# Friends or Foes?
# Gyrfalcon – Golden Eagle Interactions in the Scandinavian Mountains

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# Abstract

Climate change, habitat loss and human persecution are threatening raptor populations globally, making science based conservation strategies essential to preserve healthy populations in the future. The importance of a multi-species or community approach in conservation is increasingly recognized, especially for species utilizing the same resources. However, in arctic and sub-arctic environments, extensive knowledge on factors affecting population dynamics of sympatric raptor species is limited. This exploratory study used over 20 years of monitoring data on gyrfalcons (*Falco rusticolus*) and golden eagles (*Aquila chrysaetos*) in the Swedish mountain region to analyse spatial and temporal trends of distribution and productivity of these two species in relation to environmental variables and interspecific presence. Two main questions were addressed; 1) How do fluctuations in prey populations, weather variables and topography of nesting sites affect the territorial occupancy and productivity of gyrfalcons and golden eagles? and 2) Do gyrfalcons and golden eagles affect each other's territorial occupancy and productivity? Regression modeling and model selection based on Corrected Akaike Information Criterion (AICc) were used to identify key predictors. Results indicated that out of the environmental variables golden eagles seemed to be more affected by prey densities and gyrfalcons by spring weather conditions. A positive effect of interspecific presence was seen for golden eagle occupancy, while remaining tests of interspecific impact showed neutral effect. Limited or no significant effect in either direction for many of the models likely indicate that different factors act simultaneously and influence population dynamics in complex ways. Additionally, quality of the monitoring data varied across years, and results should be interpreted with caution. Future research should incorporate variables such as exposure of nesting sites and habitat characteristics of nesting territories, in addition to replication of the key analyses in this study to confirm the validity of the results. A more comprehensive monitoring of these species and ecosystem, and understanding built on it, will provide a stronger foundation to create targeted, multi-species conservation strategies in areas where climate and resource dynamics may change rapidly in the future.

*Keywords:* Gyrfalcon, *Falco rusticolus,* Golden Eagle, *Aquila chrysaetos*, interspecific interactions, population dynamics, distribution, reproduction, Scandinavia

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# Abbreviations

| | |
|---|---|
| AICc | Corrected Akaike Information Criterion |
| CAB | County Administrative Board |
| ES | Early Season |
| GE | Golden Eagle |
| GF | Gyrfalcon |
| ICC | Intraclass Correlation Coefficient |
| LS | Late Season |
| NRM | Swedish Museum of Natural History |
| SCB | Statistics Sweden |
| SEPA | Swedish Environmental Protection Agency |
| SLU | Swedish University of Agricultural Sciences |
| SMHI | Swedish Meteorological and Hydrological Institute |

# 1. Introduction

Knowledge about how species interact and affect each others populations is crucial to understand and successfully address conservation and human-wildlife conflicts (Fryxell et al. 2014). Many examples exist of how conservation measures for one species have led to unexpected ecosystem alterations in the environment, showing the need to evaluate potential implications of planned measures on the ecosystem rather than just the targeted species (Smedshaug et al. 1999; Courchamp et al. 2003; Bergstrom et al. 2009). Presence of and interactions among predators often play a crucial role for the structure of vertebrate communities, a fact recognized in various ecosystems across the globe (Crooks & Soulé 1999; Fedriani et al. 2000; Elmhagen et al. 2010).

In the arctic and subarctic regions, gyrfalcons (*Falco rusticolus*) and golden eagles (*Aquila crysaetos*) – two long-lived, sympatric raptors – often occur in the same habitats in mountainous areas. Living in these areas means facing pronounced seasonal changes, particularly in regard to weather and food availability, making the endeavor to survive and reproduce a constant challenge. Aspects of climate change like increased air temperature are showing to be more rapid in arctic regions (Lemke et al. 2007; Box et al. 2019), and negative impacts observed so far include increased winter precipitation and higher frequencies of rain-on-snow events limiting access to forage for herbivores (Descamps et al. 2017). However, factors like higher temperature will presumably enhance primary production and increase vegetation (Sturm et al. 2001), which could gain native species like willow ptarmigan (*Lagopus lagopus*), an important prey species for gyrfalcons and golden eagles in the arctic and subarctic regions (Ehrich et al. 2012). But a higher temperature in general may also lead non-native species to expand their ranges further north (Chen et al. 2011), contributing to a change in ecosystem functioning and food-web structure (Legagneux et al. 2014; but see van Beest et al. 2021).

By occupying the same niche in the northern mountain regions, gyrfalcons and golden eagles become potential competitors for key survival components like prey, nesting territories and nesting sites. Several researchers have reported on violent interactions between the species, especially around nests (Poole & Bromley 1988a; Barichello 2020), and indicated negative interspecific effects on density (Johansen & Østlyngen 2011; McCaffery et al. 2011). Still, gyrfalcons do not build nests themselves and are dependent on nest structures built by other species, mainly ravens (*Corvus corax*), golden eagles and rough-legged buzzards (*Buteo lagopus*), making them reliant on potential competitors (Poole & Bromley 1988a; Barichello 2020). Ravens are generally chased off by gyrfalcons rather than the opposite, but they are opportunistic feeders known to mob and pirate from gyrfalcons (Ratcliffe

& Rose 1997; Barichello 2020). They might also compete with gyrfalcons for similar nest structures to a larger extent than golden eagles and rough-legged buzzards (Poole & Bromley 1988a).

While specific details of competition between gyrfalcons and golden eagles are still being uncovered, numerous studies on raptors suggest that distribution and reproductive success is shaped by a complex interplay of spatial and spatiotemporal factors. Prey density has been demonstrated to influence reproductive success in raptors across many studies (Newton 1980; Steenhof et al. 1997). In arctic environments, quite a few prey populations experience strong fluctuation in numbers over a period of years, referred to as cycles and often implied to be enhanced by pressure from one or several predator species (Gauthier et al. 2004; Schmidt et al. 2012). Negative impacts on prey populations can give cascading effect on predators (Descamps et al. 2017), more or less pronounced depending on the degree of prey specialization of the predator (Schmidt et al. 2008; Terraube et al. 2011). In addition, other prey populations can be affected as a consequence of prey-switching by predators (Lecomte et al. 2008), as seen in the population dynamics of microtines and willow ptarmigan in Scandinavia — two important prey groups for raptors in the region (Breisjøberget et al. 2018). A relationship between prey density and reproductive success in long-lived species may however be challenging to detect, as time-lags of several years may be occurring between a period of food shortage and subsequent declines in reproductive success (Watson 2010).

The effect of weather on distribution and reproductive success depends largely on the reproductive biology of the species, such as where they nest and when they initiate breeding. The pattern of increased precipitation could be a serious threat to raptors in arctic and subarctic regions, especially those nesting on cliffs or in open stick nests as several studies show a correlation between increased precipitation and lower reproductive success (Mearns & Newton 1988; Kostrzewa & Kostrzewa 1990; McDonald et al. 2004). In addition, weather conditions often correlate with food availability, reducing access to food and requiring increased hunting effort in adverse weather conditions (Schifferli et al. 2014).

The composition and characteristics of a nesting territory is yet another factor frequently studied in relation to distribution and reproductive success among raptors, since access to food and shelter is crucial to make it through the breeding season. The spatial scale and level of analysis within a species (i.e. individual or entire population) may yield varying results and must be specified before drawing conclusions on habitat preferences (Johnson 2007). Ultimately, while habitat characteristics – closely linked to prey densities (Ekblad et al. 2020) – are essential for reproductive success, the role of intra- and interspecific competition can be equally decisive, potentially deterring individuals from otherwise suitable areas due to heightened competitive pressure (Martínez et al. 2008).

Increased age and prior breeding experience are other variables commonly correlated with higher reproductive success in raptors (Clum 1995; Snyder & Smallwood 2022). Consecutive occupancy of the same nesting site, likely linked to increased age and breeding experience, has also been positively linked to brood size (Bente 2011). Additionally, differences in individual ability, including skills like hunting efficiency, may be important to consider as it has been suggested to explain variation in reproductive success among raptors better than effect of habitat composition and available resources within a home range (Zabala & Zuberogoitia 2014; but see Terraube et al. 2014). However, individual behavior is complex to study and tracking individuals over a longer time-period requires extensive time and resources not available in most cases, including this study.

As indicated earlier, interactions between spatial and spatiotemporal factors are often suggested when studying what affects distribution and reproductive success in raptors, although distinct results might be hard to present (Steenhof et al. 1997). Still, modelling different factors simultaneously may reveal whether predictable abiotic factors like topography are more influential compared to biotic or less predictable abiotic factors like prey density and weather. Integrating interspecific influences into such models can further enhance our understanding of the relative importance of mechanisms like resource partitioning in a multi-species system, offering clues to their effect on the dynamics of the populations.

This study aims to determine drivers of distribution and reproductive success of gyrfalcons and golden eagles in areas of shared habitat in the Scandinavian mountains. The importance of studying species at a community level is increasingly recognized, yet research on raptor guilds in the Swedish mountain region are limited and predominantly centered on diet (Nyström 2004; Dalerum et al. 2016). I aim to explore trends in spatial and temporal patterns of occupancy and productivity of the two species over time and analyze it in relation to data on prey populations, weather, topography of nesting sites and effects of interspecific presence. Corresponding patterns may indicate competition for limiting resources like food or nests, which in turn can affect the long-term conservation of the species.

I intend to answer the following questions:

1. How do fluctuations in prey populations, weather variables and topography of nesting sites affect the territorial occupancy and productivity of gyrfalcons and golden eagles?

2. Do gyrfalcons and golden eagles affect each other’s territorial occupancy and productivity?

# 2. Materials and Methods

## 2.1 Terminology

Varied and undefined terminology is a recognized issue when comparing studies on raptor biology and distribution, which lead to difficulties interpreting research findings correctly, preventing comparisons of studies and complicating conservation work (Steenhof et al. 2017).

Key measurements of raptor distribution and reproduction in this study are occupancy and productivity of nesting sites (hereafter generally referred to as "nests"). Occupancy is defined as "occupied" (1) or "not occupied" (0) and confirmed by observation of a pair occupying a nesting territory or obvious signs thereof, like fresh twigs or guano at the nest. For occupancy measures on population level, total number of occupied nesting territories are divided by total number of checked nesting territories in a given year. Productivity is defined as number of live chicks observed in the nest by late June. For productivity measures on population level, total number of live chicks are divided by total number of occupied nesting territories in a given year. A list defining relevant terms used in the study can be found in Appendix 1.

## 2.2 Study species

### 2.2.1 Gyrfalcon (*Falco rusticolus*)

*Taxonomy and morphology*

The gyrfalcon (Figure 1) is the largest member of the Falconidae family. As most raptors, gyrfalcons are sexually dimorphic in body size (Leonardi 2020). The body mass of males is about 800 - 1500 g and females 1250 - 1800 g (Potapov & Sale 2005), and the wingspan range between 109-134 cm (Rasmussen n.d.). The plumage color varies from white to grey to dark over its range, with a variation of color morphs appearing in most populations (Johnson et al. 2012). Aside from periods of migration, courtship and nesting, gyrfalcons are generally solitary (Jones 2001).

*Figure 1. Gyrfalcon (Copyright © Hoorn 2018)*

*Distribution and conservation status*

The gyrfalcon has a circumpolar breeding distribution, inhabiting subarctic and arctic areas between 55º and 82º N (Cade 2011). The global population size is estimated to between 12 600 – 55 300 mature individuals and is evaluated as least concern according to the IUCN Red List (Birdlife International 2024b). The European population is estimated to about 2000 – 3500 mature individuals and the European range constitutes approximately 13% of the global range for gyrfalcons (Birdlife International 2024b). Major threats to the species include a changing climate, habitat loss and decline of prey populations (Koskimies 2005; Radcliffe et al. 2024). Gyrfalcons are protected under Swedish law (*Artskyddsförordningen (2007:845)* 2007) and the national population is classified as endangered in the Swedish Red List (SLU Artdatabanken 2020).

*Diet*

The gyrfalcon is diurnal and considered a specialist when it comes to diet, dominated by Lagopus species in most of its range (Barichello & Mossop 2011; Potapov 2011; Nielsen & Cade 2017). Alternative prey are arctic hare (*Lepus arcticus*) and mountain hare (*L. timidus*), other birds like ducks (Anseriformes), waders (Charadriiformes) and passerines (Passeriformes**)** as well as microtines like lemmings (Cricetidae) and ground squirrels (Sciuridae) (Potapov 2011). In

Fennoscandia (comprising of Norway, Sweden, Finland and the Russian regions of Kola and Karelia) willow ptarmigan and rock ptarmigan (*Lagopus muta*) are clearly the dominating prey (Koskimies & Sulkava 2011) and a range-wide reluctance to shift prey species has been shown (Nielsen & Cade 1990; Nyström et al. 2005). A preference for Lagopus species is believed to be explained in part by them being of optimal prey size (c. 400 – 650 g) for gyrfalcons and often permanently resident in an area (Nielsen & Cade 2017). The fact that Lagopus species are exploited by humans through hunting in many parts of its range may affect gyrfalcons negatively, although human hunting activity could simultaneously aid in exposing and flushing out prey for the raptor (Bente 1981; Smith & Willebrand 1999).

### *Habitat and home range*

The preferred habitat of gyrfalcons is alpine areas above the tree line with sparse vegetation which offer good hunting opportunities, and cliffs or mountain areas for nestings (Koskimies 2005). In Sweden, breeding pairs are found in the mountain region of the three northern-most counties, with the addition of one known nest in the county of Dalarna (Falkdalen 2024). Estimations of home range size varies depending on location, season, age-group and sex. Data from Alaska revealed a mean core home range (50 % of the calculated utilization distribution of tracked individuals) of 65 km$^2$ (adults, breeding season May - September; Eisaguirre et al. 2016) while the same area based on data from Greenland was 53 km$^2$ (adult females, breeding season) and 28 km$^2$ (adult males, breeding season; Burnham & Newton 2011). The nesting territory, here assumed to roughly equal core home range, is aggressively defended during the breeding season (Davis 1995) and male presence at nests during this time vary little between years with variations in ptarmigan density, indicating importance of keeping a good home range rather than increasing the hunting effort in scarce ptarmigan years (Barichello 2011).

### *Sexual maturity and breeding*

Gyrfalcons reach sexual maturity between two to four years of age (Potapov & Sale 2005). They nest in areas with clifflike structures and eggs are laid in abandoned stick nests, mainly built by ravens, golden eagles or rough-legged buzzards, or occasionally on rock ledges (Bente 2011; Barichello 2020). Protected sites like cliffs with overhang have been shown to be selected by gyrfalcons (Poole & Bromley 1988a), and a preference for large cliffs at a mean elevation of 368 m have been recorded in Alaska (Ritche et al. 2003). They are considered monogamous (Davis 1995) and show great home range fidelity, but low fidelity to nests and alternate between nests within the home range (Booms et al. 2011; but see Bente 2011). Time of egg laying differs somewhat across the range with more northern populations starting later, but initiation is generally happening in April (Poole & Bromley 1988b; Koskimies 2005; Burnham 2008; Nielsen 2019). Gyrfalcons lay clutches of one to five eggs and incubation goes on for about 34-36 days, followed by a synchronous hatching (Potapov & Sale 2005). The nestlings are altricial, i.e. completely dependent on parental care for thermoregulation and food deliveries when born, making them highly vulnerable to environmental variables during their first weeks (Henderson 2019). They leave the nest around 45-50 days of age, males generally earlier than females (Moen 2022).

