Habitat Selection and breeding ecology of Golden Eagles in Sweden

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Cover: Sketch of an adult Golden Eagle
(by Edward Moss)

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Habitat Selection and Reproduction of Golden Eagles in Boreal Sweden

Abstract

The red-listed Golden Eagle (*Aquila chrysaetos*) population is estimated between 1200-1400 reproductive individuals in Sweden. This population is unusual as eagles predominantly nest in trees unlike most others that prefer cliffs. The central aim of this thesis was to study 1) reproductive performance in relation to food supply, 2) habitat composition of territories at different scales, 3) breeding home range size, and 4) habitat selection of Golden Eagles in Sweden. Data on annual breeding performance in 1980-2009 were obtained by regional Golden Eagle monitoring groups and data on indicators of food supplies by a long-term monitoring of small rodents, and for main prey species by hunting bag statistics for mountain hare and forest grouse. Adult Golden Eagles were trapped on their territories and fitted with GPS backpack transmitters in autumn 2010 and 2011, and position data from 2011 and 2012 breeding seasons were used for studying home range and habitat selection. Landcover maps and elevation data were used to characterize habitat properties in territories.

Reproductive performance was highly variable among years, for example number of nestlings per breeding attempt ranged from 0.5-1.4 with a mean of >1, but this and other measures did not show 3-4 yr cycles as previously thought. However, both proportion of territories with nestlings and number of nestlings per occupied territory was positively related to primary prey (small game) indices in the same year. Habitat composition of territories was scale-dependent, with rugged terrain and old forest being overrepresented at the nest site scale, while clear-cuts on intermediate scales away from the nest. The GPS position data revealed some of the largest home ranges in Golden Eagle literature when derived from 50 and 95% kernel density estimators (KDE). In 2012, 50% KDEs ranged from approx. $5 - 110 km^2$, while 95% KDEs ranged from $70 - 580 km^2$. Home range size displayed a negative relationship to the proportion of clear-cuts within each home range. Analyses based on position data confirmed that the Eagles preferred coniferous forest, clear-cuts and steeper slopes. The here identified habitat and landscape preferences can be used for landscape management in the boreal region to support Golden Eagles.

Keywords: Aquila chrysaetos, raptors, reproduction, food supply, territories, habitat composition, spatial scale, rugged terrain, clear-cut, forestry, GPS tracking, home range, kernel density estimates, habitat selection, wind farms.

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Dedication

To my family

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Moss, E.H.R., Hipkiss, T. Oskarsson, I. Häger, A. Eriksson, T. Nilsson, L-E. Halling, S. Nilsson, P-O. Hörnfeldt, B. (2012). Long-term study of reproductive performance in Golden Eagles in relation to food supply in boreal Sweden. *Journal of Raptor Research* 46: 248-257.

II Moss, E.H.R., Ecke, F. Hipkiss, T. Sandström, P. Sjöstedt-de Luna, S. Hörnfeldt, B. (2015). Scale-dependent habitat composition of Golden Eagle (*Aquila chrysaetos*) territories in northern Sweden. (Manuscript)

III Moss, E.H.R., Hipkiss, T. Ecke, F. Dettki, H. Sandström, P. Bloom, P.H. Kidd, J.W. Thomas, S.E. Hörnfeldt, B. (2014). Home range size and examples of post-nesting movements for adult Golden Eagles (*Aquila chrysaetos*) in boreal Sweden. *Journal of Raptor Research* 48: 93-105.

IV Moss, E.H.R., Hipkiss, T. Ecke, F. Dettki, H. Sandström, P. Bloom, P.H. Kidd, J.W. Thomas, S.E. Singh, N.J. Hörnfeldt, B. (2015). Habitat use by a large boreal raptor and implications for wind farm establishment. (Manuscript).

Papers I & III are reproduced with permission from the publisher.

The contribution Edward H.R. Moss made to the papers included in this thesis were as follows:

I Moss conducted the majority of data analysis and writing for this paper.

II Moss performed all the data analysis and most of the writing for this manuscript.

III Moss carried out all data analysis and most writing in this paper.

IV Moss performed the majority of data analysis and wrote most of the manuscript.

1 Introduction

Golden Eagles are rare, widely ranging apex predators inhabiting a range of habitats within the largely mountainous environments of the northern hemisphere, preferring open habitats and avoiding human settlements (Tjernberg 1983b, Marzluff *et al.* 1997, McIntyre *et al.* 2006, Lopez-Lopez *et al.* 2007, Watson 2010). Golden Eagles are listed under Annex I (species in need of special habitat conservation measures) of the EU Birds Directive (European Commission 2014). In recent decades land use change through habitat loss and destruction alongside an increasing demand to replace fossil fuels with renewable energy resources through wind farms, is a major driver that increases conflicts with Golden Eagles. Attempts to unravel direct and indirect effects of changing land uses on Golden Eagles include those conducted by Fielding *et al.* (2003) in Scotland who used newly developed terrain modelling techniques in a geographical information system. Whitfield *et al.* (2001) focused on the effects plantation forestry had on Golden Eagles on the Isle of Mull, Scotland. However, other land uses in Europe that negatively affect Golden Eagles are the intensification of modern agricultural practices, the persecution of Golden Eagles that result from the management of eagle prey species (Watson 2010), increased tourism and an increased accessibility for humans into remote areas (Kaisanlahti-Jokimäki *et al.* 2008). In conjunction with increased urbanization and land-use change come knock-on effects from increased powerlines, roads, railways and settlements (Guil *et al.* 2011).

