smith & Nydegger 1985; Caley & Morley 2002; Twigg et al. 1998). The survey methodology was inspired by Caley and Morley (2002) but adapted based on economic restraints and local conditions on Gotland. For instance, Caley and Morley (2002) used a 4WD ATV travelling at 5 – 8km/h with a spotlight mounted on a helmet. The project budget did not fit the rental costs of an ATV, and most transect routes did not allow for surveillance from

cars. Therefore, transects were surveyed by foot with a handheld 550 Lumen LED-searchlight of model Nightsearcher Trio 550 (Figure 4).



Figure 4. Rabbit spotted along a surveyed transect on southern Gotland.

Locations of transects were selected through stratified random sampling to control random environmental stochasticity among territories. Using the habitat types calculated from the NMD dataset, territories were divided into four strata determined by dominating habitat types (coniferous forest, arable land, other open land, or mixed). For each stratum, five territories were randomly selected for survey. For each selected territories, between two or three suitable candidate transect routes were identified using satellite maps and the NMD dataset in QGIS. Open areas suitable for spotlight surveys on Gotland mainly comprise privately owned farmland not suitable for traversing. Fortunately, public roads and paths are abundant on Gotland. Therefore, candidate transects were allocated along seemingly accessible roads and paths in open habitat types with high detectability like dry and rocky areas with low or no vegetation, arable land, and clearcuts. Straight transect segments were prioritized to avoid double counting. Human settlements were avoided when possible. The transects were approximately 2 km long and 200 m wide, each covering 0.4 km². One candidate transect was chosen for survey in each territory. The selection among candidate transects was carried out in situ, based on suitability and availability. For instance, certain transect sections were intercepted by fences, or intruding on private property.

The character of each surveyed transect was described using the field protocol in Appendix 3. Each observation was described by species, number of individuals, time of observation, estimated perpendicular distance from transect, angle from observer, and coordinate of observer. As distance measures by the provided

rangefinder proved unreliable with fast moving animals, especially during nighttime, perpendicular distance from transect was instead estimated visually by the observer. All participating observers synchronized their distances estimates and survey techniques before performing surveys. Angle from the observer to the observed subjects was derived using a compass and protractor. Coordinates of observer were registered using the Google Maps application. Fieldwork was carried out in late October 2023. The survey was conducted in late autumn when detectability is less obstructed by crops and summer vegetation (Barnes et al. 1983), and the rabbit population number is relatively stable (Tittensor 1981). The main survey target was the European rabbit, but observations of additional golden eagle prey species were recorded opportunistically as well. European rabbit populations close to human settlements are mainly crepuscular and nocturnal (Poole et al. 2003). Therefore, transects were surveyed between 30 minutes after sundown and 6 hours after sundown. Evenings with substantial fog, mist, wind, or rain could potentially influence rabbit behavior and detection rates and were thus avoided. Surveys were carried out at a steady walking pace, only stopping to register observations. Time spent in each transect varied between 30 and 60 minutes depending on number of observations. As the initial 20 territories selected for spotlight transects were surveyed quicker than expected, additional territories and transects were selected using the same methodology until the fieldwork session on Gotland concluded. Ultimately, 38 territories were surveyed. Density and distribution of European rabbit among surveyed territories was estimated using distance sampling of transect data (Buckland et al. 1993) in R (R Core Team 2023). Akaike Information Criterion (AIC) was utilized to determine relative statistical fit of candidate models. The same statistical approach was used for estimating roe deer density and presence as well. However, as field methodology was adapted for rabbits, calculated estimates for roe deer are crude, and mainly included to provide a sense of relative distribution across the study area. Nevertheless, distance sampling using line transects is a legit method for estimating abundance and density of roe deer and other ungulates when the methodology is adapted for it (McCullough 1982; Focardi et al. 2002; Collier et al. 2007).

2.3.3 Roe deer related traffic accidents

Carcasses from traffic accidents provide valuable scavenging opportunities for golden eagles (Singh et al. 2024). Roe deer killed by traffic in Sweden is bestowed to the landowner in question. However, according to the Gotland police, remains of roe deer are usually unsalvageable for humans and are instead left in nature for scavengers (Kenneth Kronberg pers. Comm 2024). Coordinates of each roe deer related traffic accidents between 2021 and 2023 was gathered from the National Wildlife Accident Council (NWAC) (Viltolycka 2024). NWAC is a collaboration between governmental agencies and hunter associations for managing wildlife

related traffic accidents in Sweden. Roe deer related accidents constituted 99.3 % of all reported wildlife related traffic accidents during this period on Gotland. The number of roe deer related traffic accidents in each territory in each territory was calculated in QGIS.

2.3.4 Roe deer bag statistics

Hunting bag statistics are a common source of information about abundance, trend, or spatial distribution of game species populations (Grauer et al. 2015; Acevedo et al. 2019). For this study, the yearly number of shot roe deer on Gotland functioned as a proxy for roe deer abundance. Bag statistics in Sweden are managed by the Swedish Association for Hunting and Wildlife Management and open for public access. The number of roe deer shot on Gotland between 2002 and 2023, which is reported by hunters and hunting teams, was gathered from the bag statistic database (Viltdata 2024).

2.3.5 Wind turbines

Using the estimated radius of each territory, and Vindbrukskollen, a nationwide map service for existing and planned wind turbines in Sweden, wind turbine presence in each territory was calculated in QGIS (Länsstyrelsen 2024). Vindbrukskollen is a governmental service and maintained by the Swedish Energy Agency and the County Administrative Boards of Sweden. Locations of wind turbines on Gotland were extracted from the provided dataset using GIS. Distance to nearest wind turbine was calculated in QGIS by constructing a distance matrix of core area coordinates for each territory. As wind turbines usually are aggregated in windfarms, some territories had many nearby wind turbines while others had none. Therefore, each territory was classified as either being a wind turbine territory or not, for analysis purposes. Wind turbine territories were defined as territories with at least one wind turbine inside the estimated territory range.

2.4 Analysis

The R package “ape” was used to control for spatial autocorrelation in productivity among territories. R package “ggplot2” was used to generate plots to visually examine data. Correlation matrix was used to measure correlation among candidate predictor variables and productivity using the R package “stats”. “stats” was also used to fit linear regression models for numeral and categorical predictor variables and generalized linear regression models with family = “binomial” for binary predictor variables. Simple regressions were used as the limited dataset resulted in univariate regression models over-fitting data. By critically evaluating the ecological equity of model results, and confirming statistically using stepwise

reduction, the most important predictors for reproductive success was identified. R package “MuMIn” was used to distinguish relative importance for reproductive success among important predictor variables. R package “lmtest” was used to inspect model diagnostics. All analyses were conducted in R (4.3.2) and R studio (2023.12.0-369). All R packages used are compiled in Appendix 4.

3. Results

3.1 Temporal and spatial trends in reproductive success

The average population productivity between 2002 and 2023 for Gotland and Sweden was 0.50 (SD = 0.170) and 0.49 (SD = 0.129), respectively (Figure 5). On Gotland it fluctuated between 0.20 and 0.85 while for overall Sweden, it fluctuated between 0.26 and 0.69.

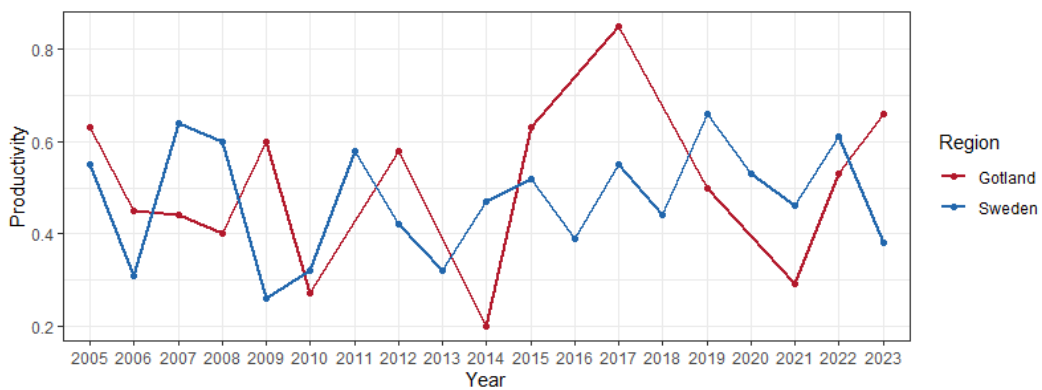


Figure 5. The population productivity for Gotland and Sweden between 2002 and 2023. Due to lack of nestling information, data is missing for Gotland in years 2002, 2004, 2011, 2018, and 2020. Data was collected by the County Administrative Boards of Sweden and NGOs administered by Kungsörn Sweden.

