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Long-Term Dynamics of Three Types of Black Grouse Habitat in the Centre and at the Edge of the Distribution Range in Sweden 1850 – 2000 (*)

by
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Key words : *Tetrao tetrix*, Black Grouse, Central Sweden, habitat dynamics, long-term trends.

SUMMARY

Being a habitat specialist with a large area requirement and a complex social system the Black Grouse is a good candidate for an umbrella species in conservation planning. Gradual land use changes are usually the major forces behind trends in the distribution and abundance of such species. Throughout its range, the black grouse is found in open to semi-open vegetation types that range from natural moors and bogs, and young seral stages in the forest succession to cultural landscapes.

Using historical land use cover statistics for the trends in these three vegetation types and black grouse densities in them we modelled the long-term population trends in one landscape at the edge and one in the centre of the range in Sweden over a period of 150 years. The dynamics of these three types of black grouse habitats was very different. At the edge of the distribution a wide range of factors apparently caused the long-term negative trend, while in the centre of the distribution range the amount of the different habitat types fluctuated, but without any overall long-term trend. Using the long-term trend in hunting-bag records to validate the main outcome of the model did not contradict the results.

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Introduction

Habitat selection results in certain sets of species occupying particular habitat types (CODY 1985). Consequently, as the amount and distribution of particular habitat types change, the population size of species specialising in that habitat may «rack» the amount of preferred habitat (ROUGHGARDEN 1974, WIENS 1976, SWENSON and ANGELSTAM 1993, ÅBERG 2000). An obvious starting point for understanding the reasons behind trends and differences in the population size of a species is therefore to understand differences, trends and dynamics of the available habitat

The black grouse *(Tetrao tetrix)* is a large bird with a lek mating system where males form social flocks that are closely confined to the lek site and its surrounding, while females occupy home-ranges further away from leks (ANGELSTAM *et al.* 1985). Throughout its range the black grouse is found in open to semi-open vegetation types. These range from natural moors and raised bogs (e.g. GLUTZ *et al.* 1973, ANGELSTAM 1983, KLAUS 1990), young stages in the forest succession after large-scale disturbance (e.g. SEISKARI 1962, GLUTZ *et al.* 1973, KLAUS *et al.* 1990, SWENSON and ANGELSTAM 1993) to old cultural landscapes maintained by certain types of management (e.g. GLUTZ *et al.* 1973, KLAUS 1990, ROSENBERG 1995).

In large areas throughout the edge of the Eurasian range of the black gouse in Western Europe, the size and number of local populations have declined markedly (KLAUS *et al.* 1990, TUCKER and HEATH 1994). During the last decades, the formerly abundant black grouse is now one of the most endangered bird species in Central and Western Europe (KLAUS 1996, LONEUX and RUWET 1997, HAGEMEIJER and BLAIR 1997, STORCH 2000). The proposed reasons behind the negative trend include a wide range of factors : exploitation and fragmentation of the landscape, increases in the application of chemicals and artificial fertilisers, airborne pollution, increased disturbance of breeding grounds, spread of human settlement, increased tourism, hunting, competition from large ungulates and predation have all been mentioned (see ANGELSTAM 1988, KLAUS 1996, BAINES and HUDSON 1995). However, according to KLAUS (1996), gradual anthropogenic changes in land use often constitute the major cause. In Western Europe, the cessation of active maintenance of open landscapes plays the key role in determining the amount and quality of suitable black grouse habitats (TUCKER and HEATH 1994).

By contrast, countries in the centre of the distribution appear not to show any negative population trend (STORCH 2000). Sweden is the only country in Western Europe where black grouse population showed a positive trend between 1970 and 1990 (TUCKER and HEATH 1994). At a continental scale it thus appears as if the peripheral populations are doing worse than the ones in the centre. However, the relationship between population and habitat trends in

the core and the periphery of the range has not been quantified. BERGMANN and KLAUS (1994) recommended that this field should be given priority in future research concerning habitat restoration in areas with declining populations.

Traditionally, population studies focus on the factors influencing black grouse population size and dynamics at the scale of local patches rather than at the scale of landscapes (reviews in ANGELSTAM 1986, LONEUX and RUWET 1997). To understand the total impact of the land use on distribution and abundance of a species, it may be fruitful to compare the situation also among landscapes in regions (WIENS 1976, ANGELSTAM 1992, BUNNELL and HUGGARD 1999, LONEUX and RUWET 1997). In particular, it is important to study the full range of situations from declining populations to those that still are stable and viable (STORCH 2000).

The aim of this paper is to attempt a retrospective approach to understand the long-term trends in black grouse density by analysing habitat trends in the core and the periphery of the range in Sweden during the past 150 years. We first document how the land cover composition has changed in two areas representing extremes in the Swedish distribution range : Bergslagen in central Sweden and NW Scania in the far south of Sweden. Secondly, based on a review of black grouse densities in the different habitats, we present an estimate of the long-term population trend. Finally, an attempt to validate the model is made by using long-term hunting-bag records.

Black Grouse habitats

Large scale disturbance

Under natural conditions, the ecological niche of black grouse over much of its range was probably young successional stages originating from forest fires, windfalls and other large-scale disturbances (SEISKARI 1962, HJORTH 1970, JOHNSGARD 1973, ANGELSTAM 1983). The studies by ZACHRISSON (1977), JOHNSON (1992) and NIKLASSON and GRANSTRÖM (2000) show how the natural fire dynamics of the boreal forest resulted in a shifting mosaic of more or less even-aged stands. Today, when forest fires have been almost totally suppressed (ZAKRISSON 1977), modern forestry practices with commercial logging create a similar pattern of successional stages in most of Fennoscandia (ESSEEN *et al.* 1992).

Habitat types in Sweden-open bog : open young forest and the cultural landscape

To quantify the amount of black grouse habitat in Sweden, at least three types of habitat must be considered, young successional stages in forest, open raised bogs, and finally habitat types of the old cultural landscape.