Home ranges in large raptors are determined by habitat productivity and available nesting sites. Home range sizes may also vary among populations, individuals and seasons (Clouet *et al.* 1999, Haworth *et al.* 2006). Previous studies concluded scarce prey or predators selecting avian over mammalian prey also contributed to larger home range sizes (Schoener 1968, Peery 2000). Habitat and resource selection by animals occurs at multiple spatiotemporal scales (Boyce 2006), meaning studies conducted at a single spatiotemporal scale may miss important selection criteria and draw incorrect conclusions (cf. Thompson 2002). Marzluff *et al.* (1997) report that Golden Eagles utilize their home ranges in unequal proportions, preferring certain types of habitat due to increased prey availability, enhanced nesting and foraging opportunities or more efficient movement across the landscape (Bohrer *et al.* 2012, Katzner *et al.* 2012).

Reproduction in Golden Eagles is conducted in a monogamous mating style where each resident pair exclusively defends a territory (Bergo 1987). Their foraging behaviour follows that of the central place foraging theory (McIntyre *et al.* 2006) where individuals usually return to chosen sites to feed their mate, or young. It is well documented that reproductive success is closely linked to food supply and that Golden Eagles feeding on cyclic or otherwise highly variable prey populations (Tjernberg 1983a, Sulkava *et al.* 1984 1999, Steenhof *et al.* 1997, McIntyre & Adams 1999) will display more variable reproductive success than eagles living in stable environments (Newton 1979). Following on this, Tjernberg (1983a) predicted that Golden Eagle reproductive performance would show 3-4 yr cycles, linked to the synchronised cycles of voles and the eagle's main prey, small game, in northern Sweden.

This thesis aims to improve the understanding of the Swedish Golden Eagle population. I approach this goal by studying Golden Eagle reproduction in relation to food supply, while technologically advancing eagle research in Sweden through the use of landscape data and GPS tracking techniques in combination with different home range estimators and habitat selection functions.

My main research questions are:

1. Does the reproductive performance of the Golden Eagle fluctuate in 3-4 yr cycles, i.e. in synchrony with the vole cycle and that of their principal small game prey species in northern Sweden?
2. Are habitat properties within Golden Eagle territories scale-dependent?
3. What are the home range sizes of GPS tracked adult Golden Eagles in boreal Sweden?
4. What are the Golden Eagle's preferred and avoided habitats in boreal Sweden, and how can we decrease potential negative effects from wind power development on eagles by more effective planning?

2 The status and management of the Golden Eagle in Sweden

2.1 The Golden Eagle

Throughout its global range, the Golden Eagle usually predates on medium-sized birds and mammals, although occasionally other taxa are consumed (Watson 2010). Golden Eagles also scavenge food when abundance of prey is low. For example, carrion is beneficial for eagles in winter (Madders & Walker 2002, Norberg *et al.* 2006) and during years of low food abundance in populations whose main prey vary considerably among years, as in Sweden (Watson 2010).

Reproduction of Golden Eagles can be divided into three distinct phases that together form the breeding cycle. The pre-breeding season is associated with display flights performed by a territorial pair usually over the nest site. These undulating flight patterns with wings partially closed may represent some form of courtship between the resident pair (Watson 2010). It is also during this period territory boundaries become re-established and nest construction occurs (Watson 2010). Following this, the eggs are laid and the incubation period begins, lasting between 43-45 days (Tjernberg 2010). Time of laying varies considerably throughout their global range due to latitude and altitude. For example, in Sweden egg laying begins in late March through to early April (Tjernberg 1983a). In Alaska, laying dates are prolonged until late April or early May due to eagles being high-latitude migrants (McIntyre 2002). The post-fledging period commences in July when nestlings fledge and abandon the nest. This period then extends through to when juveniles leave the breeding territory and become independent, usually in mid-September through to October in Sweden. Despite little being known of this phase it is likely important for juveniles to perfect their flying and hunting skills while building fat reserves before migration. Young eagles usually experience at least 4 years of independence prior to attempting to establish a territory and enter the breeding population. The presence of floaters can provide stability for Golden Eagle populations, as when territories become vacant floaters immediately move into the territory thereby reducing inter-annual variation in occupancy rates and breeding attempts. Therefore, the size and age structure of a floater population can be a good indicator as to whether a population is in decline (Balbontín *et al.* 2003).

2.2 The Swedish Golden Eagle Population

The Swedish Golden Eagle population predominantly ranges over the boreal and mountain regions of northern Sweden (61-69^{o}N), also with a dense population on the Baltic island of Gotland among an increasing number of scattered populations in the south (Figure 1). The Swedish population is unique in that over half of the Golden Eagle population is dependent on trees for nesting unlike most other Golden Eagle populations that nest on cliffs, or bare rock. With forestry being a major land-use in Sweden this tree nesting population raises numerous potential conflicts of interest between forestry and nature conservation. Golden Eagles have been protected in Sweden since 1924. The population consists of between 1200-1400 reproductive individuals and is categorised as Near Threatened (NT) on the Swedish Red List, with evidence that the population is increasing (Gärdenfors 2010).

Golden Eagles inhabit two biogeographical regions in northern Sweden; the boreal, and the alpine region. Throughout these regions eagles differ in how they meet their dietary requirements. In the mountains principal prey species are the Mountain Hare (*Lepus timidus*) Willow Grouse (*Lagopus lagopus*) and Rock Ptarmigan (*Lagopus mutus*) (Nyström *et al.* 2006), whereas in boreal regions their diet is more diverse with Tjernberg (1981) reporting additional species such as Black Grouse (*Tetrao tetrix*), Western Capercaillie (*Tetrao urogallus*), Common Cranes (*Grus grus*) from nearby wetlands and occasionally Hazel Grouse (*Bonasa bonasia*). Over large parts of northern Fennoscandia, temporal variation of grouse (*Tetraonids*) and hare (*Leporidae*) populations were largely governed by the 3-4 year vole cycles during the 1960s and 1970s (Hörnfeldt 1978, 1994, 2004, Angelstam *et al.* 1985, Small *et al.* 1993, Dahl 2005, Hörnell-Willebrand 2005), although in central Finland, Lindén (1989) found longer grouse cycles with 6-7 year periodicity.