Between 2021 and 2023, Gotland trended positively in most breeding parameters (Table 1). The number of occupied territories increased, and breeding attempts became more successful. Year 2023 was an extreme year in terms of success, where in all territories where adults attempted breeding had successful outcomes.

Table 1. Golden eagle breeding parameters in Gotland between 2021 and 2023.

Parameter	2021	2022	2023
Nr of occupied territories	65	75	77
Nr of breeding attempts	28	41	43

Nr of territories not attempting breeding	37	34	34
Nr of successful breeding attempts	19	32	43
Nr of failed breeding attempts	11	10	0
Nr of nestlings on Gotland	19	40	51
Breeding attempts per territory	0.43	0.55	0.56
Skipped breeding attempts per territory	0.57	0.45	0.44
Successful breeding per territory	0.29	0.43	0.56
Successful breeding per attempt	0.68	0.78	1.00
Failed breeding per territory	0.17	0.13	0.00
Failed breeding per attempt	0.39	0.24	0.00
Nestlings per attempt	0.68	0.98	1.19
Nestlings per nesting occupied territory	0.29	0.53	0.66
(population productivity)			

Throughout the study period, the weather during the breeding period got colder and more stable (Table 2). The yearly average temperature decreased from 11.0 to 10.3 to 10.2. Similarly, the number of unusually cold and hot days decreased from 8 to 7 to 0. In other words, in 2023, all attempted breeding attempts succeeded, as well as having stable temperatures throughout the breeding period.

Table 2. Temperature parameters in Gotland between 2021 and 2023. Cold and hot days represent the number of days with negative or positive outliers in terms of average daily temperature.

Year	Month	Min (°C)	Max (°C)	Average (°C)	Cold days	Hot days
2021	March	-7.6	17.6	3.0	0	0
2021	April	-4.0	15.7	4.6	0	0
2021	May	0.3	23.4	9.3	0	0
2021	June	4.2	29.9	17.5	1	4
2021	July	7.7	30.4	20.6	1	2
2021	Sum	0.6	117.0	55.0	2	6
2021	Average	0.1	23.4	11.0	0.4	1.2
2022	March	-9.7	14.6	2.7	0	1
2022	April	-9.6	15.6	4.5	2	0
2022	May	-0.9	19.5	9.6	0	0
2022	June	8.3	30.8	16.4	0	3
2022	July	6.5	32.7	18.4	0	1
2022	Sum	-5.2	113.2	51.6	2	5
2022	Average	-1.0	22.6	10.3	0.4	1
2023	March	-13.8	10.7	1.8	0	0
2023	April	-7.0	19.6	5.2	0	0
2023	May	-5.1	22.3	10.6	0	0

2023	June	0.6	25.5	16.3	0	0
2023	July	9.7	23.5	17.2	0	0
2023	Sum	-15.6	101.6	51.2	0	0
2023	Average	-3.1	20.3	10.2	0	0

Territory productivity was analyzed for 62 territories and varied between 0 and 2, with an average of 0.96 (Figure 6). In general, territories were evenly distributed across the study area, except the area surrounding Visby, where a noticeable gap emerged. Furthermore, the average territory productivity of three of the four closest territories to Visby ranged between 0 and 0.5. Out of 62, 9 territories had zero average productivity. 11 territories had low average territory productivity (0 – 0.5). 27 territories had medium average territory productivity (0.5 – 1.5). 12 territories had high average territory productivity (1.5 – 2).

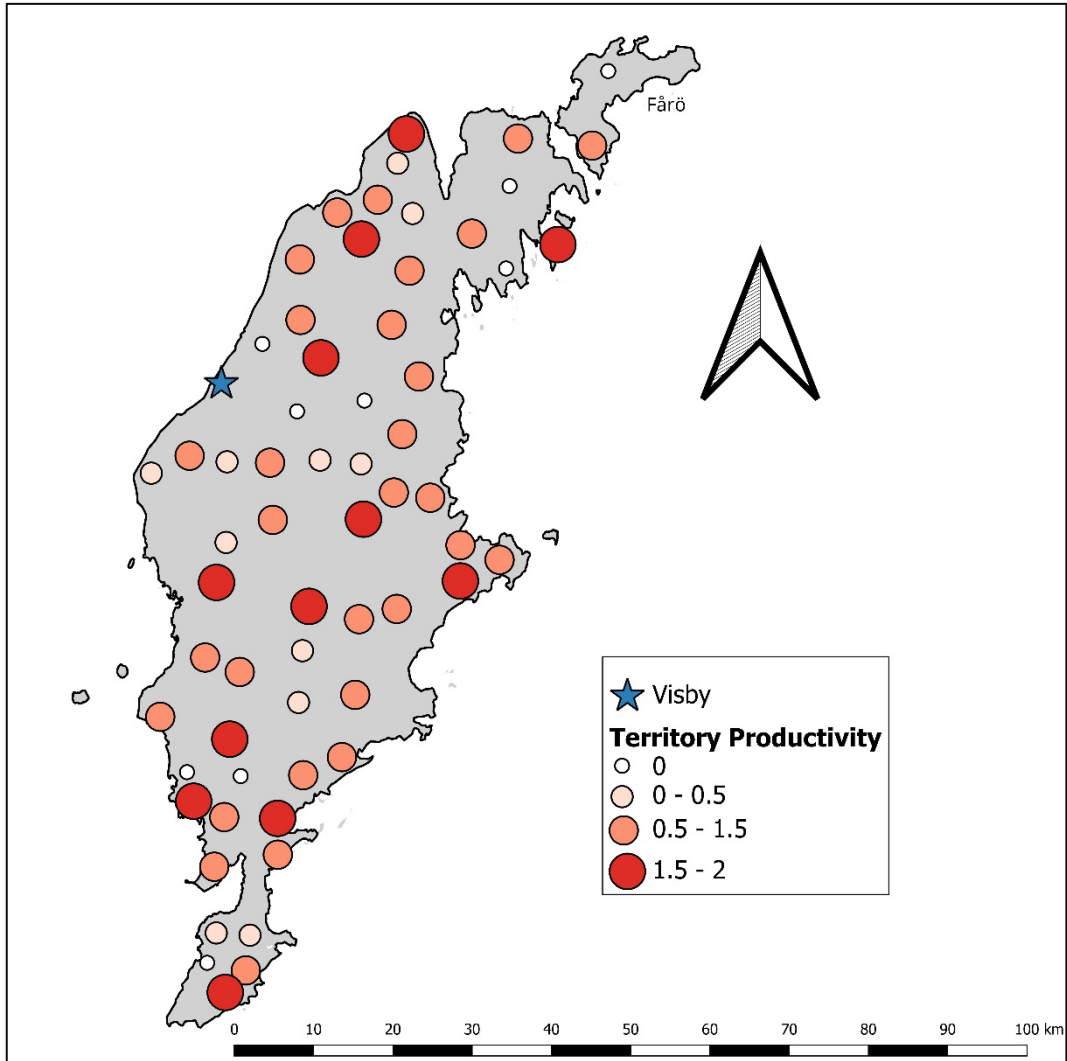


Figure 6. Spatial variance in average territory productivity across Gotland between 2021 and 2023.

The yearly number of roe deer shot on Gotland was strongly correlated with number of occupied territories on Gotland between 2002 and 2023 (Table 3). Territories with more neighboring territories had significantly higher territory productivity than isolated territories.

Table 3. Summary of analysis. Significant results ($p < 0.05$) are highlighted with bold font. Predictors were analysed using individual simple or generalized linear regression models.