Young successional stages in forest

In the boreal forest, black grouse prefer seedling and young stands while fresh clearcuts and older forests are generally avoided (BÖRSET and KRAFFT 1973, MARCSTRÖM *et al.* 1982, ANGELSTAM 1983). In addition, the size of the habitat patch has to be sufficiently large, usually in the order of 100 ha for a lek (ANGELSTAM 1983). Today, clear-felling almost exclusively creates this habitat type. Such patches usually become inhabited within five years after logging and last for 25 up to 35-40 years depending on the productivity of the forest, being high in southern parts of the country but low in the north (ANGELSTAM unpubl.). As patches become unsuitable, local populations should go extinct, while other local populations should be established as new patches arise.

In southern Sweden the duration of the young successional stages are usually much shorter because the forest rapidly grow too dense to constitute a suitable habitat (SVENSSON *et al.* 1999). In addition grasses and herbs rather than the required ericaceous plants dominate the ground vegetation (ODELL and DRAKENBERG 1991).

The open bog

Raised bogs and bog/fen complexes constitute natural black grouse habitats. Their quality is largely constant relative to the anthropogenically changing surrounding habitat types (BERGMANN and KLAUS 1994). Among several types of bogs and mires described by BYRKJEDAL *et al.* (1997), the open sparsely vegetated ones are preferred.

During the last decades several mires and bogs in southern Sweden have been exposed to airborne nitrogen, which acts as a fertiliser, and this has caused a succession of Scots pine and deciduous shrubs (ELLENBERG *et al.* 1989). As a consequence, the encroachment of shrubs is gradually changing the bogs from an open habitat type to a forest.

The most serious threats to the mires and bogs, listed in order of importance in European areas by BYRKJEDAL *et al.* (1997) are ; afforestation, peat extraction, tourism, other agricultural improvement, pollution (i.e. nitrogen deposition and acid rain), and hydropower.

Habitat types of the old cultural landscape

Meadows

Few terms have been so confusing and misused as the concept of meadows (IHSE 1997). While cultural historians usually focus on man and his traditional management of habitats and landscapes, botanists focus on plant

species, plant communities and biotic factors. Here the old cultural landscape aspect is adopted and the meadows are viewed as usually permanent grasslands, traditionally maintained by the cutting of hay often combined with the lopping or pollarding of deciduous trees, which were commonly present in the meadow (BERGENDORFF and EMANUELSSON 1996). The tree species used as cattle winter fodder were mainly *Betula*, *Carpinus*, *Fagus*, *Fraxinus*, *Tilia* and *Ulmus* (e.g. SLOTTE 2000).

Since this habitat is barely present in Sweden, a look at historical situations or countries still using old methods of agricultural management is necessary. Such a situation is still found in parts of the Alps (GLUTZ *et al.* 1973) and areas where the old cultural landscape has been maintained (e.g. WALDVIERTEL in N Austria and Rhön in Germany, A. SCHMALZER and K.-H. KOLB, pers. comm.).

The presence of black grouse populations in old cultural landscapes was a result of the anthropogenic mosaic of different habitats such as fields and meadows lined with various habitats suitable for retreat, breeding and winter foraging (KLAUS *et al.* 1990, KOLB 1996, A. SCHMALZER, pers. comm.). In the Åland archipelago in the Baltic, where the cutting of hay in meadows was practised quite recently, the population size of black grouse declined along with the cessation of the traditional management of wooded grasslands, and the subsequent re-growth of trees (SLOTTE 2000). According to HAILA *et al.* (1980) the Åland black grouse population declined by 80% since the 1940s, attributed to afforestation of open, grazed heath and small agricultural field and forest mosaics. Similarly, SCHERZINGER (1976) argued that the cultural landscape reflects the black grouse habitat requirements. As an example he mentioned that leks often are situated in heaths, pastures and meadows.

Pastures and forest grazing

While the meadows often were placed in connection to the farm, the pasture evolved in peripheral land, or as a result of grazing in former meadows (IHSE 1997). Along with the change in structure of the forest by woodland pasturing, the dense forests gradually were converted to more open forest structures with openings and glades in the forest (BERGLUND *et al.* 1991, ALMQUIST-JACOBSON 1994, LAGERÅS 1996, SKÅNES 1996, NILSSON 1997, BJÖRSE 2000). Historically, the forests for a long time provided pasture and fodder for a range of livestock. In all European countries, however, the general trend over the last four decades has been to abandon such pastures (TUCKER and HEATH 1994). In open forests, more light reached the ground, which gave higher insect abundance (HANSSON 1983), thus providing an important feeding habitat to the newly hatched chickens.

Also old literature supports the idea that the old cultural landscape was important for black grouse. EKSTRÖM (1894) mentioned that the black grouse inhabited open fields, heathlands and pasturelands, which were surrounded by

forests. In the dark coniferous forest, these birds were never found. In historical literature, there is evidence that the pastureland and the edges between forest and pasture were important habitats (ANDERSÉN 1861, Anonymous 1865, Anonymous 1881, Anonymous 1883, SJÖGRÉEN 1885, EKSTRÖM 1894).

Lowland Atlantic heathland

REBANE and WYNDE (1997) defined lowland Atlantic heathland as an open, mainly treeless habitat dominated by dwarf shrubs of the heath family (Ericaceae), usually heather *Calluna vulgaris*, or other species of similar appearance. Heathland gradually evolved through forest clearance and subsequent grazing (SCHAGER 1909), as an effect of increasing needs as the human population grew. In southern Sweden, the heaths were maintained by a combination of grazing and turf cutting («plaggen»). This ancient agricultural system was practised for around 1,000 years until it ceased in the twentieth century (DAMMAN 1957, MALMER 1965).

Material and methods

The model

By using historical and current maps, official statistics and local history, we compiled data about the amounts of young forest, open bog and the different forms of old cultural landscape habitats in Bergslagen (i.e. largely the Ramsberg parish) and NW Scania (i.e. largely Örkelljunga commune) (**Fig. 1**). The two study areas were 400 and 300 sq. km in size respectively. Together with a compilation of breeding densities (BD) in the three main habitat types, we made a simple model for a 100 Sq. km area to estimate the past development of the local black grouse population density (BD) in the centre and at the periphery of the distribution range :

to validate the model predictions about habitat trends in the core (Bergslagen) and the periphery (NW Scania) of the range of black grouse in Sweden, we used hunting statistics for the two regions studied as well as current densities.

