Introductory Research Essay

Golden eagle *(Aquila chrysaetos)* ecology and forestry.

Edward Moss

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Department of Wildlife, Fish, and Environmental Studies
Swedish University of Agricultural Sciences
901 83 Umeå, Sweden

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Principal supervisor: Birger Hörnfeldt

Assistant supervisors: Frauke Ecke, Tim Hipkiss, Mats Nilsson

1 Background

The widespread growth of commercial forestry in the second half of the 20th century has led to an increasing concern over the effects it may have upon species dependent on old growth forests. The golden eagle *(Aquila chrysaetos)* inhabits mainly mountainous environments throughout the northern hemisphere and is an example of just one species that is affected by forestry practices (Whitfield *et al.* 2001, Pedrini *et al.* 2001b). Tjernberg (1983a) studied 97 nesting trees in boreal Sweden and found golden eagles nested predominantly in older trees with a mean age of 335 years. This review aims to discuss all current literature concerning the effects of forestry on the golden eagle, the eagle's food supply, reproduction and habitat requirements. Where there is little, or no previous research relevant to the golden eagle, references to other *Aquila* species will be used to better illustrate the point.

2 Terminology

A number of studies have defined terms differently or even used words interchangeably making comparisons difficult and discussions unclear. In order to avoid similar problems in this review I define some basic terminology below.

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 is within 2-3km 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 1997).

Sub-adult – an individual aged 3-4 years old but not yet usually part of a breeding population. Note that sub-adults can hold breeding territories (Watson 1997).

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

Afforestation – the process of converting land from a non-forested area to a forested area.

Deforestation – the removal of forest cover as a result of human cutting activity.

3 Global range of the golden eagle

The golden eagle inhabits most montane environments throughout the northern hemisphere and has a remarkable ability to cope with climatic extremes and a diverse range of habitats. With reference to their global distribution, Watson (1997) identified nine different biogeographical regions in the Palearctic and seven in the Nearctic, with six sub-species being recognised today primarily upon plumage colouration and size differences. These sub-species with approximate geographical locations are *Aquila chrysaetos chrysaetos* (Northwest Europe and into Russia), *A.c.homeyeri* (North Africa), *A.c.daphanea* (Himalayas), *A.c.kamtschatica* (Siberia and Russia), *A.c.japonica* (Japan) and *A.c.canadensis* (Nearctic).

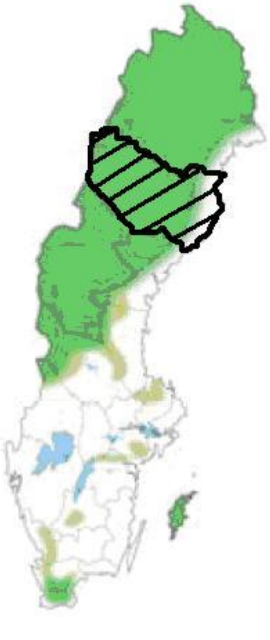
The *Palearctic range* stretches from eastern Siberia, west to the Kola Peninsula and through Scandinavia down into Scotland where mere fragments of the original boreal forest remain in Scotland. Further south, populations occur in the Pyrenees, Alps, Carpathians and Caucasus mountain ranges, extending into the deserts of Kurdistan and Afghanistan and east into the Himalayas. More scattered populations are found in the deserts of Ethiopia and Arabia (Watson 1997, Clouet *et al.* 1999). Throughout the *Nearctic*, the golden eagle *(Aquila c.canadensis)* is widely distributed. With their northern limit following roughly that of the tree line, their distribution spans from western Alaska to eastern Canada stretching down the Rocky mountains south to California and Mexico (Kochert & Steenhof 2002).

All biogeographical regions with golden eagles feature similar characteristics typical of the eagle’s preferred environment, namely that of open habitats for hunting and with minimal human disturbance. Similarities are also seen with respect to prey as sufficient medium sized birds and mammals are the key requirement in all but a few regions where other taxa are consumed more readily (Watson 1997).

4 The Swedish golden eagle population

The Swedish golden eagle population ranges over primarily that of the mountain and boreal regions of northern Sweden (61-69^{o}N) with scattered patches throughout the south (see Fig. 1). The terrain varies from high alpine slopes with mountain tundra to coniferous forests and mires with a tree line around 900 m.a.s.l. Above the tree line, golden eagles usually nest on suitable cliff edges (Tjernberg 1985), as is also the normal case throughout most of the golden eagle's distribution worldwide (Watson 1997). Agricultural land may also be among different habitats used in the south of Sweden. In boreal Sweden, golden eagles predominantly nest in trees (Tjernberg 1983a, Watson 1997) as in other parts of the boreal forest such as in Finland (Ollila 2005), but which is otherwise uncommon in most parts of the world (Watson 1997). In America, north-east Wyoming also holds a small population of tree nesting golden eagles, although this population is poorly documented (Menkens & Anderson 1987).

The Swedish Red List categorises the golden eagle as near-threatened (Gärdenfors 2010) as does additional legislation under Annex 1 (species in need of special protection) of the EU Birds Directive. Despite the status of the golden eagle being stable (or slightly increasing), its categorisation on the Swedish Red List has not been downgraded as a sudden rise in mortality (e.g. from increased persecution, train collisions or with wind turbines) could have a profound impact at a population level (Gärdenfors 2010). Current population estimates have put the size of the Swedish golden eagle population between 1200-1400 reproductive individuals (Gärdenfors 2010).



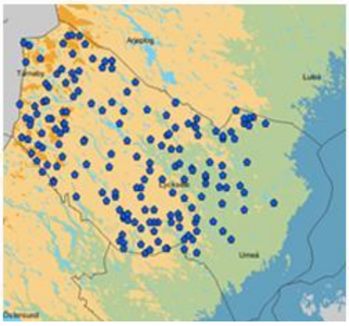


Figure 1: Range of the Golden eagle (shaded) in Sweden (left) (Tjernberg 1983a), where I have highlighted my forthcoming core study area in Västerbotten. Map of nest sites with breeding pairs in Västerbotten county, 2008 (right) (Nilsson *pers. comm.*).

5 Food supply with links to eagle reproduction

The aim of this section is to discuss prey ecology and distribution, and to review food availability for golden eagles, with emphasis on the situation in Sweden. Examples of dietary breadth derived by the proportional percentages of different families in the diet are also provided, alongside the mechanisms underlying fluctuating food resources. The influence that prey has upon reproduction is then mainly reviewed in section 6.

The majority of dietary research has been carried out in America (Olendorff 1976) and Europe (Lockie & Stephen. 1959, Brown & Watson. 1964, Tjernberg 1981, Högström & Wiss 1992, Sulkava *et al.* 1999), although in recent years similar research has also been undertaken in Japan (Takeuchi *et al.* 2006). Both indirect and direct approaches to dietary analysis are seen throughout the literature. For example, indirect measures result from prey remains and pellet analyses (Tjernberg 1981), but these are known to overestimate the relative importance of mammalian prey while underestimating the total quantity of prey delivered to the nest (Watson 1997). Direct measures on the other hand constitute observational data and stomach analyses (Tjernberg 1981). While observational data is more time consuming than indirect measurements, it does not account for food consumed away from the nest or outside the breeding season (Watson 1997). Stomachs were frequently used for dietary analyses at the start of the 20th century prior to legislation banning the killing of golden eagles. However, nowadays golden eagle stomachs are rarely used for dietary analysis due to their lack of availability (Watson, 1997). As a result, comparative analyses are difficult to interpret as long term datasets may incorporate different methodologies and thus biases in prey representation.