Resp. var	Expl. var	Est.	Std. dev	t/z-value	P-value	N	D.O.F
Productivity	Prop. Coniferous forest	0.65	0.52	1.44	0.16	61	59
Productivity	Prop. Arable land	-0.40	0.54	-1.10	0.28	62	60
Productivity	Prop. Other open land	0.11	0.53	0.15	0.88	61	59
Productivity	Prop. Dec/mixed forest	0.32	0.54	0.23	0.82	62	60
Productivity	Prop. Clearcut	1.81	0.52	0.92	0.36	61	59
Productivity	Prop. Wetland	-0.37	0.54	-0.10	0.92	62	60

Productivity	Prop. Inland water	-13.6	0.53	-0.96	0.34	60	58
Productivity	Coastal territory	0.08	0.54	0.58	0.56	62	60
Productivity	Prop. Bedrock	-0.03	0.54	-0.08	0.94	62	60
Productivity	Prop. Sand	-0.12	0.54	-0.28	0.78	62	60
Productivity	Prop. Moraine	-0.04	0.54	-0.14	0.89	62	60
Productivity	Rabbit presence	0.01	0.54	0.06	0.95	62	59
Prod. 2023	Rabbit presence	0.03	0.67	0.12	0.90	62	59
Productivity	Rabbit density	-2.15	0.53	-0.29	0.77	37	35
Prod. 2023	Rabbit density	-9.89	0.65	-1.11	0.28	37	35
Rabbit pres.	Prop. Bedrock	1.02	1.46	0.70	0.48	62	60
Rabbit pres.	Prop. Sand	1.58	1.88	0.84	0.40	62	60
Rabbit pres.	Prop. Moraine	-2.05	1.24	-1.66	0.10	62	60
Productivity	Roe Deer presence	0.19	0.53	1.08	0.28	62	59
Productivity	Roe Deer density	7.07	0.51	0.91	0.37	38	34
Productivity	Roe Deer traffic accidents	-0.01	0.53	-1.87	0.07	62	60
Nr. terr.	Roe Deer shot	7.85	5.68	5.49	< 0.001	18	16
Productivity	Prop. Buildings	-0.95	0.53	-1.79	0.08	62	60
Productivity	Prop. Road	-17.2	0.53	-1.14	0.26	61	59
Productivity	Wind turbine presence	0.22	0.53	1.41	0.17	62	60
Productivity	Dist. Nearest wind turbine	-0.01	0.53	-0.11	0.91	60	56
Productivity	Dist. Nearest neighbor	-0.05	0.54	-0.66	0.51	61	58
Productivity	Prod. Nearest neighbor	-0.12	0.54	-0.94	0.35	62	60
Productivity	Nr. Neighbor territories	0.14	0.53	2.07	0.04	62	60
Productivity	WTE presence	0.26	0.53	1.82	0.07	62	60

3.2 Habitat composition

The two most prevalent habitat types in golden eagle territories were coniferous forest and arable land (Figure 7). Coniferous forest covered much of northwest Gotland, while arable land dominated in central and southern Gotland. Other open land was most prevalent along the coasts, with higher concentrations in the north and south edges of Gotland. Deciduous and mixed forest was evenly distributed across Gotland except in the north edge, where it was rare. Clearcuts corresponded with coniferous forest, although more prevalent in central Gotland. Wetlands were rare, and mostly existed on northern Gotland. Gotland had few lakes, and most of them were located in the north. Open bedrock was common everywhere except the central parts of Gotland. Sand was more common in the south. Moraine was common across the whole island, although rarer along the northern and southern shorelines/coastal areas.

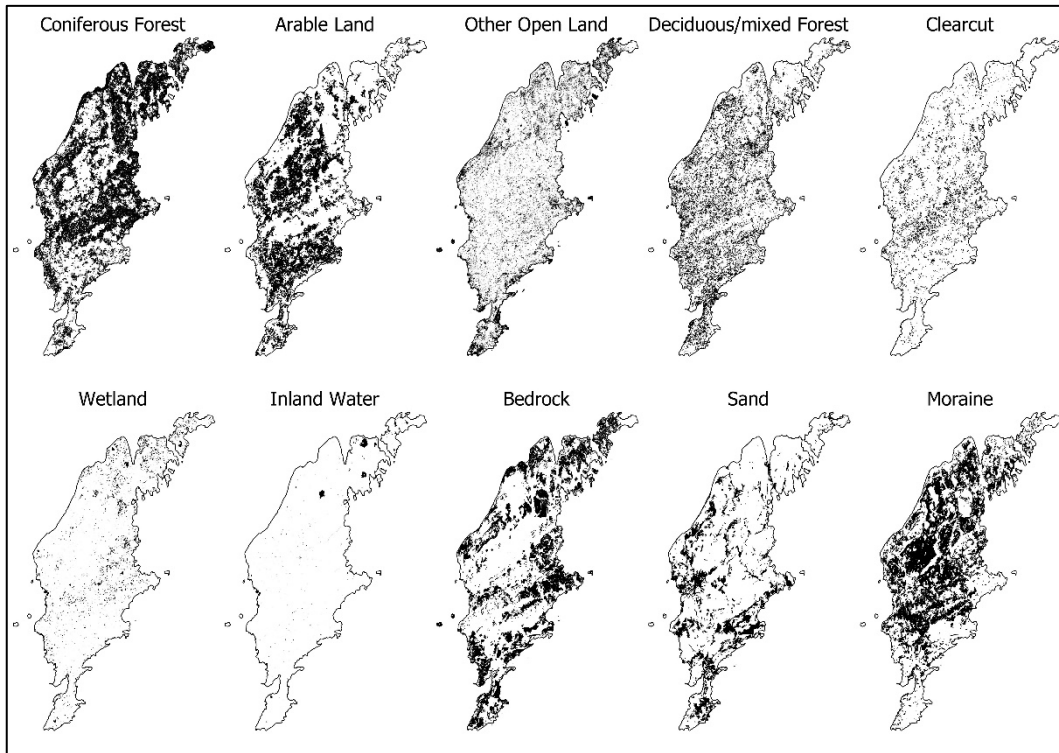


Figure 7. Surface cover of habitat types and soil types on Gotland.

Coniferous forest and arable land were prevalent in all territories to varying degrees (Figure 8). Other open land and Deciduous and mixed forest rarely covered more than 30 % of territory surfaces. Clearcuts, Wetland, and inland water existed only in small patches in territories. The proportion of marine water depended on how close the territory was to the coast. Exact values are shown in Appendix 5.

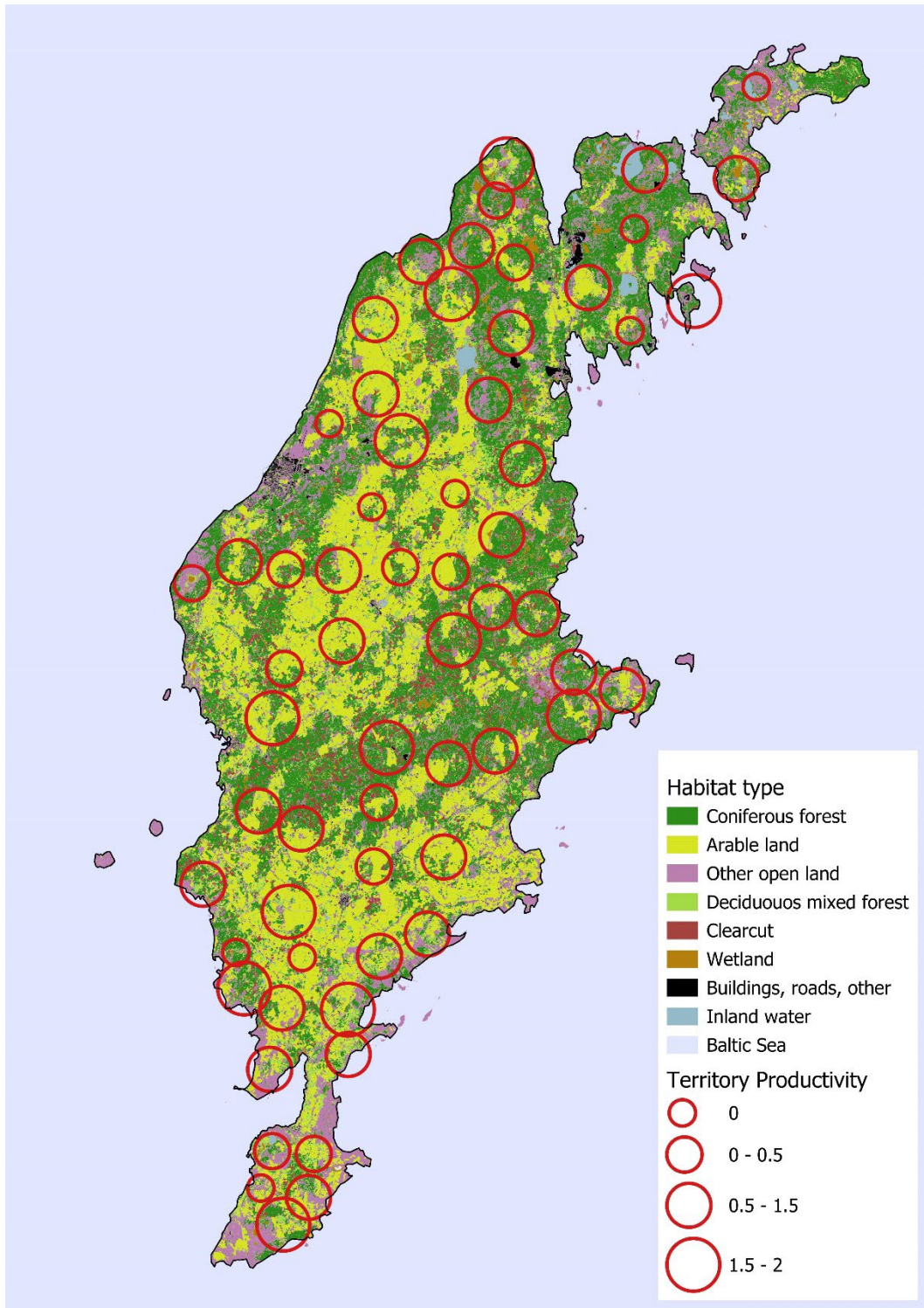


Figure 8. Habitat types across Gotland in relation to territory productivity.