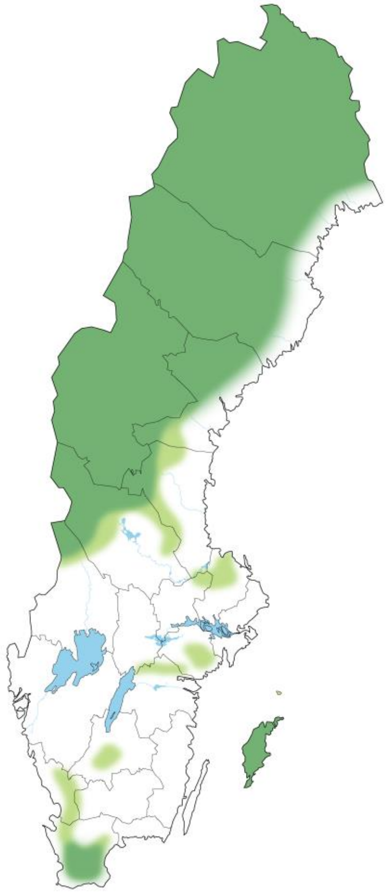

Figure 1. Distribution of Golden Eagles in Sweden 2005 (From Tjernberg & Svensson 2007)

2.3 Important land use types interacting with Golden Eagles in Sweden

2.3.1 Forestry

Modern forestry practices have developed relatively recently, evolving throughout the 20th century and affecting Golden Eagles in different ways due to the Eagles' dependence on nesting trees. Selective logging occurred in the first half of the century, cutting around 40 trees per hectare, many older than 250 years (Ericsson *et al*. 2000). The second half of the century saw mass logging schemes with shorter rotation periods. This radically changed the boreal landscape leaving younger more even aged forests with single storey canopies as opposed to the multi-storey canopies at the start of the 20th century (Andersson & Östlund 2004). This transition also significantly decreased the patch area of old forests (Ecke *et al.* 2013). If forestry in Sweden continues to take the direction of short rotation periods (Ericsson *et al*. 2000), Golden Eagle nest sites are likely to display an increasingly clumped distribution limited by the availability of old growth forest (Tjernberg 1985). In temperate latitudes Whitfield *et al.* (2001) in Scotland, and Pedrini & Sergio (2001) in Italy, found that afforestation and the expansion of woodland generated negative effects upon Golden Eagles.

Figure 2. A view from near a Golden Eagle's nest overlooking the Västerbotten landscape, northern Sweden and looking towards a clear-cut (upper left) (Photograph: Edward Moss).

2.3.2 Wind farm establishment

The rapid and continuous increase in turbine installations across Sweden totalled >2 600 operational onshore wind turbines in the final quarter of 2013 (Svensk Vindenergi, 2014), with more proposals planned in particular for the two northernmost counties. These northernmost counties contain the highest numbers of Golden Eagles (Figure 1). Consequently, concern lies over the effect this change in land use will have on Golden Eagles in future (Tjernberg 2010). Studies from outside Sweden have shown that the impact of wind farms on Golden Eagles can be through; i) habitat displacement, whereby a shift in ranging behaviour is observed due to unsuitable habitat being actively avoided, ii) collision risk, where fatalities result from direct collision with a turbine, or iii) territory abandonment, where disturbance is so extreme that the territory is no longer suitable as a breeding territory and thus abandoned (Hunt 1999, Walker 2005).

2.3.3 Reindeer herding

In Sweden, reindeer (*Rangifer tarandus*) herding has been practiced by the indigenous Sami people for centuries and herders annually migrate with their reindeer from the summer grazing pastures (and calving grounds) in the mountains to their winter grazing pastures in the lowland forest of northern Sweden. According to Nybakk *et al.* (2002), Golden Eagles predate on Reindeer calves more than Brown Bear (*Ursus arctos*) and Grey Wolf (*Canis lupus*), although to what extent is uncertain as studies suggest the Eurasian Lynx (*Lynx lynx*) and Wolverine (*Gulo gulo*) to be the most dominant predators on Reindeer across Fennoscandia. Juvenile Golden Eagles in their second and third summer, and adults that interrupted breeding and deserted their breeding home range, may undertake migratory movements of >1000 km to the mountain regions (Nilsson 2014). Movements by eagles in spring coincide with the seasonal movements of Reindeer to calving and summer grazing pastures (Figure 3). This may suggest eagles benefit from predation and/or scavenging opportunities on Reindeer (Nilsson 2014).

