

Spatial dynamics of Norwegian tetraonid populations

-as reviled by hunting statistics

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Abstract

Species in a given site, or populations of one species in different sites often fluctuate in synchrony, given that their affected similarly by factors such as spatially autocorrelated climate, predation or by dispersal between populations of one species.

Here I analysed county wise time series of hunting bag records covering 24 yrs among four Norwegian tetraonids for interspecific and intraspecific synchrony. I measured synchrony at three spatial scales; National, region (consisting of counties with similar precipitation and at county level.

The ecologically related tetraonids with overlapping distributions exhibited strong synchrony across Norway, but there were clear variation between different regions and counties. Regions with long coastline to the North Sea exhibited an overall stronger synchrony than those consisting of more continental areas. Intraspecific synchrony was generally low across all counties, but stronger synchrony between counties within regions defined by precipitations rates. Synchrony was negatively related do distance between populations in a majority of the species. Only the synchrony in willow ptarmigan showed a clear negative relationship with distance, while the other species had both strong positive and negative correlations at short distances. Strong interspecific synchrony between some species pairs within regions and weak intraspecific synchrony across counties within regions, suggest stronger synchronizing effect from environmental factors such as weather or predation and less effect from dispersal. However dispersal may have some effect in willow ptarmigan as this species show the strongest intraspecific synchrony.

It is suggested that a large scale driving force, presumable weather related drive different species into synchrony at national-, region- and county level. At lower levels, local factors such as local predators and small-scale habitat features are important.

It is important to interpret data based on hunting statistics with caution, since there exists some indications that catch per unit effort are unaffected by density. It is also probable that the hunting statistics are affected by hunter behaviour during different weather conditions.

Sammendrag

Arter som lever i samme område eller populasjoner av en art svinger ofte i synkroni så sant de påvirkes likt av faktorer som autokorrelert klima, predasjon eller gjennom spredning mellom populasjoner.

I denne oppgaven har jeg analysert tidsserier på 24 år basert på jaktstatistikk fra fire hønefuglarter for å finne mellomart- og innenart synkroni i artene. Jeg har målt synkroni i tre romlige skalaer; Nasjonalt, regionalt (bestående av fylker med lik nedbør) og på fylkes nivå.

De økologisk beslektede hønefuglartene med overlapp i utbredelse viste sterk synkroni, men det var tydelig variasjon blant regioner og fylker. Regioner med lang kystlinje mot Nordsjøen viste sterkere samlet synkroni mellom arter enn regioner med mye kontinentale områder. Innenart synkronien var generelt lav på landsbasis, men ble sterkere blant fylkene innen regionene. Synkronien avtok med avstand mellom populasjonene hos mesteparten av artene. Kun lirype viste en klar negativ sammenheng mellom synkroni og avstand mens de andre artene hadde sterke negative og positive korrelasjoner ved korte avstander.

Sterk mellomart synkroni mellom noen artspaar innen regioner og svak innenart synkroni mellom populasjoner innen regionene indikerer sterkere synkroniserende effekt fra ytre krefter enn effekten av spredning. Likevel, kan spredning ha noe effekt på synkronien i lirype siden arten viser den sterkeste innenarts synkronien. Antagelig er det en ytre stor-skala effekt, mest sannsynlig vær relatert som synkroniserer artene. På de lavere skalaene er det mye som tyder på at lokale forhold som små-skala habitat egenskaper og lokalt predator regime virker sterkt på artene.

Det er viktig å være varsom når man tolker data basert på jaktstatistikk siden det finnes eksempler på at mengden skutt fugl per tidsenhet er uavhengig av tetthet. Det er også mulig at jaktstatistikken er påvirket av jegernes adferd under forskjellige værforhold.



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Introduction

Population dynamics are driven by abiotic and biotic environmental factors through their effects on demographic rates, potentially resulting in synchronous dynamics of populations influenced by the same forces (Moran 1953; Ranta et al. 2006). When these environmental forces are spatially autocorrelated, spatially separated populations of one species may fluctuate synchronously. Also sympatric populations of different species may show synchronous dynamics if the same environmental forces affect them similarly (Ranta et al. 2006). Driving factors like predation (Smedshaug et al. 1999; Ims and Andreassen 2000), climate (Moran 1953; Grenfell et al. 1998; Grotan et al. 2005; Houlahan et al. 2007) and food availability (Erikstad 1985) may all work alone or simultaneously to affect population dynamics through changes in reproduction, mortality or dispersal.

Interspecific synchrony refers to temporal match in fluctuations across species at a given site (Krebs et al. 2002). An early study of Canadian mammals showed that several pairs of species tended to have population peaks in closely matching years (Butler 1953). Furthermore, in Finland (Linden 1988; Ranta et al. 1995), Italy (Cattadori et al. 2000) and Sweden (Small et al. 1993), several grouse species fluctuated synchronously. Other known studies include small mammals (Krebs et al. 2002; Huitu et al. 2004). Common for these studies is that the synchronized species are taxonomically related or inhabit closely located habitats. In fact, Cattadori et al. (2000) showed that different species in neighbouring habitats exhibited stronger synchrony than those separated with several habitats, and this is probably due to a force (climatic and/or predatory) working locally and affects the species similarly.

Intraspecific spatial synchrony refers to temporal match in the fluctuations among populations of one species and is well documented in many taxonomic groups, (Tetraonids; (Ranta et al. 1995; Lindstrom et al. 1996; Cattadori et al. 2000; Hornell-Willebrand et al. 2006; Kerlin et al. 2007), small rodents; (Bjornstad et al. 1999; Ims and Andreassen 2000; Krebs et al. 2002; Huitu et al. 2008), moths and aphids; (Hanski and Woiwod 1993; Klemola et al. 2006) ungulates; (Grenfell et al. 1998; Grotan et al. 2005). A common pattern is that populations may fluctuate in synchrony over large areas (Cattadori et al. 2000; Huitu et al. 2008), with decreasing synchrony with increasing distance between the populations (Hanski and Woiwod 1993; Lindstrom et al. 1996; Klemola et al. 2006; Kerlin et al. 2007).

