Ongoing population decline and range contraction in Norwegian forest grouse

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Gregersen, F. & Gregersen, H. 2009. Ongoing population decline and range contraction in Norwegian forest grouse. – Ornis Norvegica 32: 179-189.

Forest grouse diverge in niche, where Capercaillie *Tetrao urogallus* thrives in older forests, Hazelgrouse *Bonasa bonasia* is a habitatspecialist (middle-aged decidous-rich coniferous forest) and Black Grouse *T. tetrix* is an early succesionalist. We analysed the hunting statistics over four decades in Norway to explore divergence among forest grouse in spatio-temporal trends and discuss these findings in relation to factors changing habitats for these species. Overall, modern forestry has continuously modified the forests, especially Hazelgrouse and Capercaillie habitats. In the same time, climate has become warmer and more humid pushing climate zones northwards. In this study, all species revealed declines compared to the 1970s, especially profound into south and in the northernmost county. This response was strongest for Hazelgrouse and next Capercaillie. Central, inland counties along the Swedish border reveal smaller declines and are probably source areas. We propose that the effect of climate and forestry interact to reduce habitat optimality for forest grouse, and that these effects are stronger in sinks, potentially initiating range-contraction.

Key words: Hunting, grouse, boreal forest, climate, niche, forestry

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INTRODUCTION

Bags of forest grouse are a positive function of population density, in turn dependent of ecosystem quality and hunting pressure (Kurki *et al*. 2000, Ranta *et al*. 2008). Population density of forest grouse has changed with underlying changes in the ecosystem at large scale. Modern forestry has changed the forest community (Esseen *et al*. 1997, Löfman & Kouki 2001), and climate change comes on top of this (Sæther *et al*. 2004, Jonzen *et al*. 2006, Kausrud *et al*. 2008). Old forest species and habitat specialists have shown severe declines and even extinctions (Helle & Järvinen 1986, Jansson & Andren 2003, Pakkala *et al*. 2003). Since the 1950s, almost all forest area is converted to managed forests and the density of timber per area has tripled the last decades (Essen *et al*. 1997, Löfman & Kouki 2001). In the same time as forestry has converted the landscape to industrial forests, climate has become warmer and pushed climate zones northwards, and vegetation zones and other biotic responses will follow (Brommer 2008, Teplitsky *et al*. 2008).

In Europe, the density of forest grouse has fallen dramatically and large-scale range-contraction are evident (Kurki *et al*. 2000, Storch 2000), parallel to radical changes in climate and forestry practices (Ludwig 2007). The three forest grouse species Capercaillie *Tetrao urogallus*, Black Grouse

T. tetrix and Hazelgrouse *Bonasa bonasia* use different habitats in the coniferous forest mainly along axis as late to early succession, old-growth to disturbance biotopes or marginal to productive forest (Swensson & Angelstam 1993). Capercaillie prefer the late-succession old coniferous forests with rich bilberry field layer (Rolstad & Wegge 1987), whereas Black Grouse prefer the early-succession, moor-like and less productive parts of the forest (Baines 1996). Hazelgrouse, as a habitat-specialist, occupy moist, productive stream-alder valleys and deciduous-rich mosaics in the coniferous forest (Åberg *et al*. 2003). As these species diverge in niche they can be expected to respond differentially to forestry which reduces the old natural forest proportion and the deciduous component and productive parts of it (Esseen *et al*. 1997, Hanski & Walsh 2004). Relative to Black Grouse, Capercaillie and Hazelgrouse responses to forestry is expected to be larger (Swenson & Angelstam 1993).