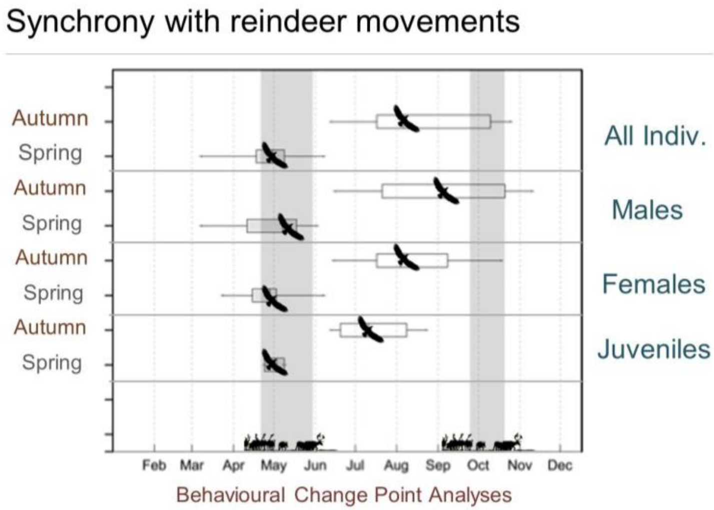

Figure 3. Timing of Golden Eagle movements in spring and autumn in relation to Reindeer migration; grey shading depicts seasonal timing of reindeer migration (Figure 4 in Nilsson 2014)

2.4 Management of Golden Eagles in Sweden

In a predominantly forested landscape the management of Golden Eagles requires close collaboration between logging companies and other land-owners. Tjernberg (2010) advised a minimum of a 200 m radius when clearing forest around nesting trees (including alternative nest sites). However, the actual area of forest that needs to be saved may vary between nests from one hectare (0.01 km^2) to several tens of hectares (>0.1 km^2) depending on the topography, wind exposure and visibility of the nest (Tjernberg 2010). When referring to wind power development, legislation from the Swedish Environmental Court states wind turbines must not be placed closer than 2km from known Golden Eagle nests (Sveriges Ornitologiska förening 2014).

Managing disturbance at a nest site scale is becoming increasingly more challenging and Golden Eagles are particularly sensitive to human activities (Kaisanlahti-Jokimäki *et al.* 2008). Therefore, management in Sweden should be avoided close to an eagle's nest between January/February - 31st July (Tjernberg 2010). During this time eagles are breeding and thus particularly vulnerable to breeding failure or territory abandonment.

3 Terminology

Throughout the raptor literature some studies have used terms differently or even used words interchangeably. To avoid similar problems I have listed some commonly used terms in this thesis to be clear as to how I intend them to be used.

Home range - a restricted area containing breeding individuals with their nest(s) and hunting ranges.

Territory - a portion of the home range used exclusively by the breeding pair and actively defended against intruders. McLeod *et al.* (2002) also refer to a "core area" within the territory where Golden Eagles are expected to spend >50% of their time. This core area (in their Scottish study area) is within 2-3 km radius from the territory centre (McLeod *et al.* 2002).

Nestling – a young eagle still dependent on the nest.

Juvenile – an individual aged 1-2 years typically displaying its juvenile plumage (Watson 2010).

Sub-adult – an individual aged 3-4 years old but not yet usually part of the breeding population. Note that some sub-adults can hold breeding territories (Watson 2010).

Adult – an individual that has reached full breeding status and displays its adult plumage.

Floaters - Birds in either sub-adult or adult plumage that are not associated with specific nesting territories and do not reproduce. Floaters may be physiologically capable of breeding, but are prevented from doing so by lack of a territory or nesting site. They are usually unpaired (Steenhof & Newton 2007).

Post-nesting movements – Movements made by an adult Golden Eagle after successfully breeding or interrupting/failing to, breed. Movements occur after any juveniles have left the territory.

Post-fledging period – The period from when a juvenile Golden Eagle has fledged and abandoned the nest up until when it leaves the breeding territory and becomes independent.

4 Material and Methods

4.1 Data collection and handling

Golden Eagle dataset (Paper I): In Sweden, monitoring of Golden Eagles dates back to the late 1960s (Ekenstedt & Schneider 2008) and local ornithologists have attempted to visit most nests 2-3 times a year ever since. The first visit is made around mid-March to confirm any pre-breeding activity such as nest building and territory establishment. This is determined from eagles displaying over the nest or from fresh green foliage within the nest bowl indicating recent nest building activity. The second visit is during incubation or the early nesting period in May, and is occasionally left out as this is treated as the least important of the three visits. Finally, the third visit occurs prior to fledging to confirm territory status and breeding success. With these three visits a five point criteria is used to assess the status of individual territories (Table 1).

Table 1. Swedish Golden Eagle monitoring criteria

0	Not visited
1	Visited but unknown occupancy status
2	Occupied but unknown breeding status
3	Breeding failed at an early stage (probably during incubation)
4	Breeding failed at a late stage (nestlings died)
5	Breeding successful (≥4week old nestlings)

Standardisation of Golden Eagle monitoring in the Nordic countries was adopted in 2004 with minor discrepancies between regions, but are now referred to as the Nordic criteria (Ekenstedt 2004). Throughout Västerbotten and Norrbotten (Sweden's two northernmost counties) the Nordic criteria have been used with one simplification, namely chicks of unknown age and small chicks have been categorised together as chicks (Ekenstedt & Schneider 2008).

Small mammal dataset (Paper I): Snap-trapping of voles has been conducted in a 100×100 km^2 trapping grid north-west of Umeå during spring and autumn since the autumn of 1971 (for detailed methods see; Hörnfeldt 1978). In paper I data from Bank Voles (*Myodes glareolus*) and Field Voles (*Microtus agrestis*) were pooled between 1980-2009 since their cycles were fairly synchronous (Hörnfeldt 1978, 1994, 2004).