Three principal factors have been identified as possible causes of synchrony: (1) Interactions between predators and prey where mobile predators covering large areas may cause spatial synchrony (Ims and Andreassen 2000). It is also reasonable to assume that local predators affect local tetraonid populations similarly. (2) Ever since Moran (1953), spatially

autocorrelated climatic factors have been regarded as synchronizing agents within and between species (Hanski and Woiwod 1993; Ranta et al. 1995; Lindstrom et al. 1996; Grenfell et al. 1998; Cattadori et al. 2000; Koenig 2002; Grotan et al. 2005). The “Moran effect” states that spatially correlated environmental effects, such as weather may synchronize physically separated populations sharing the same density dependent structure. More recently, it has been stated that equal density dependent structure is not an essential requirement in the driving force of “Moran effect” (Ranta et al. 2006). Since correlation in climate is usually strongest in nearby sites and levels off with distance between sites (Ranta et al. 1999; Koenig 2002), one might expect strongest synchrony between species with overlapping distributions and within species where populations are close, and that this synchrony will decrease with less distribution overlap and increasing distance between populations. (3) Dispersal between populations is also frequently regarded as an explanation for spatial synchrony within species (Lindstrom et al. 1996; Paradis et al. 1999; Cattadori et al. 2000). Often it is assumed that dispersal is most dominant between closely located populations (Paradis et al. 1999) and that dispersal levels off with distance (i.e. distance dependent dispersal) as in Lindström et al. (1996) where simulations showed that synchrony levelled off with decreasing dispersal (or increasing distance between populations). On the other side, local dispersal may over time yield large-scale synchrony (Ranta et al. 2006). Many studies have tried to disentangle the most important synchronizing factor of dispersal and “Moran effect”, and many suggest that “Moran effect” is the strongest driving factor (Hanski and Woiwod 1993; Cattadori et al. 2000; Grotan et al. 2005; Klemola et al. 2006), but others suggest equal strength (Lindstrom et al. 1996). Predation, “Moran effect” and dispersal may thus synchronize spatially separated populations of one species while predation and “Moran effect” may synchronize populations of different species in a given site.

Capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*), willow ptarmigan (*Lagopus lagopus*) and rock ptarmigan (*Lagopus mutus*) are widely distributed game bird species in Norway. Although showing many similar ecological characteristics, there is also a clear ecological gradient through this species assemblage in their life histories and habitat use (spatial distribution). The largest species, capercaillie and second largest, black grouse are sympatric, forest dwelling, promiscuous, lekking birds. Their distributions overlap largely over the boreal forest zone in Scandinavia, although capercaillie preferring old forest patches and black grouse preferring younger successional stages (Seiskari 1962; Swenson and Angelstam 1993). Willow- and rock ptarmigan are smaller, sympatric, alpine dwelling species that form pair during breeding season. Willow ptarmigan is slightly larger than rock

ptarmigan and their distributions usually overlap in the alpine zone in Norway, but the rock ptarmigan is restricted to the upper mountain slopes. In many mountain forest areas the willow ptarmigan distributions overlap with both black grouse and capercaillie. A generalized illustration of distribution overlap between the species is presented in Fig 1a.

All these species are subject to predation from a number of avian and mammalian predators, but egg loss (Myrberget 1988; Wegge and Storaas 1990), chick loss (Myrberget 1988; Wegge and Kastdalen 2007) and adult survival (Bergerud and Gratson 1988) vary largely between years, and cause autumn densities of these species to vary accordingly (Solvang et al. 2005; Solvang et al. 2007). These large variations of autumn density between years suggests that populations of tetraonids are to a large degree affected by some environmental driving forces like other tetraonid populations in Europe (Ranta et al. 1995; Lindstrom et al. 1996; Cattadori et al. 2000).

No study has yet been conducted on spatial and temporal synchrony between and within Norwegian tetraonids. Neither do we know if any of the known synchronizing agents; predation, climate or dispersal force populations into synchrony, or if the synchrony, if any, follows a similar pattern as in other European tetraonid populations (Ranta et al. 1995; Lindstrom et al. 1996; Cattadori et al. 2000; Kerlin et al. 2007). The long-term hunting bag records collected by Norway statistics (Norway statistics 2007) from 1971 and onwards is a large dataset containing county-wise annual bag records from capercaillie, black grouse, willow- and rock ptarmigan from all 19 counties in Norway. From this dataset, the patterns of synchrony in Norwegian tetraonid populations may be analysed (Cattadori et al. 2003). In this paper, I will use hunting bag records from the four tetraonids as an index of population fluctuations and I will attempt to answer the following questions: (1) Do ecologically related tetraonid species fluctuate in synchrony in Norway; at national level, within weather-defined regions (i.e. counties of similar precipitation) and within counties? (2) Can a simple index of species overlap explain the observed patterns of synchrony? (3) Do the species exhibit intraspecific synchrony between all populations (i.e. counties) that decrease with distance between the populations, and (4) do the synchrony increase when I measure synchrony between populations within weather-defined regions?

Birds of closely distributed populations are likely to be affected by the same weather regime, have a relatively high exchange probability (i.e. dispersal) and share a similar predator-guild. On the basis of this I expect ecologically related species with substantial distribution overlap to show temporal match in their fluctuations within regions or counties, and that this will to some extent vary between counties, as the regions and counties differ in

structure, and geography. In addition, I expect populations of one species to be synchronized across counties and that synchrony will level off as distance between counties increase.

Methods

Hunting statistics

The time series analyses based on annual, county-level hunting bags between 1982 and 2006 were obtained from Statistics Norway (<http://www.ssb.no>). Different sampling methods were used in different time periods. The statistics from 1982-1992 were based on interviews with a random sample of hunters registered in the Norwegian hunter register and the bags were statistically estimated (Bjørk 2006). From 1992-2000 all hunters were instructed to report their bags, but due to low response this was supplemented with statistical estimations. After 2000, 90% of the hunters reported their bags so no estimation was needed (Bjørk 2006).