### *Migration*

Knowledge of seasonal movements of gyrfalcon is limited but migrating or partially migrating behavior is seen in many populations in the northernmost part of the range while others are believed to remain sedentary (Schmutz et al. 1991; Burnham 2008; McIntyre et al. 2009). Recent GPS-data revealed a variation of migration patterns of gyrfalcons in Greenland with individuals migrating to over-winter in southern Greenland, Canada, Iceland and also spending long periods on the sea ice, indicating high adaptability depending on seasonal variations (Burnham 2008; Burnham & Newton 2011). The northernmost recorded wintering range from the study on Greenland was located at 67.9°N (Burnham & Newton 2011). Degree of migration is likely influenced by fluctuations in prey populations and weather conditions (Bente 1981).

### *Intra- and interspecific interactions*

Pirating of killed prey occurs in regions where multiple raptor species coexist. Species with a size advantage, such as bald eagles (*Haliaeetus leucocephalus*), often intimidate gyrfalcons and have been observed stealing prey killed by the latter (Dekker et al. 2012; Dekker & Court 2024). Gyrfalcons in return have been recorded to pirate from the smaller peregrine falcon (*Falco peregrinus*), although peregrine falcons have been seen dominating gyrfalcons as well (Burnham 2008; Dekker et al. 2012). In addition, an indirect interaction with the peregrine falcon is, together with climate change, believed to be part of the reason for retraction of the gyrfalcon population on Greenland, displacing the larger falcon as the peregrine range expands north and their population on Greenland increase (Burnham 2008).

Records of direct intraspecific interactions between gyrfalcons are rare. Distance between nesting gyrfalcons has been calculated to a minimum of 1000 m, although reproductive success was significantly lower with nesting conspecifics within 5000 m than when nesting distance was greater (Poole & Bromley 1988a). Distance between nesting gyrfalcons and nesting golden eagles has been estimated to a minimum of 1800 m and a corresponding minimum of 700 m to nesting peregrine falcons (Poole & Bromley 1988a). Higher density of golden eagles have been suggested to correspond with declining numbers of gyrfalcons (Johansen & Østlyngen 2011; McCaffery et al. 2011), and gyrfalcons in Alaska have been recorded to steer clear of occupied golden eagle nests (Weir 1982, cited in Watson 2010).

Few observations of intra- or interspecific predation exist, although gyrfalcon remains have sometimes been found in the nests of other raptors (Moen et al. 2023). Among documented cases an Eurasian Goshawk (*Accipiter gentilis*) has been recorded killing gyrfalcon nestlings in Norway (Moen et al. 2023) and adult peregrine falcons likely killed a subadult gyrfalcon when it attacked their nestlings in Russia, based on observations shortly after the attack (Pokrovsky et al. 2010). Siblicide in gyrfalcons is likely occurring during periods of food stress (Cade 1960, cited in Leonardi 2020).

Although competition and rivalry are the main themes when studying raptor assemblages, the gyrfalcons dependence on nest structures built by ravens, golden eagles or rough-legged buzzards signify the importance of their presence for the gyrfalcon to persist in any part of its range.

### 2.2.2 Golden eagle (*Aquila crysaetos*)

*Taxonomy and morphology*

The golden eagle (Figure 2) is a member of the family Accipitridae, and the species has six recognized subspecies across its global range (McIntyre & Watson 2019). The one present in Sweden is the nominate subspecies, sometimes referred to as the European golden eagle. Sexual dimorphism is exhibited through size difference, where the body mass of males range around 3500 - 4000 g and females around 5000 g (Watson 2010; Hjernquist 2011). The wingspan ranges between 185 - 220 cm (Hjernquist 2011). Juvenile plumage of golden eagles are characterized by chocolate brown pigmentation with the majority of the tail being pure white as well as patches of white at the base of the secondaries and the inner primaries (Watson 2010). At around five years of age the adult plumage is attained, characterized by a dark brown pigmentation with paler, almost yellow feathers around the back of the head and on the covert wings (Watson 2010).

*Figure 2. Golden eagle (Copyright © Otero 2024)*

*Distribution and conservation status*

The distribution of golden eagles is widespread, ranging across the Nearctic and Palearctic regions with some populations even reaching into Indomalaya and the Afrotropics (Birdlife International 2024a) and covering latitudes of 70°N to 20°N (Watson 2010). Globally golden eagles are considered as least concern with a population size of 85 000 - 160 000 mature individuals (Birdlife International 2024a). Population estimates in Europe range from 19 200 – 25 600 mature individuals and the European range equals approximately 16% of the global range (Birdlife International 2024a). Change of land use impacting hunting and availability of prey, poaching, collision with wind turbines, lead poisoning and electrocution from power poles are some of the threats recognized as most severe for the conservation of the species (Watson 2010). In Sweden, golden eagles are protected by law (*Artskyddsförordningen (2007:845)* 2007) and the population is classified as near threatened in the Swedish Red List (SLU Artdatabanken 2020).

*Diet*

Golden eagles are more of a generalist compared to gyrfalcons when studying diet (Sulkava et al. 1999; Nyström 2004). They are diurnal (James & Sandilands 2014) and a variety of prey is utilized across the range, mainly from the families Leporidae (hares and rabbits), Sciuridae (squirrels and marmots), Tetraonidae (grouse) and Phasianidae (pheasants and partridges), with additional options such as carrion of deer or livestock, reptiles and hedgehogs being important for populations in certain areas (Tjernberg 1981; Nyström et al. 2006b; Watson 2010). In the Swedish mountain region reindeer (*Rangifer tarandus*) husbandry of semi-domesticated reindeer is practiced by the indigenous people of Sweden, the Sami, and golden eagles in northern Sweden have a diet largely dominated by species of Tetraonidae, mountain hare and reindeer fawns during breeding season (Tjernberg 1981; Nyström et al. 2006b). However, it is debated whether reindeer fawns are killed by eagles or mainly fed on as carrion after dying from other causes, with limited proof of live killings.

### *Habitat and home range*

Considering the wide distribution of the species, the golden eagle can adapt to an impressive range of climates in environments from tundra to deserts (Watson 2010). Preferred habitat is varied, but often include flat or mountainous open habitats at elevations between sea level and 4000 m a.s.l. (Birdlife International 2024a). Golden eagles are breeding all over Sweden, but the six northern-most counties host 85% of the known home ranges, although the largest subpopulation is located on the island of Gotland in the south (Åsbrink & Källman 2024). Home range size is highly variable over the range, but also over seasons and by age-group, and core home ranges has been estimated to be between 5 – 30 km$^2$ (adults, breeding season March-August) in northern Sweden (Singh et al. 2016), 5 - 110 km$^2$ (adults, breeding season March – October) in northern and central Sweden (Moss & Hipkiss 2014) and averaging 41.3 km$^2$ (adults, breeding season March-October) in northern Finland (Tikkanen et al. 2018). Golden eagles have been documented to show strong aggressive behavior when holding or searching for a new nesting territory, indicating a fitness advantage to having a high quality home range similar to gyrfalcons (Hunt et al. 2021). Undulating flight displays by resident eagles are often seen directed at intruders, but also during courtship and pair bonding, indicating that such a display is more complex than we might think (Harmata 1982; Reid et al. 2019).

### *Sexual maturity and breeding*

The golden eagle has a slow reproduction and becomes sexually mature around six years of age (Tjernberg 1988, cited in Hjernquist 2011). Pairs are considered to mate for life, but lost mates are often replaced (James & Sandilands 2014) and occasional mate-switching is suspected to occur without the death of a partner (Watson 2010; Kylmänen et al. 2023). Golden eagles show strong fidelity to nests, although nest-switching within home ranges between years is common in many areas (Johnsen et al. 2007; Kylmänen et al. 2023). They generally nest on cliffs with a few exceptions in trees, especially in populations inhabiting more densely forested areas (McGahan 1968). An overlap of preferred nesting site characteristics is seen between golden eagle and gyrfalcon (Ritche et al. 2003). However, in Canada a preference for south-facing nests was seen in golden eagles, while no pattern regarding aspect was seen among gyrfalcons (Poole & Bromley 1988a).

Laying date for golden eagles is closely related to latitude and ranging from mid-November to early May depending on location (Watson 2010). In northern Sweden egg laying is initiated in the end of March, a brood is generally consisting of one to three eggs and incubation is ongoing for 41–45 days (Hjernquist 2011). Just as gyrfalcons, golden eagle nestlings are altricial and only weigh about 100 g when born, making them highly dependent on their parents (Watson 2010). Nestlings stay in the nest until between 60-80 days of age, and just like gyrfalcons males generally leave the nest earlier than females (Moen 2023).

### *Migration*

Most golden eagle populations are sedentary, and long-distance migration is mainly seen in populations at latitudes above 60°N, as staying put secures the ownership of the obtained nesting territory while also giving the opportunity to start breeding as soon as conditions allow (Brodeur et al. 1996; Watson 2010). The species tend to migrate singly or in small groups and seldom remain in one place more than two days (James & Sandilands 2014). Young individuals generally migrate longer than adults and aside from age, factors like weather and experience determine time, length and route of migration (Miller et al. 2016; Singh et al. 2017). Better understanding of migration patterns for northern populations of golden eagles is an important matter for conservation and should be prioritized as the interest for industrial wind power development is increasing, to mitigate hazards for the species (Bedrosian et al. 2018).

### *Intra- and interspecific interactions*

Many other raptor species avoid sites occupied by golden eagles, likely due to the risk of predation (Poole & Bromley 1988a; Ratcliffe & Rose 1997; Sergio et al. 2004). Golden eagles have also been known to displace other raptor species from their nests (Radcliffe 1962, cited in Watson 2010). Although white-tailed eagles (*Haliaeetus albicilla*) are bigger, golden eagles have been documented being dominant and more aggressive when competing for access to carcasses (Halley & Gjershaug 1998). Distance between occupied golden eagle nests in Canada measured a minimum of 1400 m (Poole & Bromley 1988a). On rare occasions golden eagles are seen forming larger groups and interacting with each other, possibly for hunting or playing (O'Connell & Kochert 2013).

## 2.3 The Swedish mountain region

The Swedish mountain region is part of the Scandes mountain range, which stretches along the border between Norway and Sweden, its northern and central part being shared between the countries while the southern part is located in Norway (c. 58.2 – 71.1°N, 4.5 – 31.0°E, Figure 3). The region covers almost 40% of the total area of Sweden, although it is inhabited by less than 2% of the total population (Moen 2006). It falls within the cold climate region (Köppen Climate Classification; Beck et al. 2018), in the subgroup continental subarctic climate (Arnfield 2023). Precipitation is rich year-round as the majority of wind is coming from the west or south-west bringing humid air from the Atlantic Ocean (Swedish Meteorological and Hydrological Institute; SMHI 2024b). The ground is snow covered approximately 200 days per year (SMHI 2024a).

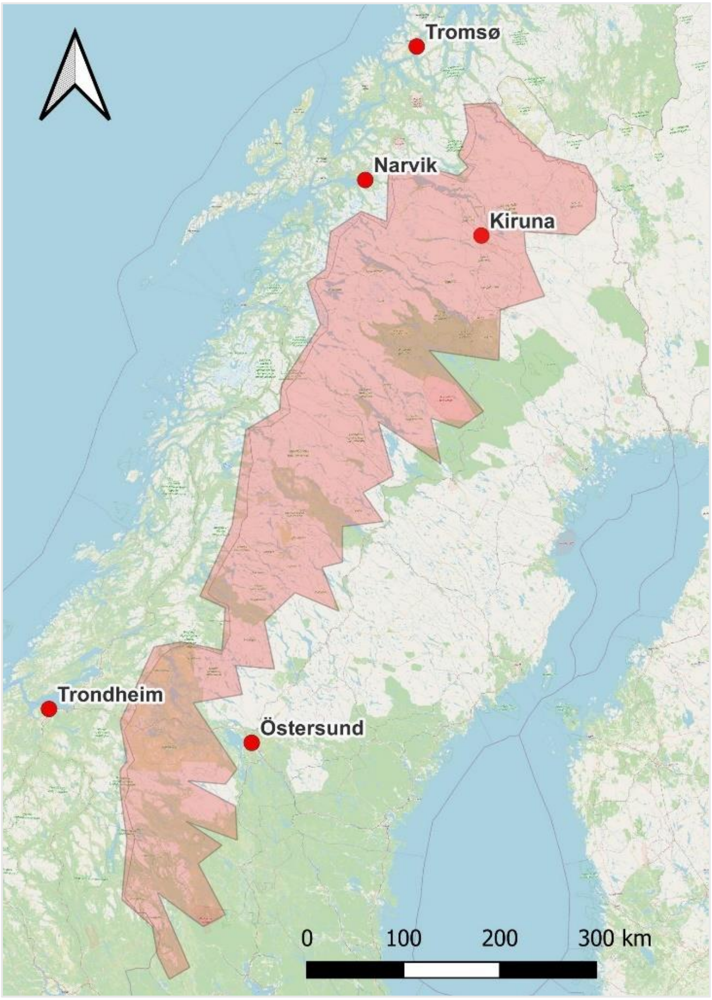

*Figure 3. Approximate map of the Swedish mountain region.*

The habitat composition is diverse with a landscape largely covered by shrubland, open wetland, forests, lakes and rivers, while bare alpine terrain is dominating above the timber line (at elevations of 600-950 m a.s.l. depending on latitude; Rafstedt 1984). The mountain range is built up by a variety of rock types, resulting in heterogeneous vegetation across the region (Andersson et al. 1985). Type of rock also affect the shape of the terrain, and smooth, rolling hills as well as steep alpine mountains are found across the mountain range (Rafstedt 1984). The highest mountain in the Swedish part of the Scandes, Kebnekaise, is located in Norrbotten County, measuring 2097 m a.s.l. (Tarfala Research Station 2024).

Different types of land use have dominated the mountain region throughout history, with reindeer husbandry, forestry, hunting, tourism, mining and hydroelectric development being some of the most important ones (Moen 2006). Traditional reindeer husbandry is still practiced, although infrastructure development and modern forestry are creating challenges by limiting migration paths and reducing lichen abundance (Anttonen et al. 2011; Kivinen et al. 2012). 51.1% of the land area in the subalpine region (i.e. above the boundary for mountain forests in accordance with the Swedish Forest Agency delimitation) is formally protected (Statistics Sweden; SCB 2023).