Hunting bag statistics (Paper I): Game bird and Mountain Hare data were collected in the form of hunting bag statistics. These were provided by the Swedish Association for Hunting and Wildlife Management which is an organization formed from many local hunting groups within counties reporting to one national database. From this database I retrieved hunting bag statistics for the Golden Eagle's principal prey; forest grouse (e.g. Black Grouse, Willow Grouse and Western Capercaillie) and Mountain Hare. To somewhat control for hunting effort, I expressed all game species per 1 000 hectares within the three most intensively monitored Golden Eagle municipalities (Lycksele, Vindeln and Åsele). This hunting index was calculated for the hunting season in autumn - early winter. However, a change in the reporting system occurred in 1995 causing a gap in the dataset for this year.

Landcover dataset (Paper II, III, IV): In an attempt to mimic the landscape available to Golden Eagles in northern Sweden, I extracted landscape data from two datasets, the Swedish Landcover map (SMD, Lantmäteriet 2004, for paper II, III & IV) and *k*nn forestry data (*k*nn 2005 for paper II, SLU 2005, *k*nn 2010 for paper III & IV, SLU 2011) both with 25×25m resolutions. *K*nn data is derived from a combination of satellite imagery, field data and algorithms that validate and determine *k*-nearest neighbour distances (Reese *et al.* 2003). To minimise any error, in paper II and IV *k*nn data was further supplemented with data on registered clear-cuts from the Swedish Forestry Agency (Skogsstyrelsen 2014) between 2001-2005 and 2006-2010, respectively. I used a 50×50m resolution digital elevation map (Lantmäteriet 1999) to calculate a terrain ruggedness index in paper II, and slope and aspect in paper IV. For paper III I calculated the proportion of clear-cuts within each home range.

In an attempt to minimise error after *k*nn data was imported into ArcGIS, I used a majority filter smoothing parameter that requires at least four of the eight neighbouring pixels to share the same code before the central pixel is changed. This removed isolated pixels within the raster layer thus generalising data towards areas with distinctive habitat codes.

Movement data (Paper III, IV): In 2010 and 2011 a team of specialist trappers captured 29 adult Golden Eagles on their territories, using remote controlled bow nets (Bloom *et al.* 2015). Individuals were initially sexed by body mass (later confirmed genetically with blood samples). Each eagle was fitted with one of two types of GPS backpack transmitter: i) Microwave Telemetry Inc, USA (MT) units, or ii) Vectronic Aerospace GmbH, Germany (VA) units (Paper III). These transmitters were scheduled with the aim of conserving battery power while accounting for variation in daylight hours throughout the course of the year (Table 2). All trapping was conducted in accordance with the required permits from the Swedish Environmental Protection Agency, the Animal Experiment Ethical Committee in Umeå, and the County Administrative Boards of Västerbotten and Västernorrland.

Table 2. Programmed schedules for Golden Eagles fitted with either VA or MT backpack transmitters.

Period	Interval-VA[1]	Interval-MT[2]	Start-MT[3]	Stop-MT[3]
Jan-Feb	2hr	2hr	10:00	16:00
Mar-Apr	30min	1hr	09:00	17:00
May-Aug	10min	1hr	04:00	20:00
Sep-Oct	30min	1hr	09:00	17:00
Nov-Dec	2hr	2hr	10:00	16:00

1. VA units contained a horizontal accuracy of 2m and were activated by a tilt mechanism

2. MT units contained a horizontal accuracy of up to 18m

3. All times are displayed as local times

I used data from individuals holding positions within the specified breeding seasons 1st of March – 31st of October during 2011, or 1st of March - 15th of August during 2012. I excluded eagles with <100 positions since they were assumed unreliable for the construction of home range size, leaving the mean number of positions per individual at >2 500 positions (Paper III). The VA unit has a horizontal accuracy of ±2m (Robert Schulte, Vectronic Aerospace GmbH *pers.comm.* 2012) and the MT unit a horizontal accuracy of up to 18m (Microwave Telemetry Inc. 2013). The VA unit reports the number of satellites in range (unlike MT units) from which I selected data points with ≥3 satellites thus ensuring an acceptable horizontal accuracy (±2m). VA units also calculate a HDOP (horizontal dilution of precision) value which was set to ≤10 so to select GPS points with the highest degree of certainty (c.f. Langley 1999). MT units provided no HDOP value but I included all previously WRAM (Wireless

Remote Animal Monitoring) validated positions from these units to increase sample size of individual eagles.

4.2 Analytical approaches

This thesis has used different analytical approaches including time series analyses in paper I and spatial analyses in papers II – IV. Paper I focused on analysing the reproductive success of eagles in relation to their prey using autocorrelation and regression analysis on data from 1980-2009. Autocorrelation analysis was used as it enabled detection of any periodicity within the Golden Eagle population, while testing Tjernberg's (1983a) prediction that reproductive performance of Golden Eagles shows 3-4 yr cycles along with their main small game prey. In the remaining papers (Papers II – IV) I used spatial modelling techniques, although the complexity of these models developed with each paper. The simplest models were circles and concentric bands (with fixed radii) representing individual home ranges (Paper II). These home ranges also required some statistical modelling in an attempt to reduce spatial autocorrelation. The most sophisticated models were constructed in papers III & IV using minimum convex polygons (MCP) and kernel density estimators (KDE). Both these are commonly used throughout the Golden Eagle literature and thus comparable to similar studies. For both estimators, I selected 50 (fine) and 95% (coarse) volume contours (VC) as scales for analysis, which delineate i) the core area, and ii) home range (minus extreme points), respectively.