Hörnell-Willebrand et al. (2006) showed that hunting statistics underestimated the willow ptarmigan chick production and they suggested that this was caused by hunter behaviour. Also, hunters shot a smaller portion of the population in high-density areas than low-density areas (Hörnell-Willebrand 2005) so that the variation in the hunting bag will underestimate the true variation in densities. However such errors are likely to affect all counties and species equally (Small et al. 1993). As no time series based on transect line census is available that covers all Norway, I assume that long-term hunting statistics provide an acceptable index of fluctuations in abundance in tetraonid populations (Cattadori et al. 2000; Cattadori et al. 2003; Kerlin et al. 2007).

Due to difference in county size and amounts of preferred habitats, there were large variations in numbers of birds shot within counties. The coefficients of variation were negatively correlated with the mean number of birds shot, thus indicating that the time series from counties with few birds were harvested was less reliable. Time-series of shot individuals from a county with 5 or more missing or outlying (see chap. "*Statistical analysis of time series*" further down) values in the raw data were excluded from further analysis. Four time series of willow- and rock ptarmigan were not included due to only sporadic or no occurrence of the species in the bag records (Vestfold, Oslo, Akershus and Østfold). In the analysis, I used capercaillie, black grouse, willow and rock ptarmigan time series data from 18, 17, 15 and 15 counties, respectively (Fig. 1b).

Weather data

Monthly means of precipitation (measured as mm) from all weather stations that were operational between 1980 and 2007 were obtained from Norwegian Metrological Institute (www.met.no). Some stations were operational during the whole period while others only partly, but all were included in the calculation of county-level mean values. An average of 62 (total 1044) stations registered precipitation in each county. Some stations were manually monitored and thus located close to human settlement, whereas others registered precipitation automatically and were distributed to give the representative value at the county level. I estimated mean summer (May-August) precipitation in the 18 counties from where I had time series of hunting statistics.

To define regions with similar precipitation in summer months, I clustered the time-series using a cluster analysis. Mean summer precipitation was rescaled to euclidian distances between precipitation rates between counties and applied as a dissimilarity matrix (PROC DISTANCE in SAS statistical software). In the agglomerative hierarchical clustering (PROC CLUSTER in SAS statistical software), each time series first formed a cluster itself. Then, the two closest clusters were merged to form a new cluster that replaced the old ones. The procedure was repeated until only one cluster was left. The distance between two clusters was computed by the Ward's minimum variance method (Ward 1963). To validate the clusters, I calculated mean cross-correlation within regions and compared it to the national mean correlation coefficient.

The cluster analysis revealed four regions consistent with geography (Fig. 1b) and with similar summer precipitation means (mean within-cluster correlations; North: $r = 0.57$, Centre: $r = 0.62$, West: $r = 0.43$ and East: $r = 0.66$).

Species habitat overlap

To obtain an index of distribution overlap between pairs of species, I used data from the Norwegian bird atlas database (www.fugleatlas.no). This database contains UTM-positions with an accuracy of 1*1 km for reported observations of all four tetraonid species from 1970-2007. The data collection was based on voluntarily work by ornithologists, who observed grouse, noted the UTM-position and registered this in a database. In total 4505 observations of all grouse species (willow ptarmigan: 1565, rock ptarmigan: 791, capercaillie: 875 and black grouse: 1274) were used. To calculate an index of habitat overlap at the county level between pairs of species, buffers with radius 1km were placed around all positions. Then, the number of buffers of a species that overlapped with the other species was counted. A small

number of buffers that crossed a county border were counted as one observation in both counties. All calculations on overlap data were executed in ArcGIS 9.2 (www.esri.com). To calculate an overlap index for each pair of species within a county, I divided the number of overlapping buffers with the total number of buffer for both species in the comparison, and obtained a proportion of overlap between the species. The overlap index turned out to be lower than expected. However, as the ornithologists should be as able to observe both species as they visited all areas, the overlap index should reflect the real distribution overlap

Statistical analysis of the time series

All time series were log-transformed before calculating rates of change. This removed an overall downward trend in the data (Turchin 2003) and stabilised the variance, and most important, it changed the subject to fluctuations in population growth. To avoid unnecessary high influence from single extreme rates of change, values that were located outside a 4% threshold set by the 2.5% and 97.5% percentiles in county-wise distributions was characterized as outliers and removed from the time-series.

I analysed patterns of synchrony at three spatial scales. First, I pooled all time series from each species, and investigated the national-level interspecific synchrony by constructing a matrix of pairwise Pearson cross-correlations between each pair of species (Ranta et al. 1995; Cattadori et al. 2000). Second, I performed the same procedure on region- (regions reviled from the cluster analysis on precipitation rates) (Fig. 1b) and county level.

To examine the relationship between habitat overlap index and interspecific synchrony at national scale, I estimated the correlation between the interspecies correlations and overlap index. Further, at regional and county level, I fitted linear mixed effect models, implemented by the *lmer* function in the library *lme4* (Bates 2005) in the software R (R Development Core Team 2006). This function allowed for crossed random effects (Bates 2005), which were appropriate here since there was no nested structure in the data. The models were fitted with county or regions, respectively, and species pairs as random effects, and the amount of variation attributable to each factor was assessed by variance decomposition analysis (Borger et al. 2006; Nilsen et al. 2007). To investigate the effect of habitat overlap index on interspecific synchrony, I fitted the models with and without habitat overlap index as fixed effect, and compared the total residual variance to obtain a measure of this effect.

Spatial intraspecific synchrony was also initially assessed by constructing matrices of pairwise Pearson cross-correlations between all pairs of time series (within species), both between all counties and between counties within each region. A corresponding inter-county,

distance matrix was also constructed, containing distances between centroid-points in each county. Then at county level, a two-step approach was used to assess the spatial scaling of the synchrony. First, I estimated the correlation between bootstrapped (see next paragraph) intraspecific correlations and distance between counties to achieve a robust estimate on the relationship between synchrony and distance. Thereafter, to describe the relationship visually, I analysed the relationship between synchrony and distance with a generalized additive model (GAM) using software R (R Development Core Team 2006). The GAM is based on a non-parametric regression and smoothing techniques. Non-parametric regressions reveal structures in the relationship between the predictor and response variable that might otherwise be missed, which is useful in assessing the spatial scaling of synchrony.