Coastal forests in Norway are warmer, more humid and lack a stable snow-cover in winter (Ahti *et al*. 1968). They may therefore be natural sink habitats with lower habitat optimality for boreal grouse, for example through effects on the field layer (Pulliam 1988, Bokhorst *et al*. 2008, Kausrud *et al*. 2008). Most coastal counties are situated in the South Boreal, even Nemoral, climate zone (Ahti *et al*. 1968), with fewer conifers, a denser bush layer and reduced field layer of ericaceous shrubs. As global climate change pushes these suboptimal climate zones northwards, grouse will increasingly be negatively affected. Further, the forests in inland Norway are connected to massive boreal forests shared by Sweden, whereas those on the coast are isolated along the coast of Norway. This separation may introduce island effects strengthening the negative effects of environmental change (Rosenzweig 1995, Åberg *et al*. 2000). This is evident for old-growth forest dependent biodiversity in Finland with distance from pristine source areas in Russian Karelen (Kouki & Väänänen 2000, Brotons *et al*. 2003). Based on this, we predict larger effects in coastal areas for grouse during population declines and range-contraction can finally occur.

We aim to explore the Norwegian hunting statistics as a measure of population density and discuss the findings in light of relevant habitat and climate hypothesis. Specifically, we analyse the recent (36 years) temporal responses of forest grouse and test various spatial and ecological effects. In light of different niche requirements we can predict differential responses to modern forestry. As areas in the south, and along the coast, are climatically different, and isolated in the periphery of the central taiga, we expect these areas to be sinks for forest species.

MATERIAL AND METHODS

We used the national hunting statistics from all 18 counties in Norway (Table 1, Statistics Norway). The counties stretches 1 752 km from 57° N to 71° N and occupies several climatic zones (Fig. 1). We assumed that the hunting bags are positively correlated to population density and that the hunting efficiency among species is unchanged in this period (see Ranta *et al*. 2008). Ranta *et al*. (2008) found consistent effects of species and geography in correlations between forest grouse hunting bag and population counts. However, these effects are minor compared to trends discussed in this study. To standardize catches per effort we converted the catch statistics to CPUE (catch-per-unit-effort) data (Harley *et al*. 2001, Maunder *et al*. 2006). The CPUE measure relates the bags of grouse shoot in a county to the hunting effort (see below). However, CPUE data often underestimate high density and overestimate low density resulting in underestimation of temporal declines (Hatter 2001).

Statistics Norway have estimated or recorded total county-wise grouse bags from all hunters each year in the period 1971-2007 (Statistics Norway, Smedshaug *et al*. 1999, Selås 2001). The total numbers of hunters has steadily increased in the period ($r = 0.94$, $p < 0.0001$). Hunting effort

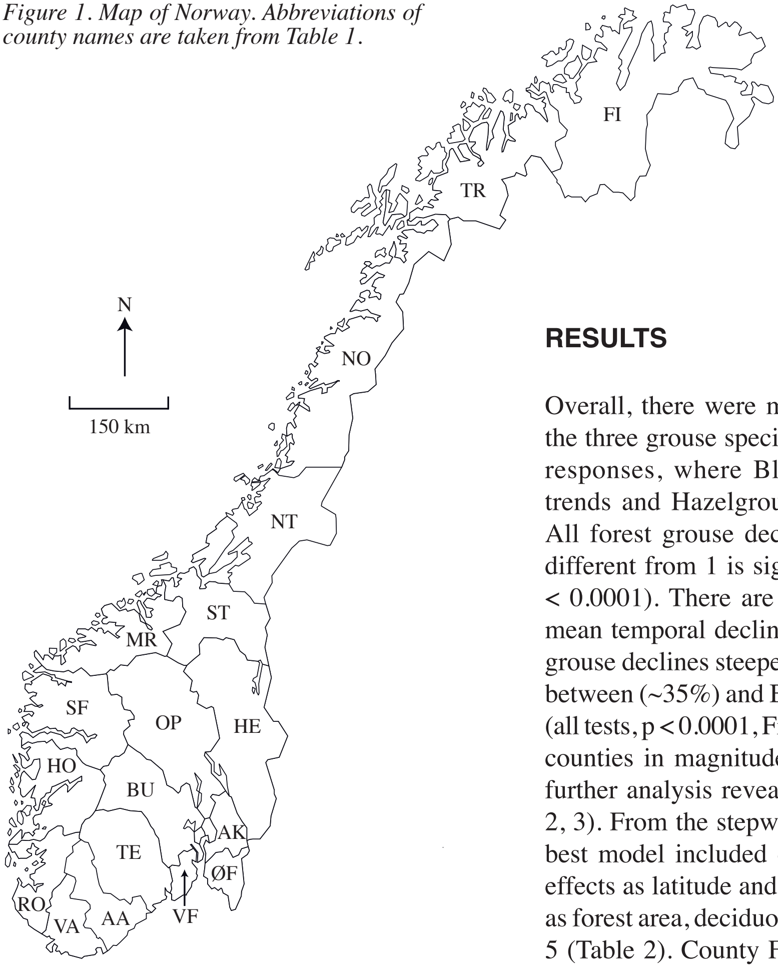
*Table 1. Environmental data - Regional statistics as geographic position, forest statistics and total grouse bags for the different counties of Norway used in this study. Forest statistics are taken from Norwegian Forest and Landscape Institute (*www.skogoglandskap.no*) (# Deciduous = deciduous forest percent in a county, logging class 5 = percent mature forest, forest area = total forest area, & = manually positioned from the «midpoint of a county» on a map). Total bags are all bags from the period 1971-2007 taken from Statistics Norway.*