5 Results and Discussion

5.1 Reproductive success of Golden Eagles in relation to food supply (Paper I)

This paper rejected Tjernberg's (1983a) initial prediction of a 3-4 year cycle in Golden Eagle reproductive performance. It is possible Golden Eagles were cyclic in the 1970s, but the structure of the predator-prey community changed in the early 1980s after an outbreak of sarcoptic mange (a parasitic mite [*Sarcoptes sacbiei*]) hit the Red Fox (*Vulpes vulpes*) population in Sweden (Danell & Hörnfeldt 1987, Lindström *et al.* 1994). In agreement with the alternative prey hypothesis, this epidemic resulted in an increase in forest grouse and Mountain Hare due to reduced predation pressure as fox populations declined (Danell & Hörnfeldt 1987, Lindström *et al.* 1994). This led to less regular fluctuations among Mountain Hares in Sweden from the mid-1980s onwards (Newey *et al.* 2007) when compared to the 3-4 yr cycles they displayed previously. The regularity of small game fluctuations may also have been disturbed by a dampening of the 3-4 yr vole cycles starting in the 1980s in northern Sweden and elsewhere in Fennoscandia (Hörnfeldt 2004, Ims *et al.* 2008).

Despite rejecting Tjernberg's (1983a) prediction in paper I, we also demonstrated the importance of food on reproductive success, as shown in similar studies (Tjernberg 1983a, Watson *et al.* 1992, Steenhof *et al.* 1997, Nyström *et al.* 2006). Multiple regression found the percentage of territories with nestlings was associated to current indices of primary prey (F=5.99, P=0.006). The same applied to the index for annual population production, which was also associated to numbers of voles in the previous autumn (F=6.30, P=0.021). Together these two explanatory variables explained 28% of the total variation in the annual population production. Vole supply in the previous autumn appeared to explain almost as much variation in the index for annual population production as the Golden Eagles' principal prey in the current year. However, along with the alternative prey hypothesis (Hörnfeldt 1978, Angelstam *et al.* 1984) this higher vole supply in the previous autumn could act as a buffer against overwinter predation on small game by other predators, which would be a more plausible explanation than Golden Eagles switching to prey on voles when they were abundant.

In Alaska, McIntyre and Adams (1999) explained nearly 90% population productivity from changes in spring prey (Snowshoe Hare [*Lepus americanus*] and Willow Grouse) densities. I believe McIntyre and Adams (1999) were able to explain more variation since they used line transects that were better geographically matched with eagle data than hunting bag statistics to measure prey densities. Further, hunting bag statistics in paper I were from autumn - early winter, a period when Golden Eagles start scavenging more to replace live prey (Watson *et al.* 1993, Watson 2010). Therefore, McIntyre and Adam's (1999) results may reflect the transition back from more scavenging in winter to predating on live prey in spring.

Relating to paper I, we have also found a high variation in territory quality of Golden Eagles, in the sense of how frequently Golden Eagles breed successfully in different territories (Hipkiss *et al.* 2014). Such variation has long been recognised across many raptor species, in for example Sparrowhawks (*Accipiter nisus*, Newton 1991), Goshawks (*Accipiter gentilis*, Krüger & Lindström 2001) and Black Kites (*Milvus migrans,* Sergio & Newton 2003, Sergio *et al.* 2009).

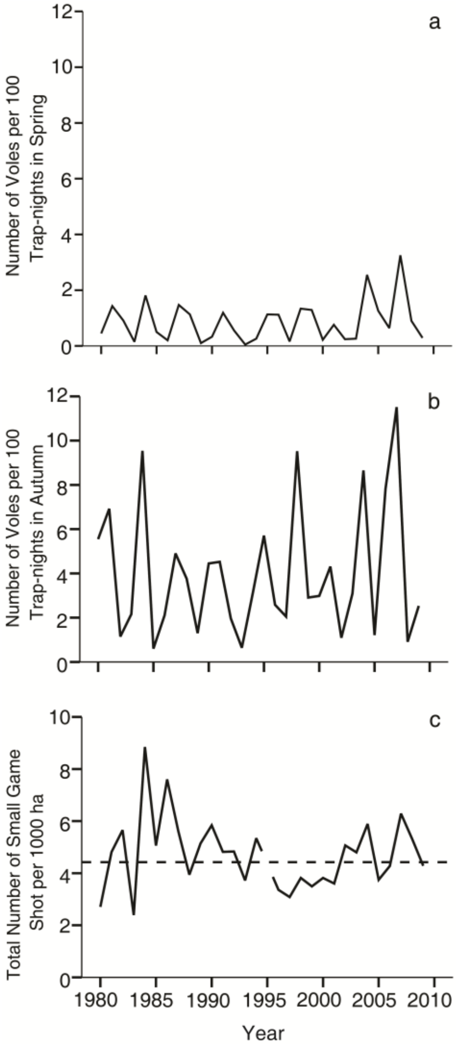

Figure 4. The number of snap-trapped voles (Bank Voles, *Myodes glareolus* and Field Voles, *Microtus agrestis*) in (a) spring and (b) autumn, 1980-2009 in Västerbotten county, northern Sweden and (c) the pooled number of principal prey species for the Golden Eagle, i.e. small game, Mountain Hare (*Lepus timidus*) and Tetraonidae species, as indexed by hunting bag statistics. The dashed line indicates the mean number of small game shot per hunting year throughout the study period. (Figure 5 in paper I).