No habitat type was significantly correlated with territory productivity (Table 3). The only habitat type or soil type that displayed a trend for territory productivity was coniferous forest, which was positive. There was a negative correlation between coniferous forest and coastal territories (estimate \pm standard deviation = -

0.09 ± 0.14 , $t = -2.25$, $p = 0.03$, $N = 62$). The other dominant habitat type, arable land, did not correlate to productivity in any way. Territories with more arable land have more roe deer related traffic accidents (estimate \pm standard deviation = 0.005 ± 12.47 , $t = 3.01$, $p = 0.004$, $N = 62$). Arable land was uncommon in coastal territories (estimate \pm standard deviation = -0.17 ± 0.17 , $t = 4.24$, $p = 0.0001$, $N = 62$) and WTE presence is rare in arable land dominated territories (estimate \pm standard error = -3.82 ± 1.56 , $z = -2.45$, $p = 0.014$, $N = 62$). Territories with abundant other open land were common in coastal territories (estimate \pm standard deviation = 0.13 ± 0.076 , $t = 6.85$, $p = 4.5e-09$, $N = 61$) and often had WTE presence (estimate \pm standard error = 11.62 ± 4.07 , $z = 2.85$, $p = 0.004$, $N = 61$). Furthermore, roe deer related traffic accidents were rare in other open land habitats (estimate \pm standard deviation = -52.93 ± 12.34 , $t = -3.06$, $p = 0.003$, $N = 61$). None of the soil types displayed any statistically significant correlation with territory productivity or rabbit presence.

3.3 Food Supply

3.3.1 Prey species in golden eagle territories

The majority of prey species observed in territories included European rabbit, roe deer, red fox, and field hare (*Lepus europaeus*). Rabbits and roe deer were regularly encountered in clusters, and the only species common enough to estimate density in territories (Figure 9). Territory productivity was not significantly correlated with either rabbit or roe deer density (Table 3). The absence of observations in several territories resulted in zero-inflated data, and questionable density estimates. Therefore, two new 3-level categorical predictor variables (rabbit presence and roe deer presence) were created, based on whether a species was either present (observed at least once), not present, or unknown (territory not surveyed). Neither rabbit nor roe deer presence were significantly correlated with territory productivity, although territories with confirmed or unknown roe deer presence showed a slight trend towards having higher productivity than territories with no roe deer presence.

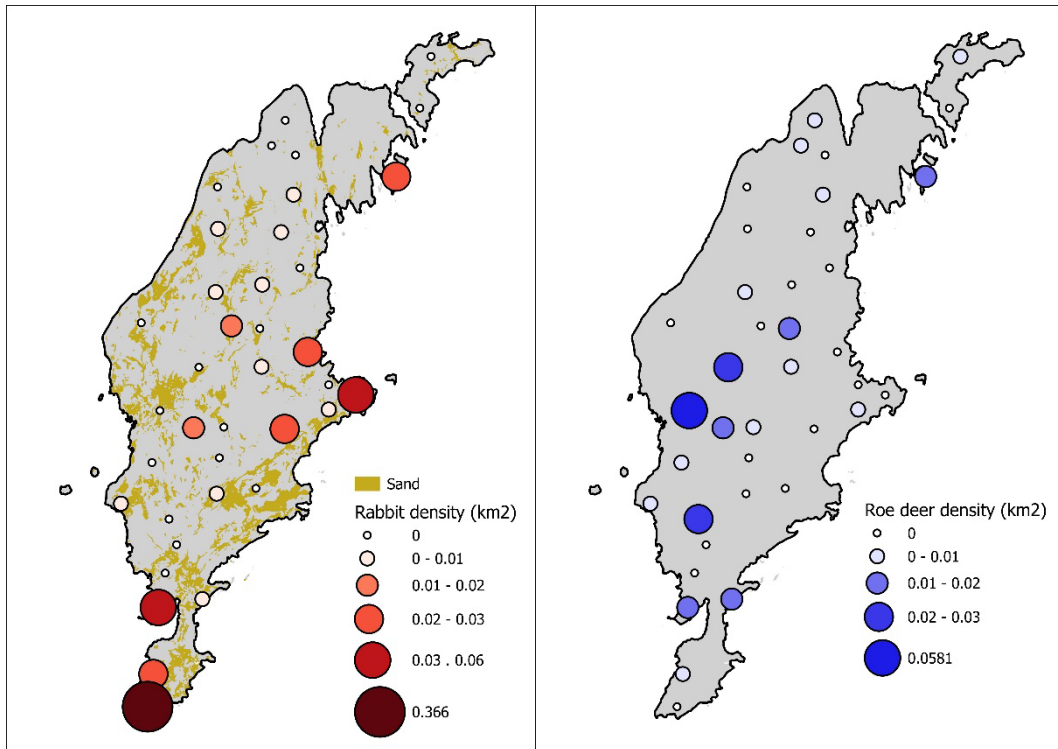


Figure 9. Distribution and density of European rabbit (left) and roe deer (right) in golden eagle territories on Gotland.

3.3.2 Roe deer carcasses from traffic accidents

Roe deer related traffic accidents were most common in central Gotland, particularly in areas surrounding Visby. Although not significant, there was a weak negative correlation between accidents and golden eagle territory productivity (Table 3). There was no significant correlation between roe deer related traffic accidents and roe deer presence. Instead, accidents correlated significantly with roads (estimate \pm standard deviation = 1315.15 ± 11.68 , $t = 4.33$, $p = 5.73e-05$, $N = 62$) and buildings (estimate \pm standard deviation = 50 ± 11.71 , $t = 4.27$, $p = 6.98e-05$, $N = 62$).

3.3.3 Roe deer population on Gotland

During the last two decades, the roe deer population on Gotland has increased greatly, which is reflected in the yearly bag count of roe deer (Figure 10). There is a strong positive correlation between the number of roe deer shot and number of golden eagle territories on Gotland between 2003 and 2022 (Table 3).

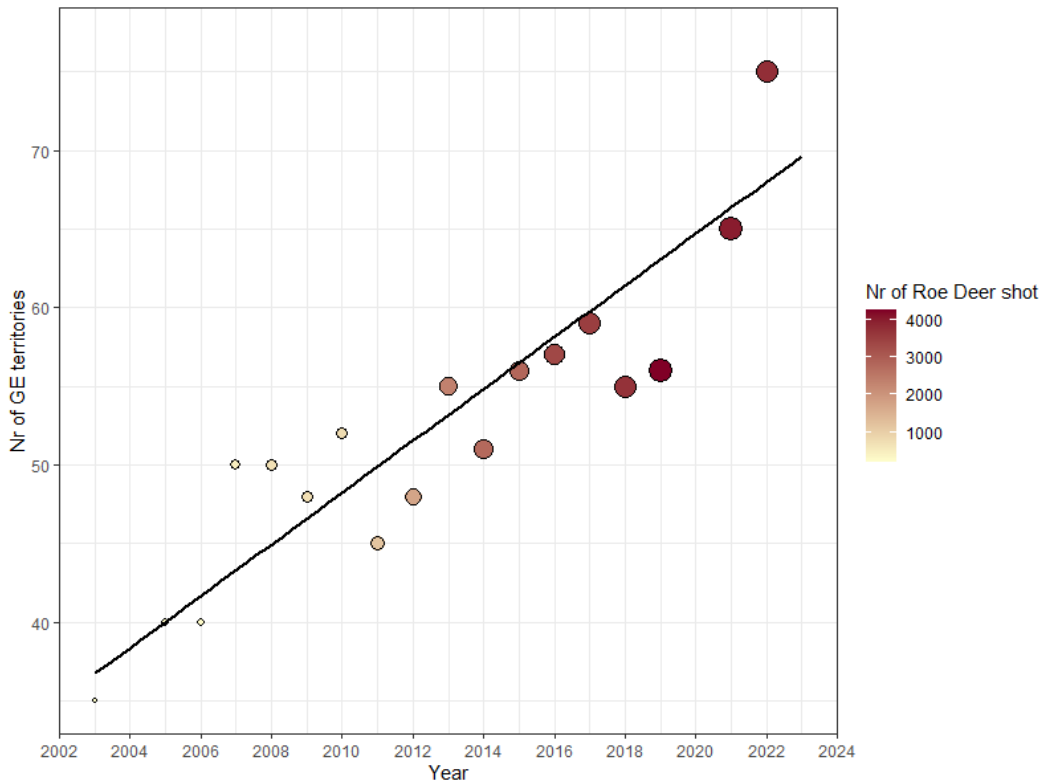


Figure 10. The number of shot roe deer reported each year on Gotland, in relation to nr of golden eagle territories. Increasing size and darker color of datapoints = larger number of roe deer shot.