$BD = (\%Habitat_A * Density_A) (\%Habitat_B * Density_B)+(\%Habitat_C * Density_C)*100$

Source material for habitat analyses

To estimate the proportions of the land area of different black grouse habitats in Scania and Bergslagen several types of sources were used (For details see **Table I, II**).

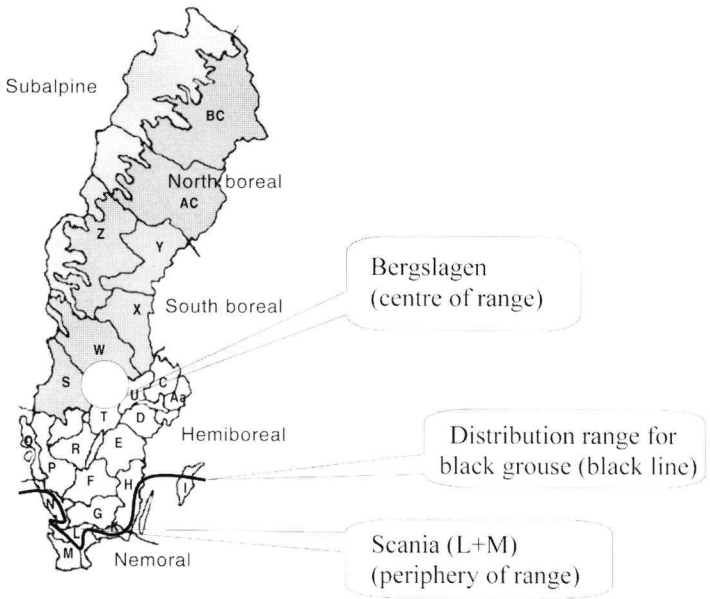

Fig. 1. The study areas
Les aires d'étude.

The agricultural statistics

Since 1927, Swedish agricultural statistics is available for approximately every fifth year (Statistiska Centralbyrån 1930). This statistics was used to describe changes of the old ancient cultural landscape. The classification of grasslands varied between years, which made direct comparisons difficult because both the definition and number of categories have changed. The different classifications used were :

(1) 1927-1944 ; mowed meadow and other grazed meadow («annan betesäng»)
(2) 1951 and 1956 ; natural meadow («naturlig äng»).

Areas included in edge study area in Scania were the forest regions («skogs- och mellanbygd») in Kristianstad and Halland counties. Areas used for Bergslagen were Örebro and Västmanland counties and 1932 to 1961 the counties of Kopparberg and Värmland were also included.

Maps and local history

Historical and current maps were used together with several sources of local history (**Table I, II**). The present amount of open bogs in the landscape was estimated by extracting the theme from digitised topographic map using a geographical information system.

Breeding densities

Data about breeding densities in the different habitats were collected by reviewing the literature and from direct correspondence with researchers involved in black grouse work in different parts of Europe.

Table I. Estimates of the proportions of the land area of different black grouse habitats in Bergslagen.
In this study «Bergslagen» is defined as the parishes of Ramsberg and Skinnskatteberg (EK 1995). WIESLANDER (1936) shows that the whole Bergslagen area had a similar development
Estimations des proportions de l'étendue des différents habitats des Tétras lyres dans le Bergslagen. On entend ici par « Bergslagen » les paroisses de Ramsberg et de Skinnskatteberg (EK 1995). WIESLANDER (1936) a montré que l'ensemble du Bergslagen a connu un développement similaire.

Bergslagen			
Period	% Young forest	% Open bog (6)	% Ancient cultural landscape
1850	67 (1)	9	4
1875	67 (1)	9	4 (7)
1900	67 (1)	9	3 (8)
1925	10 (2)	9	2 (9)
1950	>5 (3)	9	2 (9)
1975	23 (4)	9	0 (9)
2000	32 (5)	9	0 (9)

1. (1903) EK 1995
2. (1935) EK 1995 Assuming no long-term we used the values from the 1998 Swedish land survey (all bogs except wet ones).
3 (1947) Aerial photographs
4. (1975) ANGELSTAM 1983.
5. Ecological landscape plan for the study area made by the owner Assi Domän AB in 1998.
6. (2000) Extracted theme from digitised topographic map. Assuming no long-term trend we used the values from the 1998 Swedish land survey (all bogs except wet ones).
7. (ca 1870) Häradskartan
8. (1900) Kopparbergs county. BRATT and LJUNG 1993.
9. (1927, 1951, 1976) Agricultural statistics (Statistika Centralbyran 1930,1936,1941,1946,1956,1958,1963,1968,1972).

Table II. Estimates of the proportions of the land area of different black grouse habitats in Scania «Scania» was defined as the Örkelljunga commune.
Estimations des proportions de l'étendue de différents habitats des Tétras lyres en Scanie. Celle-ci est assimilée ici à la commune d'Örkelljunga.

Scania		
Period	% Open bog	% Ancient cultural landscape
1850	23 (1)	40 (3)
1875	20 (1)	20 (4)
1900	17 (1)	15 (5)
1925	15 (1)	8 (6)
1950	15 (1)	4 (6)
1975	13 (2)	0 (6)
2000	13 (2)	0 (6)

1. Wolter ARNBERG, Mats LEINE pers. comm.
2. (2000) Extracted theme from digitised topographic map. Assuming no long-term we used the values from the 1998 Swedish land survey (all bogs except wet ones).
3. (1862) HÄRADSKARTAN.
4. (1885) EMANUELSSON, U. In : BIRKS *et al.* 1988.
5. Interpolation between 1875 and 1925.
6.(1927,1951,1976) Agricultural statistics (Statistika Centralbyran 1930,1936,1941,1946,1956,1958,1963,1968,1972).