5.2 Scale-dependent habitat composition of Golden Eagle territories in northern Sweden (Paper II)

In paper II we demonstrate, using circles and concentric bands, that scale-dependent habitat composition is an important factor in Golden Eagle territories. Despite this simple representation of a Golden Eagle's territory we still manage to identify how individuals partition their territory. Perhaps the most pronounced result was that of the terrain ruggedness index. In support with McIntyre *et al.* (2006) who used a similar index we found more rugged terrain closer to the nest. Clear-cuts were overrepresented between 400 and 3240m from the nest, i.e. in line with paper IV and studies referring to the eagles' preference for open hunting grounds (Idaho USA Marzluff *et al.* 1997, Scotland Watson 2010, Sandgren *et al.* 2014). Young forest was underrepresented throughout the study. This complements studies in temperate latitudes, where Whitfield *et al.* (2007) found plantation forestry in Scotland threatened Golden Eagles requiring open landscapes for hunting. Finally, closed canopy forest was overrepresented close to the nest reflecting their preference for suitably old growth trees when nesting. On the other hand canopy closure restricts access to the forest floor consequently inhibiting potential prey detectability for eagles which may explain why clear-cuts were overrepresented at intermediate scales.

In conclusion, where advanced spatial models are lacking, multi-scaled simplistic modelling can reveal comparable results for the management of Golden Eagles. However, with these simplistic approaches it is important to recognise the biological meaning behind each scale. This study emphasizes the need to focus on the nest site scale (≤400m), and scales up to ~3km from the nest, where better access to clear-cut areas lie. The only previous study involving Golden Eagles in boreal Sweden has focused on the nest site scale (Tjernberg 1983b). However, managers should acknowledge the importance of different habitats throughout an eagle's territory and that the preference/avoidance towards these habitats are scale-dependent.

5.3 Adult home range size and post-nesting movements in the boreal forest (Paper III)

In paper III we found some of the largest home ranges in Golden Eagle literature when derived from minimum convex polygons (MCPs) and kernel density estimators (KDEs). Compared to other parts of the world (e.g. Marzluff *et al.* 1997, Clouet *et al.* 1999), I believe this is largely explained by decreased prey detectability within a predominantly forested landscape. This supports Schoener's (1968) conclusions of scarce prey resources, or predators selecting avian over mammalian prey contributing to large home range sizes. Such large home ranges also suggest Golden Eagles in boreal Sweden are forced to expand their home ranges (in contrast to those of other regions) so to include a greater proportion of clear-cut habitat. This is shown in Figure 5 where home range size is inversely related to the proportion of clear-cuts. Thus, forestry likely benefits the species by opening up the forest through clear-cutting, thereby creating suitable hunting habitats and allowing for smaller home ranges. It is unknown whether eagles require a certain proportion of clear-cuts within their home range. Figure 5 was only significant (P<0.05) for females (r=−0.94, P<0.01, n=7) and not for males (r=0.04, P=0.93, n=8). We explain this by females being larger in size and thus requiring more open space for hunting, although I do recognise that sample sizes were small.

In paper III we also provide the first reported case of post-nesting movements northwards for adult Golden Eagles, although such movements have been reported for other raptor species (Prairie Falcons, Steenhof *et al.* 2005, Red-tailed and Red-shouldered Hawks, Bloom 2011). We also found Golden Eagle pairs reunited after migration on northern summer-use areas following long-distance post-nesting movement (Figure 6). This phenomenon may be an example of one of the first accounts in any raptor species (Karen Steenhof, Associate Editor, Journal of Raptor Research *pers.comm.*).

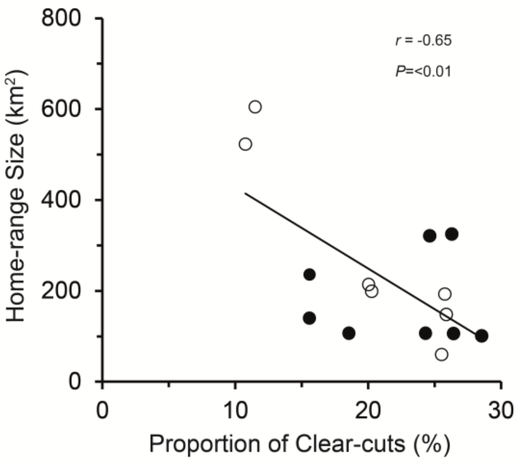

Figure 5. Relationship between home-range size (95% MCPs) and proportion of clear-cuts within the home ranges for adult Golden Eagles (n = 15) during the 2012 breeding season in northern Sweden with the correlation coefficient shown for the pooled number of males and females. Open circles denote females whereas closed circles denote males (Figure 3 in paper III).

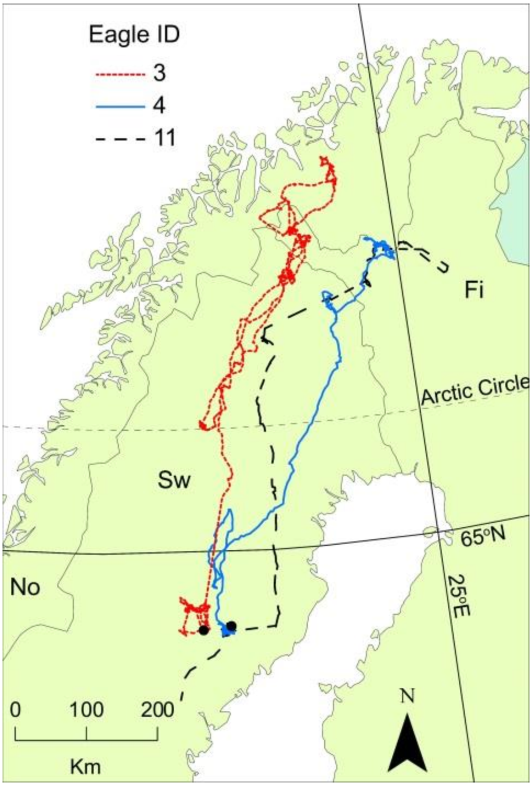

Figure 6. Long-range directional movements displaying ranging behaviour for adult Golden Eagles (n=3) with IDs 3, 4 and 11 during 2012 from when breeding home ranges were first deserted through to the 15th August. Nest sites are represented by the solid black circles, while No, Sw and Fi represent Norway, Sweden and Finland respectively (Figure 4a in paper III).