3.4 Human disturbance

Buildings were abundant across the whole study area, but most concentrated on the west side of central Gotland (Figure 11). There were also clusters of settlements along certain coastal areas. Territories appear to be more common in areas with less buildings. Roads are highly abundant on Gotland and distributed across the entire islands. Territory productivity is not significantly correlated with the proportion surface covered by buildings or roads (Table 3). However, there is a trend towards buildings and roads being negatively correlated with productivity. Roads are more common in the habitat type arable land (estimate \pm standard deviation = 13.68 ± 0.18 , $t = 2.66$, $p = 0.01$, $N = 61$).

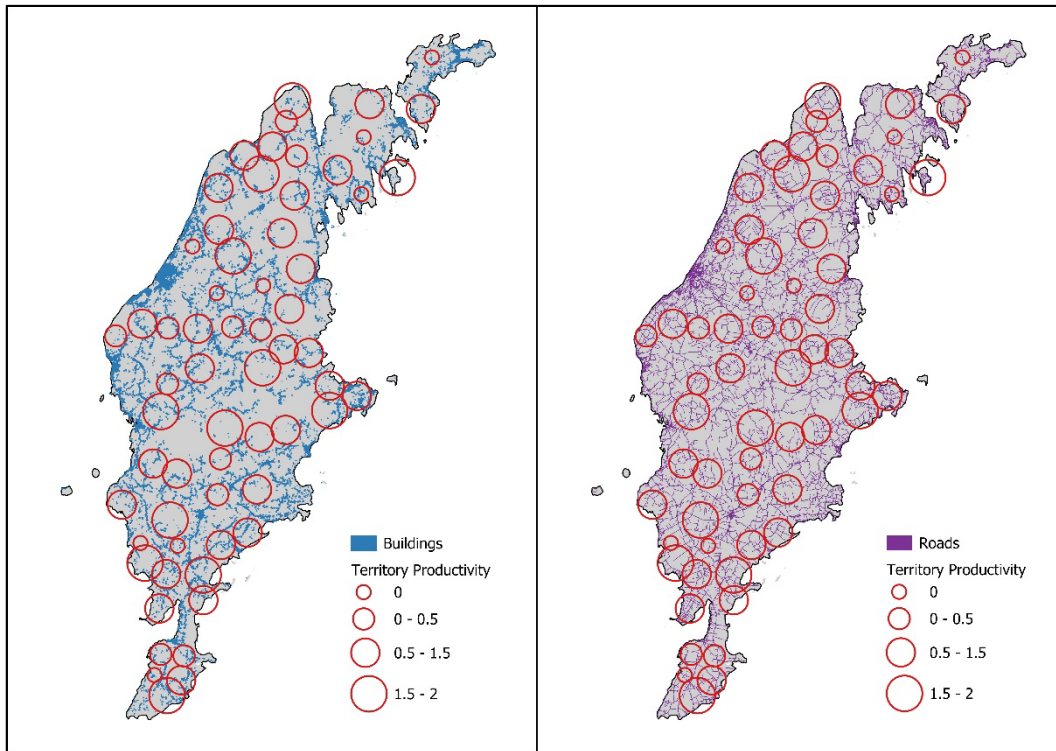


Figure 11. Distribution of buildings (left) and roads (right) in relation to golden eagle territory distribution and productivity.

3.5 Wind power

In total, there were 141 wind turbines in the study area and 92 located within golden eagle territories. 76 % of analyzed territories had zero wind turbines, 16 % of territories had between 1 and 3 wind turbines, and 8 % of territories had more than 3 wind turbines. In other words, 75 of the 92 wind turbines within territories were distributed among 5 territories, maximum being 42 wind turbines in one territory. The average distance to the nearest wind turbine was 6.5 km. Nor territories with wind turbines presence (at least one wind turbine within territory) or the distance to nearest wind turbine correlated significantly with territory productivity (Table 3). However, a weak trend of territories with wind turbine presence having higher territory productivity was observed. Wind turbines were more common in coastal territories (estimate \pm standard deviation = 1.35 ± 0.63 , $t = 2.16$, $p = 0.03$, $N = 62$) and less common in territories with more coniferous forest (estimate \pm standard deviation = -0.09 ± 0.15 , $t = -2.05$, $p = 0.04$, $N = 62$).

3.6 Golden eagle density dependence

The average distance to the nearest neighboring territory on Gotland was 5387 m (SD = 1239), ranging from 3763 to 9619 m. The two territories on Fårö were outliers and more isolated than other territories. Territory productivity did not correlate significantly with distance to nearest neighbor or productivity of nearest neighbor (Table 3). However, territory productivity did correlate positively with increasing number of neighboring territories (estimate \pm standard deviation = 0.14 ± 0.53 , $t = 2.07$, $p = 0.04$, $N = 62$) (Figure 12).

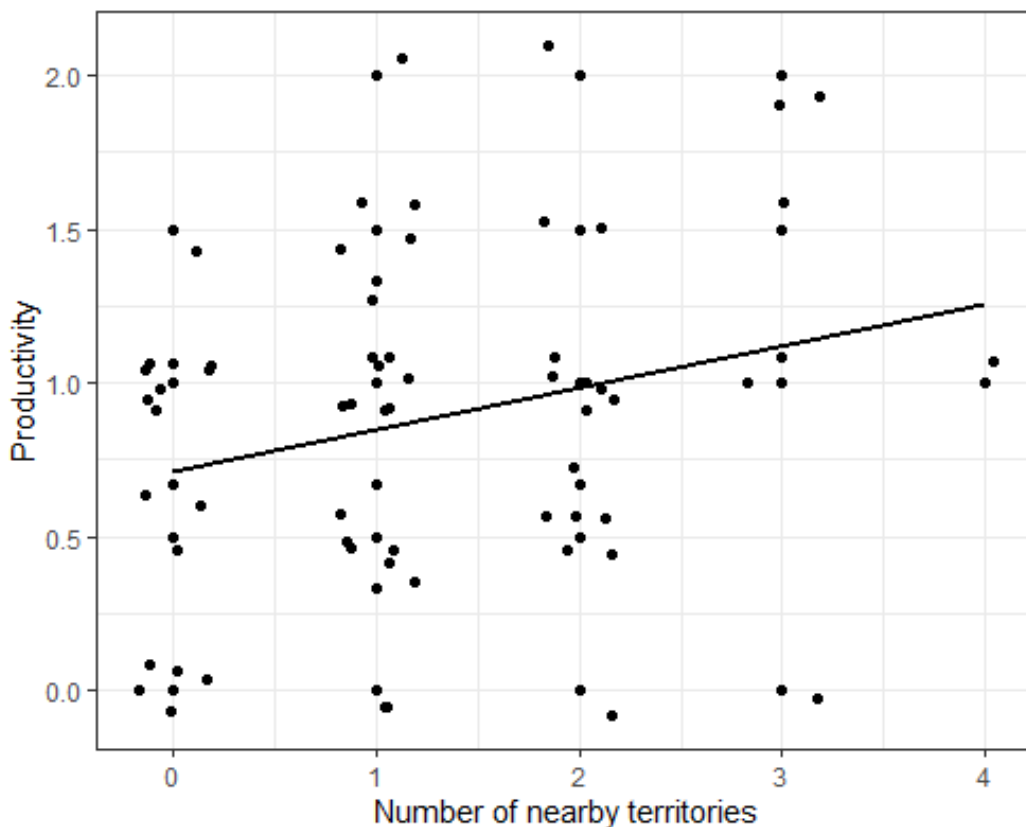


Figure 12. Number of neighbouring golden eagle territories in relation to territory productivity.

3.7 White-tailed eagle presence

WTE activity was confirmed in 43 of 62 analyzed golden eagle territories during the study period. WTE was prevalent across the entire east coast, and the northern and southern edges of the study area. WTE was less active in the central western areas of Gotland. All territories with high golden eagle productivity (1.5 – 2) except one had WTE presence. There was no significant correlation between WTE presence and territory productivity (Table 3), however, a weak trend of positive correlation was observed (Figure 13). WTE were more common in coastal

territories (estimate \pm standard deviation = 2.37 ± 0.81 , $z = 2.94$, $p = 0.003$, $N = 62$) and uncommon in arable land (estimate \pm standard deviation = -3.82 ± 1.56 , $z = -2.45$, $p = 0.01$, $N = 62$) and territories with high level of human settlement (estimate \pm standard deviation = -4.98 ± 2.31 , $t = -2.16$, $p = 0.03$, $N = 62$).