Due to lack of statistical independence of intraspecific pairwise cross-correlations, I calculated median cross-correlation coefficients and confidence limits with a bootstrap procedure (Ranta et al. 1995; Cattadori et al. 2000; Klemola et al. 2006; Kerlin et al. 2007) in R (R Development Core Team 2006). Pairwise cross-correlation coefficients were sampled with replacement to generate 10 000 matrices of sampled coefficients. Calculation of the median for each of these matrices produced a normally shaped frequency histogram. This histogram was then used to estimate the median together with 2.5% and 97.5% percentiles of the original matrix of pairwise cross-correlation coefficients.

All cross-correlation coefficients used in this study were estimated using the PROC CORR procedure in SAS statistical software. Correlations that are presented without confidence limits are significant if not stated.

Results

Interspecific synchrony

Capercaillie and black grouse ($r = 0.811$), willow ptarmigan and rock ptarmigan ($r = 0.672$), and black grouse and willow ptarmigan (0.515) fluctuated in synchrony at national level (Fig 2). Willow ptarmigan and capercaillie (0.374 , $p = 0.072$), and rock ptarmigan and black grouse showed weak synchrony (0.331 , $p = 0.11$) and the two most unrelated species, rock ptarmigan and capercaillie showed no synchrony at all on national level (0.254 , $p = 0.23$) (all Table 1). Also at region and county level, ecologically related species pairs (capercaillie and black grouse, and willow ptarmigan and rock ptarmigan) fluctuate in rather close synchrony, while black grouse show weak and capercaillie no synchrony with neither willow- nor rock ptarmigan (Table 1). When comparing correlations at the different scales, there was a tendency that the mean synchrony was stronger at larger spatial scales (Table 1). However,

the synchrony between species varied among regions and counties, and in some counties and regions the synchrony between species was higher than at the higher scales (Table 1).

I found a strong, positive relationship between the synchrony and the overlap index at the national level ($r = 0.954$, Fig 3). At the region- and county scale, the mixed effect model with habitat overlap index fitted as fixed effect revealed a similar pattern, i.e. species pairs with high overlap index tended to fluctuate in stronger synchrony than those with low overlap index. The variance decomposition analysis further revealed that on both scales, area (i.e. region or county) and species attributed almost equally to the variation in synchrony when the model was fitted without any fixed effects, whereas area attributed much more to the total variation than species pairs (region: nine times, county: five times) when species overlap index was fitted as fixed effect, (Table 2). The relative difference in total residual variance between models with and without overlap index as fixed effect, showed that the overlap index is attributable to ~25% and ~50% of the variation in synchrony at county and region scales, respectively. Best linear unbiased predictions (BLUP) from the region scale mixed model fitted with overlap index, indicates an overall stronger interspecific synchrony in west and centre than in east and north (in ranking order) (Fig 5).

Intraspecific synchrony

Different spatial patterns were observed within the species. Bootstrapped cross-correlation between counties indicated overall weak synchrony in capercaillie (median correlation, [97.5%, 2.5% percentiles]: 0.10 [0.15, 0.04]) and rock ptarmigan (0.12 [0.17, 0.06]), stronger, but still low in black grouse (0.21 [0.26, 0.15]) and willow ptarmigan (0.21[0.28, 0.15]).

Synchrony in willow ptarmigan, rock ptarmigan and capercaillie are negatively correlated with distance (bootstrapped correlation \pm [97.5%, 2.5%]: $-0.70 \pm [-0.64, -0.75]$, $-0.35 \pm [-0.24, -0.44]$, $-0.16 \pm [-0.06, -0.27]$, respectively) while synchrony in black grouse is more or less unrelated to distance ($-0.09 \pm [0.015, -0.19]$), as the confidence limits includes zero. Similarly, the GAMs indicate a negative relationship between distance and synchrony in all species except black grouse (Fig. 4). Willow ptarmigan populations were mainly positively correlated at distances less than 750km, beyond that the populations were mainly negative correlated before a positive trend began around 1200km. Both capercaillie and rock ptarmigan showed a weak, negative linear relationship with distance. The scatter plots in Figure 4 show large variation in all species even at short distances, and in capercaillie, black grouse and rock ptarmigan the variation seems to be almost equal throughout the scale.

Mean intraspecific correlation between counties within precipitation-defined regions, was stronger than between all counties (mean r , [max, min]; capercaillie: 0.202 [0.724, -0.35], black grouse 0.296 [0.813, -0.321], willow ptarmigan 0.435 [0.727, 0.172] and rock ptarmigan 0.164 [0.616, -0.191]), however lower than the correlation between several species pairs in regions and counties (Table 1).

Discussion

Using long-term, large-scale hunting bag records, I have documented interspecific and intraspecific synchrony in Norwegian tetraonids. As in other studies, ecologically related species (Butler 1953; Small et al. 1993; Ranta et al. 1995; Cattadori et al. 2000; Krebs et al. 2002; Huitu et al. 2004) were highly synchronous all over Norway and the synchrony was dependent on overlap index. Also within precipitation-defined regions and within counties, I found strong mean synchrony between ecologically related and overlapping species. There were however clear variation between regions and counties. The synchrony observed at county level corresponded to what Small et al. (1993) and Ranta et al. (1995) found at county level in Sweden and Finland, respectively.

Species with overlapping distributions showed strong synchrony in population changes, and when this was accounted for in linear mixed effects models, a large portion of the variation in synchrony between species pairs was caused by area differences (i.e. differences between regions and counties), and less to species pairs. Consequently, it might seem as species living in close proximity share a common dynamics and that this proximity is more important than differences in their life histories and body size. The two regions, Centre and West have long coastlines and short distances between shore and inland. These regions showed an overall stronger interspecific synchrony than the regions North and East, which have shorter coastlines and include more continental/inland areas.

Mean intraspecific synchrony across counties was low in all species, but stronger between counties within the precipitation-defined regions. The synchrony typically declined as the distance between populations increased for all species except black grouse. Capercaillie and rock ptarmigan showed both positive and negative correlations through the scale, even inside 500 km. Black grouse showed no relationship with distance at all and had mainly positive, but also some negative correlations inside 600 km, outside that limit, there were virtually only positive correlations. Willow ptarmigan showed the clearest negative relationship with distance and virtually all correlations were positive inside 750 km and mainly negative beyond that.