Hunting is common in Sweden, both for sport and as a tool for conservation. All hunting is regulated by law and the use of dogs is an integral part of the Swedish hunting tradition. The five large predator species in Sweden, brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), grey wolf (*Canis lupus*), wolverine (*Gulo gulo*) and golden eagle can all be found in the mountain region. However, wolves are just sporadic visitors as they are prohibited to establish territory in reindeer herding areas, often causing significant damage by killing individuals and breaking up herds of reindeer. At present, hunting quotas are issued yearly for brown bears, lynx, wolves and wolverines, while permits to hunt golden eagles only can be issued for cases where a specific individual is causing damage. Other hunted species inhabiting the mountain region are moose (*Alces alces*), red fox (*Vulpes vulpes*), mountain hare and different bird species like rock and willow ptarmigan, while the arctic fox (*Vulpes lagopus*), also inhabiting mountain areas in Sweden, is protected by law without any hunting allowed. Main raptor competitors for the gyrfalcons and golden eagles in the area are rough-legged buzzards, white-tailed eagles and occasionally peregrine falcons.

This study examines two large areas in the Swedish mountain region. The study area located in the county of Västerbotten (hereafter referred to as “Västerbotten”) covers approximately 13 000 km$^2$ and the study area in the county of Norrbotten (hereafter referred to as “Norrbotten”) covers approximately 30 000 km$^2$.

## 2.4 Data collection

Data used in the study included distribution and reproductive outcome for gyrfalcons and golden eagles, harvest data on ptarmigans, trapping index data on microtines, weather data and topography data (including latitude) for nesting sites (Table 1).

The spatial variables (topography variables like elevation and aspect) did not change between years, while the remaining variables (all spatiotemporal) varied between years.

*Table 1. Overview of data from Västerbotten and Norrbotten used for analyses.*

| Data type | Time period | Comment |
|---|---|---|
| **Gyrfalcon reproduction Västerbotten** | 1998 – 2010;<br>2016 - 2024 | 57 nests in total as of 2024 in Västerbotten (not all nests surveyed each year). |
| **Golden eagle reproduction Västerbotten** | 1998 – 2024 | 67 nests in total as of 2024 in Västerbotten (not all nests surveyed each year). |
| **Gyrfalcon nest quality Norrbotten** | 1998 – 2024 | 104 nests in total as of 2024 in Norrbotten. |
| **Ptarmigan harvest Västerbotten** | 2013 - 2023 | Ptarmigan harvest data available for areas surrounding 24 gyrfalcon nests and 26 golden eagle nests in Västerbotten. |
| **Microtine catch index Västerbotten** | 2001 - 2023 | One catch site for the entire study area in Västerbotten. |
| **Weather variables** | 1998 - 2024 | Two locations used within the study area in Västerbotten, data missing for a few variables/years. Specifications in Appendix 2. |
| **Topography** | - | Topography data available for 53 gyrfalcon nests and 54 golden eagle nests in Västerbotten and for 104 gyrfalcon nests in Norrbotten. |

### 2.4.1 Gyrfalcon and golden eagle data

Data on gyrfalcon breeding performance has been collected in the Swedish mountain region for decades thanks to dedicated volunteers and the County Administrative Boards (CABs), although not always in a systematic way due to lack of finances and coordination between regions. Since the gyrfalcon only nests in the mountain region, field work is time-consuming and costly due to inaccessible nest locations in steep terrain, generally requiring a helicopter to be efficient. Ideally, known nests are visited twice yearly, once in the spring to determine occupation of nests and breeding attempts (i.e. signs like brooding) and once in the summer to confirm breeding success and count nestlings (Ekenstedt 2006). New nesting sites are added when found. To protect sensitive information, nest locations and monitoring results remain confidential, and only general reproductive outcomes are made public.

The Swedish Museum of Natural History (NRM) is coordinating monitoring of golden eagles in Sweden, while the CABs have the main responsibility for the field work (Kungsörn Sverige 2023). Field work is executed by representatives from the CABs and regional experts from Kungsörn Sverige, a non-profit association with the mission to aid and promote the work of maintaining a healthy golden eagle population in Sweden (Kungsörn Sverige 2023). Data on reproduction is collected yearly by visits to known home ranges and nests within the home ranges, once during the spring to collect observations of occupied nests and confirmed breeding attempts and once in the summer to determine whether breeding attempts were successful and potentially mark young with rings (Swedish Environmental Protection Agency; SEPA 2024). Just like with the gyrfalcon monitoring, the monitoring of golden eagles in the mountain regions often requires the use of a helicopter and new nesting sites are added when located. Standardized methods for collecting breeding data are determined by the SEPA and the results are submitted in Rovbase, a Swedish-Norwegian data base for wildlife survey data (NRM 2024). However, as data on nests for golden eagles are confidential, imprecise coordinates for nests are registered in the shared data base (NRM 2024). For both species, the aim is to collect the highest quality data possible, but weather conditions and financial constraints largely dictates the extent to which this can be achieved.

In this study, the main analyses were based on data from Västerbotten with nest occupation and productivity representing variables of distribution and reproduction of the two raptor species. An overview of the raptor data from Västerbotten is found in Appendix 3. Data from Norrbotten was also analyzed, but available variables were restricted to gyrfalcons and the reproductive data was not available per year but rather as a nest quality index over the period between 1998 - 2024 (Table 2). Therefore, analyses were limited to compare nest quality with topographic variables since remaining predictor variables aside from ptarmigan harvest data were unavailable on nest level. Comparisons with ptarmigan data were excluded due to a large mis-match in time, as ptarmigan data from Norrbotten only covered a portion of the years of which the nest quality index was based. Nest locations were used to derive data on elevation, slope and aspect of nests in both areas.

*Table 2. Overview of the quality index for gyrfalcons in Norrbotten for the years 1998 – 2024.*

| Quality | Requirement |
|---|---|
| **5** | A nest occupied at least 70% of the years with successful breeding at least 50% of the years |
| **4** | A value between 3 and 5 |
| **3** | A nest occupied at least 40% of the years with successful breeding at least 20% of the years |
| **2** | A value between 1 and 3 |
| **1** | A known nest location but rarely occupied and very rarely any breeding attempt observed |

### 2.4.2 Prey species data

Data on microtine rodents was acquired from the Swedish University of Agricultural Studies (SLU; Ecke & Hörnfeldt 2023). Trapping of microtines was done over three days on two occasions yearly (spring and fall) and made into a trapping index of number/100 trapping nights (Ecke & Hörnfeldt 2023). The microtine species used for analysis were Norwegian lemming (*Lemmus lemmus*), grey-sided vole (*Myodes rufocanus*) and field vole (*Microtus agrestis*), based on occurrence of species in the diet of gyrfalcon and golden eagle in previous studies from the Swedish mountain region (Nyström et al. 2005, 2006b). Trapping index from spring and fall was used and tested with different time lags in this study. The data was collected in the Ammarnäs area, Västerbotten.

Harvest data for willow and rock ptarmigan was used as a proxy for population density of both species. Hunting of ptarmigan in the mountain region is administered by the CABs or, in one instance, the local Sami village (an organization of reindeer herders with rights to use a determined area). A time-limited license is required to hunt and reporting of the result (whether successful or not) is encouraged and mandatory to be able to issue a new license at a later occasion (Länsstyrelsen Norrbotten n.d.)

Ptarmigan harvest data from Västerbotten were available as seasonal totals for each small game hunting area. Although the hunting season of ptarmigan in northern Sweden generally begins in late summer and continue until early spring—with slight variations between years—the year in which the season started was used to label the data (i.e. the sum of the season 2022/2023 was recorded as 2022 since the majority of the season took place before the new year). Summed harvest data from the three main small game hunting areas within circular buffer zones with a radius of 10 km (approximately 314 km$^2$) around nests were derived and analyzed in relation to raptor occupancy and productivity with different time lags.

### 2.4.3 Historical weather data and topography

Historical weather data was derived from the Swedish Meteorological and Hydrological Institute (SMHI 2025). Data for the months of March – June was used, divided into early breeding season (1st of March – 30th of April, ES) and late breeding season (1st of May – 30th of June, LS). Although the breeding events of gyrfalcon and golden eagle in the mountain region of Sweden are differing slightly, both species will normally lay eggs in the early period and chicks will be hatched in the late period (Figure 4).

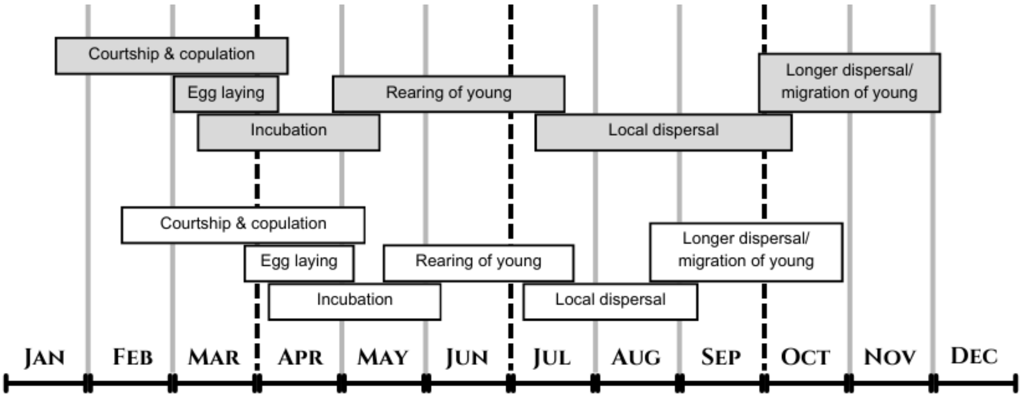

*Figure 4. Approximate timing of breeding season events for golden eagles and gyrfalcons in the Subarctic region. Golden eagle events are depicted in grey and gyrfalcon events are depicted in white.*

The variables of interest included mean temperature (°C), amount of precipitation (mm, rain and snow), number of days with heavy precipitation (over 8 mm), number of storm events (minimum 5 consecutive days of precipitation), mean snow depth (only for ES) and onset of spring (first day of the year out of six with a mean day temperature of +5,0°C or higher). These were selected based on their relevance to the biology of the study species. Weather data were sourced from two different locations within Västerbotten, and whichever location was closer determined which data were associated with individual nests. Some data was sourced from nearby weather stations due to lack of consecutive observations, introducing a bit of local variation in the data. Onset of spring was only available for a larger area constituting of the northernmost part of Sweden, delimited by the southern border of the county of Västerbotten. An overview of the weather stations used are found in Appendix 2.

Topographic variables at nests were analyzed using data derived from Lantmäteriet (Lantmäteriet 2024) and extraction of spatial data and distances between nests was made in QGIS version 3.34 (QGIS Development Team 2023).

## 2.5 Data analysis

All statistical tests were performed using R Statistical Software (v. 4.4.3; R Core Team 2025). A variety of linear models were used to perform analyses both on nest and population level (Table 3).

*Table 3. Specifications for analyses of the effect of spatial and spatiotemporal variables on occupancy and productivity. All analyses were performed with data from Västerbotten except for the analysis of nest quality and topography in Norrbotten.*

| Response variable | Variable type | Predictor variable | Variable type | Scale | Test |
|---|---|---|---|---|---|
| **Occupancy** | Binary | Occupancy nearest interspecific neighbor | Binary | Nest | Generalized linear model |
| **Productivity** | Numeric | Productivity nearest interspecific neighbor | Numeric | Nest | Negative binomial regression |
| **Occupancy** | Numeric | Interspecific occupancy | Numeric | Population | Beta regression |
| **Productivity** | Numeric | Interspecific productivity | Numeric | Population | Linear regression |
| **Occupancy** | Binary | Ptarmigan density | Numeric | Nest | Generalized linear model |
| **Productivity** | Numeric | Ptarmigan density | Numeric | Nest | Negative binomial regression |
| **Occupancy** | Binary | Microtine density | Numeric | Population | Beta regression |
| **Productivity** | Numeric | Microtine density | Numeric | Population | Linear regression |

| | | | | | |
|---|---|---|---|---|---|
| **Occupancy** | Binary | Weather variables | Numeric | Population | Beta regression |
| **Productivity** | Numeric | Weather variables | Numeric | Population | Beta regression |
| **Occupancy** | Binary | Topography variables | Numeric | Nest | Generalized linear model |
| **Productivity** | Numeric | Topography variables | Numeric | Nest | Beta regression |
| **Quality** | Ordered | Topography variables | Numeric | Nest | Ordinal logistic regression |

In addition to these models, the variance of individual nest productivity was tested with a random intercept model and intraclass correlation coefficient (ICC) was calculated to assess the consistency of productivity within nests relative to between-nest variation. A permutation test was also conducted to assess nest fidelity and distribution of nesting site aspect was analyzed with a Chi-Squared test for given probabilities.

Missing data points (marked not applicable, NA) were mainly found among the raptor reproduction data and were excluded from the analyses as they represented unknown values. Due to large differences in monitoring effort between years, mean occupancy and productivity was used for analyses on population level. Ptarmigan harvest data was log transformed before analysis due to many zero values. Aspect was transformed into two categories before running regression models; northness (cosine of aspect) and eastness (sine of aspect). Correlation matrices (threshold 0.7) were used to detect multicollinearity among ptarmigan, microtine and weather variables.

Model selection was performed for the multivariate analyses of topography and weather variables, based on Corrected Akaike Information Criterion (AICc) suitable for small sample sizes (Burnham & Anderson 2002). The AICc was calculated in R Statistical Software using the formula

$$AICc = AIC + 2K(K + 1) / (n - K - 1)$$

where K is the number of parameters and n is the number of observations. An overview of all specific R packages used for analyses are found in Table 4.

*Table 4. Overview of specific R packages used for analyses (general packages excluded).*

| R package | Reference | Analysis |
|---|---|---|
| **MASS** | (Venables & Ripley 2002) | Interspecific productivity, ptarmigan density vs productivity, topography vs nest quality |

| | | |
|---|---|---|
| **corrplot** | (Wei & Simko 2024) | Correlation matrix of weather and prey variables |
| **betareg** | (Cribari-Neto & Zeileis 2010) | Interspecific occupancy, microtines and weather vs occupancy, weather and topography vs productivity |
| **MuMIn** | (Bartón 2025) | Model selection of weather and topography models |
| **lme4** | (Bates et al. 2015) | Nest productivity |
| **lmerTest** | (Kuznetsova et al. 2017) | Nest productivity, extension of lme4 with test values |

Rather than applying a strict significance threshold of the p-value at 0.05, greater weight was placed on the value of the test statistic (t or z), particularly when it deviated substantially from zero in either direction.