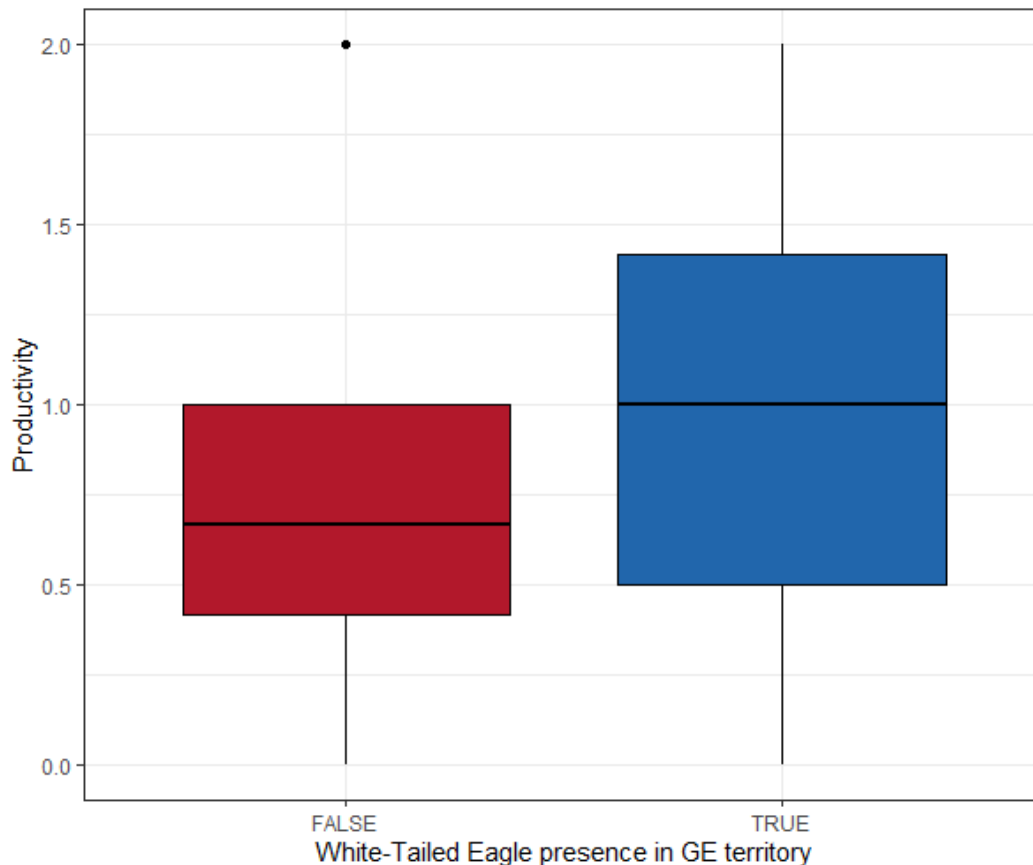


Figure 13. Golden eagle territories where white-tailed eagle activity has been confirmed, in relation to golden eagle territory productivity.

3.8 Most significant predictors for golden eagle territory productivity

After visually and statistically analyzing a large set of predictor variables and their respective correlation with territory productivity, one predictor displayed significant correlation. Territories with many closely neighboring territories had higher productivity than territories with few neighbors. Although not statistically significant, five other predictors displayed interesting patterns in relation to territory productivity. Coniferous forest, wind-turbine presence, and WTE presence displayed weak positive correlation, while buildings and roe deer related traffic accidents displayed weak negative correlation. These predictors were chosen for

analysis of relative significance for territory productivity and assigned a corresponding value of weight. WTE presence = 0.58, coniferous forest = 0.53, wind turbine presence = 0.49, buildings = 0.44, and roe deer related traffic accidents = 0.38. According to the analysis, WTE presence was the most important predictor for golden eagle territory productivity on Gotland between 2021 and 2023.

4. Discussion

Since 40 years ago, the golden eagle sub-population on Gotland has gone through a remarkable increase in breeding pairs (Tjernberg 1983; Åsbrink & Källman 2023). The purpose of this study was to investigate factors driving this increase, by exploring landscape level variation in breeding ecology of golden eagle on Gotland. As a first step, temporal variance in population reproductive success was summarized on Gotland and Sweden in its entirety. The average yearly population productivity since 2002 was 0.50 for Gotland and Sweden both (Figure 5). This was low in relation to previous estimates, where Tjernberg (1983) calculated it to 0.64 for northern Sweden between 1975 and 1980. It's also low in comparison to the neighboring countries Norway (0.58 between 1970 and 1990) (Gjershaug 1996) and Finland (0.64 between 1970 and 1989) (Virolainen & Rassi 1990). Population productivity was less irregular in mainland Sweden, ranging between 0.26 and 0.69, and Gotland between 0.20 and 0.85 on Gotland (Figure 5). Despite low population productivity, numbers of territories occupied by breeding pairs has increased, particularly on Gotland (Figure 2). During the last three years, the number of occupied territories on Gotland has increased from 65 to 77 (Table 1). It's possible that weather conditions during the breeding period on Gotland have been favorable, especially during 2023 when temperatures were mild and stable compared to previous years (Table 2). Interestingly, the golden eagle breeding season of 2023 was among the most successful ones since the start of recording. However, weather effects on temporal population productivity were not statistically analyzed in this study due to limited temporal reproductive data on Gotland. To identify the underlying reasons for the increasing golden eagle sub-population on Gotland, three years (2021 – 2023) of reproductive data from individual territories on Gotland was analyzed in relation to several subjects relevant to breeding success.

The first subject was habitat composition. Eight different predictor variables relating to different habitat types in territories were analyzed. Furthermore, three predictor variables relating to ground and soil composition were analyzed, due to its potential relation to prey abundance, in particular European rabbit. No habitat or soil type was statistically correlated to territory productivity. However, territories with higher proportion coniferous forest trended towards having higher territory productivity. The proportion of coniferous forest in territories was the second most important predictor for territory productivity. The positive impact of coniferous

forest was unsurprising, given the habitats importance for adult nesting sites in Sweden (Tjernberg 1982). It's even less surprising on Gotland, considering golden eagles on Gotland nests exclusively in trees, while mainland eagles in Sweden alternates between trees and cliffs. There might be several explanations for the lack of statistical correlation between coniferous forest and productivity. Due to limited data on the movement of golden eagle on Gotland, the method for simulating territories is rudimentary. Territories were defined as 20 km² large spheres surrounding their main area of occupancy, based on field surveys. In reality, the sizes vary greatly, with complex configurations according to natural structures in the landscape (Watson 2010). Simulated territories in this study might be insufficient for detecting significant patterns regarding effects of different habitat types on reproductive success. Unrealistic territory simulations are a consistent shortcoming for predictor variables in this study. Furthermore, the habitat type surface cover dataset extracted from NMD is based on environmental data gathered between 2017 and 2019, while the reproductive parameters are based on data gathered between 2021 and 2023. There are likely areas with discrepancy between surface data and reality, particularly in relation managed coniferous forest and clearcuts. However, while pine stands are preferred nesting sites for golden eagles on Gotland, they do show adaptability in regard to nesting habitats (Wiss 2008). All territories contained at least 0.95 km² coniferous forest, and the average coverage was 6.3 km². Perhaps small patches of coniferous forest are sufficient to provide suitable nesting habitats in territories on Gotland? Nonetheless, further studies are required to properly assess the relation between coniferous forest and reproductive success on Gotland.