The strong synchrony between species inhabiting areas in close proximity indicates that the tetraonids reacts similarly to some environmental forces. These forces may be the cause of synchrony between ecologically related species with overlapping distributions all over Norway. At region and county level however, the synchrony varied; some species pairs exhibited stronger- and some weaker synchrony than at higher scales. This suggests that local factors are important and that they work differently among regions or counties and has strong local influence on the dynamics in these populations. Within regions with similar precipitation rates, there was stronger interspecific synchrony between some of the species than the intraspecific synchrony between populations of single species. This implies that space is more important than taxonomy and it may also indicate that environmental forces are more important than dispersal in synchronising populations. Low intraspecific synchrony across all counties, which declined with distance in most species and stronger synchrony between counties in the regions suggests that the synchronizing force(s) are correlated in space, but the large variation, even at short distances indicates that local factors may be predominant (Tavecchia et al. 2008).

Unfortunately, the identity of the synchronizing agents that are causing these synchronous fluctuations, are still unknown. Strong interspecific synchrony contra weak intraspecific synchrony suggests however those extrinsic factors are more important than dispersal. Previous modelling studies have showed that dispersal-induced synchrony caused a stronger negative relationship between synchrony and distance than synchrony caused by stochastic events (Lindstrom et al. 1996). Except willow ptarmigan, this is not the case among the species in this study. Paradis et al. (1999) predicted that if dispersal had an effect on synchrony, species with the greatest dispersal distances should have the highest mean synchrony, however this was not a clear pattern. Willow ptarmigan that showed the highest mean synchrony at all scales and clearest relationship with distance has a mean female dispersal distance around 10 km (Hornell-Willebrand 2005), these dispersal distances may indeed result in high exchange rates of individuals between spatially structured populations. Paradis et al. (1999) suggested that an effect of dispersal on synchrony should be more noticeable at low scales, so if there was an effect of dispersal in this study, it might easily have been “washed” away due to the large scale measurement in this study.

If a factor only have slight effect on demographic rates, it is likely that this factor also is unable to promote synchrony. Driving environmental forces, such as predation, harvest, climate and food availability are known to affect demographic rates (Moran 1953; Erikstad 1985; Grenfell et al. 1998; Smedshaug et al. 1999; Ims and Andreassen 2000; Pedersen et al.

2004; Grotan et al. 2005). Since synchrony between species were stronger in regions that are exposed to rough weathers from west and stronger intraspecific synchrony in the regions than across all of Norway, it is reasonable to assume that a weather variable is involved in the synchronizing process. However there are few studies showing direct effect of weather on tetraonids and Haakenstad (2003) found no connection between weather and chick production in willow ptarmigan at all. This is most likely because the birds are well adapted to small deviations from the mean weather conditions. However, when an extreme stochastic event in weather occurs, Wegge and Kastdalen (2007) found a slight increase in capercaillie chick mortality directly caused by a weather event. Cattadori et al. (2000) showed that stochastic events in weather played the dominant role in synchronizing populations, and Ranta et al. (1995), using simulations, found that a stochastic hit of breeding failure was able to synchronize different species. However, the identity of this stochastic event was unidentified. If chicks die due to extreme weather conditions (Wegge and Kastdalen 2007) weather could be capable of synchronizing tetraonid populations. Further, if the same extreme weather hits large areas synchronously one might also expect large scale intraspecific synchrony. If weather have only slight effect on demographic rates however, it is unlikely that weather is the direct cause of synchrony. Nevertheless, weather might also work indirectly or in concert with other driving factors. From Wegge and Kastdalens (2007) study, it is important to notice that chick mortality due to weather was only a small percentage of the total mortality. However, chick mortality due to predation was high during and immediately after heavy rainfalls (Wegge and Kastdalen 2007), suggesting that adverse weather could have predisposed chicks to predation. Finally, it is also possible that weather affects tetraonid populations indirectly, as climate is known to strongly affect the dynamics of other predator-prey systems in the boreal region. For instance, if densities of alternative prey or predator species are affected by weather, it is reasonable that this somehow will affect the tetraonids. We might suspect that this most likely happens through alteration of the predator-prey relationship. The strong synchrony between species with high overlap index may also indicate that a shared predator-guild that works similarly on all species is more important than species-specific predators. In addition, the strength of the interspecific synchrony contra the intraspecific spatial synchrony may indicate that stationary predators are more important than migrating avian predators (Ims and Andreassen 2000).

During this study, I have found answers to the questions stated earlier in the introduction. (1) Ecologically related species fluctuated in synchrony at national, region and county level. However, clear variations at the lower scales. (2) Species with large overlap

index fluctuated in strong synchrony. (3) There was low intraspecific synchrony in all species (willow ptarmigan strongest) all over Norway and synchrony decreased slightly with distance in most species, but willow ptarmigan showed a clear decrease. (4) Intraspecific synchrony was stronger within regions than all over Norway. Some large-scale forces may cause the observed patterns, but it is uncertain which factors that is dominant. However, local conditions seem to be very important as closely located populations often are out of phase, but from unknown reason. Further studies are needed to disentangle the factors that are causing these patterns.