Distance between nests were calculated by creating distance matrices in QGIS. Intraspecific nests within 1000 m of each other were considered to be alternate nests in the same nesting territory and all but one nest within 1000 m were therefore excluded before re-creating the matrix. Interspecific distance matrices were created last and nests within 1000 m of each other were removed as these also were considered to be alternate nests in the same nesting territory although assigned to different species. Most likely, the species have only been using alternate nests of the same nesting territory in different years. No new matrices were created as it was not possible to decide which of the species nests should be removed in profit of the other, instead all nests within 1000 m of each other were excluded.

# 3. Results

## 3.1 Västerbotten

The response variables used for analyses of data from Västerbotten were occupancy and productivity for both raptor species. Number of occupied nests for gyrfalcons varied between 0 – 27 in the same year, while the same number varied between 0 – 30 for golden eagles. Mean yearly productivity varied between 0 – 2.5 for gyrfalcons and 0.06 – 2 for golden eagles. Number of produced chicks per year varied between 0 – 44 for gyrfalcons and 1 – 19 for golden eagles.

Distances of inter- and intraspecific nests were calculated between all known nests, regardless of occupation status (Table 5). Distance between nearest neighboring gyrfalcon nests within Västerbotten ranged from 2796 m to 16 301 m and distance between nearest neighboring golden eagle nests ranged from 1655 m to 21 450 m. Distance between gyrfalcon nests and nearest neighboring golden eagle nests within Västerbotten ranged from 1026 m to 23 401 m and distance between golden eagle nests and nearest neighboring gyrfalcon nests ranged from 1026 m to 34 375 m, since nearest neighbors are not always corresponding pairs (Figure 5).

*Table 5. Distance (m) between nearest nests within and between species in Västerbotten. Nests within 1000 m of each other were considered to be alternate nests in the same nesting territory and were therefore excluded.*

| **Species** | **Shortest** | **Longest** | **Mean** |
|---|---|---|---|
| **Gyrfalcon** | 2796 | 16301 | 7840 |
| **Golden eagle** | 1655 | 21450 | 9302 |
| **Gyrfalcon – Golden eagle** | 1026 | 23401 | 7806 |
| **Golden eagle – Gyrfalcon** | 1026 | 34375 | 11001 |

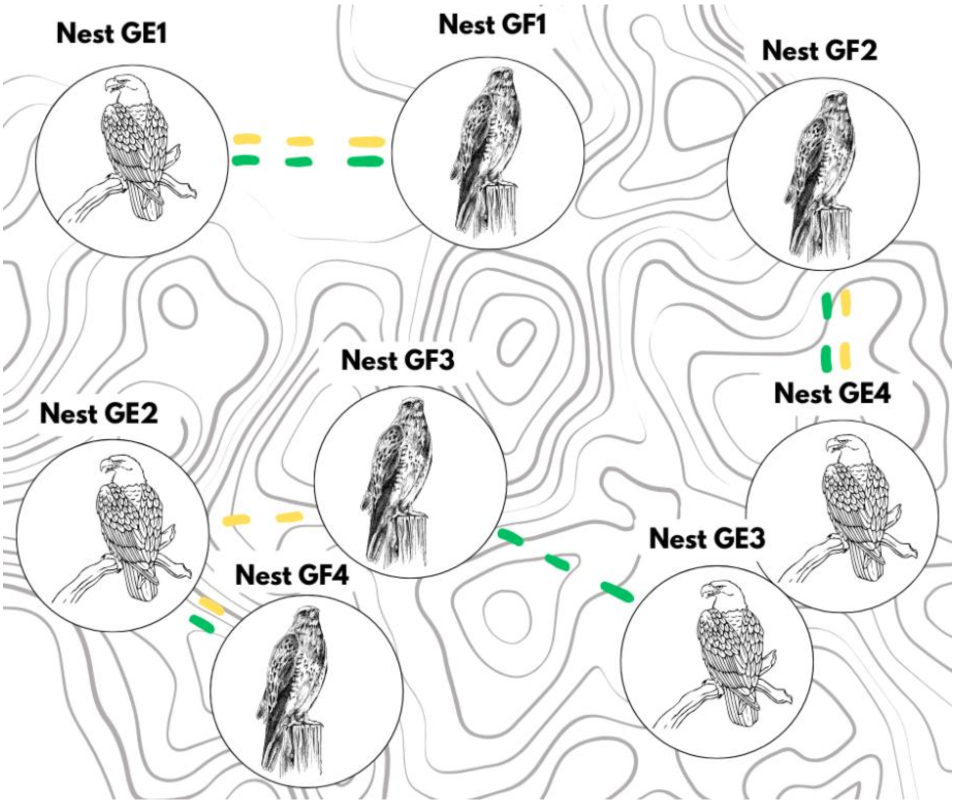

*Figure 5. Example of spatial interspecific relationships between gyrfalcons (GF) and golden eagles (GE) on nest level. Yellow lines mark nearest golden eagle nest to each gyrfalcon nest and green lines mark nearest gyrfalcon nest to each golden eagle nest.*

### 3.1.1 Nest fidelity, productivity and variance of productivity for individual nesting sites

Nest fidelity in Västerbotten was analyzed with a permutation test, and the observed variance in occupancy was significantly higher than expected for both gyrfalcons (observed variance 14.42, $p < 0.001$) and golden eagles (observed variance 41.45, $p < 0.001$), indicating strong site fidelity. Plots of mean productivity and coefficient of variance of productivity for individual nests suggest a relationship between higher productivity and lower variance of productivity for both species (Figure 6 and Figure 7). However, tests on productivity of individual nests revealed low variability (ICC), with only 7.5 % of the variance explained by nest identity for gyrfalcons and 8 % for golden eagles. The low ICC values indicate that most variation in productivity occurred within nests across years rather than between different nests.

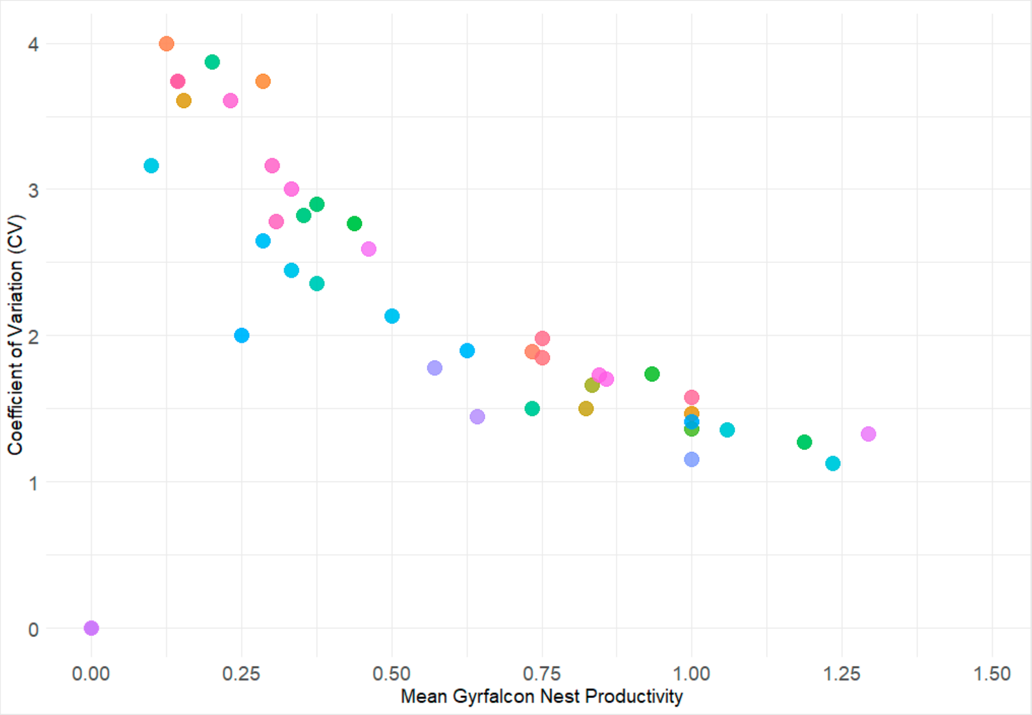

*Figure 6. Relationship between mean nest productivity and its variation for gyrfalcons in Västerbotten.*

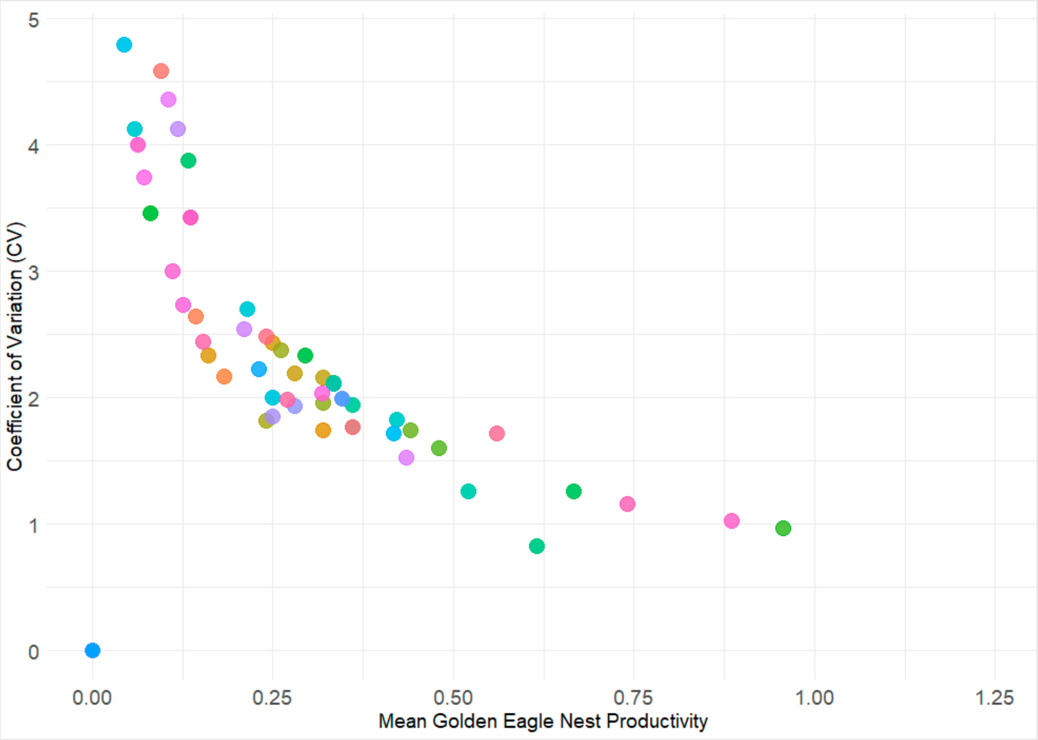

*Figure 7. Relationship between mean nest productivity and its variation for golden eagles in Västerbotten.*

### 3.1.2 Impact of prey population density on occupancy and productivity

Univariate models were used to analyse the effect of ptarmigan density on occupancy and productivity on nest level with time lags of one and two years. No effect was seen for the analyses of ptarmigan and gyrfalcon occupancy and productivity. Willow ptarmigan density and pooled ptarmigan density were positively correlated to golden eagle occupancy with a two-year time lag (willow ptarmigan; estimate = 0.29, S.E. = 0.14, z-value = 2.11, p = 0.03, pooled ptarmigan; estimate = 0.28, S.E. = 0.14, z-value = 2.02, p = 0.04). No effect was seen for the analyses of ptarmigan and golden eagle productivity. No multivariate models of ptarmigan were run due to high correlation between the predictor variables. A complete table of test results for all univariate linear models are presented in Appendix 5.

Univariate models were used to analyse the effect of microtine density from spring and fall both on occupancy and productivity data in the same year (only spring microtine density) and on occupancy and productivity data with a one-year time lag (both spring and fall microtine densities). No effect was seen for the analyses of microtines and gyrfalcon occupancy and productivity. Density of field voles in fall had a positive effect on golden eagle occupancy with one-year lag (estimate = 0.18, S.E. = 0.1, z-value = 1.84, p = 0.07, Figure 8). No effect was seen for the analyses of microtines and golden eagle productivity. No multivariate models of microtines were run due to high correlation between the predictor variables.

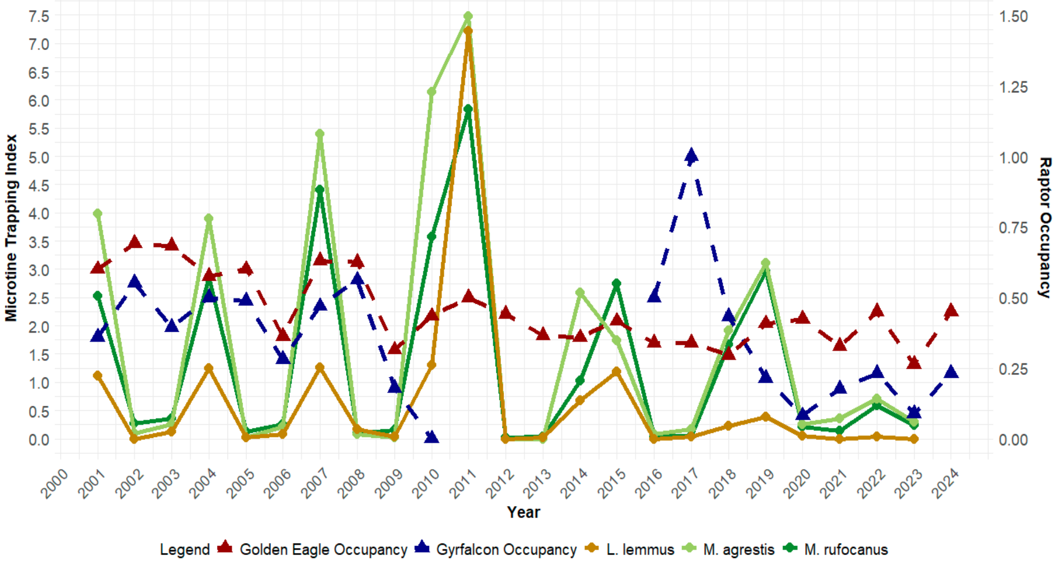

*Figure 8. Mean occupancy of gyrfalcon (blue dashed line) and golden eagle (red dashed line) in relation to mean trapping index of lemmings (orange solid line), field voles (lightgreen solid line) and grey-sided voles (dark green line) in Västerbotten 2001 - 2024.*

When plotted, pooled ptarmigan densities and pooled microtine densities showed synchronized fluctuations between 2013 – 2024, though clear correlations with raptor occupancy were absent (Figure 9).