Golden eagles maintain a rather broad food niche consuming medium-sized birds and mammals in addition to amphibians and even reptiles such as spiny-tailed lizards *(Uromastix microlepis)* in more arid regions of Arabia (Watson 1997, Sulkava *et al.* 1999). Whether golden eagles are seen as generalists or specialists varies spatially and temporally dependent on their need to exploit alternative food resources when and where their preferred prey (e.g. grouse and hare in Sweden) are low in numbers (Watson 1997). Watson (1997) suggested a typically narrow diet may comprise 85% in one taxon whereas in contrasting broader diets 5 prey taxa may each hold 12% of the diet. The case on the Swedish island of Gotland (57°30′N 18°33′E) shows an example of a fairly narrow and particularly unusual diet. Grouse are absent and lagomorphs are only present in limited numbers. Instead, eagles have exploited a niche with hedgehogs *(Erinaceus europaeus)* and ducks (Tjernberg 1981, Högström & Wiss 1992). These prey size classes (0.5-1.0kg), which are smaller than those of mainland Sweden (2.0-4.0kg), have resulted in eagles almost doubling their catch rate in comparison to that on mainland Sweden to obtain the equivalent quantities of food (Högström & Wiss 1992). Throughout their global range, prey size is considered a major factor in ecologically separating golden eagles from other *Aquila* species (Watson 1997).

5.1 Prey species, their main habitats and distribution in Sweden

The range of bio-geographical regions (see section 3) inhabited by golden eagles clearly corresponds to differing prey bases and distributions. In Sweden the golden eagle's dietary requirements in mountain regions are met through consumption of mainly willow grouse *(Lagopus lagopus)*, mountain hare *(Lepus timidus)* and ptarmigan *(Lagopus mutus)* (Tjernberg 1981, Nystöm *et al.* 2006). In forest habitats the main diet is made up of black grouse *(Tetrao tetrix)*, capercaillie *(Tetrao urogallus)*, hazel grouse *(Bonasa bonasia)*, willow grouse and mountain hare. Reindeer *(Rangifer tarandus)* carcasses are likely an important food source during winter for golden eagles. Reindeer range in the herding district limiting their distribution on a national scale to the north, where they migrate seasonally in the fall and spring bringing them to the lowlands in winter and to the mountains in summer for calving.

Willow grouse are found in both mountain and forest habitats selecting willow thickets, forest edge habitats or forest clearings (Hörnell-Willebrand 2005) suggesting their preferred habitat would lie to the left of Fig. 2 with black grouse. The mountain hare selects different landscape features throughout the year based on the availability of food or shelter (Dahl 2005). Dahl (2005) assumed seven different landscape features to be important for mountain hare: mature deciduous forest, mature spruce forest, mature pine forest, mature mixed forest, young forest (up to 3m), open mires and agricultural land. Ptarmigan is a mountain species and only found in the mountain regions of Sweden. In the forest, the diversity of grouse is greater than in the mountains, with black grouse favouring forest edges and areas characteristic of early forest succession from 0-20 years old (Seiskari 1962, Swenson & Angelstam 1993, Lande 2011). In contrast, capercaillie select older pine forests (≥90 years old) with natural openings but few deciduous trees (Seiskari 1962, Swenson & Angelstam 1993, Lande 2011). The hazel grouse, favours the early secondary successional stage (20-50 years old) and old growth spruce forest patches, both of which meet one of the hazel grouse's key habitat requirements of having thick undergrowth (Swenson & Angelstam 1993, Åberg *et al.* 2000, Lande 2011). Swenson & Angelstam (1993) also found hazel grouse selected habitats with 1-10% deciduous trees whereas capercaillie selected stands with no deciduous trees.

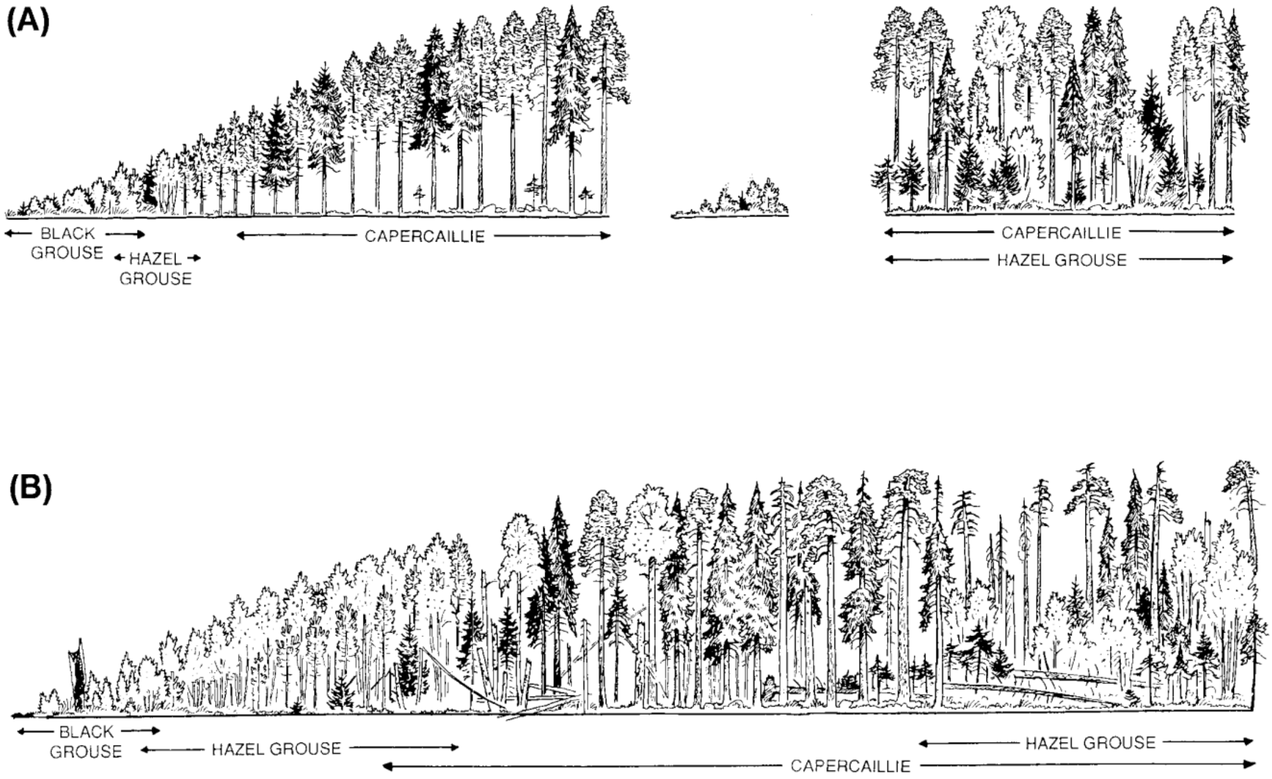


Figure 2. (A) Graphic portrayal of the forest structures studied; intensively managed forest on the left, farmer's forests on the right. (B) Hypothesized structure of primeval forest. The age-classes found or hypothesized to be used by the three forest grouse species are indicated (reproduced from Swenson & Angelstam 1993).