The second subject explored was food supply. The main food source explored in this study was European rabbit, due to their strong presence on Gotland compared to other parts of Sweden. Nocturnal spotlight transects were carried out in 38 territories in order to estimate variance in rabbit density across territories and analyze in relation to golden eagle territory productivity. There was no statistical correlation between rabbit density and eagle productivity. However, the precision of the density estimates is likely low, and the result must be used with care. Firstly, observers lacked tools for accurately measuring the distance to observations. Instead, perpendicular distances to observations were estimated by eye, using 10 m distance classes. The perpendicular distance is important in order to calculate detection rates. Secondly, due to time restraints, territories were surveyed using one transect that was surveyed once, making density estimates influenced by random variation. As many transects were absent of rabbits, the resulting dataset was zero-inflated, making analysis less reliable. In an attempt to decrease statistical noise in the analysis, a three-level categorical predictor variable (rabbit presence) was designed, based on whether rabbits were present (at least one spotted), not present (none spotted), or unknown (territory not surveyed). As with rabbit density, no

statistical correlation was detected with territory productivity. Furthermore, neither sand nor any other soil type correlated with rabbit parameters. During the field studies, observations of additional animals were recorded. In particular, roe deer observations were abundant across the study area. Roe deer numbers on Gotland have increased greatly in the last twenty years (Pettersson et al. 2019; Jägareförbundet Mitt 2020). Variables roe deer density and roe deer presence were calculated for each territory using distance sampling. However, as roe deer parameters were calculated using a methodology adapted for rabbits, the result should be met with caution, and viewed as a crude estimate. Regardless, no correlation was detected between territory productivity and roe deer density or presence. The increasing roe deer population Gotland has subsequently led to increasing roe deer related traffic accidents. Ungulate carrion might be an important source of food for golden eagle, particularly during winters (Watson et al. 1992). The correlation between food supply from roe deer related traffic accidents and territory productivity was analyzed statistically. Surprisingly, although insignificant, territories with more accidents, and presumably more food to scavenge on, trended towards lower productivity. Roe deer related traffic accidents in territories was the fifth most important predictor for territory productivity. One reason for this result might be that accidents seem to be more correlated with human activity than roe deer presence. The proportion of buildings and roads trended towards having negative correlation with territory productivity. Traffic accidents revolving golden eagles remain rare on Gotland (Viltolycka 2024). However, a high number of roe deer related accidents might indicate a stressful environment for golden eagles, with high levels of human disturbance. Nonetheless, the development of roe deer as food source was investigated further by comparing it to the increase of occupied golden eagle territories on Gotland. Before roe deer were introduced to Gotland around 1990, Gotland hosted ten occupied golden eagle territories (Tjernberg 1983). Both populations have gone through incredible increases since then. Using roe deer bag statistics as proxy for roe deer population development, the correlation with number of occupied golden eagle territories since 2002 was analyzed, which resulted in a strong statistical correlation (Figure 10). However, considering the simple nature of the statistical analysis, alternative explanations must be explored before conclusions can be made. The roe deer population's role in golden eagle breeding ecology on Gotland remains an interesting topic for future studies.

The next subject explored was human disturbance. Human activities might, intentionally or unintentionally, disturb eagles' ability to hunt prey or scavenge (Watson 2010). During the breeding season, human disturbance might impede the reproduction process, or the parenting of young, ultimately reducing reproductive success (Suter & Jones 1981). The proportion of territory surface covered by buildings and roads was used as a proxy for human disturbance. Buildings were an

important predictor for territory productivity and showed trend of correlating negatively to territory productivity. However, using the dataset from NMD as proxy for human disturbance has shortcomings. The dataset comprises all types of buildings, including non-residential buildings like barns, outhouses, and industrial complexes. The road layer contains everything between large, heavy traffic roads and small farmers tracks. As building and road variables are based on surface coverage, large buildings have more statistical impact than small buildings. Some buildings may be vacant, at least during large parts of the year. Furthermore, when compared against satellite images, some buildings were not included in the NMD dataset. Roads have the same statistical impact regardless of the amount of traffic. As such, estimates for human disturbance in this study might be too imprecise to detect significant variation among territories. Furthermore, this study did not discriminate between disturbances during different seasons. The huge influx of summer tourists and vacation homeowners presumably impair some territories more than others, depending on location and nesting habitat. Thus, the effects of human disturbance on Gotland are a subject for future studies.

Next, the impact of wind turbines on golden eagle reproductive success was explored. Two predictor variables were analyzed, each territory's distance to the nearest wind turbine, and wind turbine presence (whether or not a territory included at least one wind turbine). Wind turbine presence was the third most important predictor for territory productivity. Although not statistically significant, territories with wind turbines trended towards having higher territory productivity. Wind turbines are known to increase eagle mortality (Hunt 2002; Smallwood & Thelander 2008; Watson et al. 2018) and functional habitat loss (Fielding et al. 2021). The simple territory simulations for this study did not capture detailed flying patterns around wind turbines. Breeding golden eagles, which are relatively stationary, might be vigilant of nearby wind turbines and actively avoid them. According to Hunt (2002), non-breeding adults, or "floaters", are at higher risk of getting stricken by wind turbine blades, compared to breeding adults. This might even be beneficial for breeding eagles, by decreasing conspecific competitive effects. Additionally, as reproductive parameters are calculated on a per-territory basis, mortality on breeding eagles might go statistically unnoticed if deceased individuals are quickly replaced by floaters. Lastly, wind turbines are installed in areas with windy conditions. Eagles generally prefer windy conditions as they use it to travel efficiently and hunt prey (Watson 2010). If breeding eagles can avoid being killed by wind turbines, perhaps the environmental conditions provide beneficial fitness effects. Furthermore, as wind turbines kill many other bird species in addition to raptors (Smallwood & Thelander 2008), wind turbine territories might provide increased scavenging opportunities. As of now, the relation between wind turbines and breeding ecology of golden eagle on Gotland requires further studies for conclusion to be made.

Interspecific density dependence among territories was explored by analyzing the number of neighboring territories, and the distance and reproductive success of the nearest neighboring territory. The golden eagle sub-population on Gotland is incredibly dense, suggesting that self-limiting density effects might take place (Newton 1979 see Whitfield 2013). However, a significant correlation was detected between territories with many neighbors and high territory productivity. This contradicts the hypothesis that the high density of golden eagles on Gotland causes detrimental competitive effects among territories. This, however, assumes that resources are limited. It is possible that the most important raptor resources, nesting sites and food supply (Newton 1979 see Whitfield 2013), are abundant enough on Gotland to support more territories than usual. Since golden eagles display high adaptiveness for tree nesting habitats, nesting sites might not be as limiting on Gotland as other areas of its distribution. Furthermore, the large roe deer population, or the clusters of European rabbit across Gotland, might play crucial roles in sustaining eagles. If resources are abundant enough to support additional territories, the result might simply indicate that territories cluster around high resource areas, rather than receiving beneficial effects by having many neighbors. The golden eagle diet and food supply on Gotland should be studied further. There are several potential prey species not accounted for in this study, most notably waterbirds and hedgehogs (Högström & Wiss 1992). It's also worth noting that hunting grounds of breeding pairs might be located relatively far away from territories (Watson 2010), which is not accounted for in this study. The environment in areas containing clusters of high productive territories could be investigated more thoroughly in future studies. As of now, there is no evidence of population limiting effects caused by conspecific competition.

Finally, competitive effects with white-tailed eagles were explored. Historically, competitive effects between species are rare due to niche separation (Whitfield 2002; Whitfield 2013), but resource usage overlap on Gotland might be higher than usual due to similar food preferences (Högström & Wiss 1992) and nesting site preferences (Wiss 2008). According to the relative weight calculated for important predictors, WTE presence was the best predictor for golden eagle territory productivity. Territories with WTE presence trended towards having increased productivity. This was unexpected, although Whitfield (2002) noticed similar patterns. One reason for this result might be the speculative nature of WTE presence as a predictor variable. The data, gathered during field surveys by the County Administrative Board of Gotland, did not include the specific activity performed by WTE in golden eagle territories. For instance, WTE might have overlapping breeding territories, overlapping hunting ranges, or simply passing through the golden eagle territory. The result might be different with more detailed information. However, following the absence of many small- and medium sized prey animals on Gotland, golden eagle dietary preference resembles WTE

preferences more than for mainland eagles, especially in relation to waterbirds (Högström & Wiss 1992). Furthermore, if roe deer and sheep carrion serve as important food sources on Gotland, dietary overlap may be even higher. Golden eagles are superior to WTE when competing for carrion (Halley & Gjershaug 1998). Perhaps WTE presence indicates valuable resources for eagles, such as important feeding grounds? Furthermore, as both species nest in trees on Gotland, there might be an overlap in nesting preferences as well (Wiss 2008; Evans et al. 2010). Perhaps golden eagles can overtake old WTE nests, providing easy access to nesting sites? The potential relation between golden eagles and WTE on Gotland requires further studies.

4.1 Future studies

This study served as an exploratory analysis that briefly evaluated potential reproductive impact of many environmental subjects. To reach conclusive results regarding breeding ecology of golden eagle on Gotland, detailed studies of individual subjects should be carried out. It is important that surveillance of breeding parameters is continued on Gotland, as quantity of data for this study was limited. With more data, complex multivariate models could be utilized instead of simple linear regression models. Furthermore, the parameter “years of occupancy” of each territory could be used to calculate territory productivity, instead of “number of breeding attempts”, making territory productivity more statistically comparable with population productivity.