Region	**Coastal/inland (see MM)**	**Latitude&**	**Deciduous forest#**	**Logging class5# (Hk5)**	**Forest area#**	**Caper-caillie**	**Hazel-grouse**	**Black Grouse**
Østfold (ØF)	Inland	6616650	9.9 %	31.1 %	239029 ha	14746	5494	18743
Akershus (AK)	Inland	6645428	15.8 %	23.9 %	334990 ha	20264	16669	57990
Hedmark (HE)	Inland	6757223	15.8 %	28.9 %	1370119 ha	125828	38799	183727
Sør-Trøndelag (ST)	Inland	6903330	22.3 %	38.9 %	422776 ha	51021	50105	70923
Nord-Trøndelag (NT)	Inland	7139095	13.6 %	36.9 %	630820 ha	82295	69246	94423
Vestfold (VF)	Inland	6593405	35.6 %	22.7 %	127114 ha	3670	5415	6665
Buskerud (BU)	Inland	6671993	18.2 %	34.8 %	582243 ha	37017	44711	86869
Oppland (OP)	Inland	6800391	26.6 %	33.7 %	759061 ha	33035	15639	92940
Telemark (TE)	Inland	6626611	20.3 %	37.9 %	539939 ha	22520	15955	59099
Aust-Agder (AA)	Coastal	6538061	15.1 %	36.3 %	326313 ha	12825	640	59097
Vest-Agder (VA)	Coastal	6500428	29.6 %	30.2 %	250586 ha	10401	143	81889
Rogaland (RO)	Coastal	6589124	35.9 %	24.3 %	136867 ha	2445	125	39436
Hordaland (HO)	Coastal	6719951	29.9 %	23.6 %	262096 ha	3689	204	55817
Sogn & Fjordane (SF)	Coastal	6856894	37.5 %	39.3 %	251707 ha	2938	338	25848
Møre & Romsdal (MR)	Coastal	6989320	48 %	32.4 %	289715 ha	11234	822	58802
Nordland (NO)	Coastal	7285202	51.2 %	33.4 %	592024 ha	20071	9477	66653
Troms (TR)	Coastal	7772071	69.4 %	36.1 %	415968 ha	9238	404	48394
Finnmark (FI)	Coastal	7914127	72.5 %		125000 ha	8929	951	1699

has increased by 67% from the 1970s to 2004 where 197 000 hunters paid their license (Selås 2001, Statistics Norway). We assumed that the relative increase in effort was approximately equal in every county and similar to the national increase. To give CPUE data, we standardized for this bias in effort by dividing bags on the proportion of hunters a given year compared to the mean number of the 1970s. This correction factor is therefore ~1 in the 1970s, and increases to 1.67 in 2004, indicating that effort has risen by 67%. To give an easily interpretable statistic to explore potential declines further, we divided each year's standardized bags in 2000-2007 to the mean values of the 1970s. We can therefore interpret the statistic as what proportion the bags of today (2000-2007) are compared to the 1970s shot by an equal number of hunters.