5.4 Adult habitat use and wind farm establishment in Sweden (Paper IV)

In paper IV we found differences (P<0.05) between used and expected values for habitat and topographic variables within 50 and 95% volume contours (VCs). I utilised position data from 15 adult Golden Eagles with GPS tracking devices and found eagles preferred clear-cuts and suitably old coniferous forest, the latter being in line with the findings by Tjernberg (1983b) that Golden Eagles use trees with a mean age of >335 yr for nesting. Eagles avoided open and wooded mires alongside young, mixed and other forest habitats (Figure 7). We found increasing preferences for steeper slope classes in both 50 and 95% VC which supports the findings by McIntyre *et al.* (2006), and reinforces the importance of rugged terrain within Golden Eagle territories. However, Golden Eagles displayed a general avoidance of northern aspects, while preferring east and west facing slopes at both spatial scales. At both fine and coarse scales Golden Eagles showed stronger preferences towards coniferous forest with ground lichens, rather than regular coniferous forest habitat (Figure 7). I believe this may reflect how coniferous forest with ground lichens is often less dense than other forest types, and thus more suitable for hunting. These results confirm the more simplified analyses of paper II. Paper IV demonstrates how wind farms, that require similarly windy habitat, must be managed with eagles in mind, both in the planning and operational phases of wind farm construction. The results imply that potential conflicts between Golden Eagles and wind energy exploitation can be substantially reduced if wind farms are placed away from steep slopes and ridges, and if clear-cutting of forest is minimized within the wind farm area.

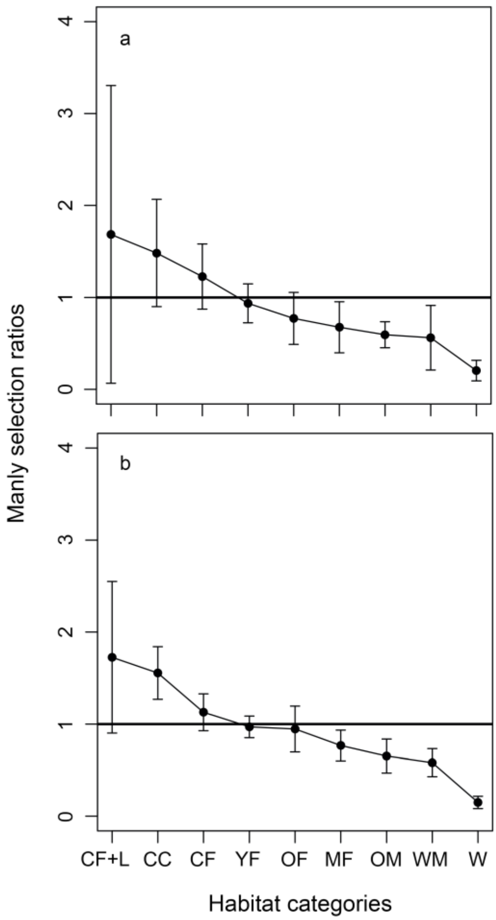

Figure 7. Manly selection ratios for different habitat categories by adult GPS tracked Golden Eagles during the breeding season in 2012, northern Sweden, shown for a) the 50 % and b) 95 % kernel density estimator home ranges. Habitat categories are defined as CF+L= coniferous forest with ground lichens, CC = clear-cut, CF= coniferous forest, YF= young forest, OF= other forest, MF= mixed forest, OM = open mire, WM = wooded mire, and W=Water bodies. Ratios >1 indicate a preference, while ratios <1 indicate an avoidance of habitats (Figure 2 in paper IV).

6 Conclusions

This thesis has considerably increased the knowledge on Golden Eagles in Sweden, and contributed on a global scale to the understanding of boreal nesting Golden Eagle populations.

I believe we have conducted one of the first formal tests of cyclicity on a long-term Golden Eagle time series (Paper I). Despite finding large inter-annual fluctuations, we concluded there was no cyclicity in the reproductive performance of Golden Eagles although performance was linked to supply of small game in the same year and to vole supply in the previous autumn.

In paper II the importance of different habitats within an eagle's territory was found to be scale-dependent. This paper also concluded that simplistic models can draw similar conclusions to advanced spatial models (KDEs) as in paper IV regarding habitat preferences. In paper III we found some of the largest home ranges that have been reported for the Golden Eagle. These large home ranges in boreal environments are likely due to the expanse of closed canopy forest forcing Golden Eagles to compensate for reduced prey detectability by increasing home range size (Paper III & IV). This was in line with finding a decreased home range size with an increased proportion of clear-cuts (Figure 5). Paper III also found what I believe is the first case of Golden Eagles reuniting on their northern summer-use areas during post-nesting movements (Figure 6).

Finally, this thesis attempted to understand how land use change may be modified to reduce disturbance of Golden Eagles in boreal Sweden. With the number of wind farms set to increase in northern Sweden the eagle's preference for steep slopes along with east or western facing aspects must be considered in future exploitation and Golden Eagle management plans. Therefore, if wind farms are placed away from steep slopes and ridges, and if clear-cutting of forest is minimized within wind farm areas, these actions will help minimise disturbance for Golden Eagles in boreal Sweden. Habitat analyses within this thesis also suggest forest management could be used as a tool for encouraging eagles away from otherwise poorly-sited wind farms.

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