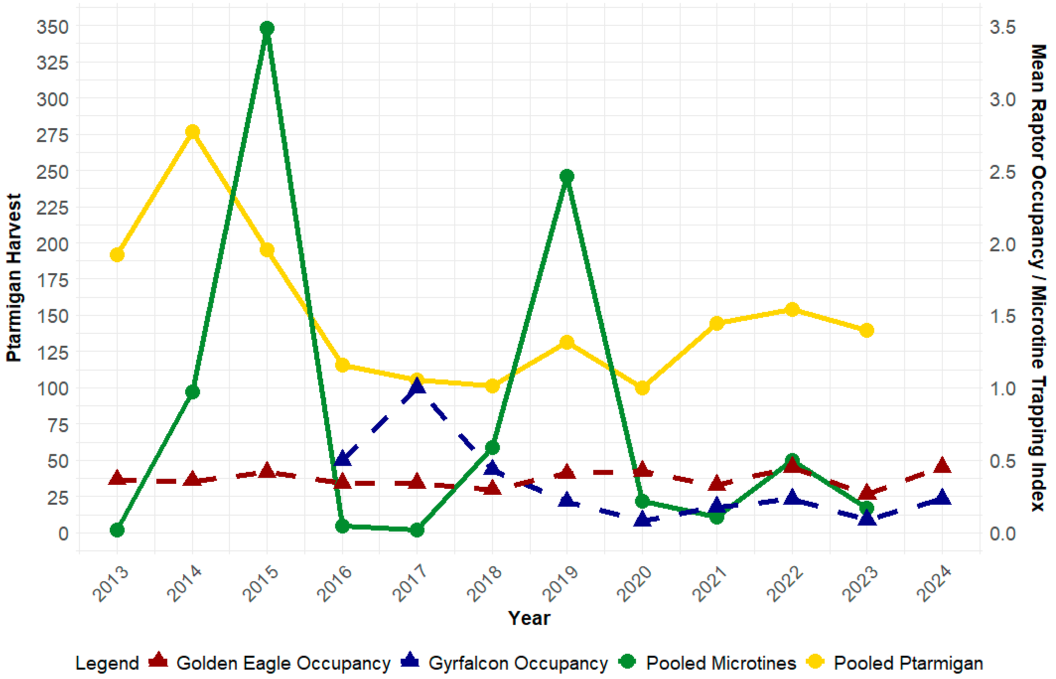

*Figure 9. Mean occupancy of gyrfalcon (blue dashed line) and golden eagle (red dashed line) in relation to mean ptarmigan harvest (yellow solid line) and mean microtine trapping index in spring (green solid line) in Västerbotten 2013 - 2024.*

### 3.1.3 Impact of weather variables on occupancy and productivity

Univariate models were produced for all weather variables. Yearly mean occupancy was tested against weather variables ES and onset of spring, while yearly mean productivity was tested against all weather variables, based on relevance of timing for each of the response variables.

For univariate models of gyrfalcon data, storm events ES had a positive effect on occupancy while temperature ES affected productivity positively and snow depth ES affected productivity negatively. For univariate models of golden eagle data and weather variables no effect was seen.

A correlation matrix was run to determine highly correlated weather variables, resulting in removal of the variable days of heavy precipitation for both early and late breeding season. Subsequently, multivariate models were run followed by model selection based on AICc. Among the models assessing the effects of weather variables on gyrfalcon occupancy, the highest ranked model (Table 6) included the predictor variable storm events ES (estimate = 0.48, S.E. = 0.24, z-value = 2.0, p = 0.05).

*Table 6. Full model, best model and null model for weather variables and gyrfalcon occupancy in Västerbotten.*

| **Model** | **Variables Included** | **df** | **logLik** | **AICc** | **Delta** | **Weight** |
|---|---|---|---|---|---|---|
| **Null Model (intercept)** | None | 2 | 0.185 | 4.3 | 0.97 | 0.377 |
| **Full Model** | Temperature ES,<br>Storm events ES,<br>Onset of spring,<br>Precipitation ES,<br>Snow depth ES | 7 | 5.578 | 11.5 | 8.13 | 0.011 |
| **Best Model (highest ranked)** | Storm events ES | 3 | 2.041 | 3.3 | 0.00 | 0.612 |

Among the models assessing the effects of weather variables on gyrfalcon productivity, the highest ranked model (Table 7) included the predictor variables snow depth ES (estimate = -5.42, S.E. = 1.7, z-value = -3.194, p < 0.01) and onset of spring (estimate = 0.1, S.E. = 0.05, z-value = 1.99, p = 0.05).

*Table 7. Full model, best model and null model for weather variables and gyrfalcon productivity in Västerbotten.*

| **Model** | **Variables Included** | **df** | **logLik** | **AICc** | **Delta** | **Weight** |
|---|---|---|---|---|---|---|
| **Null Model (intercept)** | None | 2 | 0.758 | 3.2 | 2.66 | 0.209 |
| **Full Model** | Temperature ES + LS,<br>Storm events ES + LS,<br>Onset of spring,<br>Precipitation ES + LS,<br>Snow depth ES | 10 | 8.337 | 27.8 | 27.24 | 0.00 |
| **Best Model** | Snow depth ES, Onset of spring | 4 | 5.067 | 0.5 | 0.00 | 0.791 |

No variables were statistically significant when assessing the effects of weather variables on golden eagle occupancy and productivity with univariate models, making further modelling unnecessary. An overview of relative predictor variable importance for all four response variables is summed below (Table 8).

*Table 8. Sum of weight (sw, relative variable importance) for weather variables in relation to different response variables of gyrfalcon and golden eagle reproduction in Västerbotten.*

| | **Response variable** | | | |
|---|---|---|---|---|
| **Predictor variable** | Occupancy gyrfalcon | Productivity gyrfalcon | Occupancy golden eagle | Productivity golden eagle |
| **Storm events ES** | 0.67 | 0.18 | 0.207 | 0.216 |
| **Temperature ES** | 0.24 | 0.37 | 0.202 | 0.21 |
| **Onset of spring** | 0.35 | 0.44 | 0.233 | 0.193 |
| **Precipitation ES** | 0.32 | 0.16 | 0.226 | 0.194 |
| **Snow depth ES** | 0.26 | 0.76 | 0.224 | 0.227 |
| **Temperature LS** | - | 0.16 | - | 0.226 |
| **Precipitation LS** | - | 0.15 | - | 0.2 |
| **Storm events LS** | - | 0.14 | - | 0.204 |

### 3.1.4 Impact of nesting site topography on occupancy and productivity

The distribution of elevation of nesting sites in Västerbotten varied between 565 m – 1149 m (mean 811 m) for gyrfalcons and 395 m – 986 m (mean 655 m) for golden eagles, and most nests were situated at intermediate elevations within the observed ranges for both species.

For distribution of aspect of nesting sites, a south-facing direction was clearly favored for both species. Mean aspect for gyrfalcon nests was 170.2° and 180.6° for golden eagle nests. Nest aspect of gyrfalcon nests was significantly non-random ($\chi^2 = 928.7$, df = 7, $p < 0.01$), indicating a strong directional preference in nest selection. Residuals from the Chi-squared test revealed that nests were disproportionately oriented toward the south, southeast, and southwest, while remaining aspects were underrepresented. Nest aspect of golden eagle nests was also significantly non-random ($\chi^2 = 958$, df = 7, $p < 0.01$). Residuals revealed that nests were disproportionately oriented towards the south and southwest, while remaining aspects were underrepresented.

Slope distribution of nests varied between 4° - 47° for gyrfalcons and 0° – 52° degrees for golden eagles.

No variables were statistically significant when assessing the effects of topographic variables on gyrfalcon occupancy with univariate models, making further modelling unnecessary. Univariate modelling of topographic variables and gyrfalcon productivity showed a positive effect of elevation on productivity. However, subsequent multivariate modelling and model selection identified the null model as best model, indicating limited effect of the predictor variables (Table 9).

*Table 9. Full model, best model and null model for topography variables and gyrfalcon productivity in Västerbotten.*

| Model | Variables Included | df | logLik | AICc | Delta | Weight |
|---|---|---|---|---|---|---|
| **Null Model (intercept)** | None | 3 | -213.314 | 432.6 | 0.00 | 0.5 |
| **Full Model** | Elevation, Slope, Aspect_Cos, Aspect_Sin, Latitude | 8 | -229.655 | 475.4 | 42.79 | 0.0 |
| **Best Model** | None | 3 | -213.314 | 432.6 | 0.00 | 0.5 |

Univariate models revealed a positive effect of latitude on golden eagle occupancy. Among the multivariate models assessing the effects of topography variables on golden eagle occupancy, the highest ranked model (Table 10) included the predictor variables latitude (estimate = 0.24, S.E. = 0.03, t-value = 7.09, $p < 0.01$) and elevation (estimate < 0.01, S.E. < 0.01, t-value = 1.72, p = 0.09).

*Table 10. Full model, best model and null model for topography variables and golden eagle occupancy in Västerbotten.*

| Model | Variables Included | df | logLik | AICc | Delta | Weight |
|---|---|---|---|---|---|---|
| **Null Model (intercept)** | None | 2 | -828.521 | 1661.1 | 47.38 | 0.000 |
| **Full Model** | Elevation, Slope, Aspect_Cos, Aspect_Sin, Latitude | 7 | -801.944 | 1618.0 | 4.31 | 0.104 |
| **Best Model** | Latitude, Elevation | 4 | -802.819 | 1613.7 | 0.00 | 0.896 |

No variables were statistically significant when assessing the effects of topography variables on golden eagle productivity with univariate models, making further modelling unnecessary.

### 3.1.5 Interspecific ecological influence on occupancy and productivity

Univariate analyses were performed to determine if occupancy and productivity of individual nests of one species were affected by occupancy and productivity of the nearest neighboring nest of the other species. No effect was seen when analyzing the impact on occupancy status of gyrfalcon nests by occupancy status of the nearest neighboring golden eagle nest (estimate = 0.2, S.E.= 0.18, z-value = 1.11, p = 0.27).

However, the corresponding analysis of occupancy status of golden eagle nests and the impact of occupancy status of the nearest neighboring gyrfalcon nest showed a positive effect (estimate = 0.35, S.E. = 0.19, z-value = 1.89, p = 0.05). Additional figures of the relationships of occupancy across nests and years are presented in Appendix 4.

No effect was seen when analyzing impact of productivity of individual gyrfalcon nests on productivity of the nearest neighboring golden eagle nest (estimate = 0.15, S.E. = 0.17, z-value = 0.85, p = 0.39), nor for the opposite analysis of productivity of individual golden eagle nests on the productivity of the nearest neighboring gyrfalcon nest (estimate = 0.06, S.E. = 0.07, z-value = 0.8, p = 0.43).

Additionally, the interspecific analysis of productivity was carried out on a cleaned data set where all vacant nests were removed beforehand, resulting in a lack of effect as well (gyrfalcon; estimate = 0.15, S.E. = 0.11, z-value = 1.29, p = 0.2, golden eagle; estimate = 0.01, S.E. = 0.06, z-value = 0.22, p = 0.83).

When analyzing impact of mean yearly occupancy and productivity of gyrfalcon nests by golden eagle nests and the opposite on population level, no effect was seen on either of the response variables.

## 3.2 Norrbotten

The response variable used for analyses of data from the study area in Norrbotten were quality of gyrfalcon nests on a scale from 1 – 5 (Figure 10).

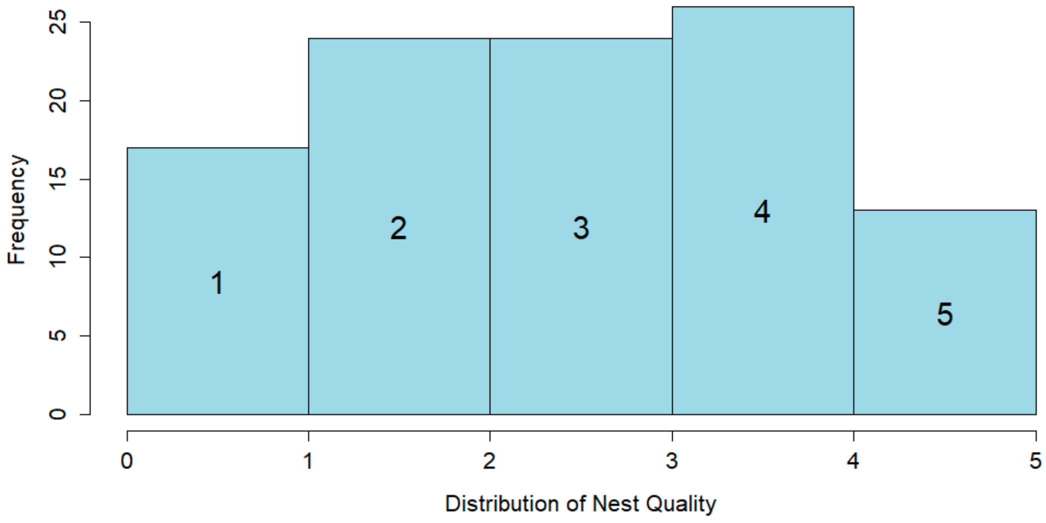

*Figure 10. Distribution of quality of nests for gyrfalcon nesting sites in Norrbotten.*

Distance between nearest neighboring gyrfalcon nests within Norrbotten ranged from 1468 m to 72 720 m (mean 10 126 m).

### 3.2.1 Impact of nesting site topography on nest quality

Elevation of nest sites in Norrbotten ranged from 393 m – 1142 m with a mean of 741 m. Slope of nest sites ranged from 0° - 67° with a mean of 33°. Aspect of nest sites ranged from 22.3° - 350.5° with a mean of 172.1°. The analysis of aspect revealed a significantly non-random distribution ($\chi^2 = 64.923$, df = 7, $p < 0.01$), indicating a strong directional preference in nest site selection. Residuals from the Chi-squared test revealed a disproportionate orientation of nests toward the south and southwest, while remaining aspects were underrepresented.

Univariate models of the effect of topography variables on quality of gyrfalcon nests revealed a positive effect of latitude. After running multivariate models with model selection, the highest ranked model (Table 11) confirmed latitude as the most influential variable (estimate = 0.49, S.E. = 0.18, z-value = 2.78, $p < 0.01$).

*Table 11. Full model, best model and null model for topography variables and gyrfalcon nest quality in Norrbotten.*

| Model | Variables Included | df | logLik | AICc | Delta | Weight |
|---|---|---|---|---|---|---|
| **Null Model (intercept)** | None | 4 | -164.251 | 336.905 | 5.791 | 0.050 |
| **Full Model** | Elevation, Slope, Latitude, Aspect_Cos, Aspect_Sin | 9 | -158.823 | 337.561 | 6.447 | 0.036 |
| **Best Model** | Latitude | 5 | -160.25 | 331.114 | 0.00 | 0.913 |

# 4. Discussion

In this study I investigated patterns of coexistence of gyrfalcons and golden eagles in the Swedish mountain region. Specifically, I explored the effect of spatial and spatiotemporal variables of chosen nesting territories as well as interspecific influence on distribution and reproductive success in areas of shared habitat. I was fortunate to get access to over 20 years of monitoring data on distribution and reproductive success for gyrfalcons and golden eagles in the region.