Climate varies from coastal Nemoral, Boreonemoral or South Boreal in South-West into inland Semiboreal, Boreal and Northboreal in the North-East (Ahti *et al*. 1968), and vegetation varies according to this (Fremstad 1997). As we aimed to study relative temporal and spatial patterns the details in these gradients are not presented here, but we believe these broad-scale climate zone differences to be important. In the statistical tests we test various spatial variables, i.e. latitude and coastal influence or forest statistics, as deciduous component, forest area and old forest proportion (Table 1). In the tests we have divided counties into two ecologically different groups, coastal and inland, those who have their major forest area towards west or not. Most coastal counties have most of its forested area to the west, except for Sør-Trøndelag and Nord-Tøndelag, with its major forest area connected to the eastern boreal forests. Thus, Sør-Trøndelag and Nord-Trøndelag are defined as inland (Table 1). Bags of Hazelgrouse and Capercaillie per area at the coast, respectively, are 7% and 22% compared to central, inland counties. For Black Grouse there is no significant difference between bags in neither cline, but it seems to be higher bags in SW. Since climate changes northwards we also test the latitudinal effect.

Figure 1. Map of Norway. Abbreviations of county names are taken from Table 1.



The temporal and spatial variation in grouse hunting bag declines was tested with various linear models (ANCOVAs) (SAS Institute). Initially, we used stepwise regression with forward selection to select the best models. A priori, all possible effects were tested and the most supported model was chosen based on the AIC criteria (Burnham & Anderson 1998). In short, the AIC criteria evaluate how much the model improves when introducing an effect at the expense of degrees of freedom. All analysis was performed on ln-transformed responses, in order to obtain normally distributed residuals.

RESULTS

Overall, there were major differences between the three grouse species in spatial and temporal responses, where Black Grouse had weaker trends and Hazelgrouse revealed strong ones. All forest grouse declines and a test of mean different from 1 is significant for all species ($p < 0.0001$). There are significant differences in mean temporal declines among species. Hazelgrouse declines steepest (~80%), Capercaillie in between (~35%) and Black Grouse least (~20%) (all tests, $p < 0.0001$, Fig. 2). The variation among counties in magnitude of declines is large and further analysis revealed spatial patterns (Figs. 2, 3). From the stepwise regression process the best model included effects of species, spatial effects as latitude and cline, and forest statistics as forest area, deciduous forest and logging class 5 (Table 2). County FI was excluded from this analysis due to its large deviation from overall trends. In the best model, species explained most of the variance ($F = 712.64$), but all other variables where highly significant, except for forest area. Models with single effects yielded AIC values 100-400 units lower than the best model. The overall pattern is larger declines for Hazelgrouse, and least for Black Grouse, larger declines into south and at the coast, and slightly smaller declines with increased older forest stand proportion and forest area.

Declines among counties range from 0.04 to 0.55 for Hazelgrouse, from 0.24 to 1.05 for Capercaillie and from 0.16 to 1.63 for Black Grouse (Fig. 3). For the mean grouse response, the counties with the 50% lowest decline are mostly situated

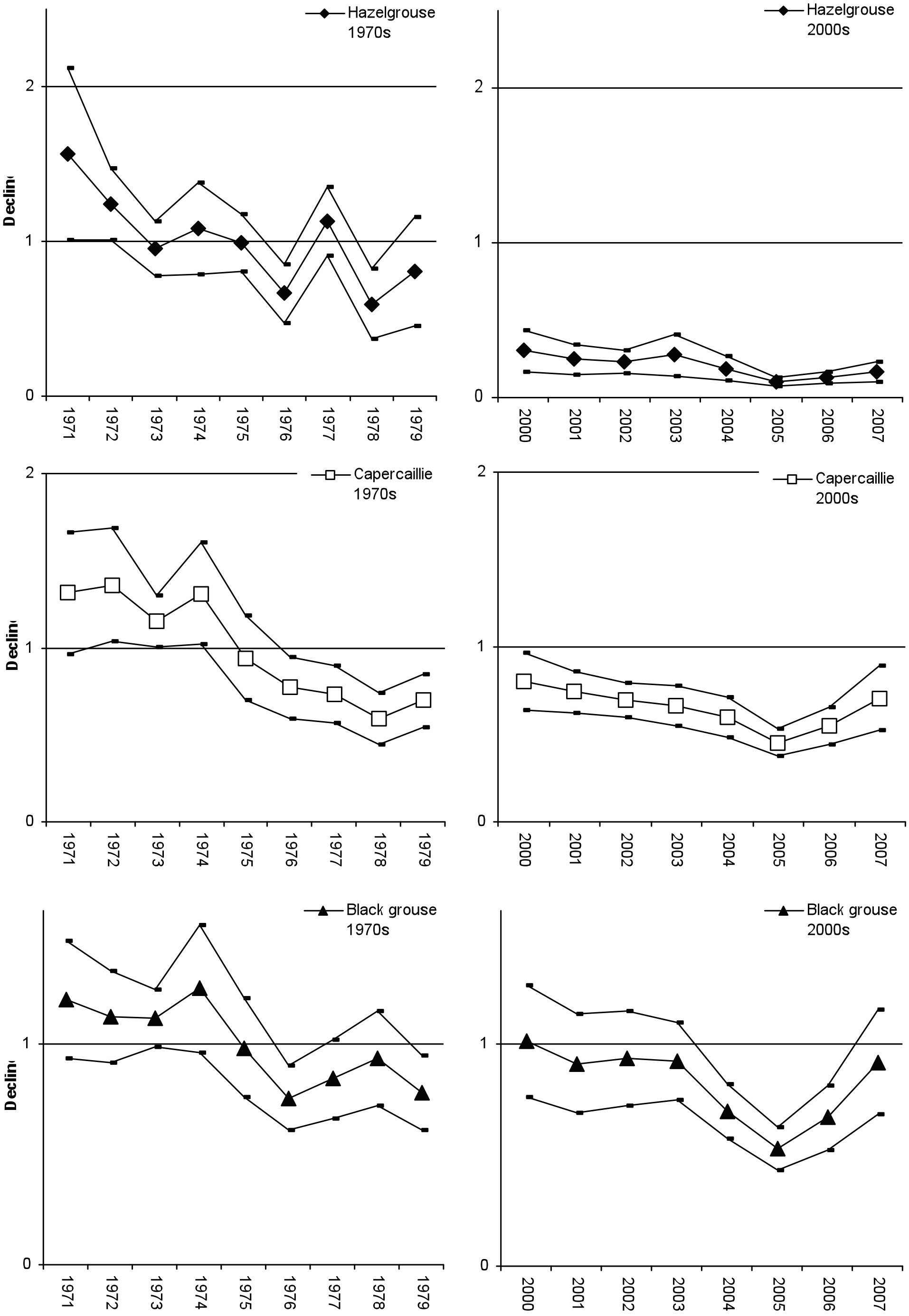


Figure 2. Temporal patterns of declines in Norway for Hazelgrouse, Capercaillie and Black Grouse. The response is bags of the periods 1971-79 and 2000-7 as a proportion of mean bags in 1970s (Mean and 95% confidence interval, see MM). Values below 1 indicate decline responses and values above indicate increases.

Table 2. *A) Model selection for linear models fit to predict declines in grouse bags in counties in Norway. Model selection criteria are based on AIC values and the best model has the lowest AIC and highest rank. Various spatial variables and forest statistics are tested as covariates. All continuous variables (including the response variable) were ln-transformed. Models are ranked after the step-wise inclusion of new variables (mod. 6-11) and examples of less influential models are given (mod. 1-5). B) Test statistics for the most supported model. Overall model results: A): $R^2 = 0.67$, $P < 0.0001$, $N = 392$.*

A) Model structure	**AICc**	**deltaAIC**	**Rank**
1) Deciduous	-76.92	423.91	10
2) Coastal/inland (CI)	-77.00	423.83	9
3) Latitude	-89.04	411.79	8
4) Forest area	-89.42	411.41	7
5) Hk5	-90.50	410.33	6
6) Species	-412.74	88.09	5
7) Species+Hk5	-461.69	39.14	4
8) Species+Hk5+Forest area	-480.95	19.88	3
9) Species+Hk5+Forest area+Latitude	-490.69	10.14	2
10) Species+Hk5+Forest area+Latitude+CI	-500.83	0	1

B) Summary statistics

Source	**Effect**	**Sum of squares**	**F**	**P**
Intercept	-52.58			
Species (Hazel vs Black and Caper)	-0.75	191.58	699.68	<0.0001
Species (Caper vs Black)	-0.12	3.55	12.96	0.0004
CI	0.11	3.32	12.11	0.0006
Latitude	3.03	5.67	20.70	<0.0001
Forest area	0.11	1.005	3.67	0.06
Hk5	0.69	4.37	15.95	<0.0001

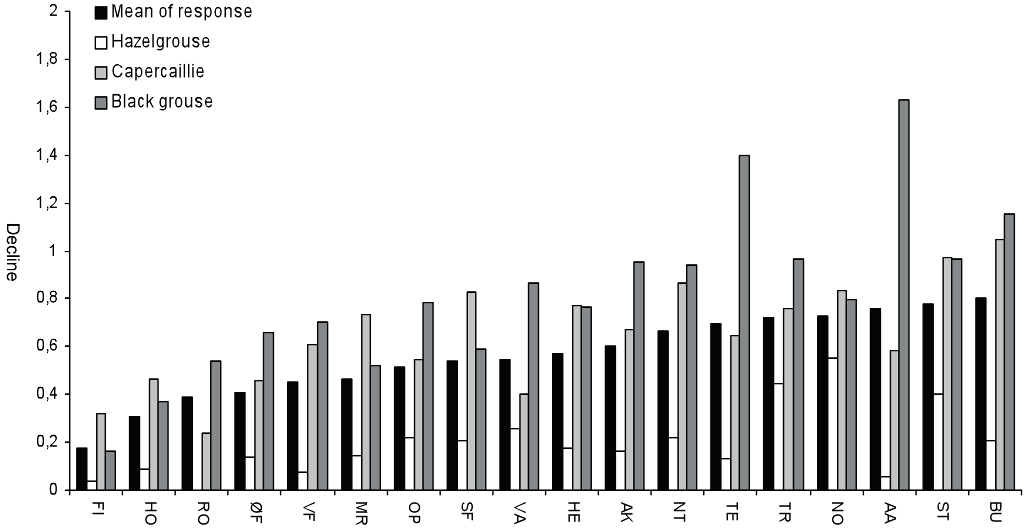


Figure 3. County-wise declines in grouse hunting bags in Norway. Counties are ranked from largest to smallest decline in mean grouse response, where FI has the largest decline and BU the smallest decline. The decline is the mean bags in 2000s as a proportion of the mean of the 1970s. Values below 1 indicate decline responses and values above indicate increases.

into south or being the northernmost county. These counties reveal twice or triple as large declines as opposed to inland counties (Hazelgrouse: 0.10 vs 0.30, Capercaillie: 0.47 vs 0.83 and Black Grouse: 0.56 vs 1.07). 88% of the 50% lowest counties for all species are situated south of Sør-Trøndelag. All the border-counties to Sweden, AK, HE, ST, NT, NO and TR are those with least declines.

DISCUSSION

We document declines in forest grouse hunting bags, species divergence in response and a spatial pattern in these declines in Norway. This is discussed in relation to their habitat requirements and the influence of climate and forestry. Peripheral counties had severe declines and maybe natural sink areas enforced by environmental change. The strength of the response diverged among species revealing strongest response for Hazelgrouse and least for Black Grouse reflecting different habitat requirements.

This study verifies that grouse populations have fallen with major differences between inland and more peripheral southern counties. This may be related to how combined effects of climate and forestry have restructured vegetation and forest biota. That forest grouse populations falls is probably related to complex large-scale forest community changes as discussed thoroughly by others (Storch 2000, Ludwig 2007, Ranta *et al*. 2008). Consistently lower declines for forest grouse in counties more connected to the taiga may be area- and source effects where habitat is more optimal, larger and more connected (Andren 1994, Beshkarev *et al*. 1994, Rosenzweig 1995). On the other hand, counties in the south, especially at the coast, and the northernmost county, are probably sink (suboptimal) areas for forest grouse. This may be related to vegetation components which are sub-optimal for grouse. These areas may therefore produce too few recruits to sustain mortality and depends on immigration from surrounding areas when populations fall off (Rosenzweig 1995, Hanski & Gaggiotti 2004). The habitat optimality may sink even further in these areas due to climate change and forestry. All these effects may together explain larger declines here and may be indicative of ongoing range-contraction. The same pattern is evident southwards in Finland or with distance to Russian Karelia (Hanski & Hammond 1995, Kouki & Väänänen 2000, Ludwig *et al*. 2008a).

Temperature, humidity and oceanic influence is higher southwards, especially at the coast, potentially explaining sink characteristics and larger declines for boreal grouse species. Climate change last decades may strengthen this pattern by pushing optimal habitat zones and distribution ranges northwards (Brommer 2008). From Finland, Ludwik *et al*. (2006) relate grouse declines last century to climate change and argue that a negative divergence between optimal hatching time and foraging seasons occur. The same is seen for other bird species but effects vary (Jonzen *et al*. 2006, Sæther *et al*. 2004). In the case of grouse, climate and forestry may interact to suppress vital bilberry cover (Atlegrim & Sjøberg 1996, Bokhorst *et al*. 2008).

This study confirms the habitat divergence hypothesis as proposed by Swenson & Angelstam (1993). The most severe temporal declines are evident for Hazelgrouse and secondly for Capercaillie. This is in line with predictions from what is already familiar knowledge about habitat requirements for forest grouse and effects of forestry on these habitat characteristics (Rolstad & Wegge 1987, Swenson & Angelstam 1993, Åberg *et al*. 2000). Hazelgrouse and Capercaillie biotopes and niche requirements are those most affected by modern forestry. We have not yet reasons to expect that climate change should lead to the differential response among grouse species, although it likely partially contributes to the overall decline. The most severe effects to grouse are probably large clear-cuts, plantations, too dense and homogene later successions, suppression of the field layer, and drainage of swamped forest and mires (Ludwig 2007, Ludwig *et al*. 2008a). Although complex, a switch in forest community clearly occurs, from old-growth forest to younger, denser, more homogen managed forests, reducing the niche for old and mixed forest species (Hanski & Hammond 1995, Löfman & Kouki 2001, Hanski & Walsh 2004).

The habitat requirements of Hazelgrouse is older deciduous succession (especially alder) interspersed into the multilayered, coniferous forest and forest stream valleys (Swenson 1993, Åberg *et al*. 2003). These vegetation types are severely affected by modern forestry, as they are the most productive (Framstad *et al*. 2002, Rolstad *et al*. 2002). They are clear-cut and often regenerated by planting dense spruce plantations. Thus, the most optimal habitat for Hazelgrouse is lost in intensely driven managed forests. Stronger responses for Hazelgrouse are also expected in view of their lower ability to and aversion to disperse (Beshkarev *et al*. 1994, Saari *et al*. 1998). The old-growth bilberry-rich spruce forests mixed with pine are optimal Capercaillie habitat (Storch 1993, Wegge *et al*. 2005, Gregersen & Gregersen 2008). Like the situation for Hazelgrouse, the clear-cut practice and establishment of plantations and monocultures results in habitat loss also for the Capercaillie. However, the area of second-best habitat is a bit larger, and forestry practices do not plant less productive soils, so low density populations in sub-optimal habitat may survive (Rolstad *et al*. 2007, Miettinen *et al*. 2008). The weaker population decline for Black Grouse suggests that effects of habitat change are a bit different. Black Grouse had traditionally a stronghold in early successions after forest fires or in open moore-land. Open deciduous bush-landscapes or open land-forest transitions, sustained by moderate cattle and sheep grazing, burning or cutting for wood, were especially suited for Black Grouse (Baines 1996). This habitat is now in a phase of forest recovery after centuries with traditional agricultural use (Ludwig *et al*. 2008b). Forestry mimics these disturbance regimes and creates a larger area of second-best habitat (Swenson & Angelstam 1993). It will be less optimal though, because the regeneration and fertilisation process through release of nitrogen during the burning or grazing process is absent (Nordin *et al*. 1998).