Efforts should be aimed at exploring movement patterns of individual eagles and eagle pairs. The biggest shortcoming of this study was the limited knowledge of territory structure- and size. One approach assessing this issue is to track land usage of individual eagles using GPS-tracking collars (Singh et al. 2016). This could provide proper insight into habitat preference of nesting sites and hunting grounds. Identifying hunting grounds for breeding pairs could provide further insight into dietary preference and competitive effects with neighboring pairs and WTE. GPS data could illustrate how golden eagles react to long term and sudden human disturbance, and aid in future decisions regarding new facilities and tourist attractions. Furthermore, effects and movement patterns in relation to wind turbines could be studied (Fielding et al. 2023).

The abundance and distribution of food supply for golden eagle on Gotland is a potential topic for future studies, particularly the relevance of roe deer. According to pellet counts, densities of roe deer vary across Gotland (Jägareförbundet Mitt 2020). Pellet count data could provide more accurate estimates of roe deer prevalence in golden eagle territories. Additionally, the transect surveys carried out for this study could be adapted to the ecology of roe deer in order to calculate more accurate density estimates. For instance, transects would be surveyed in the summer

between hunting seasons (15 June to 16 August) as hunting may increase shyness (Focardi et al. 2002), and summer vegetation does not impede detection rates as much for roe deer. Furthermore, the detection rates and flushing distances of roe deer would be higher than for rabbits. The biggest shortcoming of the field methodology during this study was the lack of precise distance estimates. To combat this issue, a night vision range finder would prove useful. The dietary preferences of golden eagles could be studied further using camera traps installed in nests (Melin 2020), particularly the relative preference for roe deer. Camera trap data could be complemented with pellet analysis. Additionally, the dietary importance of species like European rabbit and domesticated sheep could be assessed using camera data. Gotland has a strong tradition of breeding sheep, and in 2019, there were over 68 300 sheep on Gotland (Jordbruksverket 2019). The approach could be expanded to WTE as well, to understand the level of competition among the species. The activity of WTE in golden eagle territories should be studied, as well as dynamics surrounding nesting competition.

The effects of Human disturbance on golden eagles on Gotland should be studied in detail. The human disturbance proxy variable could be improved by integrating up to date population data in different parts of the island, in order to include the actual number of people in the area. The roads across the island could be divided into disturbance classes depending on their size and level of traffic. One approach could be to divide disturbance into different types, at different times of the year, and in different parts of Gotland. Some territories endure constant disturbance throughout the year, from heavily trafficked roads, tractors in farmland, or large industrial sites. In the summer, during the sensitive breeding season, human activity escalates across the island as 12 500 summer house owners arrive, and 900 000 tourists pass through the island (Holm 2015; SCB 2023). This undoubtedly results in sudden disturbances for certain territories, such as tourists hiking in the forests, houses being inhabited, small roads receiving heavy traffic. The relative impact of different types of disturbance on breeding ecology of golden eagle is important knowledge for understanding breeding ecology. Finally, future studies on temporal and spatial variance in reproductive success should consider the effects of weather conditions.

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Popular science summary

Why have this Swedish island become an unexpected paradise for eagles?

The golden eagle is one of the largest and most iconic eagles in the world. Large carnivores, such as golden eagle, are important for the well being of ecosystems by killing and controlling the number of prey animals. Golden eagles are good at adapting to different types of habitats. Most golden eagles in Sweden exist in the north, among mountains and boreal landscapes. These habitats provide eagles with strong winds to fly in, trees and cliffs to nest in, and patches of open areas where they can hunt. However, there is an island outside mainland Sweden that contains unusually many eagles on a relatively small surface. This island, called Gotland, does not contain typical golden eagle habitats. There are no mountains, few trees to nest in, and a lot of people that might disturb them. Still, the density of golden eagle are ten times higher on Gotland than anywhere else in Sweden. The purpose of this study was to understand why there as so many golden eagles on Gotland. This was done by comparing how breeding success varied over time and space in relation to factors that typically affect the wellbeing of golden eagle. These factors included habitat type, food supply, human disturbance, wind turbines, and competition with neighboring golden eagles and another eagle species. Roe deer might be an important food source on Gotland, as the study found that the number of roe deer on Gotland seems to correlate with the number of golden eagle territories. Furthermore, golden eagles with more neighboring eagle territories had higher breeding success. This does not necessarily mean that they gain benefits from having more neighbors. Rather, it may be the result of eagles clustering around areas that are beneficial for them. Normally, eagles compete for limited resources and would suffer by having many competitors. However, if resources are abundant enough to sustain all eagles, competition does not become an issue. Coniferous forest seemed to be important for golden eagles. Eagles in territories containing wind turbines or white-tailed eagles, also seemed to breed more successfully. Buildings and roads in territories seemed to have negative effects on breeding success. However, as many alternative explanations to these results remain, further studies are required to draw conclusions. Particularly, future research should focus on mapping territory borders, study food type preferences, and explore how different types of human disturbance affect the golden eagles on Gotland.

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Appendix 1

Term	Definition
Fledgling	A chick able to fly
Breeding attempt	One of the following must be confirmed for the occupied territory in question: mating, incubation, egg or eggshells In or around the nest, living or dead chicks observed, or recently maintained nest.
No breeding attempt	Territory not surveyed again between 1 June and 15 September, or no observations of egg remains or living/dead chicks between 1 June and 15 September.
Successful breeding attempt	A living chick is observed in the nest or elsewhere in the territory between 1 June and 31 August or together with a sexually mature eagle between 1 and 15 October and that all chicks are not found dead before 15 September.
Unsuccessful breeding attempt (one of the following):	<ul style="list-style-type: none"> • No chicks observed in a nest where breeding has been confirmed or no chicks observed within 100 days in a nest where breeding has not been initiated but observed later. • All eggs are still in the nest between 1 June and 1 July or within 45 days in nest where nesting has been initiated. • All chicks found dead before 15 October or after 100 days where in a nest where breeding has not been initiated.
Unknown Breeding attempt (one of the following):	<ul style="list-style-type: none"> • Breeding, eggs, or living chicks is observed before 1 June I a nest where no more visits is done. • A dead chick or eggshells in or around a nest before 15 October that has not been visited before or where only incubation has been observed.
Estimating territory limits:	<ul style="list-style-type: none"> • Nests with breeding happen simultaneously belongs to different territories. • If two or more GE pairs are being observed simultaneously, they count as belonging to different territories.

- If GE pairs have distinguishable plumage, they can be divided into separate territories.
 - DNA samples
 - If territories have not yet been divided, sexually mature GE and nests within 10 km is being grouped, while above 10 km is defined as separate territories.
-

Appendix 2

Variable	Topic	NMD classes included
Coniferous forest	Habitat composition	Pine forest not on wetland Spruce forest not on wetland Mixed coniferous forest not on wetland Pine forest on wetland Spruce forest on wetland Mixed forest on wetland
Arable land	Habitat composition	Arable land
Other open land	Habitat composition	Vegetated other open land Non-vegetated other open land
Deciduous and mixed forest	Habitat composition	Mixed forest not on wetland Deciduous forest not on wetland Deciduous hardwood forest not on wetland Deciduous forest with deciduous hardwood forest not on wetland Mixed forest on wetland Deciduous forest on wetland Deciduous hardwood forest on wetland Deciduous forest with deciduous hardwood forest on wetland
Clearcut	Habitat composition	Temporarily non-forest not on wetland Temporarily non-forest on wetland
Wetland	Habitat composition	Open wetland
Artificial surface	Human disturbance	Artificial surfaces, buildings Artificial surfaces, roads/railways Artificial surfaces, not buildings or road/railway
Buildings	Human disturbance	Artificial surfaces, buildings
Roads	Human disturbance	Artificial surfaces, roads/railways

Appendix 4

Package	Version	Author	Functions
Base	4.3.2	R Core team	General data manipulation, removing outliers
Stats	4.3.2	R Core Team	Linear regressions, correlations matrix
Dplyr	1.1.4	H. Wickham	General data manipulation
Ggplot2	3.4.4	T.L. Pedersen	Plotting and visualizing data
Ggpubr	0.6.0	A. Kassambara	Manipulating plots
Distance	1.0.9	D. L. Miller	Distance sampling, abundance and density
Utils	4.3.2	R Core Team	Create CSV files
lmtest	0.9-40	A. Zeileis	Diagnostic checking in linear regression models
ape	5.7-1	E. Paradis	Controlling for spatial autocorrelation

Appendix 5

Habitat type	Min	Max	Median	Average	Standard deviation
Coniferous forest	4.75	65.16	26.6	31.52	15.46
Arable land	0.00	64.76	23.00	27.41	18.19
Other open land	3.66	57.45	14.92	16.92	10.74
Deciduous/mixed	0.24	20.37	9.26	9.46	4.92
Marine water	0.00	72.12	0.00	4.97	10.76
Clearcut	0.17	17.33	3.14	4.81	3.89
Wetland	0.01	8.03	0.92	1.70	1.85
Inland water	0.00	0.27	0.14	0.76	3.30

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