Validation of the model using hunting-bag records

To validate the model we compiled statistics of hunting-bag records from the Swedish Sportmen's Association and from local estates in Scania. We also compiled data on the present number of black grouse males in spring from the two study areas (i.e. Örkelljunga commune and the Grimsö Wildlife Research Area in Ramsberg parish).

Results

Habitat trends

Bergslagen

While the amount of open bogs was stable over time, the cultural landscape with meadows and wood pastures declined dramatically. The amount of suitable successional stages in the boreal forest succession fluctuated over time (**Table I, Fig. 2**).

NW Scania

The amount of bogs and the old cultural landscape with meadows and wood pastures decreased throughout the study period. The old agricultural landscape gradually disappeared from the statistical record of agriculture in 1961. The size of young forest stands did not exceed 5 ha, i.e. it was well below the minimum area requirements even for a single cock (ANGELSTAM 1983). Therefore, young forest is not considered as black grouse habitat in NW Scania. The results are summarised in **Table II** and **Fig. 3**.

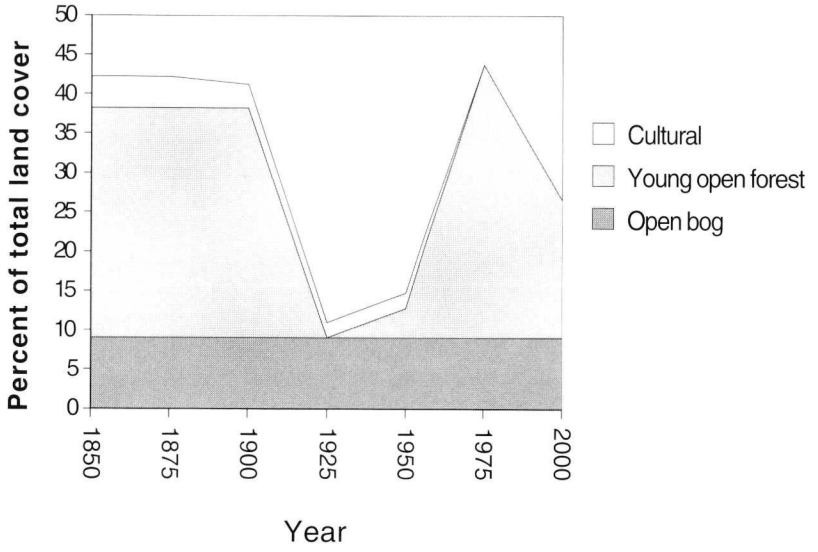

Fig.2. Changes in the amount of open bogs, open young forest and cultural landscape habitats (heaths, pastures etc.) in Bergslagen during the past 150 years.
Changements au cours des 150 dernières années des proportions de tourbières ouvertes, de stades forestiers jeunes et ouverts, et d'habitats des paysages culturaux (lande à bruyères, pâtures) dans le Bergslagen.

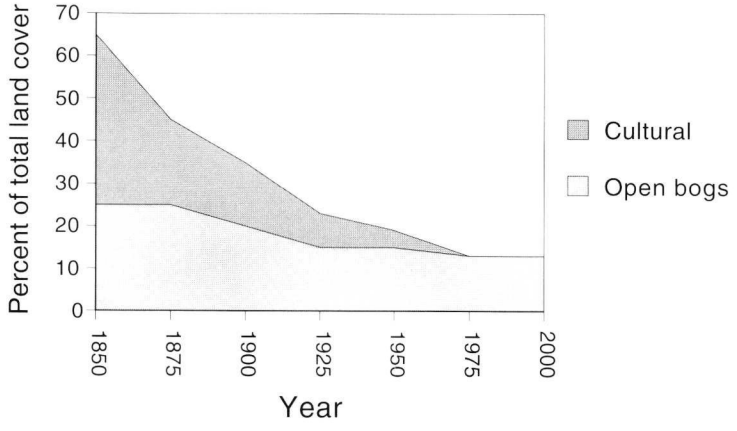

Fig. 3. Changes in the amount of open bogs and cultural landscape habitats (heaths, pastures etc.) in Scania during the past 150 years
Changements au cours des 150 dernières années des proportions des tourbières ouvertes et des habitats des paysages culturaux (landes à bruyères, pâtures) en Scanie.

Table III. Compilation of estimates of the density of black grouse males (lekking and solitary) in spring
Compilation des estimations des densités des Tétras lyres mâles (paradant en arène ou en solitaire) au printemps.

Locality	Habitat type	Patch size	Birds per patch		Density	Reference
Wales/Llandegla	Young forest	heath/young forest	1400	60	4.3	Ron Plummer
N England	Young forest	Young forest			4-6	David Baines
Grimsö	Young forest	Young forest			5	Angelstam 1983
Fagnes NE	Bog	Heath/bog	1404	28	2.0	Ruwet *et al...* 1998
Barache Michel	Bog	Heath/bog	2040	59	2.9	Ruwet *et al...* 1998
Elsenborn	Bog	Heath/bog	2200	13	0.6	Ruwet *et al...* 1998
Scania	Bog	raised bog			1	Angelstam unpubl.
Grimsö	Bog	raised bog			1	Angelstam unpubl.
Grünwald (1998-2000)	Bog	bog/young forest	1400	22-26	1.7	Petra Malkova pers. comm.
Loucna (1994-2000)		young stands with large immission clearcuts	6000	20-75	0.7	Petra Malkovapers. comm.
Sallandse Heuvelrug	Cultural landscape	Heath	1000	15	1.5	Roelof Heringa pers. comm.
Rhön	Cultural landscape	Cultural landscape	2666	38	1.4	Karl-Heinz Kolb pers. comm.
Waldviertel	Cultural landscape	Heath (military training area)	5000	90	1.8	Alois Schmalzer pers. comm.
Brembana	Cultural landscape	Alpine pasture/treeline habitat	5800	145	2.5	Ivano Artuso pers. comm.
Mont Avic	Cultural landscape	Alpine pasture/treeline habitat			2.2 – 4.1	Massimo Bocca pers. comm.
Cervieres	Cultural landscape	Alpine pasture/treeline habitat	750		1.9	Ellison *et al...* 1982
Mercantour	Cultural landscape	Alpine pasture/treeline habitat	1330		3.2	Ellison *et al...* 1982
Fretes	Cultural landscape	Alpine pasture/treeline habitat	>1000		3.5	Ellison *et al...* 1982
Bauges	Cultural landscape	Alpine pasture/treeline habitat	>700		2.3	Ellison *et al...* 1982

Black Grouse densities in different habitats

The results of the review of black grouse densities are presented in **Table III**. The mean densities for the three main black grouse habitats were 4.5 males per sq. km in young forest, 1.5 in open bog and 2.4 in cultural landscape habitats.

Estimated Black Grouse trend

Bergslagen

The estimated numbers of black grouse fluctuated over the study period (**Fig. 4**). Estimated numbers were high in the end of 19th century but showed a decline in the first half of the next century. After 1950, the estimated trend was positive, but never reached the high level estimated for the late 19th century.

NW Scania

In NW Scania the estimated numbers of black grouse was lower compared to Bergslagen (**Fig. 4**). Throughout the period the overall trend was negative.

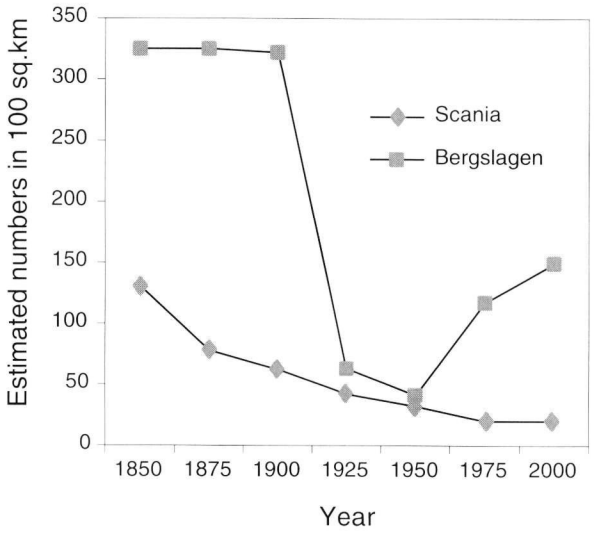

Fig. 4. Estimated black grouse numbers in a 100 sq. km landscape in Bergslagen and NW Scania
Estimation des effectifs des Tétras lyres dans un paysage de 100 km2 dans le Bergslagen et en Scanie.

Validation of the model

Bag records in Bergslagen and NW Scania

In Bergslagen the numbers of birds shot fluctuated during the period 1900-1960 but the long-term trend was negative and reached its minimum level around 1960 (**Fig.5**). In the middle of the 1960s the numbers once again started to increase and continued up to 1986. Thereafter the numbers shot declined up to present days.

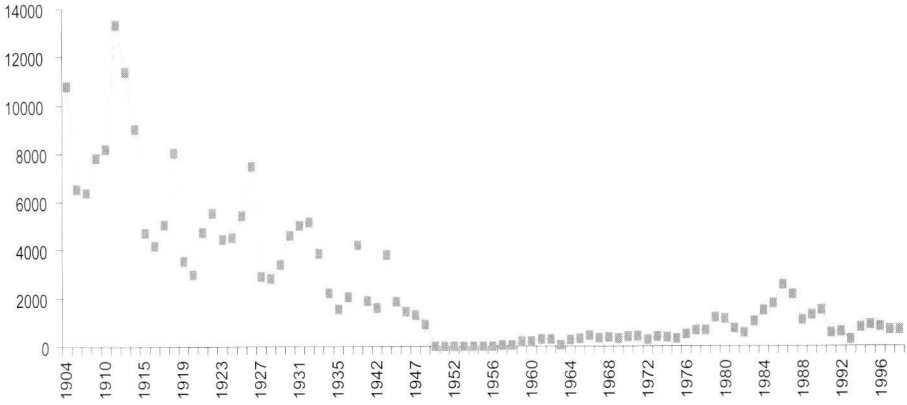

Fig. 5. Black grouse hunting records from Kopparberg county, Bergslagen 1904-1962 and during the period 1963-1998 from Örebro and Västmanland counties, Bergslagen.
Nombre de tétras lyres tués à la chasse dans le comté de Kopparberg, Bergslagen, de 1904 à 1962 et dans les Comtés de Örebro et Västmanland, Bergslagen, de 1963c à1998.

The province of Scania consisted formerly of two counties ; Kristianstad in the NE and Malmöhus in the SW. Although the numbers shot in the two counties of Scania fluctuated over time and showed some peaks, the overall trend was negative (**Fig 6**). However, in the NE county the number of birds shot were three times higher than in Malmöhus county. According to the bag records, there was no further hunting in Malmöhus county after the mid 1930s and after about 1950 in Kristianstad county.

Black Grouse counts in Bergslagen and NW Scania

Within the Grimsö Wildlife Research area (90 sq. km) the numbers of black grouse males from 1974-1982 averaged 1.2 cocks per sq. km, or 120 cocks per 100 sq. km. The model predicts about 140 cocks per 100 sq. km.

Within the Örkelljunga commune the number of black grouse males was estimated to 46 (i.e. 0.14 per sq. km) in both 1998 and 1999. The model predicts about 20 cocks per 100 sq. km.

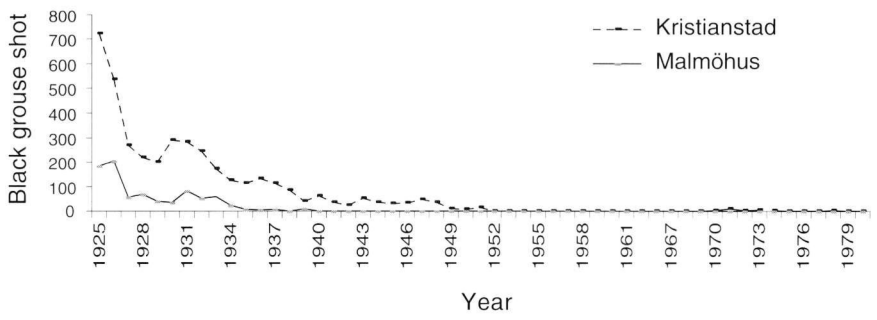

Fig. 6. Black Grouse hunting records from Kristianstad and Malmöhus counties, Scania during the period 1925 - 1980.
Relevés des nombres de Tétras lyres tués à la chasse pendant la période 1925-1980 dans les comtés de Kristianstad et Malmöhus, en Scanie.

Discussion

Modelling is an attempt to catch the true world in a simplified way. In this study, a model (amount of habitat * breeding density of black grouse males) was used to estimate the differences in black grouse population trends in the centre and in the periphery of the distribution range in Sweden. While the long-term trend predicted by the model was stable in the centre of the range, it was estimated to be strongly negative in the periphery. Neither long-term hunting bag records nor the present densities contradict the outcome of the model.

The assumed pattern of habitat tracking following succession is supported by several studies. ANGELSTAM (1983) analysed habitat composition and black grouse densities in a gradient of forest and agricultural landscapes and found a clear relationship between the amount and size of habitat patches and black grouse density. The size and numbers of patches of the preferred habitat types explained a large (73 %) fraction of the observed variation in total density of cocks between areas. The amount of habitat alone, irrespective of the required minimum size of a patch, explained 68 % in total density. Similarly, KLAUS (1991) showed that a population in the Thuringian forest, Germany, following a hurricane and subsequent succession with rowan and birch, increased from about 10 individuals in 1945 to about 300 in the late 1960s, 15 years after the hurricane.

A similar pattern was found in the old cultural landscape. Agricultural methods in the 18th and 19th century in Western Europe created large areas of *Calluna* heaths (SCHAGER 1909, SCHOTTE 1921, DAMMAN 1957, MALMER 1965, EMANUELSSON *et al.* 1985). The opening of the landscape and the large amounts of food available favoured black grouse, and the numbers of birds increased. However, as old-fashioned agricultural methods and afforestation of heaths commenced, black grouse numbers declined (BIJLSMA 1990, SVENSSON *et al.* 1992, EKBERG and NILSSON 1994, SVENSSON *et al.* 1999).

Differences in land use history as an explanation to the estimated trend

Young open forests

The amount of successional stages suitable for black grouse has fluctuated in relation to the contemporary ways of forest management. In the Bergslagen area, the coniferous forest areas were managed to satisfy the need for charcoal by the numerous ironworks (FURUSKOG 1924, WIESLANDER 1936, EK 1995). As the economic profit of the iron industry declined, charcoal production was replaced by management for timber and pulpwood around the turn of the 20th century (ANDERSSON 1960). The decreased need for charcoal and the increased interest for timber and pulpwood was responsible for the gradual ageing of the forests that ensued during the coming 50 years. In the 1960s intensive large scale clear-cutting became common and the age distribution changed in favour of young forest stands. The present forest landscape still bears a clear imprint of the forest history during the 20th century by a large proportion of stands younger than 40 years and low amount of middle-aged forest (ANGELSTAM in press).

In NW Scania, the landscape was dominated by Calluna heath (SCHAGER 1909, SCHOTTE 1921, DAMMAN 1957, MALMER 1965) and grazed forest up to the end of the 19th century (SJÖBECK 1976, BERGENDORF and EMANUELSSON 1996) Bergendorf and Enamulsson 1996. Later, the amount of young forest gradually increased due to afforestation on drained land and abandoned agricultural land (SCHOTTE 1921). In parallel with Bergslagen, around the 1960s large scale forestry was practised. However, the size of clear-cuts was at least one order of magnitude lower (ca. 2-3 ha) compared with the boreal forest (Nils ROSENLUND, pers. comm.).

Since young open forests constitute the most important habitat type in Bergslagen the estimated trend in black grouse dynamics can to a major extent be explained by the dynamics of this habitat type.

In the last decade forest management has changed. As an attempt to reach the political goal to increase and maintain biodiversity the forest management practise is less large-scale and clear-cuts smaller. The proximate future black grouse trend is therefore predicted to be negative. In Scania, young forest is much less important as habitat and was therefore not included in the model (see results).

The open bog

Around the end of the 19th century, the human population in Sweden grew rapidly (ANDERBERG 1991, BERGLUND *et al.* 1991, HÄGERSTRAND and LOHM 1993). In Scania, several bogs were drained to meet the increased needs for agricultural land. As a result the amount of bogs gradually declined. In the 1960s, draining and forest plantations on abandoned agricultural land and less productive forest areas were subsided, which lead to an additional decrease of bog areas (BERGENDORF and EMANUELSSON 1996). During the last decades, several mires and bogs in southern Sweden have been exposed to airborne nitrogen, which acts as a fertiliser, and this has caused a succession of Scots pine and bushes (Naturvårdsverket 1993, Naturvårdsverket 1994).

Since the South Swedish heaths went afforested (SCHAGER 1909, SCHOTTE 1921, DAMMAN 1957, MALMER 1965), mires and bogs play an important role to the existence of black grouse because they constitute the last remaining suitable habitat found in southern Sweden (JOHNSSON 1979). Therefore, the loss of this habitat type had far-reaching consequences and contributed to the negative trend in Scania.

By contrast, the bogs in Bergslagen were not attractive for the agricultural development. They are also located further away from the sources of airborne pollution. As a consequence they remained stable over time.

Cultural landscape habitats - meadows, heaths and pastures

In both study areas the old cultural landscape has decreased dramatically during the last 150 years as the profitability in agriculture declined. The traditional agriculture in Scania was characterised by extensive farming methods with coppice, shifting agriculture and large areas of grazed semi-open to open land (SJÖBECK 1973, SKÅNES 1996, BERGENDORF and EMANUELSSON 1996). Pollen records indicate that forest grazing from livestock become widespread as well as farming on semi-wooded land (LAGERÅS 1996, BJÖRSE and BRADSHAW. 1998). In the middle of the 18th and 19th centuries large heaths were the major land use in SW Sweden (SCHAGER 1909, SCHOTTE 1921, DAMMAN 1957, MALMER 1965).