Increased competitor and predator abundance may reinforce the habitat loss and climate effects, and is in fact effects of the same human-induced factors (Storch 2000). Moose, red deer, roe deer and voles has increased in abundance as a result of the same forest community change (Melis *et al*. 2006, 2007, Ludwig 2007). Grazing may strongly modify the forest vegetation contributing to indirect and direct effects on forest grouse. Grazing reduce bilberry vegetation and therefore have direct effects as competitors to grouse (Melis *et al*. 2006, 2007, Baines 1996, Gregersen & Gregersen 2008). All forest grouse depend on ericaceous shrub vegetation, and Capercaillie and Hazelgrouse thrive in the most moist and herbaceous, which is especially affected by grazing. Also, partially contributing to long-term declines is increased generalist predation, but this effect is expected to contribute to the opposite temporal differences among species (Storaas & Wegge 1987, Smedshaug *et al*. 1999).

The environmental management in Norway established the hunting statistics as a surveillance measure. Our explorations of these data now warrant response and we propose some conservation implications. International science has signalled that the populations of Hazelgrouse and Capercaillie in southern parts of Scandinavia are low and at risk of regional extinction (Hanski & Walsh 2004, Ludwig 2007). At some point, grouse species is expected to reach critical environmental thresholds in which the forests can not sustain viable populations (Andren 1994, Saari *et al*. 1998, Kangas & Kurki 2000). Further logging may therefore bring the populations below such critical thresholds of productive old or deciduous multi-layered coniferous forest. As the overall quality of Norwegian forests today may be near (or below) such thresholds the future is uncertain (Framstad *et al*. 2002, Rolstad *et al*. 2002). This is especially profound in counties into South because of sink characteristics. Remaining Capercaillie and Hazelgrouse source habitats should be conserved at local and regional scales from clear-cutting practice in line with predictions presented in Hanski & Walsch (2004).

In conclusion, we revealed a spatial and temporal pattern in forest grouse bags likely structured by climate and forestry. Forest grouse reveal densities according to distribution of major climate zones and reveal sink effects in peripheral counties. Sources are into North-East nearer to the Scandinavian taiga where oceanic influence is less and habitat larger. Forest grouse had also declines according to predicted niche requirements, where the old forest species Capercaillie and the habitat specialist Hazelgrouse are most sensitive to forestry. The temporal trends are cause of concern if habitat loss continuous and habitat optimality still falls.

ACKNOWLEDGEMENTS

We thank Statistics Norway for letting us use the hunting statistics. We are gratefull to Vidar Selås, Odd Henning Stuen, Eivind Østbye and Kjartan Østbye who improved the manuscript considerably, and to Svein Gausemel preparing the map.

SAMMENDRAG

Pågående bestandsnedgang og utbredelsesinnsnevring for norske skogshøns

Skogshøns divergerer i nisjekrav, der storfugl trives i gammelskog, jerpe er en habitatspesialist (middelaldret, løvrik barskog) og orrfugl er en tidlig-suksesjonsart. Vi analyserte skuddstatistikken fra fire årtier fra Norge for å avdekke forskjeller mellom skogshønsene i romlige og tidsmessige trender, og diskuterer resultatene i lys av faktorer som endrer habitatene deres. Moderne skogbruk har kontinuerlig endret skoglandskapet, spesielt for jerpe og storfugl. I samme tidsrom har klimaet blitt varmere og fuktigere, og klimasoner har forflyttet seg nordover. Dette studiet avdekket at alle artene viste en nedgang i forhold til 1970-tallet, spesielt tydelig i sør og i det nordligste fylket. Denne responsen var sterkest for jerpe, deretter storfugl. Sentrale innlandsfylker inntil Sverige avdekket lavere nedganger og er trolig kilde områder. Vi antar at effekten av klima og skogbruk samvirker om å redusere habitatkvaliteten for skogshøns, og disse effektene er sterkere i sink-områder.

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