Results of the study revealed strong fidelity to nesting sites for both species although variance of productivity at individual nesting sites was primarily driven by year-to-year fluctuations within nests. Occupancy of golden eagles was affected by prey densities in the years prior, while gyrfalcon occupancy and productivity were affected by weather variables in winter and spring the same year. Although both species favored south-oriented nests, aspect did not seem to affect occupancy or productivity of either species. Among the topographic variables only latitude had any significant effect, influencing golden eagle occupancy in Västerbotten and gyrfalcon nest quality in Norrbotten positively. Positive interspecific effect of occupancy on nest level were seen between golden eagles and their closest neighboring gyrfalcon nest, while the opposite relationship and the tests of interspecific effects on productivity as well as tests of interspecific effect on population level lacked effect in either direction.

## 4.1 Prey populations

Many studies on gyrfalcon diet have found a strong dependency on ptarmigan by the gyrfalcon (Barichello & Mossop 2011; Koskimies & Sulkava 2011; Nielsen 2011), yet my results only revealed a positive effect by ptarmigan density on golden eagle occupancy. Still, a positive correlation between gyrfalcon density and ptarmigan density has been shown among Swedish gyrfalcons previously (Nyström et al. 2006a), and the lack of effect in this study could be due to the complexity of other variables simultaneously influencing reproduction as well as inconsistencies in the data collection. I am aware that the gyrfalcon monitoring in Västerbotten has varied across the time period, both in terms of observers, effort and possibly methods. I was also unable to account for ptarmigan hunting effort, which, along with a bias of more accessible hunting areas likely being used to a larger extent, may reduce the reliability of the ptarmigan density data. However, seeing as ptarmigan density had a positive effect on golden eagle occupancy, harvest data may still give a good measure of the broader fluctuations of the ptarmigan population since a correlation between the two was expected. Despite not being as specialized towards ptarmigan, golden eagles in similar regions are commonly utilizing ptarmigan to a large extent during the breeding season as well, along with mountain hares and microtines (Nyström et al. 2006b; Moss et al. 2012).

Microtines are less associated with gyrfalcon diet, and even in the analyses of golden eagle data, field vole density in fall was the only variable within the microtine prey group that had a positive effect on golden eagle occupancy the following year. Local differences in microtine populations could be a potential reason for limited effects found in my data. Habitat composition is a factor known to affect the distribution of main prey for arctic raptors (Oksanen et al. 1999; Gustafson et al. 2025), and since one single site within Västerbotten was used for trapping microtines the data is likely not representative for the entire study area.

No prey variables had any traceable effect on productivity of either species. This may be explained by the general increase in available prey species later in spring and summer, reducing the reliance on these two resident prey groups for the pairs who decided to breed. In previous studies, however, an opposite result regarding effect on occupancy and productivity has been shown with similar prey groups. McIntyre (2003) found a close relationship between productivity of both raptor species and willow ptarmigan and snowshoe hare density in Alaska, while they were unrelated to number of territorial pairs present in the study area. Similarly in Idaho, occupancy did not correlate with densities of jackrabbit, but it had a positive effect on percentage of pairs that laid eggs (Steenhof et al. 1997). Golden eagles breeding in reindeer calving areas have shown to have a higher proportion of reindeer (mainly fawns) in their diet compared to pairs in other areas (Johnsen et al. 2007), potentially resulting in less competition for prey with gyrfalcon during the later part of the breeding season as reindeer generally calve in May in Scandinavia. As I lack data on utilization of reindeer by the raptors in my study area, the impact of reindeer presence in this study system remains unknown. A more comprehensive study of prey would likely reveal effects related to productivity, although it may still be blurred by interactions of other factors.

Because prey densities in this study are inferred from ptarmigan harvest data and national monitoring of microtines, the actual use of prey species and different age groups (i.e. juveniles or adults) in the diet is unknown. Nevertheless, utilization of ptarmigan in the gyrfalcon diet have been shown to correlate with ptarmigan density, suggesting that ptarmigan harvest data can serve as a reasonable, if imperfect, proxy for prey availability in this context (Nyström et al. 2006a).

## 4.2 Weather

The positive correlation between storm events during early breeding season and occupancy of gyrfalcons appears odd, seeing as other studies have found negative correlations between raptor reproduction and similar measurements of severe weather and precipitation (Steenhof et al. 1997; Nielsen 2011). The effect of severe weather on occupancy has been somewhat mixed in previous studies, with most reporting either no effect or negative effects (Kostrzewa & Kostrzewa 1990; Fairhurst & Bechard 2005). Potentially, severe weather makes it even more important for the gyrfalcons in my study area to hold their nesting territory, to asure the opportunity to breed is there if conditions improve. Other reasons might be observation bias when weather is bad, suppressing hunting and resulting in higher observation counts as more time is spent by the nest, although it could simultaneously suppress monitoring efforts. Nevertheless, given the atypical nature of this result and the marginal test values, it should be interpreted as suggestive rather than conclusive evidence until validated by replication and confirmation in other studies. I believe it is possible that the use of consecutive days of precipitation – including days with minimal amounts – is a bad measure of severe weather in this study area, and the observed effect is attributable to random variation.

The positive correlation between gyrfalcon productivity and onset of spring (i.e. later start of the vegetation period) and the negative correlation between gyrfalcon productivity and snow depth during early breeding season are more in line with previous discoveries, although they might appear counteracting. The positive correlation with onset of spring was seen in a recent study of gyrfalcons in Norway, as well as the negative correlation with snow depth also documented earlier in Iceland (Nielsen 2011; Slettenhaar et al. 2025). However, the results of both these previous studies showed negative correlations with snow depth during nestling period, approximately around May-June, while my results covered snow depth in March-April. Data on mean snow depth in May-June was missing from my study since the ground generally was snow free in early June at the weather stations used. Snow depth during the two time periods should however be correlated and indicate an overall negative correlation between snow depth and gyrfalcon productivity, although it has not been formally tested.

The negative relationship between snow depth and gyrfalcon productivity could be explained by a few different reasons. First, deep snow makes nests inaccessible during early season and might suppress courtship and initiation of egg laying. Early laying-date has been shown to correlate positively with gyrfalcon productivity in the Yukon (Barichello & Mossop 2011). Although positive effects from laying eggs early in the spring, with colder temperatures and low prey availability, seem strange, Barichello argues that it might be the associated timing of fledging that actually has an important impact on productivity, having the chicks leave the nest at a time when easy prey is most abundant. Inhibition of breeding early may therefore result in skipped breeding altogether. Second, nestlings are likely to have a higher mortality when more snow remains during the nestling period. Gyrfalcon nestlings have been estimated to thermoregulate independently at around 21 days of age, while relying on their parents for heat regulation until then, especially in wet and cold conditions (Jenkins 1978).

The positive effect of a later onset of spring is, as argued by Slettenhaar et al. (2025), more likely acting indirectly by effecting ptarmigan negatively. Previous studies have seen correlations between lower reproductive success and later appearance of snow-free ground (Novoa et al. 2008) and between mortality rate and late springs in ptarmigan (Eriksen et al. 2025). As herbivores, ptarmigan feeding opportunities are largely reduced by snow cover, potentially reducing body condition and forcing individuals to take greater risks when foraging. There might also be a camouflage mismatch in years of late onset of spring, amplifying their vulnerability when they moult into their summer plumage while snow is still dominating the ground. Microtines, in contrast, generally seem to benefit from a persistent snow cover, offering shelter from the cold and from avian predators (Heisler et al. 2014; Fauteux et al. 2015). However, although showing a statistically significant correlation the positive effect of onset of spring on gyrfalcon productivity was rather small (0.1) while snow depth had a much larger negative effect (-5.42).

The absence of correlation between weather variables and golden eagle distribution and reproduction may indicate limited importance in relation to other factors. When analyzing weather, timing may also be of great importance, explaining lack of traceable relations. Courtship and egg laying are generally initiated a few weeks earlier by golden eagles compared to gyrfalcons in the study area, potentially making unexamined time periods like February weather more influential of golden eagle reproduction than assumed beforehand. January and February weather might influence initiation of breeding for both species and is recommended to include in future studies.

Although weather surely affect gyrfalcons and golden eagles, both are examples of large, tough raptors adapted to endure harsh conditions. It is possible that weather have a more important indirect effect by influencing their main prey populations, in particular prey activity patterns and timing of courtship in ptarmigan (Fairhurst & Bechard 2005). Integration of such factors into the monitoring data could also help to map out what elements are more influential in predicting raptor distribution and productivity.

## 4.3 Habitat characteristics and topography

Strong non-random patterns of nest use were seen among gyrfalcons as well as golden eagles in Västerbotten, similar to several other raptor studies (Sergio & Newton 2003; Kochert & Steenhof 2012; Anderson et al. 2019). Some variability in productivity was seen between nests for both species, but most of the variability was within nests. These results suggest a preference for certain nests, although reproductive success is largely explained by year-specific environmental variability and chance. Reasons for the strong patterns of nest use warrants further investigation about specific individuals or pairs and their utilization of nests across years, as well as habitat characteristics of high-used nests which could provide deeper insight into the factors driving nest preference.

Preference of certain topographic characteristics at nesting sites in the two areas were quite unclear aside from aspect, with both species clearly favoring south-oriented nests. Poole and Bromley (1988a) found golden eagles to favor south-facing nests in Alaska, while no specific aspect was favored for gyrfalcons or ravens. Instead, the latter two preferred nests protected by complete overhang, covering the nest from severe weather and improving chances of successful breeding. Golden eagles did not select for protected nests based on results from the same study, a choice argued by the authors to be due to a disadvantage to the high aspect of the sun early in the year, limiting exposure to the warming sun (Poole & Bromley 1988a). However, golden eagles are adapted to inhabit a variety of climates while gyrfalcons only live in arctic and subarctic environments, making the former able to handle heat in a better way. South-facing nests without cover make the risk of heat-stress for nestlings higher, but this is likely a larger threat to gyrfalcons than golden eagles.

Despite the over-representation of south-oriented nests, I found no positive effect of south-facing nests on reproduction for either species. In general, I only saw a clear positive correlation between latitude and golden eagle occupancy in Västerbotten and latitude and gyrfalcon quality in Norrbotten. The correlation with more northern latitudes may however be a coincidence explained by more suitable mountainous habitat available and less human presence in the northern part of both areas. Few studies have looked at topographic variables on nest level in relation to gyrfalcon and golden eagle reproduction, but rather at modelling suitable habitat on a landscape level (McIntyre et al. 2006, 2009; López-López et al. 2007). In the relevant studies I found, protection or exposure has been shown to be a determinant of reproductive success in gyrfalcon (Barichello & Mossop 2011; Henderson 2019), while afforestation has been negatively correlated with golden eagle reproduction (Marquiss et al. 1985; Whitfield et al. 2001). Henderson (2019) found the same over-representation of south-facing gyrfalcon nests in Alaska, but also lacking correlation with reproduction. Possibly an advantage of sun-exposure during the early part of the breeding season is erased by a negative effect due to heat-stress for nestlings later in the spring.

Targeting other factors on nest level like exposure of the nest and overview of the surroundings to spot predators and competitors may be more relevant in future studies. General wind direction and human development are other factors that have been suggested to effect where raptors choose to nest (McLeod et al. 2002). Habitat characteristics on a larger scale might also be more suitable to analyze to determine reproductive output, including elements like distance to water and suitable habitat for main prey species within the home range.

## 4.4 Ecological interactions between gyrfalcons and golden eagles

Golden eagles are known to displace and generally be avoided by other raptor species (Poole & Bromley 1988a), and the positive correlation between occupancy of individual golden eagle nests and occupancy of the nearest neighboring gyrfalcon nest in this study system may therefore seem surprising. However, the result likely demonstrates a shared habitat preference in regions of mountainous terrain, while also suggesting that competition of nesting territories between the species in Västerbotten is low and available nests are not the main limiting factor. Mean distances between nests, both inter- and intraspecific, indicate a similar conclusion. Distances are quite large considering that all known nests are included in the calculation, although not all nests are occupied each year, likely keeping interactions on a low level. In contrast it could rather suggest shared prey as the limiting factor in this case, making more pairs of both species occupy nests in years of high prey densities while resulting in low numbers for years when prey is scarce. No correlation – positive or negative – was seen between productivity of nearest neighbors, suggesting that other factors might play a more important role for the result when breeding is attempted. It may also be another proof of sufficient spacing between the species.

However, since both gyrfalcons and golden eagles have a tendency to alternate nests between years (Booms et al. 2011), assigning a fixed nest as the nearest neighbor throughout the study period likely oversimplifies their spatial behavior and undermines the reliability of such comparisons. This consideration should be kept in mind when interpreting patterns of nest proximity and occupancy, particularly when drawing conclusions about ecological interactions across years. The lack of correlations, both for occupancy and productivity, when analyzing interspecific effect on population level might be testimony to that. Therefore, I believe the question of whether the species affect each other in this study system warrants further investigation, although my results suggest there is likely no clear negative relationship.

Another factor to consider when trying to understand interspecific relations is the presence of other sympatric species. Although I only have occasional notes of sightings and breedings in my study areas, it is known that ravens, rough-legged buzzards, peregrine falcons, common kestrels (*Falco tinnunculus*) and white-tailed eagles are all inhabiting the same areas to some extent. Poole and Bromley (1988a), who studied a guild of these species (aside for common kestrels and white-tailed eagles) in Alaska, established that gyrfalcons, golden eagles and ravens highly overlapped in resource use in their study area, while the two smaller species arrived later in the season and generally took smaller prey. Ravens likely compete with gyrfalcons and golden eagles in my area, but the extent is unknown. However, peregrine falcons have been shown to choose nests close to ravens, proposed to be due to the advantage of ravens warning them for incoming predators (Sergio et al. 2004). Ravens in Alaska were often nesting very close to gyrfalcons while keeping the same distance to golden eagles as the gyrfalcons tend to do, indicating that gyrfalcons might take advantage of ravens in the same manner by accepting them in close proximity, the benefits of their presence outweighing the costs. Golden eagles, only beaten by white-tailed eagles in terms of size in my study area, might not experience the same trade-off, in addition to not needing the presence of other species for construction of nests to use.

## 4.5 Threats and future directions

Several researchers have pointed out climate change and loss of habitat through land use alterations as major threats for many raptor populations, including gyrfalcons and golden eagles (Koskimies 2005; Watson 2010; Booms 2011; Christensen et al. 2013; Radcliffe et al. 2024). As climate change progress even more rapidly in arctic regions (Lemke et al. 2007; Box et al. 2019), related consequences like change of distribution for native and non-native species, altered food-web structures and increased risk of diseases are likely to happen more quickly than elsewhere (Jessup & Radcliffe 2023). Land use alterations in arctic and subarctic areas include activities like forestry, wind farm establishments and mining operations, and may affect raptors directly by reducing nesting and hunting habitat, but also indirectly by affecting prey populations negatively (Imperio et al. 2013; Dwyer et al. 2018; Watson et al. 2018).

Effects of these threats have been proposed as reasons for decline in several gyrfalcon and golden eagle populations already, making continued monitoring and conservation efforts of immediate importance (Whitfield et al. 2001; Burnham 2011; Lobkov 2011). Consistent monitoring over time is a key tool to be able to detect and act on changes likely to alter the living conditions of gyrfalcons and golden eagles.

With that and the results of this study in mind, I encourage increased collaborations between regions, standardization of monitoring protocols and expansion of relevant data variables collected, especially exposure of nesting sites, when monitoring these species in the Swedish mountain region. Extended use of acoustic monitors, only tested in part of the study area so far, is also recommended as it has potential to be a useful and cheap tool to determine occupancy at know nests, as well as to detect unexplored nests in areas of suitable habitat. In addition, studies using nest cameras could shed light on several factors not possible to determine with the data on hand, such as actual intra- and interspecific interactions, effect of local weather conditions at the nest sites and what prey species are brought back to the nest.

I encourage future studies to follow up on the relevant correlations found in this study and to aim for the use of more exact, localized data on the predictor variables, especially weather conditions and prey densities. Effects of habitat characteristics on nesting territory level is likely also of importance. A logical next step would be to incorporate raptor presence into the modelling of environmental predictors to assess whether this inclusion further enhances model performance.

In addition, future research on gyrfalcons and golden eagles should adopt a community-level approach by including relevant sympatric species or even key species of the shared food web. The influence of ravens on gyrfalcons and golden eagles is highly relevant and above other species, data on ravens should be included in future monitoring in areas of shared habitat.

## 4.6 Conclusions

The complexity of factors influencing gyrfalcon and golden eagle distribution and productivity makes it difficult to draw conclusions of any certainty, but this study represents a novel attempt to explore the issue in an area where studies on this topic are limited. Previous studies have indicated a segregation of prey utilization rather than habitat, as the species have shown to utilize the same habitat and even use the same nests in different years. My study provides limited answers to resource partitioning between gyrfalcons and golden eagles, but indicates that distribution of either species does not seem to be negatively affected by the other and that occupancy of nests is driven by similar factors for both species. Although few environmental variables clearly affected distribution and productivity, the results indicated that golden eagle occupancy was influenced by prey densities of the previous years, while gyrfalcon occupancy and productivity appeared to be more sensitive to spring weather conditions. Weak data quality may be the reason for limited results regarding effect of environmental variables, likely masking positive effects of ptarmigan density on gyrfalcon distribution and productivity which has been proved in numerous studies before. But the lack of traceable effects might also be an indication of the range of factors playing into the picture regarding distribution and productivity of gyrfalcons and golden eagles. The hope is that this study will serve as a foundation and stimulate funding for future research on these unique species, aid in decisions of what variables to survey and ultimately support informed decisions in monitoring.

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# Popular science summary

## Rivals up high – are rare raptors threatening each other's existence in the Scandinavian mountains?

Raptors are often depicted as majestic, viscous and solitary predators of the sky, controlled by no one. But how do they treat the presence of other raptors in their home areas? In the Scandinavian mountains, gyrfalcons and golden eagles are the largest of a group of raptors inhabiting the same regions. They both breed in early spring, use the same nests and eat similar prey. So, who dictates the rules of their mountainous kingdom? As it seems, it's the rough environment they choose to live in.

In past decades, human persecution, chemicals from pesticides and egg trading led to rapid declines of many raptor populations. Protection of species, restricted use of toxic chemicals and conservation work has been a great success and changed negative trends in many areas, but today other threats like habitat loss and climate change are instead becoming more pressing. To efficiently plan and execute conservation measures, a broad understanding of species and their environments is key. But some species and populations are less studied than others, due to their way of life and chosen habitat. Gyrfalcons and golden eagles in arctic and sub-arctic mountain regions are among those, appearing in low densities and nesting in steep terrain when snow still covers the ground. They hunt over large open areas and generally avoid human presence. Snowmobiles and helicopters are often required to monitor these populations efficiently, and observers need to be skilled to detect signs of raptor presence from a distance. Threats to raptor populations in these areas are mainly climate change, getting effects like warmer temperatures and more precipitation, changed vegetation cover and changed distribution of species, but also human developments like wind farm establishments and mining operations altering the landscape and posing risk of death by collision with wind turbines.

With this study we aimed to understand more of what drives distribution of gyrfalcons and golden eagles in the landscape, and what affects how many young they produce in a year. Monitoring data from the Swedish counties of Västerbotten and Norrbotten was used and the variation across years compared to environmental variables like spring weather, densities of main prey species and topography at nesting sites. To try to understand the magnitude of competition between the species we also compared presence and productivity of both species over time to determine any patterns, i.e. if one species would produce few young in a year when the other species produced many.

Despite what one would imagine, the gyrfalcons and golden eagles seemed to have neutral effect on each other while prey densities and weather influenced distribution and productivity to a larger extent. Hard environmental conditions are likely the main factor acting limiting on the populations, and as long as there is enough room for the surviving individuals there is no use in competing. It might even be one of the appeals of specializing into living in arctic and sub-arctic environments. However, it is doubtlessly many different elements determining what these raptors choose to do and what nature dictates for them in a given year. Even though prey is abundant and make conditions good for many raptor pairs to breed, a severe snowstorm in May might lead to most young dying anyway. More research is needed on the subject, digging into important factors for gyrfalcon and golden eagle to live and thrive in our mountain areas and equipping decisionmakers with a solid foundation of knowledge to base conservation strategies on.

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# Appendix 1

**Home range** – Utilized area of a sedentary individual or a migrating individual outside of migration season, comprised of nesting territory and hunting range. Measures of core and extended home range areas are often used in studies with GPS-tracking of gyrfalcons and golden eagles, by extracting 50% and 95% volume contours of the calculated utilization distribution (Singh et al. 2016).

**Nesting territory** – Defined area where nests are found, occupied only by one breeding pair at a time and assumed to roughly equal core home range from studies with GPS-tracking of gyrfalcons and golden eagles. May include alternative nesting sites.

**Nesting site** - Specific location of the nest in the landscape.

**Occupied nesting territory** - Confirmed observation of a pair occupying a nesting territory or obvious signs thereof, such as fresh twigs or guano at the nesting site, in a given year.

**Productivity** - The number of young that reach the minimum acceptable age for assessing success (51 days for golden eagles, slightly shorter for gyrfalcons) divided by number of occupied nesting territories in a given year (Steenhof et al. 2017). Due to limitations in monitoring effort, in this study productivity is defined as number of live chicks observed in the nest by late June divided by the number of occupied nesting territories, to be kept in mind when comparing results with other studies.

# Appendix 2

*Table 12. Specifications of weather stations and time periods used for analyses.*

| **Area** | **Weather variable** | **Weather station** | **Time period** |
|---|---|---|---|
| **North** | Average temperature | Hemavan | 1998-2024 |
| | Amount precipitation | Mosekälla | 1998-2018, 2021-2024 |
| | Days of heavy precipitation | Mosekälla | 1998-2018, 2021-2024 |
| | Storm events | Mosekälla | 1998-2018, 2021-2024 |
| | Snow depth ES | Mosekälla | 1998-2018, 2021-2024 |
| **South** | All except snow depth ES | Gielas | 1998-2003, 2005-2024 |
| | Snow depth ES | Kittelfjäll | 1998-2024 |

# Appendix 3

*Table 13. Raptor monitoring statistics in Västerbotten 1998 – 2024.*

| | **Gyrfalcon** | | | | **Golden eagle** | | | |
|---|---|---|---|---|---|---|---|---|
| | No of checked territories | No of occupied territories | No of breeding attempts | Young produced | No of checked territories | No of occupied territories | No of breeding attempts | Young produced |
| **1998** | 11 | 6 | 0 | 0 | 4 | 4 | 4 | 4 |
| **1999** | 2 | 2 | 2 | 5 | 16 | 12 | 12 | 13 |
| **2000** | 13 | 12 | 8 | 19 | 33 | 9 | 9 | 11 |
| **2001** | 25 | 9 | 7 | 10 | 35 | 21 | 18 | 21 |
| **2002** | 29 | 16 | 11 | 24 | 39 | 27 | 22 | 28 |
| **2003** | 33 | 13 | 11 | 20 | 41 | 28 | 14 | 15 |
| **2004** | 42 | 21 | 18 | 42 | 47 | 27 | 20 | 25 |
| **2005** | 45 | 22 | 22 | 44 | 50 | 30 | 24 | 24 |
| **2006** | 32 | 9 | 5 | 6 | 47 | 17 | 2 | 1 |
| **2007** | 49 | 23 | 16 | 31 | 46 | 29 | 17 | 18 |
| **2008** | 48 | 27 | 20 | 39 | 48 | 30 | 16 | 20 |
| **2009** | 50 | 9 | 7 | 19 | 54 | 17 | 2 | 1 |
| **2010** | 8 | 0 | 0 | 0 | 53 | 23 | 2 | 2 |
| **2011** | 0 | | | | 48 | 24 | 14 | 10 |
| **2012** | 0 | | | | 52 | 23 | 13 | 13 |
| **2013** | 0 | | | | 52 | 19 | 2 | 3 |
| **2014** | 0 | | | | 52 | 18 | 8 | 11 |
| **2015** | 0 | | | | 48 | 20 | 11 | 15 |
| **2016** | 2 | 1 | 1 | 2 | 53 | 18 | 8 | 9 |
| **2017** | 2 | 2 | 1 | 2 | 53 | 18 | 9 | 11 |
| **2018** | 30 | 13 | 6 | 14 | 54 | 16 | 8 | 8 |
| **2019** | 42 | 9 | 6 | 11 | 54 | 22 | 19 | 26 |
| **2020** | 49 | 4 | 3 | 2 | 52 | 22 | 9 | 6 |
| **2021** | 51 | 9 | 6 | 17 | 52 | 17 | 12 | 16 |
| **2022** | 39 | 9 | 5 | 7 | 51 | 23 | 15 | 20 |
| **2023** | 45 | 4 | 1 | 3 | 53 | 14 | 8 | 11 |
| **2024** | 52 | 12 | 9 | 20 | 51 | 23 | 10 | 10 |

# Appendix 4

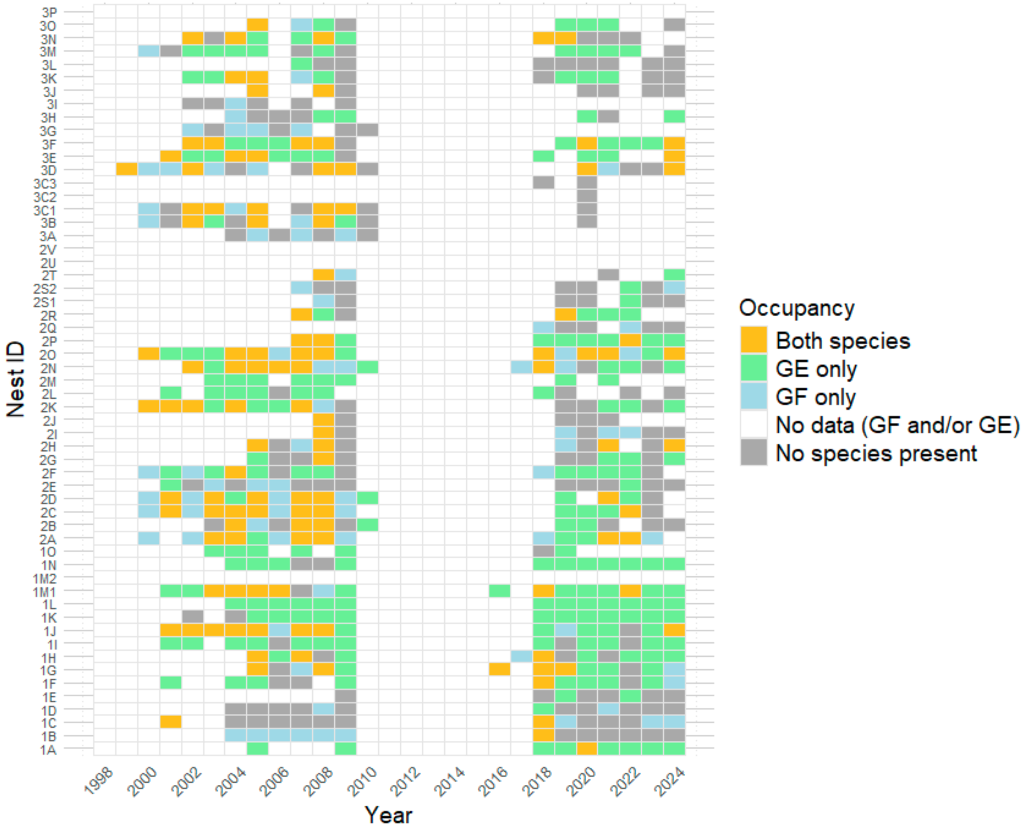

*Figure 11. Heat map displaying occupancy of gyrfalcon nests and the nearest neighboring golden eagle nest 1998 – 2024. Tiles where data is missing for one or both species (i.e. nest not checked) are displayed in white.*

*Figure 12. Heat map displaying occupancy of golden eagle nests and the nearest neighboring gyrfalcon nest 1998 – 2024. Tiles where data is missing for one or both species (i.e. nest not checked) are displayed in white.*

# Appendix 5

*Table 14. Summed test results for all univariate models. GF = gyrfalcon, GE = golden eagle, NN = nearest neighbor. All ptarmigan data is log transformed.*

| **Response variable** | **Predictor variable** | **Test** | **Level** | **Estimate** | **S.D.** | **t/z-value** | **p-value** |
|---|---|---|---|---|---|---|---|
| **Occupancy GF** | Occupancy_NN_GE | GLM | Nest | 0.1972 | 0.1777 | 1.110 | 0.267 |
| **Productivity GF** | Productivity_NN_GE | Negative binomial regression | | 0.1472 | 0.1729 | 0.852 | 0.394 |
| **Productivity GF (vacant nests removed)** | Productivity_NN_GE | Negative binomial regression | | 0.14566 | 0.11326 | 1.286 | 0.19843 |
| **Occupancy GE** | Occupancy_NN_GF | GLM | Nest | 0.34884 | 0.18501 | 1.886 | 0.0594 |
| **Productivity GE** | Productivity_NN_GF | Negative binomial regression | | 0.05681 | 0.07115 | 0.798 | 0.425 |
| **Productivity GE (vacant nests removed)** | Productivity_NN_GF | Negative binomial regression | | 0.01336 | 0.06077 | 0.22 | 0.826 |
| **Occupancy GF** | Occupancy GE | Beta regression | Pop | 1.721 | 1.37 | 1.256 | 0.209 |
| **Productivity GF** | Productivity GE | LM | | 0.1803 | 0.4171 | 0.432 | 0.67051 |
| **Occupancy GE** | Occupancy GF | Beta regression | Pop | 0.7569 | 0.5927 | 1.277 | 0.202 |
| **Productivity GE** | Productivity GF | LM | | 0.054 | 0.125 | 0.432 | 0.67051 |
| **Occupancy GF** | Rock ptarmigan (1 y lag) | GLM | Nest | 0.04284 | 0.18872 | 0.227 | 0.82 |
| | Willow ptarmigan (1 y lag) | | | 0.1264 | 0.1975 | 0.640 | 0.522 |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
|  | Pooled ptarmigan (1 y lag) |  |  | 0.1589 | 0.1978 | 0.803 | 0.422 |
| **Product-ivity GF** | Rock ptarmigan (1 y lag) | Negative binomial regression | Nest | 0.3786 | 0.3197 | 1.184 | 0.236 |
|  | Willow ptarmigan (1 y lag) |  |  | 0.00108 | 0.31838 | 0.003 | 0.997 |
|  | Pooled ptarmigan (1 y lag) |  |  | 0.1416 | 0.3253 | 0.435 | 0.663 |
| **Occupancy GE** | Rock ptarmigan (1 y lag) | GLM | Nest | -0.1970 | 0.1266 | -1.557 | 0.120 |
|  | Willow ptarmigan (1 y lag) |  |  | 0.2033 | 0.1280 | 1.588 | 0.112 |
|  | Pooled ptarmigan (1 y lag) |  |  | 0.1508 | 0.1272 | 1.185 | 0.236 |
| **Product-ivity GE** | Rock ptarmigan (1 y lag) | Negative binomial regression | Nest | -0.0551 | 0.12947 | -0.425 | 0.671 |
|  | Willow ptarmigan (1 y lag) |  |  | 0.1834 | 0.1370 | 1.339 | 0.181 |
|  | Pooled ptarmigan (1 y lag) |  |  | 01877 | 0.1382 | 1.359 | 0.174 |
| **Occupancy GF** | Rock ptarmigan (2 y lag) | GLM | Nest | 0.1501 | 0.1892 | 0.793 | 0.428 |
|  | Willow ptarmigan (2 y lag) |  |  | -0.1322 | 0.1818 | -0.727 | 0.467 |
|  | Pooled ptarmigan (2 y lag) |  |  | -0.0011 | 0.18859 | -0.006 | 0.995 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Product-ivity GF** | Rock ptarmigan (2 y lag) | Negative binomial regression | Nest | 0.3182 | 0.3171 | 1.004 | 0.316 |
| | Willow ptarmigan (2 y lag) | | | 0.03963 | 0.32068 | 0.124 | 0.902 |
| | Pooled ptarmigan (2 y lag) | | | 0.2514 | 0.3314 | 0.758 | 0.448 |
| **Occupancy GE** | Rock ptarmigan (2 y lag) | GLM | Nest | -0.0128 | 0.1319 | -0.097 | 0.9227 |
| | Willow ptarmigan (2 y lag) | | | 0.2918 | 0.1381 | 2.114 | 0.0345 |
| | Pooled ptarmigan (2 y lag) | | | 0.2793 | 0.1384 | 2.018 | 0.0436 |
| **Product-ivity GE** | Rock ptarmigan (2 y lag) | Negative binomial regression | Nest | 0.01191 | 0.13917 | 0.086 | 0.932 |
| | Willow ptarmigan (2 y lag) | | | 0.1043 | 0.1437 | 0.726 | 0.468 |
| | Pooled ptarmigan (2 y lag) | | | 0.1654 | 0.1475 | 1.122 | 0.262 |
| **Occupancy GF** | G-S vole Spring | Beta regression | Pop | -0.2212 | 0.2451 | -0.903 | 0.3668 |
| | Field vole Spring | | | -0.1583 | 0.2453 | -0.645 | 0.5187 |
| | Nor. lemming Spring | | | -0.1886 | 0.2451 | -0.769 | 0.4417 |
| | Pooled Spring | | | -0.2000 | 0.2450 | -0.816 | 0.414 |
| **Product-ivity GF** | G-S vole Spring | LM | Pop | 0.0160 | 0.1346 | 0.119 | 0.907 |
| | Field vole Spring | | | 0.02144 | 0.13454 | 0.159 | 0.876 |
| | Nor. lemming Spring | | | 0.06851 | 0.13348 | 0.513 | 0.615 |
| | Pooled Spring | | | 0.02397 | 0.13451 | 0.178 | 0.861 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Occupancy GE** | G-S vole Spring | Beta regression | Pop | 0.11659 | 0.10199 | 1.143 | 0.2530 |
| | Field vole Spring | | | 0.07363 | 0.10318 | 0.714 | 0.4755 |
| | Nor. lemming Spring | | | 0.07309 | 0.10321 | 0.708 | 0.4788 |
| | Pooled Spring | | | 0.08842 | 0.10292 | 0.859 | 0.3902 |
| **Product-ivity GE** | G-S vole Spring | LM | Pop | 0.00534 | 0.07049 | 0.076 | 0.94 |
| | Field vole Spring | | | -0.0108 | 0.07046 | -0.153 | 0.88 |
| | Nor. lemming Spring | | | -0.0313 | 0.07017 | -0.447 | 0.66 |
| | Pooled Spring | | | -0.0092 | 0.07047 | -0.131 | 0.897 |
| **Occupancy GF** | G-S vole Spring (1 lag) | Beta regression | Pop | 0.1676 | 0.2432 | 0.689 | 0.4908 |
| | Field vole Spring (1 lag) | | | 0.1068 | 0.2442 | 0.437 | 0.6618 |
| | Nor. lemming Spring (1 lag) | | | 0.1224 | 0.2437 | 0.502 | 0.6156 |
| | Pooled Spring (1 lag) | | | 0.1432 | 0.2420 | 0.588 | 0.5567 |
| **Product-ivity GF** | G-S vole Spring (1 lag) | LM | Pop | 0.07333 | 0.13372 | 0.548 | 0.591 |
| | Field vole Spring (1 lag) | | | 0.06744 | 0.13393 | 0.504 | 0.622 |
| | Nor. lemming Spring (1 lag) | | | 0.1186 | 0.1315 | 0.901 | 0.382 |
| | Pooled Spring (1 lag) | | | 0.07766 | 0.13356 | 0.581 | 0.57 |
| **Occupancy GE** | G-S vole Spring (1 lag) | Beta regression | Pop | 0.10275 | 0.0953 | 1.032 | 0.3019 |
| | Field vole Spring (1 lag) | | | 0.03400 | 0.10106 | 0.336 | 0.7365 |
| | Nor. lemming Spring (1 lag) | | | 0.04426 | 0.10086 | 0.439 | 0.661 |
| | Pooled Spring (1 lag) | | | 0.05784 | 0.10065 | 0.575 | 0.5655 |
| **Product-ivity GE** | G-S vole Spring (1 lag) | LM | Pop | 0.01281 | 0.06828 | 0.188 | 0.853 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | Field vole Spring (1 lag) | | | 0.00256 | 0.06833 | 0.037 | 0.97 |
| | Nor. lemming Spring (1 lag) | | | 0.00398 | 0.06833 | 0.058 | 0.954 |
| | Pooled Spring (1 lag) | | | 0.0061 | 0.06832 | 0.089 | 0.93 |
| **Occupancy GF** | G-S vole Fall (1 lag) | Beta regression | Pop | 0.09396 | 0.24443 | 0.384 | 0.7007 |
| | Field vole Fall (1 lag) | | | 0.1236 | 0.2423 | 0.507 | 0.6124 |
| | Nor. lemming Fall (1 lag) | | | 0.2365 | 0.2416 | 0.979 | 0.3276 |
| | Pooled Fall (1 lag) | | | 0.1303 | 0.2439 | 0.534 | 0.5932 |
| **Productivity GF** | G-S vole Fall (1 lag) | LM | Pop | 0.04771 | 0.13449 | 0.355 | 0.728 |
| | Field vole Fall (1 lag) | | | 0.03369 | 0.13477 | 0.25 | 0.806 |
| | Nor. lemming Fall (1 lag) | | | 0.1900 | 0.1258 | 1.51 | 0.152 |
| | Pooled Fall (1 lag) | | | 0.06195 | 0.13410 | 0.462 | 0.651 |
| **Occupancy GE** | G-S vole Fall (1 lag) | Beta regression | Pop | 0.15510 | 0.09681 | 1.602 | 0.1092 |
| | Field vole Fall (1 lag) | | | 0.17539 | 0.09552 | 1.836 | 0.0664 |
| | Nor. lemming Fall (1 lag) | | | 0.06172 | 0.10057 | 0.614 | 0.5394 |
| | Pooled Fall (1 lag) | | | 0.14550 | 0.09761 | 1.491 | 0.1361 |
| **Productivity GE** | G-S vole Fall (1 lag) | LM | Pop | 0.04348 | 0.06767 | 0.642 | 0.528 |
| | Field vole Fall (1 lag) | | | 0.05572 | 0.06724 | 0.829 | 0.417 |
| | Nor. lemming Fall (1 lag) | | | 0.01618 | 0.06824 | 0.237 | 0.815 |
| | Pooled Fall (1 lag) | | | 0.04315 | 0.06768 | 0.638 | 0.531 |
| **Occupancy GF** | TempEarly | Beta regression | Pop | -0.0077 | 0.24644 | -0.031 | 0.975 |
| | PrecEarly | | | 0.04197 | 0.24640 | 0.170 | 0.865 |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
|  | DaysHeavyEarly (log) |  |  | -0.1168 | 0.2461 | -0.475 | 0.635 |
|  | StormEarly |  |  | 0.4773 | 0.2409 | 1.981 | 0.0476 |
|  | SnowEarly |  |  | -0.1563 | 0.2459 | -0.636 | 0.525 |
|  | OnsetOfSpring |  |  | 0.2821 | 0.2446 | 1.153 | 0.249 |
| **Productivity GF** | TempEarly | Beta regression | Pop | 0.2048 | 0.1120 | 1.829 | 0.0674 |
|  | TempLate |  |  | 0.0727 | 0.2662 | 0.273 | 0.785 |
|  | PrecEarly |  |  | 0.00202 | 0.00745 | 0.271 | 0.787 |
|  | PrecLate |  |  | 0.00212 | 0.00935 | 0.226 | 0.821 |
|  | DaysHeavyEarly |  |  | 0.0487 | 0.12946 | 0.376 | 0.707 |
|  | DaysHeavyLate |  |  | -0.0564 | 0.15467 | -0.365 | 0.715 |
|  | StormEarly |  |  | 0.2530 | 0.2035 | 1.243 | 0.214 |
|  | StormLate |  |  | 0.06376 | 0.27629 | 0.231 | 0.817 |
|  | OnsetOfSpring |  |  | -0.0054 | 0.0389 | -0.14 | 0.889 |
|  | SnowEarly |  |  | -3.225 | 1.348 | -2.391 | 0.0168 |
| **Occupancy GE** | TempEarly | Beta regression | Pop | -0.0358 | 0.15167 | -0.236 | 0.814 |
|  | PrecEarly |  |  | -0.0823 | 0.15131 | -0.544 | 0.586 |
|  | DaysHeavyEarly (log) |  |  | -0.1053 | 0.1509 | -0.698 | 0.485 |
|  | StormEarly |  |  | -0.0550 | 0.15154 | -0.363 | 0.717 |
|  | SnowEarly |  |  | 0.08913 | 0.15121 | 0.589 | 0.556 |
|  | OnsetOfSpring |  |  | 0.09886 | 0.15105 | 0.655 | 0.513 |
| **Productivity GE** | TempEarly | Beta regression | Pop | 0.06215 | 0.11325 | 0.549 | 0.583 |
|  | TempLate |  |  | -0.1538 | 0.1983 | -0.776 | 0.438 |
|  | PrecEarly |  |  | 0.00270 | 0.00623 | 0.433 | 0.665 |
|  | PrecLate |  |  | 0.00213 | 0.00823 | 0.259 | 0.795 |
|  | DaysHeavyEarly |  |  | 0.01157 | 0.08377 | 0.138 | 0.89 |
|  | DaysHeavyLate |  |  | -0.0055 | 0.10193 | -0.054 | 0.957 |
|  | StormEarly |  |  | 0.1361 | 0.2071 | 0.657 | 0.511 |
|  | StormLate |  |  | -0.1050 | 0.2427 | -0.433 | 0.665 |
|  | OnsetOfSpring |  |  | 0.01399 | 0.03932 | 0.356 | 0.722 |
|  | SnowEarly |  |  | 1.0122 | 1.4022 | 0.722 | 0.47 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Occupancy GF** | Elevation | GLM | Nest | 0.00017 | 0.00052 | 0.329 | 0.7421 |
| | Slope | | | 0.04381 | 0.06631 | 0.661 | 0.509 |
| | Aspect_Cos | | | 0.11643 | 0.11364 | 1.025 | 0.306 |
| | Aspect_Sin | | | -0.0449 | 0.11392 | -0.394 | 0.693 |
| | Latitude | | | -0.2416 | 0.1543 | -1.566 | 0.117 |
| **Productivity GF** | Elevation | Beta regression | Nest | 0.00055 | 0.00016 | 3.393 | 0.00069 |
| | Slope | | | 0.000002983 | 0.001497 | 0.002 | 0.99841 |
| | Aspect_Cos | | | 0.00001 | 0.03333 | 0 | 1 |
| | Aspect_Sin | | | -0.0001 | 0.03219 | 0 | 1 |
| | Latitude | | | 0.02930 | 0.04484 | 0.653 | 0.513 |
| **Occupancy GE** | Elevation | GLM | Nest | 0.00037 | 0.00035 | 1.063 | 0.288 |
| | Slope | | | -0.0474 | 0.04387 | -1.08 | 0.28 |
| | Aspect_Cos | | | 0.07383 | 0.06824 | 1.082 | 0.279 |
| | Aspect_Sin | | | -0.1109 | 0.06876 | -1.613 | 0.107 |
| | Latitude | | | 0.5186 | 0.1027 | 5.049 | 4.43e-07 |
| **Productivity GE** | Elevation | Beta regression | Nest | 0.00003 | 0.00019 | 0.183 | 0.855 |
| | Slope | | | 0.00001 | 0.00159 | 0 | 1 |
| | Aspect_Cos | | | 0.00001 | 0.03614 | 0 | 1 |
| | Aspect_Sin | | | 0.00001 | 0.03524 | 0 | 1 |
| | Latitude | | | 0.00001 | 0.04897 | 0 | 1 |
| **Quality GF** | Elevation | Ordinal logistic regression | Nest | 0.15078 | 0.16832 | 0.896 | 0.37 |
| | Slope | | | 0.20935 | 0.17553 | 1.193 | 0.233 |
| | Aspect_Cos | | | -0.0573 | 0.1767 | -0.324 | 0.746 |
| | Aspect_Sin | | | 0.03937 | 0.17353 | 0.227 | 0.821 |
| | Latitude | | | 0.4926 | 0.177 | 2.783 | 0.005 |

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