Hunting statistics

Hunting bag records are widely used as population size indexes in analysis of spatial and temporal patterns in population dynamics, and it is assumed that such indexes reflect the actual fluctuations in population size (Small et al. 1993; Cattadori and Hudson 1999; Cattadori et al. 1999; Cattadori et al. 2000; Cattadori et al. 2003; Haakenstad 2003; Hornell-Willebrand 2005; Kerlin et al. 2007; Newey et al. 2007). However, there are known problems involving the use of hunting statistics as population indexes, like underestimation of chick production (Hornell-Willebrand et al. 2006). Catch per unit effort (CPUE) was only partly affected by changes in willow ptarmigan density in Sweden and the catchability increased as the population decreased (Hornell-Willebrand 2005), which suggests that hunting statistics may show lower amplitudes in the fluctuations than those of the actual fluctuations. Hunting statistics may also lag behind real fluctuations (Linden 1981). However, such problems should affect all species and time series equally (Small et al. 1993). But, if the catch per unit effort (CPUE) does not follow the actual fluctuations one could observe a high, but biased cross-correlation between overlapping species. In Sweden, 69 % of the willow ptarmigans are shot during first ten days of hunting (Willebrand 1996), similar patterns are observed in Norway (Kastdalen 1992). As the hunting methods are similar for capercaillie, black grouse and rock ptarmigan, it is likely that this is transferable to these species too. The annual bag size is therefore largely affected by the hunting success in the first period of hunting. So in a strictly hypothetical way, bad weather (i.e. unpleasant for the hunters) or poor conditions (e.g. poor scent for dugs or snow cover) during the first period of the hunting season may affect the hunting bag, given that hunters “stay home” or have “bad luck” and consequently shoot fewer birds than expected from the actual population size. If this is the true, it is likely that the observed synchrony revealed by hunting statistics could be caused by factors that are important for hunters, rather than those important for tetraonids. Such error could then

synchronize the rate of change in hunting bags of different species if the same factor affects all hunters in a given area, even if the real populations show weak synchrony.

The preceding potential problems suggest that one must show caution when drawing conclusions about data that are based on hunting bag records and that it is important take into account other factors than those that only affects the birds when studying hunted populations, namely hunter behaviour.

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Table 1. Pairwise, interspecific correlation coefficients at national scale and mean correlation with max and min values for regional and county scale.

	Norway	Region		County			
	r	Mean r	max	min	Mean r	max	min
Capercaillie vs. black grouse	0,811	0,575	0,854	0,077	0,478	0,919	0,124
Capercaillie vs. willow ptarmigan	0,374	0,292	0,593	-0,036	0,219	0,758	-0,284
Capercaillie vs. rock ptarmigan	0,254	0,154	0,429	-0,080	0,198	0,641	-0,462
Black grouse vs. willow ptarmigan	0,515	0,352	0,721	-0,001	0,325	0,704	-0,126
Black grouse vs. rock ptarmigan	0,331	0,330	0,657	0,194	0,326	0,678	-0,264
Willow ptarmigan vs. rock ptarmigan	0,672	0,733	0,831	0,583	0,580	0,773	0,279

Table 2. Amount of variation in interspecific synchrony attributed to area (county and region) and species pairs at county and region scale. Model A with only random effects and B with random effects and overlap index as fixed effect. A and B are significantly different at both scales (County: $p < 0.001$, region: $p < 0.001$), indicating a significant positive effect of habitat overlap index on the interspecific correlations.

Variance components (%)		A (%)	B (%)
<i>County scale</i>	County	25	24
	Species pair	20	5
	Residual	55	71
<i>Region scale</i>	Region	36	44
	Art	32	5
	Residual	33	52

Figure 1. a) Illustration of the four species position in the landscape and overlap between them. b) A map of the study area with colours indicating species in the hunting records includes in the analysis. White lines depict borders between regions (region east at the right, region west at the left, centre region in the middle and region north at the top). Regions are defined on the basis of similarity in precipitation rates between counties.

Figure 2. Fluctuations in rate of change in Norwegian tetraonids in the period 1982/83 – 2005/06

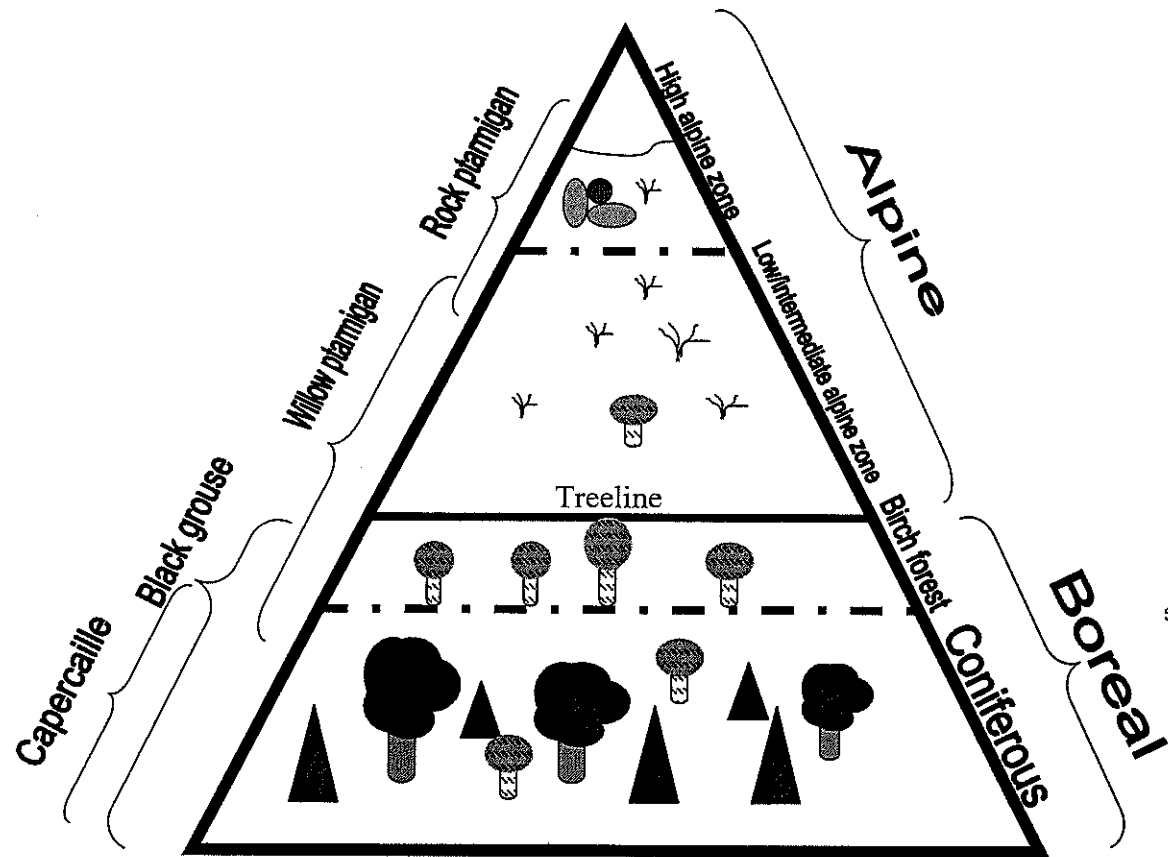
Figure 3. Synchrony plotted against overlap index between tetraonid species in Norway. C = Capercaillie, BG = Black grouse, WP = Willow ptarmigan and RP = Rock ptarmigan.