In Bergslagen, agriculture and animal husbandry occurred continuously and with increasing frequency (KARLSSON 1997) up to the late 19th century (ANGELSTAM in press). The cultural landscape during this period was characterised by several types of managed grasslands (IHSE 1997).

As a result of the declining profitability, the agricultural land declined rapidly in the 1950s. Today, the old cultural landscape can be considered as lost. Abandoned meadows and pasturelands started in the 1960s to be afforested by man and/or by spontaneous succession of trees (IHSE 1995,

NILSSON 1997, MIKUSINSKI and ANGELSTAM 1999). Today, agriculture in Sweden is intensive and large-scale (BERGLUND *et al.* 1991), and remnants of the old cultural landscape are principally only found in nature reserves.

The cultural landscape declined in both study areas. Compared to Bergslagen, Scania had large areas of cultural land. The impacts of the declining cultural landscape therefore were higher in the southern study area. In Scania, the loss of the cultural landscape largely explains the estimated trend. As an example of land use changes, in Luggude district («härad») in SW Scania, the transition of pastureland to arable land between 1830 and 1880 is mentioned as the major cause of the low numbers of birds found in 1881 (Anonymous 1881). In 1888, declines are reported in several areas of Sweden. Bogs were drained and the deciduous rich pasturelands were transformed to arable fields or dense coniferous forests was claimed (Anonymous 1888).

Additional/Alternative factors

Although changes in the amounts of black grouse habitat appear to explain the different trends in the black grouse population in the core and at the edge of the distribution range, several other factors could be included in the model, provided that the appropriate data are available.

Decreased patch size and patch density

For species with large habitat area requirements the amount of habitat alone overestimates the amount of available habitat. The reason is that only sufficiently large or smaller juxtaposed patches should be counted as habitat. Using the open bog layer in the digital topographic map for the study area in Scania and Bergslagen, we found that when removing bog patches that were smaller than 20 ha the amount of suitable habitat declined from 13 to 8 % in NW Scania and from 9 to 3 % in Bergslagen. Hence, as fragmentation is prolonged, there is a risk of overestimating the amount of habitat. When including only bog patches above the minimum area requirement, the estimated grouse density was reduced by 6% in Bergslagen and 30% in NW Scania in year 2000. By this the fit with the actual counts becomes even better.

Effect of habitat quality

Using information about land cover classes may be misleading if the quality of the land cover class changes over time. This is particularly critical in anthropogenically transformed habitat. As an example, the classification of grasslands varies between sources, making comparisons between different time periods difficult (SKÅNES 1996).

Does increased fragmentation lead to increased predation ?

The predation pressure may be higher in fragmented forest areas interspersed with agricultural land (e.g. ANDRÉN *et al.* 1985, ANDRÉN 1992, KURKI *et al.* 1998), as higher densities of generalist predators are supported by landscapes containing agricultural patches (ANDRÉN 1992, KURKI *et al.* 1998). In a Finnish study, KURKI *et al.* (2000) showed that breeding success of grouse was negatively correlated with both fragmentation of forest area per se by farmland and the decreasing proportion of older forest as a result of clear-cutting. The authors suggested that the most likely cause of observed spatial correlation was nest predation by generalist predators in fragmented forest landscapes. This could be an additional factor that contributes to the negative trend we found.

Hunting traditions and predator control

Before the decline of the cultural landscape, people lived in crofts and small farms in the countryside (BERGLUND *et al.* 1991). To protect their animals and livestock, they carefully looked after predators. Since people were spread out in the landscape, there was a higher hunting pressure on carnivores. Today most of small farms and crofts are abandoned or do not have any domestic animals. Moreover, landowners lease their land to hunters who mainly hunt moose, roe deer and hares. Hence, little attempt is made to hunt predators today.

Hunting pressure and records

Throughout the literature, there is ample evidence that the black grouse has been an important and popular game species in Sweden. Throughout the 18th and 19th century and during the first part of the 20th century, the black grouse together with other species was an economically important game for the Swedish population. Especially in the wooded districts, it constituted a valuable addition to the household. Additionally, large numbers of hunted birds were exported to the big cities (SVENSSON *et al.* 1999). FISCHERSTRÖM (1769) estimated the yearly import arriving to Stockholm to be in order of 53 000 birds. In the 1870s, the number still was around the same (Anonymous 1870).

However, in the old literature black grouse is often mentioned in context with hunting statistics. Little information (if any) is given of densities or population numbers. The large number of shot birds, and the importance of the game suggest hunting as a locally important factor to be considered when thinking of historical factors regulating the black grouse population (Michael FORSLUND, pers. comm.).

A negative effect of hunting on black grouse populations is suggested in old literature. In 1874, the black grouse was reported as declining (Anonymous 1874). Several reasons are mentioned behind the decline. Predation by goshawk *(Accipiter gentilis)* and red fox *(Vulpes vulpes)*, cold springs and the

tremendous increase of hunters is all mentioned but hunting was stressed as the main cause. The same reason is mentioned 1878 to explain the low numbers of birds observed in the northern part of Örebro county in south central Sweden (Anonymous 1878) and 1856 (SUNDEVALL 1856) in Scania.

Black grouse conservation at the edge of the range

TUCKER and HEATH (1994) proposed that key localities in central Europe should be protected and managed for black grouse, accompanied by conservation measures in the surrounding regions aimed at maintaining mosaics of suitable habitat. In the present study the two study areas showed different pattern and the model suggested that populations in the periphery do worse than the ones in the centre of the distribution range. Hence, our results suggest that all the factors/effects reviewed above affect the grouse populations earlier and stronger at the edges of the range than in the centre.

Habitat management is needed

Under natural conditions, the black grouse habitats over much of its range were created by large-scale disturbances (SEISKARI 1962, HJORTH 1970, JOHNSGARD 1973, ANGELSTAM 1983). Since naturally large-scaled disturbances nowadays are rare, the presence of black grouse is strongly restricted to man-created habitats. In the last decades black grouse numbers in Central and Western Europe have declined dramatically in parallel to the cessation of active use of cultural land, in particular grazed land and meadows. Hence, there is a active management need of understanding the mechanisms involved in habitat management. Therefore, managing these man-created black grouse habitats in an ancient, appropriate manner that integrates with the species' habitat requirements is essential to ensure survival of future black grouse populations (STORCH 2000).

Quality and quantity of patches

In conservational work the question of quality or quantity of habitat patches often arise. Which step is the most important : increasing quality or quantity of a patch ? ANGELSTAM (1983) showed that birds in larger patches do better than smaller ones. Since most patches in the edge of the distribution range are small and isolated, more attention should be focused on enlarging habitat patch size along with increasing the connectivity within the landscape.

Browsing control

Overgrazing by ungulates in heathlands is listed as one of the black grouse threats (BAINES and HUDSON 1995, BAINES 1996, BERGMANN and KLAUS 1994, STORCH 2000). Since deer and sheep graze *Calluna* and *Vaccinium*, high

stocking and deer rates can lead to excessive grazing of vegetation which can reduce the amount of food/cover available to black grouse. Browsing control is therefore important when managing heathlands.

Predator control

In a fragmented landscape surrounded by agricultural land there is a wide range of generalist predators including red fox *(Vulpes vulpes)*, Corvids and Gooshawk *(Accipiter gentilis)* (ANDRÉN *et al.* 1985, ANDRÉN and ANGELSTAM 1988, KURKI *et al.* 1998). In most regions of Europe with small and highly endangered populations at the edge of the distribution range, predation is experienced as the major proximate threat to the black grouse (KAPHEGYI 1998). A significant reduction of predators by predator control should probably result in improved black grouse survival (STORCH 2000).

Conclusions - the future of the Black Grouse

This study suggests that the different long-term trends in black grouse population most likely are explainable by changes in the amount of black grouse habitat. However, black grouse populations are also affected by other factors than landscape composition. Hence, direct and indirect landscape scale factors all contribute to the negative black grouse trend found at the periphery of the range in Southern Sweden.

Although there has been invested a lot of money and energy to restore black grouse habitats and to reverse the negative decline in central and Western Europe, few successes have been recorded (STORCH 2000). To increase future success in black grouse conservation, we stress the need to :

(1) consider that different mechanisms may affect population performance of black grouse in the core and periphery of the distribution range.
(2) realise that both direct and indirect landscape-scale consequences of land use change may be key factors in determining black grouse population size.
(3) understand the historical changes in land use when evaluating past trends and the present situation.
(4) improve the documentation of different population attributes making possible meta-analyses of several populations with different factors in com mon.

When trying to understand the mechanism of habitat selection and the dynamics of black grouse populations all over Europe, these four factors should be considered. With this in mind, the black grouse population dynamics become more understandable and the future conservation work will be more effective.

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ZUSAMMENFASSUNG : Langzeitdynamik von drei Birkhuhn-Biotopen in Mittelschweden Long-Term dynamics of three types of black grouse habitat in central Sweden

Als Biotopspezialist mit großem Raumanspruch und komplexem Sozialverhalten eignet sich das Birkhuhn hervorragend als Schirmart im Naturschutz. Oft sind graduelle Änderungen in der Landnutzung Ursache für das Vorkommen und die Häufigkeit solcher Arten. Im gesamten Verbreitungsgebiet nutzt das Birkhuhn offene und halboffene Vegetationstypen, die von natürlichen Mooren und jungen Stadien der Waldsukzession bis hin zur Kulturlandschaft reichen.

Unter Verwendung historischer Landnutzungs- und Forstwirtschaftskarten untersuchten wir Veränderungen im Vorkommen dieser drei Vegetationstypen während der vergangenen 130 Jahre, in einer Landschaft, die typisch ist für den Übergang vom hemi-borealen zum borealen Wald. Die Dynamik der drei Birkhuhn-Biotope war sehr unterschiedlich. Während der Anteil an Hochmooren über den gesamten Zeitraum nahezu stabil war, nahm der Anteil der Kulturlandschaft mit Wiesen und Waldweiden dramatisch ab. Der Anteil geeigneter Stadien der Waldsukzession schließlich variierte in Abhängigkeit von der jeweiligen Waldbaupraxis.

RESUME : Dynamique à long terme de trois types d'habitat du Tétras lyre en Suède centrale

En sa qualité d'espèce exhibant un système social complexe et requérant un vaste domaine vital comportant des habitats particuliers, le tétras lyre fait figure d'espèce phare dans la planification de la conservation. Les changements graduels de l'usage qui est fait des terres constituent généralement les forces majeures qui sous-tendent les variations de l'abondance et la répartition des espèces. A travers son aire de répartition, le tétras lyre se rencontre dans des faciès de végétation ouverts ou semi-ouverts allant des landes naturelles et tourbières, aux stades jeunes de recolonisations forestières ainsi qu'aux paysages culturaux.

En analysant dans une perspective historique l'usage des terres et en nous servant de jeux de cartes forestières, nous avons étudié les tendances manifestées dans ces trois types de végétation sur une période de 130 ans dans un paysage typique à la transition entre la forêt boréale et la forêt hémi-boréale dans la partie sud de la Suède centrale. Les dynamiques évolutives de ces trois types d'habitats du tétras lyre se révèlent très différentes. Alors que la situation des tourbières bombées est demeurée quasi complètement stable au cours de cette période, les paysages culturaux composés de prairies et de forêts pâturées ont décliné de façon dramatique. En fait, la quantité de stades appropriés de la série évolutive forestière a fluctué en fonction des pratiques en cours de la gestion des forêts.

Mots-clés : *Tetrao tetrix*, Tétras lyre, Suède centrale, évolution des habitats, changements dans le long terme