5.2 Temporal and spatial variation of prey and other food sources

Temporal variation of grouse and hare populations was largely governed by the 3-5 year vole cycles in large parts of northern Fennoscandia in the 1960s and 1970s (e.g Hörnfeldt 1978, 1994, 2004, Angelstam *et al.* 1985, Hörnfeldt *et al.* 1986, Hanski *et al.* 1991, Small *et al.* 1993, Framstad *et al.* 1997). In central Finland Lindén (1989) found longer grouse cycles with 6-7 year periodicity. The well studied vole cycles in Fennoscandia are affecting many aspects of community ecology and influencing predator population dynamics (Hörnfeldt 1978, Hörnfeldt *et al.* 1986, Ims *et al.* 2008).

When mesopredators (medium sized predators) such as the red fox are forced to prey on alternative prey sources (e.g. grouse, hare and other birds), instead of voles, the resulting decline in alternative prey densities was predicted to link also the golden eagle into the multiannual cycles (Fig.3, Tjernberg 1983b). These cyclic interactions clearly illustrate the well studied alternative prey hypothesis (APH) (e.g Hörnfeldt 1978, Angelstam *et al.* 1984, Hörnfeldt *et al.* 1986, Small *et al.* 1993, Norrdahl & Korpimäki 2000, Reif *et al.* 2001, Kjellander & Nordström 2003), where a predator makes a dietary shift towards an alternative food source when their principal prey, voles, are scarce.

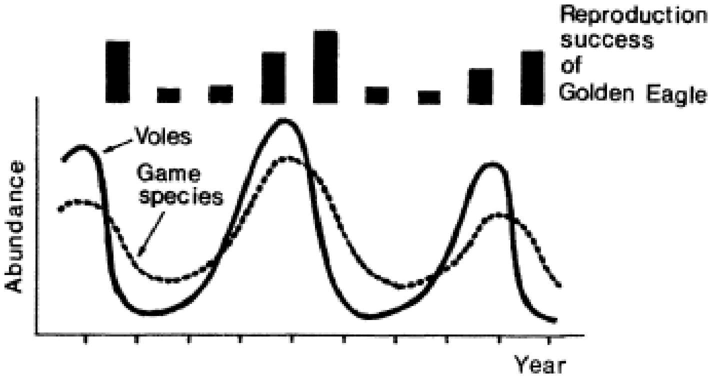


Figure 3. Predictions of reproductive success of the golden eagle in relation to fluctuations of voles and small game species. Arbitrary scales (Tjernberg 1983b).

The predation pressure from the red fox on their main prey (voles) and alternative prey (roe deer, grouse, mountain hare) was studied in Sweden during an epizootic of sarcoptic mange (a parasitic mite, *Sarcoptes scabiei*) in the late 1970s-1980s (Lindström *et al.* 1994, Kjellander & Nordström 2003). Lindström *et al.* (1994) concluded the cyclic cofluctuations of grouse, mountain hare and voles were decreased (locally), or disappeared (regionally) when mange struck the fox population (see also Danell & Hörnfeldt 1987). In support of the APH and due to a release of predation pressure, Lindström *et al.* (1994) also found densities of grouse, roe deer and mountain hare to significantly increase during the mange period (see also Danell & Hörnfeldt 1987). Tjernberg (1983b) predicted a rise in golden eagle breeding success following the cyclic peak years of their prey species (grouse and mountain hare), and he also observed such a rise during one cycle in the early 1970s (Tjernberg 1983b), but it is uncertain how the golden eagle responded to these generally increased prey densities during the mange period in the 1980s.

Besides the outbreak of sarcoptic mange, affecting the fox population and its alternative prey species another major change affected the voles, i.e. the key component of the synchronous 3-4 year cyclic small game community, namely an increased frequency and severity of winter declines among voles. This led to a decrease in vole cyclicity in northern Sweden and elsewhere in northern Fennoscandia from the mid-1980s and onwards (Hörnfeldt 1994, 2004, Hörnfeldt *et al.* 2005, Ims *et al.* 2008). Also in addition to the findings by Lindström *et al.* (1994), some other studies indicated that mountain hares have shown less regular fluctuations in the 1990s and 2000s than the 3-4 year cycles in the 1960s and 1970s (Newey *et al.* 2007).

Surviving the winter is a demanding task often resulting in eagles scavenging on ungulates killed by large carnivores (Nybakk *et al.* 1999, Norberg *et al.* 2006, Johnsen *et al.* 2007). In Scotland, the abundance of carrion in winter showed a positive correlation to the breeding densities of golden eagles the following year (Watson *et al.* 1992, 1993, Watson 1997). A similar correlation has been shown with carrion of pronghorn sheep in America (Deblinger & Alldredge 1996). Such ungulate populations are valuable sources of carrion that golden eagles may utilise during winter months when annual ungulate mortality is at its highest rate (Whitfield *et al.* 2007b). Throughout the year ungulates are consumed less frequently in the summer months than in winter months. This was suggested to be due to carrion being deficient in calcium, which is crucial for nestling growth. Ungulates are also energetically costly to hunt while breeding (Watson 1997). It has been reported from Scotland that when ungulate populations grow large, overgrazing may occur and cause a decrease in grouse and hare populations due to a deterioration and lack of suitable habitat for these two species (Whitfield *et al.* 2007b).

Watson *et al.* (1993) distinguished nine eco-regions in Scotland based upon their differing prey composition and found that reproductive success varied among them. In Sweden, Tjernberg (1981) suggested that the spatially varying composition of prey items for golden eagles throughout the coniferous forest reflected varying habitat composition across the landscape and had been caused by intensified forestry. Such habitat changes are supported by more recent studies in Finland that suggest the increased size of clear-cuts in northern regions enhance generalist predators to suppress grouse populations (Kurki *et al.* 2000).

6 Reproduction

Golden eagles may live as long as 30 years in the wild enabling them potentially to breed for many years once they establish a territory. However, they typically delay breeding until their fourth or fifth year (Watson 1997), probably to allow time to develop the hunting skills required to fulfil the needs of a family (Tjernberg 1986). Males usually delay breeding for longer than females as their parental role is essentially dominated by hunting (Collopy 1984, Tjernberg 1986).

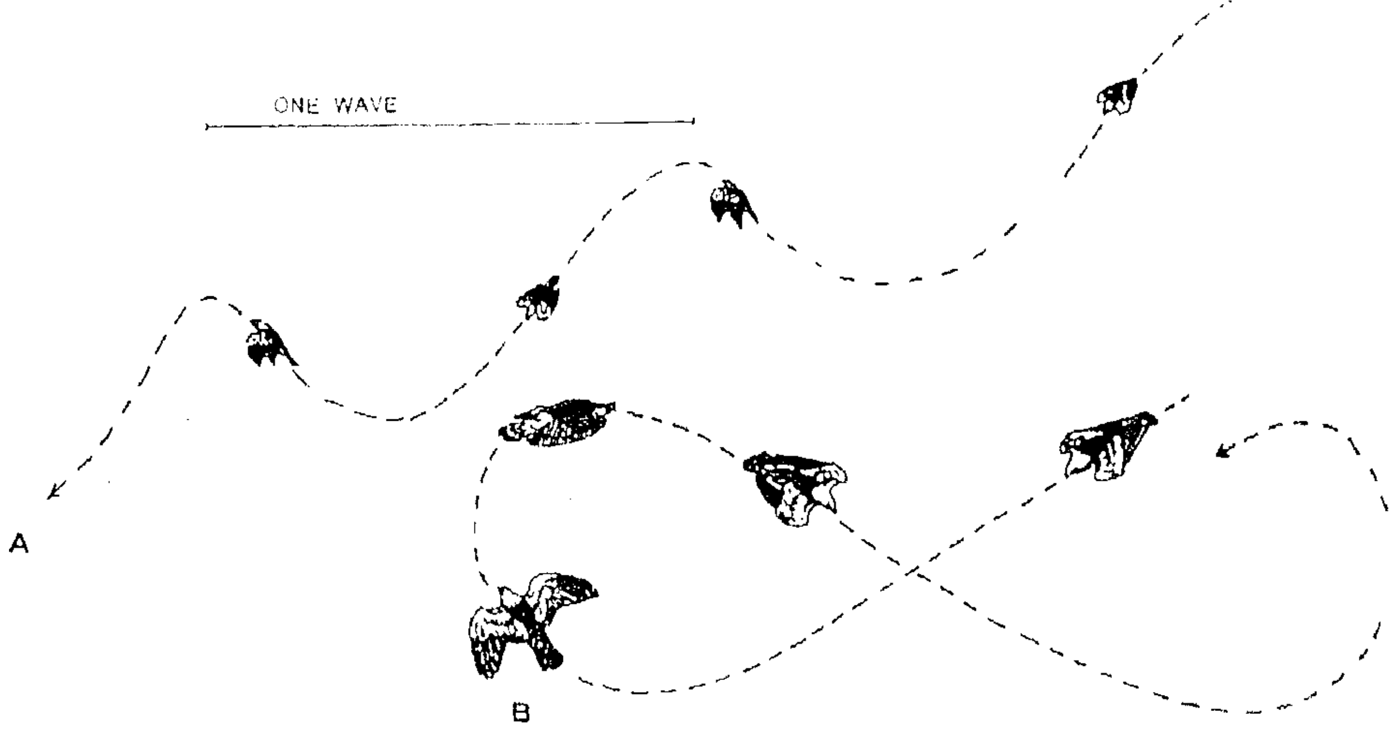


Figure 4. Pattern of undulating flights of golden eagles **A:** Eagle dives with wings partly closed, then regains height, sometimes with vigorous wing-flapping, this is repeated. **B:** a special form of undulating flight is the ‘pendulum flight’ in which the eagle dives, regains height, turns over and retraces its course repeatedly (reproduced from Bergo 1987).

6.1 Breeding cycle

Pre-breeding season: Outside the breeding season, territories are more loosely defined as individuals range further afield. Nest refurbishment may start soon after fledglings leave the territory in September and October, although in January and February nest construction substantially increases (Watson 1997). The pre-breeding season is associated with aerial display flights composed of elaborate vertical manoeuvres (Fig. 4). The purpose of these display flights is probably for territorial establishment so as to warn off neighbouring individuals, although an element of courtship may also be involved (Watson 1997).

Figure 5. Eight-day old Golden eagle chick attacking its younger sibling (reproduced from Watson 1997).

Breeding season: Laying dates vary enormously according to the literature, prompting studies to focus on the inter-annual variation of laying dates in different parts of the eagle's range (Steenhof *et al.* 1997, Watson 1997, Martinez *et al.* 2006). At one extreme there is Alaska where laying does not start until as late as May (69^{o}N). The other extreme is Oman where laying may be as early as December (20^{o}N) (Watson 1997). Further still, projections made by Watson (1997) suggest that in Ethiopia laying dates may occur in November. Steenhof *et al* (1997) provides one of the few studies in this field displaying winter severity and food abundance as two key parameters for influencing laying date. Winter severity was defined as the number of days the temperature never rose above -7 and the number of days it fell below -18. Steenhof's study in south-western Idaho showed a significant relationship between laying date and the time at which food initially became available. However, the basic principal of what regulates laying dates (winter severity and food abundance) is likely to apply also to other populations.

Laying in northern Sweden starts during late March or early April, following a period of increased nest building activities and reinforcement of territory boundaries (Tjernberg 1983b). The laying dates range from the end of March to mid April, although this can vary from year to year depending on weather and the severity of the winter (Tjernberg 1983c).

There is little literature on parental roles, but the male's role is essentially to hunt, although he may occasionally incubate for short periods merely to relieve the female who incubates most of the time. After 41-45 days of incubation the first chick hatches followed by any siblings 3-5 days later (Fig.5, Watson 1997). This resulting age difference may induce cainism, a widespread phenomenon throughout the genus *Aquila* and sometimes influenced by food availability. Nestlings will remain in the nest for around 10-12 weeks, although during years when the rate of food delivered to the nest is low (due to poor food availability or insufficient hunting from a sub-adult male), the nestling stage will be longer (Watson 1997). Throughout the initial stages of the nestling period the male dominates food deliveries bringing in 1.2 prey items/per/day as opposed to the female's 0.6 prey items/per/day (Collopy 1984). The female increases the frequency of her hunting bouts from week 7-9 of the nestling period to meet the demands of their nestlings (Collopy 1984). Through September-October adults begin to wean nestlings by considerably reducing their food deliveries to facilitate fledging (Collopy 1984, Watson 1997).

Post fledging period: When nestlings have fledged the breeding season is over. Despite the importance of the post fledging period, from here a notable decrease of literature occurs and very little is known about the activity and behaviour of immature birds (O'Toole *et al.* 1999) until they enter the breeding population several years later (Watson 1997). This trend in literature is common throughout many raptor species, and it has only been within the last decade and through the application of satellite tracking (McIntyre *et al.* 2006b, Soutullo *et al.* 2008) to raptor research that relevant literature is beginning to emerge (Weston *et al.* 2009). It is unquestionably a critical stage in an eagle's life, when hunting abilities and independence must be achieved within an unknown landscape in order to survive.

A handful of studies, mostly in America, have focused on the behaviour of golden eagles during the dispersal phase. Unlike other *Aquila* species where parental-offspring conflicts may arise to facilitate juvenile dispersal (Gonzalez *et al.* 1989), O'Toole *et al* (1999) observed no aggressive interactions from golden eagles towards their young. Following dispersal, siblings generally flew and hunted together while also feeding and preening together. During the initial stages of the post fledging phase, individuals made short excursions away from the territory only occasionally returning to the safety of the nest and reassurance of a reliable food supply. The duration of these excursions increased with time as shown from telemetry studies in Finnmark, Norway (Systad *et al.* 2007, Nygård 2009). From Finnmark, dispersing golden eagles flew to the eastern coast of Sweden and on into Finland, with males generally travelling further afield than females (Systad *et al.* 2007, Nygård 2009). The studies concluded that movements by golden eagles were greatest over their first three years of life as opposed to their fourth or fifth years when individuals returned to the vicinity of their natal territory in order to establish a breeding territory (Systad *et al.* 2007)

6.2 Factors influencing reproduction

This section focuses on the variables that may affect a breeding population. I leave discussions of forestry to section 9 as this is a large industry in Sweden that has the potential to exert both positive and negative effects on biodiversity and the availability of golden eagle nest sites and prey.

Sub-adult golden eagles normally belong to the non-breeding population, and Whitfield *et al.* (2004) called these individuals the sub-adult “security” cohort. If adult mortality increases, sub-adults will move into previously occupied territories earlier than would otherwise be expected (Whitfield *et al.* 2004). Normally, golden eagles establish a territory within 4-5 years after fledging (Watson 1997). Any increase of sub-adult breeders, decreases the average productivity at a population level as it is likely they will not breed for several years despite having left the sub-adult security cohort and becoming territory holders. The amount of sub-adult birds is therefore a good indicator of the population status, but sub-adults tend only to hold breeding territories, either when prey numbers are very high, or when adult numbers become depleted (Sanchez-Zapata *et al.* 2000).

Nest density and spacing varies considerably between regions due to carcass abundance, nest availability and persecution. Generally, breeding pairs nest as far from neighbouring pairs as possible, probably to minimise conflicts with neighbouring eagles (Watson 1997). Nest spacing has a pattern of extreme regularity in golden eagles (Tjernberg 1985). This only holds for larger raptors where intra-specific territorial spacing occurs (Martinez *et al.* 2008). A change to a more random or clumped distribution would indicate a golden eagle population under threat of habitat loss and a lack of suitable nesting sites (Tjernberg 1985). Studies have commonly used a G-index to compute nest distributions, where large values (in the interval 0-1) indicate a regular distribution and values closer to zero indicate more random distributions (Tjernberg 1985). The G-index is the geometric mean of the squares of the nearest neighbour distances divided by the corresponding arithmetic mean (Martinez *et al.* 2008). Throughout Sweden, Tjernberg (1985) found that nest densities increased in mountains compared to forested regions and, like Watson, attributed this to differences in food supply. Tjernberg concluded that prey populations had higher densities in the mountains (Tjernberg 1985). However, I suggest that this should be taken with caution, as it is likely Tjernberg (1985) referred only to carrion as this is what influences eagle densities (Watson 1997). I assume live prey is more abundant in the forest but less accessible, except in open habitats like mires and clear cuts.

The effects of prey and weather on laying dates have already been discussed (see 5 above). Studies continuously show how live prey directly influences golden eagle reproductive success (Watson 1997, Nyström *et al.* 2006). However, the nest itself may also influence reproductive success if it is poorly chosen. For example, the location and exposure of the nest may be vulnerable to human disturbance or extreme weather conditions (Watson 1997). Returning to Fig.3 (Tjernberg 1983b), Tjernberg predicted the eagle’s reproductive rate will be greatest one year after the vole peak as a result of the functional response to grouse and hare populations lagging behind the voles. Should this model be perturbed by freak weather in early spring (e.g. a late snowstorm) eagles may suffer from a year of reduced productivity (Steenhof *et al.* 1997, Watson 1997). Similarly, unusually mild weather in spring will initiate an earlier snowmelt thought to be leading to more efficient hunting and less energy expended by the female while incubating on the nest (Tjernberg 1983b). Watson

(1997) also found interesting contrasts between Europe and the United States concerning prey abundances. He concluded that the more abundant prey resources in the United States allowed larger clutch sizes on average (for example ≥ 12% were triple clutches *versus* ≤ 5% in Europe).

Through increasing the structural diversity of heather moorlands in Scotland, habitat requirements for red grouse *(Lagopus lagopus scotica)* have been met, subsequently increasing its numbers and the abundance of live prey for eagles. This has had positive effects in reaching the aim of boosting the golden eagle’s breeding success (Madders & Walker 2002).

7 Habitat selection and properties

The aim of this section is to discuss habitats that golden eagles utilise within their home range. First, I address these on a nest site scale then expand the discussion to a landscape scale introducing modelling techniques that have facilitated in habitat studies.

A wide range of studies have been published on habitat preferences across the golden eagle's range using different spatial scales to quantify habitat selection criteria (Bergo 1984, Menkens & Anderson 1987, Marzluff *et al.* 1997, Carrete *et al.* 2000, McIntyre *et al.* 2006a, Lopez-Lopez *et al.* 2007). Golden eagles often remain in one territory for many years and further breed in the same nest for consecutive years. Bergo (1984) suggests this consistency may indicate particular qualities such as protection from abiotic environmental factors or predators, views from the nest site towards special areas or energetically favourable terrain.

7.1 The eyrie

A suitable starting point to discuss the golden eagle's habitat is the eyrie itself and from here I shall build a picture of the surrounding landscape. Eyries can be phenomenal structures and may exceed 0.5-1.0m high and 1.0-1.5m diameter (Watson 1997). The largest nest Tjernberg (1983a) found in Sweden measured 4.5m in height, a product of many years of construction using sticks from fresh pine. Breeding pairs often have several eyries (up to 12 ones) in a territory (Watson 1997). However, only one is usually active, although according to Lopez-Lopez (2007), the eagle pair may switch to alternative nests. Watson (1997) observed that pairs may maintain a nest at each end of their territory. This could have two purposes: i) to reinforce ownership, or ii) act as insurance in case the primary nest collapses or is hit by a late snowfall. Thus, this could explain some degree of the nest switching seen by Lopez-Lopez (2007).

With a predominantly tree nesting population, as in Sweden, studies of habitat selection inevitably ask "Which trees do golden eagles select, and why?" By far the most detailed study in answering this question and further questions at this scale come from Sweden (Tjernberg 1983a). Tjernberg's thorough work describes the habitat selection properties of a tree nesting population. Preferences for pine trees (98.2%) over spruce trees (1.7%) are shown with a mean pine tree age over 335 years, and barely touching trees younger than 200 years. This requirement for older trees is most likely due to the immense weight of an eyrie. Watson (1997) estimated that eyries can weigh up to several hundred kilograms. Tjernberg (1983a) also recorded the height, placing and location of eyries (and stand selection, see below), concluding that the mean height of nesting trees in northern Sweden was approx.17m although nests were often located at approx.12m above ground. This supports the only other similar study of its kind (Menkens & Anderson 1987) stating that nests are usually in the top one third of the tree. Finer details such as the placement of the nest in the tree have been studied by Tjernberg (1983a) who categorised nest placement into four groups (Fig. 6).

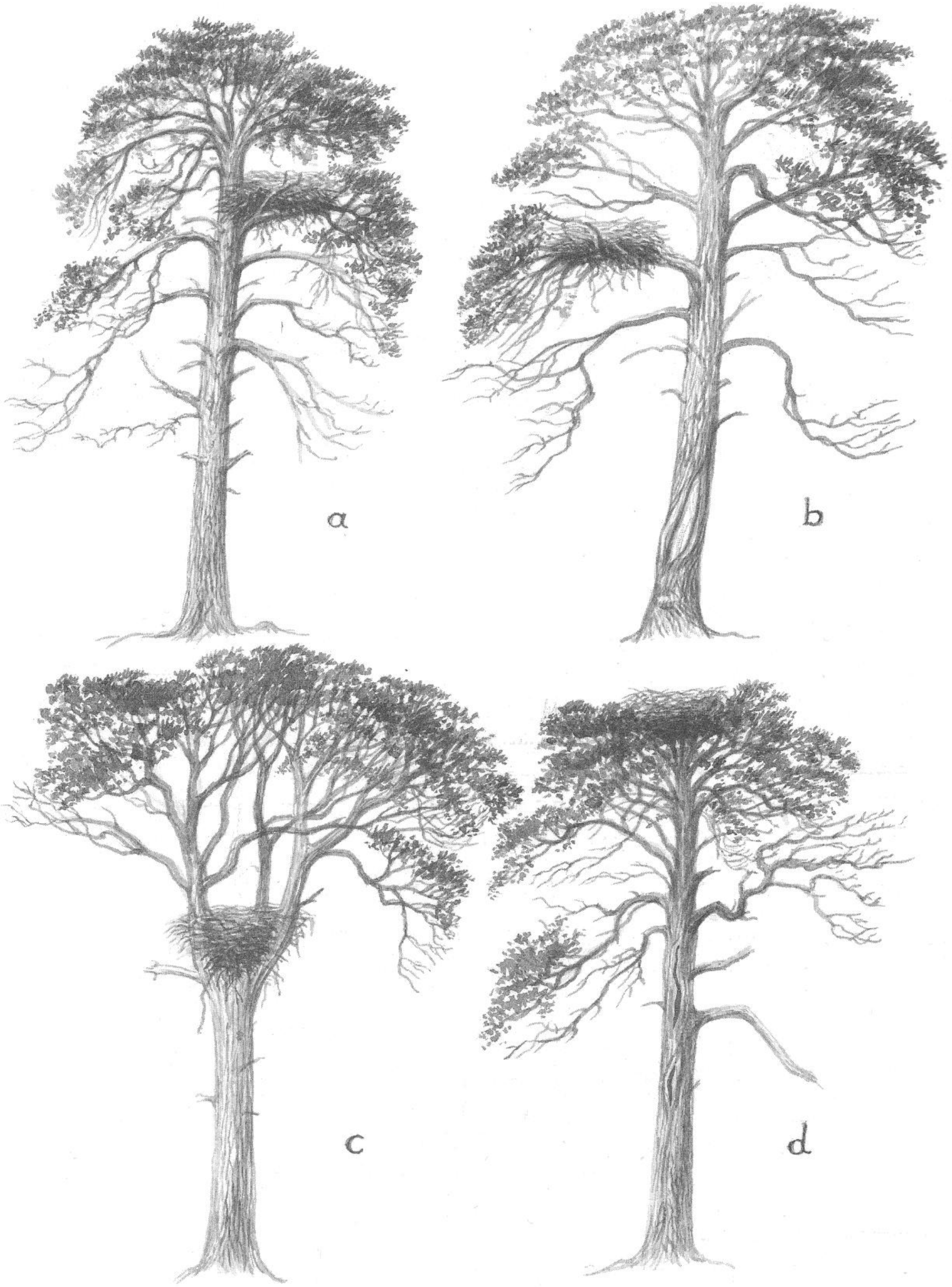


Figure 6. Main types of nest placement in trees throughout Sweden, a = 73.5%, b = 13.0%, c = 4.3%, d = 9.2% (Tjernberg, 1983a).

Interestingly, despite the golden eagle being a cliff nesting species throughout most of its range, Tjernberg found that in Sweden individuals had a preference for trees when confronted with both alternatives (Tjernberg 1983a). It is likely more tree nesting would have occurred also in Scotland prior to the destruction of native woodlands (McGrady & Petty. 2005). This would have linked Scotland into the western edge of the boreal forest where similar prey species once were found for the eagle (McGrady & Petty. 2005).

Watson (1997) compared the location of occupied nest sites (N=400) to the aspect of different nesting crags (outcrops of rock) in Scotland (assuming these crags reflected the orientation of potential nest sites). He found that 58.3% of these had a north-eastern aspect. Watson (1997) explained this directional selection in two ways; i) by avoiding excessive exposure to the sun thus reducing the risk of nestlings overheating on southern facing slopes, and ii) by being more sheltered from inclement weather that mainly comes from the south west in Scotland. It should be noted that in cooler climates bad weather can be a problem for eagles. For example, if the eyrie is over exposed the risk of a late snow fall in early spring delaying breeding or even forcing nest abandonment, is greatly increased (Steenhof *et al.* 1997, Watson 1997). Studies from continental Europe highlight the influential role bad weather may have on nest site selection (Tjernberg 1983a, Bergo 1984).

7.2 Habitat selection at a landscape scale

With raptors as large as golden eagles, it is crucial to study their habitat selection at a larger spatial scale than the nest site scale. In this section, I present the landscape scale and different habitat selection criteria that golden eagles frequently use at this scale, namely prey availability, avoidance of humans and topography (Lopez-Lopez *et al.* 2007, McIntyre *et al.* 2006a, Marzluff *et al.* 1997).

It has been demonstrated that tree age is a fundamental requirement on a nesting tree (see above), but when looking at the whole stand, the trees need not all be so old. Tjernberg (1983a) frequently found nests in isolated pines among younger stands or mixed stands. It is likely that stand size and proximity to clear felled areas has considerably changed since the study by Tjernberg (1983a), when 32.5% of nests were located in patches less than 10 hectares and 18.1% of nests in patches less than 5 hectares. In Fennoscandia, clear felling has increased prey availability for predators (Sulkava & Huhtala 1997, Kurki *et al.* 2000).

Golden eagles and humans have had a long history of conflicts, primarily over livestock, and golden eagle benefit most if they settle furthest away from humans (Kaisanlahti-Jokimaki *et al.* 2008, Lopez-Lopez *et al.* 2007). Similar conflicts are seen in the closely related black eagle, the southern hemisphere equivalent of the golden eagle (Davies 1999). Unfortunately, minimising conflicts in today’s world is increasingly difficult with human recreation and activities rapidly expanding and affecting mountain regions (Kaisanlahti-Jokimaki *et al.* 2008). This is further discussed under land use change in section 9.

The golden eagle being typically a mountain species, selects terrain generally at the higher altitudes in the landscape (Watson 1997). The optimal altitudinal positioning of eyries within the landscape were discussed by Watson (1997). He suggested that was the result of the balance between decreased human predation (at higher altitudes) and increased energy expenditure from transporting food uphill. Besides suitable nest locations, topographical features also serve additional purposes in territories. Ridges, for example, facilitate flight paths and reduce energy expenditure through the use of deflected updrafts of air currents (McLeod *et al.* 2002). This use of air currents by large raptors has prompted surprisingly few studies that incorporate any indices of topographic variance (Whitfield *et al.* 2001, McLeod *et al.* 2002, Lopez-Lopez *et al.* 2006, McIntyre *et al.* 2006a).

McLeod *et al.* (2002) have advanced the modelling of golden eagle habitat selection with the PAT (predicting *Aquila* [*chrysaetos*] territory) model. The model incorporates prey availability, avoidance of humans and topography in sophisticated spatial and terrain modelling procedures based on positions of radio-tracked adult golden eagles in Argyll, Scotland (see also McGrady *et al.* 2002). The PAT model was derived from the older and more basic RIN (Research Information Notes) model earlier developed by McGrady *et al.* (1997). Both models were designed for the non-breeding season and to model ranging behaviour. However, the RIN model is more simplistic assuming all elevations in the core range being used by eagles, as opposed to only elevations >150m outside the core range. The PAT model was constructed based on observed eagle ranging positions, ridges and peaks, and a circular range with a fixed radius around the nest centre as in the RIN model. It is assumed a higher range of elevations are explored in the core area than on the range boundary, allowing an elevation cut off point to be made below which eagles are unlikely to range (McLeod *et al.* 2002). These model parameters then calculate a new locally derived range centre and range boundary based upon the eagle’s use of different habitats throughout the territory.

Geographical information systems (GIS) are an increasingly important part of conservation management. Golden eagles have been studied with GIS for essentially two purposes, i) for monitoring ranging and migratory behavioural patterns (McLeod *et al.* 2002), and ii) for studies of habitat use (McIntyre *et al.* 2006a, Lopez-Lopez *et al.* 2007, Tapia *et al.* 2007). The studies of habitat use consistently reveal topographical features as one of the main habitat requirements for golden eagles. This is also true for other large raptors such as Bonelli’s Eagles (Lopez-Lopez *et al.* 2006) and Lesser spotted eagles *(Aquila pomarina)* (Väli *et al.* 2004). Topographical indices have been calculated in a GIS using Digital Elevation Models and raster images with numbered codes representing ridges and peaks (McLeod *et al.* 2002). Alternatively, McIntyre *et al.* 2006a used a terrain ruggedness index expressed simply as the ratio between the surface and planar areas. A topographical index in conjunction with the current habitat cover and extent of human disturbance have been the key parameters in previous golden eagle habitat suitability models (McIntyre *et al.* 2006a, Lopez-Lopez *et al.* 2007). The use of GIS has also enabled the integration of aerial photography into scientific studies, which has advanced analysis of landscape habitat composition and habitat use, also encouraging more multi-scaled approaches to develop (Lopez-Lopez *et al.* 2007). These advances are enabling more accurate landscape suitability models to be created with increased amounts of geographical data becoming available into this expanding field. For example, in Sweden *k*NN-data derived from satellite images have been successfully used for studying habitat properties of the grey sided vole *(Myodes rufocanus)* at the landscape scale (Ecke *et al.* 2006, Hörnfeldt *et al.* 2006).

Väli *et al.* (2004) studied the geographical variation of different land cover types and their proximity to landscape elements around lesser spotted eagle *(Aquila pomarina)* nests in Lithuania and Estonia. When eagle's nests were compared to random territories four variables showed significantly different distributions, namely the amount of forest within 2km of the nest, the area of optimal foraging habitat within the same 2km radius, the proximity of anthropogenic edges and the proximity to remote water bodies (Väli *et al.* 2004).

8 Golden eagle monitoring

Research and monitoring techniques for golden eagles often differ between countries and/or geographical regions. This section discusses how golden eagle monitoring has developed across Fennoscandia and provides an overview of the protocols and monitoring methods in practice today.

Raptors are a notoriously difficult group of birds to study simply due to being often sparsely distributed across the landscape and nesting in remote locations. Monitoring in northern Sweden dates back to the late 1960s when local ornithologists surveyed nests (Ekenstedt & Schneider. 2008). Since 2001 the County Administrative Boards now monitor the mountains in Västerbotten, Norrbotten and Jämtland Counties leaving the regional golden eagle groups to survey the inland regions of Västerbotten, Norrbotten, Jämtland and Västernorrland Counties. With increased monitoring efforts in recent years, discovering new territories are now less common than in earlier years enabling a better representation of the whole population.

Standardisation of golden eagle monitoring in northern Europe was first discussed at the golden eagle symposium in Trondheim 2003. In 2004 the Nordic criteria for a standard golden eagle monitoring protocol were formulated and adopted with some minor discrepancies between regions. For full details of the definitions of breeding criteria see Ekenstedt (2004). Throughout Västerbotten and Norrbotten counties, the Nordic criteria are used with one simplification, namely chicks of unknown age and small chicks have been categorised together as chicks (Ekenstedt & Schneider 2008).

Field monitoring starts in early spring to identify which territories are occupied, and in which ones incubation has commenced and therefore belong to those to be re-visited later in May-September, to check breeding success. In some cases, where it is unsure whether laying occurred, territories will be re-visited anyway (Nilsson *pers.comm.*). When eaglets hatch around mid May monitoring efforts throughout Sweden are increased with the aim to visit all known golden eagle territories. The most intensively and long term monitored areas for golden eagles lie in Västernorrland and Västerbotten with data back to 1968 in some parts of Västerbotten (Nilsson *pers.comm.*).

9 Land use change

Land use change is a real threat to numerous raptor species as it often results in direct loss of habitat or increased human disturbance (Whitfield *et al.* 2007a). Here I provide an overview of how different land uses have affected golden eagle populations around the world, followed by a more in depth discussion on how the effects of forestry may affect the species.

The long standing conflicts between golden eagles and humans were briefly mentioned in section 7.2 as this is a crucial habitat selection criterion at the landscape scale. An example is in Finland where large tourist destinations with high levels of snowmobile tracks and ski tracks proved to have a negative impact of up to 10km upon golden eagle territory occupancy (Kaisanlahti-Jokimaki *et al.* 2008). It should be mentioned that not all studies have found a negative impact from human activities. Whitfield (2007b) found little impact upon territory occupancy when using Munros (popular mountains for hill walkers >900m.a.s.l in Scotland) as the centre of recreational activity. This may be due to the simplicity of Whitfield's study in contrast to that of Kaisanlahti-Jokimaki *et al* (2008), who not only included the centres of activity but also the trails and impact they had. In Sweden, despite incorporating both trails and specific locations (fishing lakes, forest roads, paths, recreational cottages and permanent settlements), Tjernberg (1983a) did not find any significant difference in golden eagle breeding success between nest sites located near, or far from human disturbance when grouped into low, intermediate and highly disturbed nests. Despite explicit data on increased tourism in Sweden the World Tourism Organisation has predicted a growth of 3.1% per year throughout Europe between 1995-2020 (Anonymous 2003).

Whitfield (2007a) studied the habitat loss associated with afforestation in Scotland. The loss of open habitat carries a time lag of some 10-15 years after planting (Whitfield 2007a). However, since habitat requirements at a landscape scale constitute a nest site habitat, and a foraging habitat (Petty 1998), optimal breeding territories are likely achieved through a balance between afforested and deforested land. Therefore, forestry likely generates both positive and negative effects for golden eagles (Whitfield *et al.* 2001). Many studies have focused on the negative effects (Whitfield *et al.* 2001, Pedrini *et al.* 2001b). However, these studies relate to more southern latitudes (below the boreal forest) and/or study the effects of afforestation, not deforestation. Forestry is discussed further in sections 9.1 and 9.2.

Research into the effect wind farms have upon golden eagles has mainly come from Scotland and North America (Hunt 1999, Walker *et al.* 2005). That type of research must be addressed with studies before and after the construction of the wind farm (Walker *et al.* 2005). Walker *et al* (2005) found that before construction, flight paths followed normal topographical features. However, after construction eagles flew around the wind farm irrespective of topography. Avoidance and subsequent habitat loss is only one aspect, the other being collision risk (Walker *et al.* 2005). This often fatal scenario is fairly high in golden eagles and other raptors because of i) their territorial behaviour, ii) large wind turbines posing as potential perching sites (some older designs), and iii) golden eagle activity and wind turbines require similar locations due to their common preference for strong winds, usually occurring at higher elevations. In addition, both often prefer sites away from human civilisation.

Over the past decade a substantial increase in the number of proposed wind farms has been a dominant driver behind land use change in Sweden. In 2009, the number of wind farms either already built, currently being constructed or being planned for the following counties in northern Sweden are as follows: Gävleborg (0, 2, 17), Jämtland (2, 5, 19), Västernorrland (0, 1, 6), Västerbotten (0, 5, 11) and Norrbotten (2, 2, 10) (Anonymous 2009).

9.1 Golden eagles and forestry - a global perspective

It has been suggested in several studies that plantation forestry in montane areas has negatively affected the reproductive success of the golden eagle. The core literature in this field comes predominantly from Scotland (see below), but studies have not been in complete agreement as to what effect intensified forestry has had (Watson 1992, Pedrini *et al.* 2001b, Whitfield *et al.* 2001). Long term effects of habitat change may be masked by the time lag between forest re-growth and productivity declines in the eagle (Pedrini *et al.* 2001a). Initially after cutting, shrub vegetation will provide a good prey resource for the golden eagle, but after 10-15 years canopy closure occurs restricting the eagle's accessibility to the forest floor for hunting (Watson *et al.* 1992). An example is seen in Galloway (south-western Scotland) where golden eagles responded negatively to afforestation due to the decrease in land suitable for hunting (Marquiss *et al.* 1985). An initial surge in prey abundance may have been involved in the study by Pedrini *et al* (2001a), as they found no negative effect of woodland expansion in the Italian Alps but rather slight positive effects. Further, studies in Scotland have made comparisons between new native woodlands and conifer plantations, concluding that both have similar negative impacts upon potential prey biomass and the availability of prey (McGrady & Petty. 2005). Whitfield *et al.* (2001) found most golden eagles responded negatively to afforestation, with breeding success being adversely affected in most ranges with afforestation. They also cautioned against the use of over simplistic rules such as that put forward by Watson & Langslow (1987), i.e. that 40% forest cover within 4km of the range centre causes eagles to abandon their territories. Instead, Whitfield *et al.* (2001) suggested the extent of forest cover in a territory should be viewed and analysed in interaction with other variables. Such variables include the proximity of neighbouring territories and prey availability. Golden eagles in territories constrained by neighbours were more likely to abandon their territory if faced with afforestation than individuals with fewer neighbours that had the option to expand their territories (Whitfield *et al.* 2007a).

For a more global perspective of forested landscapes with golden eagle territories I now move away from the core literature to literature relating to less well known areas of their range. Japan is an example of where golden eagles have been little studied, and where eagles interact with forested landscapes. The proportion of territories that are forested is high and in recent years there has been a decline in the number pairs successfully fledging young (47.1% in 1981-1985, 40.7% in 1986-1990 and 26.7% in 1991-1995 (McGrady *et al.* 2004). This has been attributed to intensified forestry causing increased forestry coverage and reduced food availability (McGrady *et al.* 2004). McGrady *et al.* (2004) also reports that home ranges were larger throughout forested regions (171-215km^2) than in alpine areas (79-98km^2) of Austria. These differences in home range sizes are likely due to closed forests being less efficient hunting ground than more open areas. The Appalachian mountain range is one of the few mountain ranges in the northern hemisphere without golden eagles due to its very dense forest cover (Watson 1997).

9.2 Golden eagles and forestry in Sweden

Over half the Swedish golden eagle population is dependent on trees. Further, forestry is one of the largest industries in Sweden, although no decline of golden eagle populations have been directly linked to intensified forestry, in the sense of increased clear cut-cutting, during the 20th century. The likely explanation lies within Sweden's bio-geographical region and how boreal forests interact with golden eagle ecology (Watson 1997). The golden eagle is a montane species usually hunting in large open landscapes. Therefore, it can be predicted that intensive cutting of forest in Sweden may rather have benefitted this large raptor by generating more foraging habitat.

Swedish forestry practices have developed in several ways throughout the 20th century. The first half of the century saw selective logging with around 40 trees cut per hectare, many of which being older than 250 years (Ericsson *et al.* 2000). During the second half a major change in forest management occurred with shorter rotation periods and mass logging schemes, subsequently leading to a much younger forest age structure in the end compared to that at the beginning of the 20th century (Andersson & Östlund. 2004).

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 trees (Tjernberg 1985). Where such a situation arises in a population so dependent on trees, a decline is likely (Tjernberg, 1985). Tjernberg (1986b) argued that consideration according to an eight point criteria was needed to conserve tree nesting golden eagles in Sweden, as only the nesting tree was protected by legislation. These criteria advise foresters to leave potential nesting trees to grow old along with some of the surrounding trees. In addition, new road constructions and any potential disturbance should be limited to no less than 500m from a nest site particularly during the breeding season. Since these criteria were formed Swedish forestry has worked in closer cooperation with conservation, and buffer zones of 50-300m around the nest are avoided when building of roads (Ekenstedt *pers.comm.*). In addition, restrictions are put on harvesting around eagle nests between the 1st February and 31st August (Ekenstedt *pers.comm.*).

10.0 Conclusions

Changing land-uses have prompted considerable research over the past decade on the effects of these on golden eagles (Kochert *et al.* 1999, Madders & Whitfield. 2006, Kaisanlahti-Jokimaki *et al.* 2008). This review raises examples of where both positive and negative effects of forestry may be encountered. Whitfield *et al.* (2001) found that time lags associated with afforestation in Scotland may mask subsequent declines in the eagle population following canopy closure of the forest. In contrast, in Sweden clear-cutting boreal forest creates open habitats, i.e. new hunting ground, and is thus predicted to lead to a positive reproductive response of the golden eagle. Whitfield *et al.* (2001) found that most eagle territories responded negatively to afforestation on the Isle of Mull and they noted abandonment was far more complex than initially thought by Watson & Langslow (1987) and Watson (1992). Whitfield *et al.* (2001) suggested the reason why some territories did not respond negatively to afforestation was due to the ability to expand hunting ranges causing eagles to adopt a more generalist diet based on sea birds so to maintain a sufficient reproductive success.

The boreal forest landscape has changed in many ways since Tjernberg (1986b) proposed the conservation criteria for a golden eagle action plan, most of all through the change to younger and denser forest stands. For effective management of the golden eagle, it is likely that Sweden will require different strategies to countries outside the boreal forest. If practised in a sustainable way, forestry’s deforestation in combination with preserving old trees for nesting can provide a good strategy to conserve the Swedish golden eagle population in future.

With satellite tracking being now more advanced, it is important to focus on studying habitat use by adults and what juvenile eagles do and where they go during their first year of life. This will be facilitated by using habitat modelling. In addition, the extent to which individual turnover rates may explain differing reproductive success among and within territories is currently unknown in the golden eagle. Genetically mapping individuals in different territories to measure the degree of relatedness is also a major gap in the literature.

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