Figure 4. The relationship between distance and cross-correlation for willow ptarmigan (a), black grouse (b), capercaillie (c) and rock ptarmigan (d), based on GAM non-parametric regression. Black points are cross-correlations plotted against distance. Shaded area is the 95% point wise confidence limit. Estimated degrees of

freedom (EDF) for the different slopes: willow ptarmigan (edf=3.489), black grouse (edf=3.199), capercaillie (edf=1) and rock ptarmigan (edf=1).

Figure 5. Best linear unbiased predictions (BLUP) – predicted (random) intercepts at the region level. Based on the mixed effects model. The value indicate the strength of the synchrony between all species pairs in the regions.

a)



b)

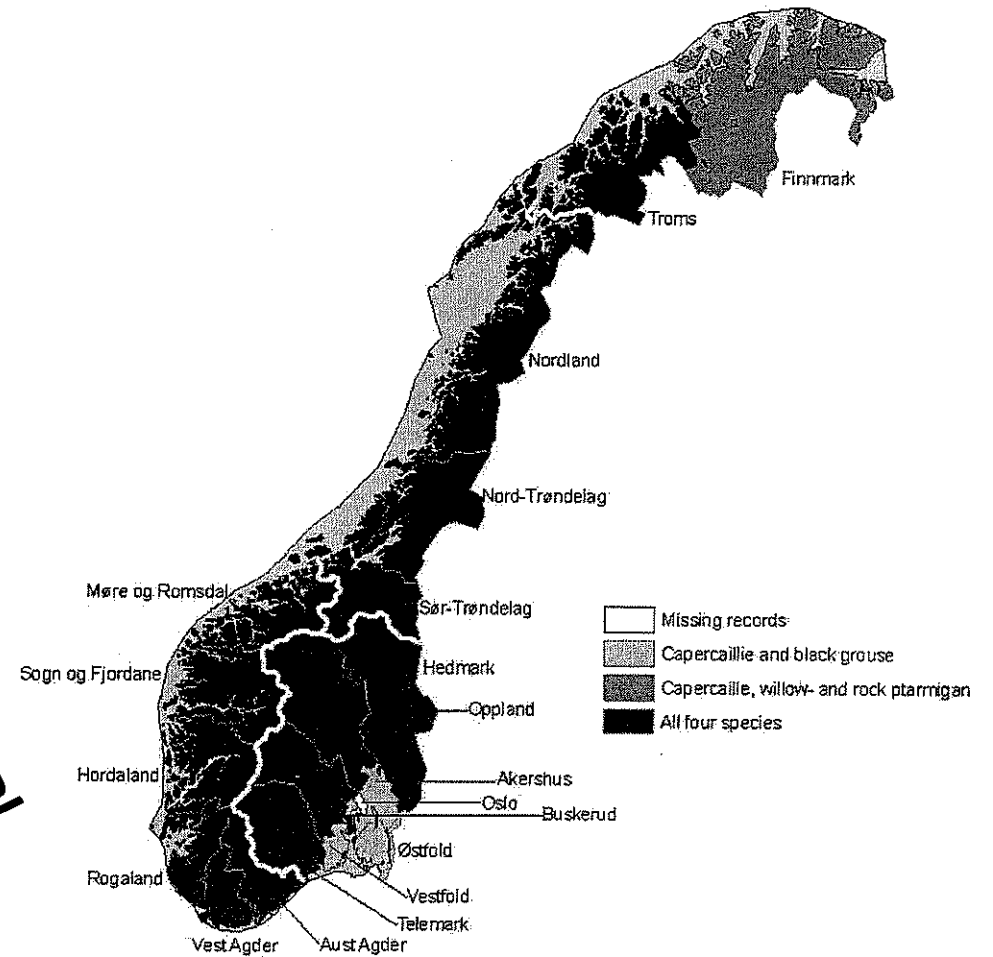


Figure 1:

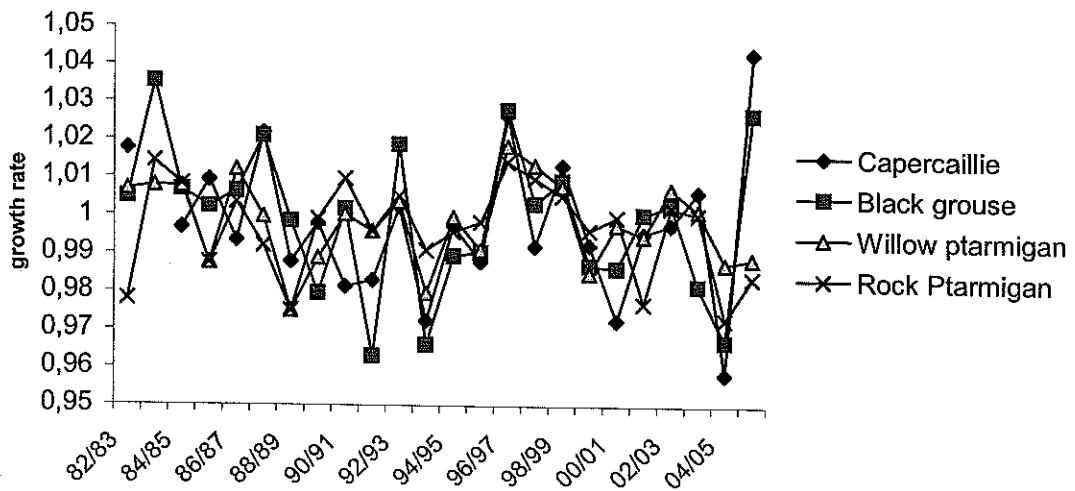


Figure 2:

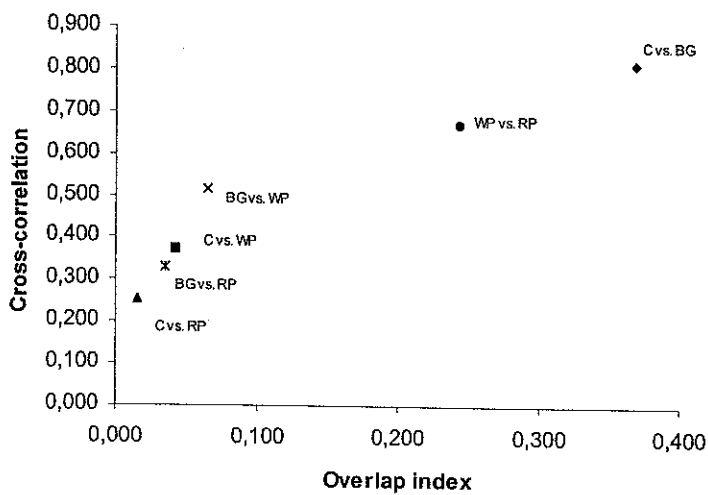


Figure 3:

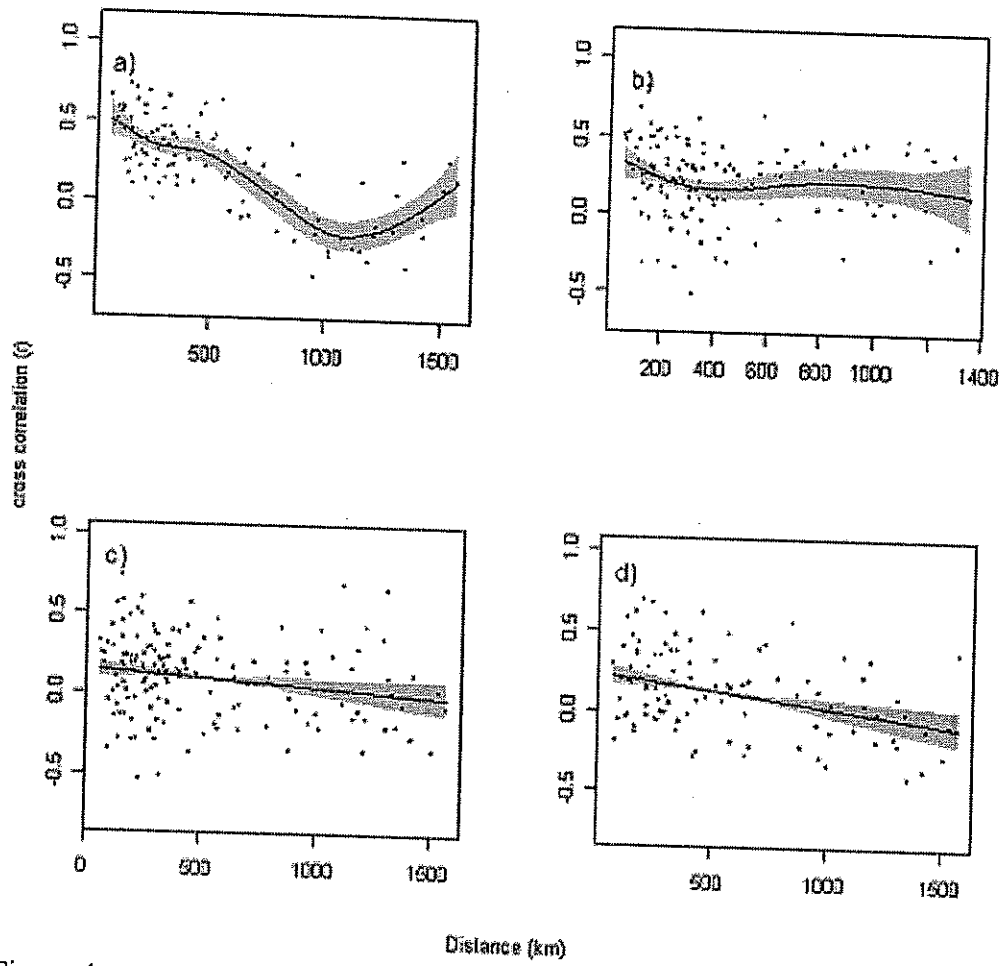


Figure 4:

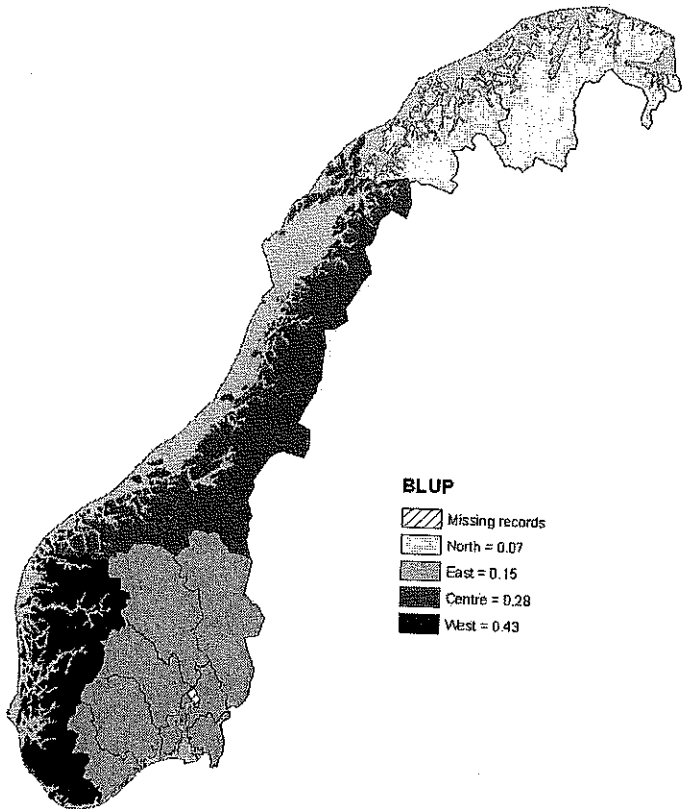


Figure 5: