

Mikkel A. J. Kvasnes · Torstein Storaas
Hans Chr. Pedersen · Svein Bjørk · Erlend B. Nilsen

Spatial dynamics of Norwegian tetraonid populations

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Abstract Different species in a given site or population of a given species in different sites may fluctuate in synchrony if they are affected similarly by factors such as spatially autocorrelated climate, predation, or by dispersal between populations of one species. We used county wise time series of hunting bag records of four Norwegian tetraonid species covering 24 years to examine patterns of interspecific and intraspecific synchrony. We estimated synchrony at three spatial scales; national, regional (consisting of counties with similar climate), and county level. Ecologically related species with overlapping distributions exhibited strong synchrony across Norway, but there was much variation between the different regions and counties. Regions with a long coastline to both the North Sea and the Norwegian Ocean 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 climatic conditions. Synchrony was negatively related to distance between populations in three of four 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 a stronger synchronizing effect from environmental factors such as weather or predation and less effect from dispersal. Our results suggest that the complete tetraonid community is structured by environmental factors

affecting the different species similarly and causes widespread interspecific synchrony. Local factors affecting the population dynamics nevertheless frequently forces neighbouring populations out of phase.

Keywords Synchrony · Growth rates · Hunting statistics · Willow ptarmigan · Rock ptarmigan · Capercaillie · Black grouse

Introduction

Population dynamics are driven by abiotic and biotic environmental factors through their effects on demographic rates, potentially resulting in synchronous dynamics in populations influenced by the same forces (Moran 1953; Ranta et al. 2006). When these environmental forces are spatially autocorrelated, segregated populations of one species might fluctuate in synchrony (i.e. intraspecific synchrony; Lindstrom et al. 1996; Hornell-Willebrand et al. 2006; Kerlin et al. 2007). Further, sympatric populations of different species may also be synchronised when the same environmental forces affect them similarly (i.e. interspecific synchrony; Ranta et al. 1995, 2006). In general, three principal factors have been identified as possible causes of synchrony: (1) predation (Ims and Andreassen 2000), (2) shared climate (i.e. Moran effect; Moran 1953) and (3) dispersal (Lindstrom et al. 1996; Paradis et al. 1999). While both shared predators and climate might cause synchrony both within and across sympatric species, dispersal is limited to cause intraspecific synchrony. Importantly, environmental factors like predation (Smedshaug et al. 1999; Ims and Andreassen 2000), climate (Moran 1953; Grenfell et al. 1998; Grotan et al. 2005) and food availability (Erikstad 1985) may all work alone or simultaneously to affect population dynamics through changes in reproduction, mortality or dispersal.

In Norway, Capercaillie (*Tetrao urogallus*), black grouse (*T. tetrix*), willow ptarmigan (*Lagopus lagopus*) and rock ptarmigan (*L. muta*) are widely distributed

M. A. J. Kvasnes · T. Storaas · H. Chr. Pedersen · S. Bjørk · E. B. Nilsen
Faculty of Forestry and Wildlife Management,
Hedmark University College, Evenstad,
2480 Koppang, Norway

H. Chr. Pedersen · E. B. Nilsen (✉)
Norwegian Institute for Nature Research,
7485 Trondheim, Norway
E-mail: erlend.nilsen@nina.no

tetraonid species. Although they share many ecological characteristics, there is a clear ecological gradient through the species assemblage in life histories and habitat use (for spatial distribution, see Fig. 1a). The largest species, capercaillie, and the second largest, black grouse, are sympatric, forest dwelling, promiscuous, lekking birds. Their distributions overlap largely over the boreal forest zone in Scandinavia, although capercaillie prefer old forest patches and black grouse prefer younger successional stages (Seiskari 1962; Swenson and Angelstam 1993). Willow and rock ptarmigan are smaller, sympatric, alpine-dwelling monogamous species. Willow ptarmigan is slightly larger than rock ptarmigan and their distributions usually overlap in the alpine zones in Norway, with the rock ptarmigan being restricted to the mid- and high alpine zones. In many mountain forest areas, the willow ptarmigan distributions overlap with both black grouse and capercaillie (Pedersen 1991; Pedersen and Karlsen 2007). The Norwegian tetraonid community is subject to predation from a number of avian and mammalian predators, and variation in egg and chick predation as well as adult survival might vary largely between years and cause autumn densities to vary accordingly (Bergerud and Gratson 1988; Myrberget 1988; Steen et al. 1988; Wegge and Storaas 1990; Steen and Erikstad 1996; Munkebye et al. 2003; Wegge and Kastdalen 2007). Little is known about the spatial autocorrelation of these processes, and to which extent they affect the complete tetraonid community in a way that causes strong interspecific synchrony.

Here we used hunting-bag statistics to examine the patterns of synchrony in Norwegian tetraonid popula-

tions, to ask the following broad questions: (1) Do ecologically related tetraonid species show interspecific synchronous population fluctuations? (2) Does the intraspecific synchrony decrease with distance between the populations? Neighbouring or overlapping 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, we expect ecologically related species with substantial overlap in distribution to show temporal match in their fluctuations. In addition, we expect populations of single species to be synchronised across counties and that synchrony will level off as distance between the populations increases.

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>). The statistics from 1982 to 1992 were based on interviews with a random sample of hunters registered in the The Norwegian Register of Hunters and the bags were statistically estimated (Statistics Norway). From 1992 to 2000, all hunters were instructed to report their bags. However, due to low response, this was supplemented with statistical estimations. The change in sampling method happened synchronously for all species and counties, and should thus not affect the interpretation of our re-

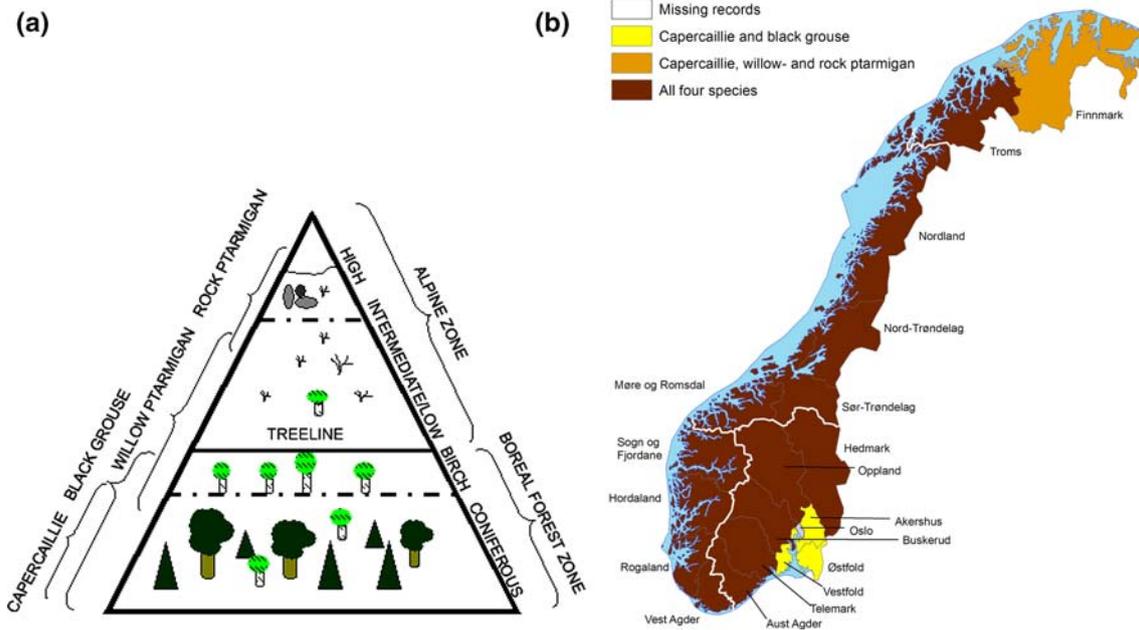


Fig. 1 a Illustration of the four species position in the landscape and the overlap between them. b Map of the study area with colours indicating species in the hunting records included in the analysis. White lines depict borders between regions (region east at the right,

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

sults. After 2000, 90% of the hunters reported their bags, and no additional estimation has been conducted (<http://www.ssb.no>).

Due to differences in county sizes and amount of preferred habitat, there were large variations in numbers of birds shot in the different counties. In general, the relative variability (i.e. coefficient of variation) was negatively correlated with the mean number of birds shot, indicating that the time series from counties with few birds harvested were less reliable. Time series of shot birds from a county with five or more missing or outlying values in the raw data were excluded from further analysis (see “[Statistical analysis of the time series](#)” further down). Time series of willow and rock ptarmigan from four counties (Vestfold, Oslo, Akershus and Østfold) were not included due to only sporadic or no occurrence of the species in the bag records. In the analysis, we used capercaillie, black grouse, willow and rock ptarmigan time series data from 18, 17, 15 and 15 counties, respectively (Fig. 1b).

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 (Cattadori et al. 2000; Slåttå et al. 2002; Kerlin et al. 2007). Although there are known problems related to the use of hunting statistics as population indexes (Linden 1981; Hornell-Willebrand et al. 2006), a recent comparison of census data and hunting bag statistics in Finland suggested largely similar conclusions for both line transect and hunting bag data (Ranta et al. 2008), with details of the models varying. As no time series based on transect line census is available that covers all of Norway, we assumed that long-term hunting statistics provide an acceptable index of fluctuations in abundance in tetraonid populations (Cattadori et al. 2000, 2003; Kerlin et al. 2007).

Weather data

We obtained monthly means of precipitation in millimetres (mm) from The Norwegian Meteorological Institute (<http://www.met.no>). In total, 1044 (average 62 in each county) weather stations were operational between 1980 and 2007. Some stations covered the whole period and a few only partly, but all were included in the calculation of county-level mean values. Some stations were manually monitored and thus located close to human settlement, whereas others registered precipitation automatically and were distributed to give a representative value at the county level. We estimated mean summer (May–August) precipitation in the 18 counties from where we had time series of hunting statistics.

To define regions with similar precipitation in summer months, we clustered the time series using a cluster analysis. Mean summer precipitation was rescaled to Euclidean distances between precipitation rates among 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, we calculated mean cross-correlation within regions and compared it to the national mean correlation coefficient. The cluster analysis revealed four regions consistent with the spatial arrangement (Fig. 1b), and in general the precipitation was well correlated within these clusters (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, we used data from the Norwegian bird atlas database (<http://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 to 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 a radius of 1 km (approximate summer home range) were placed around all positions. This buffer area represents an approximate summer range for the species, and it is assumed that individual tetraonids living in this area share similar extrinsic factors such as weather and predator regime. 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 (<http://www.esri.com>). To calculate an overlap index for each pair of species within a county, we divided the number of overlapping buffers with the total number of buffers for both species in the comparison, and obtained a proportion of overlap between the species. Although this method is likely to underestimate the true distribution overlap, the pattern obtained when comparing pairs of species largely followed the expected pattern.

Statistical analysis of the time series

Population growth rates were calculated as: $r_t = \ln(N_{t+1}/N_t)$. To avoid unnecessary high influence from single extreme rates of change, values that were located outside a 5% threshold set by the 2.5 and 97.5% per-

centiles in county-wise distributions was characterised as outliers and removed from the time series.

We analysed patterns of synchrony in population growth at three spatial scales. First, we pooled all the 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, we performed the same procedure on region scale (based on cluster analysis described above) (Fig. 1b) and county scale.

To examine the relationship between habitat overlap index and interspecific synchrony at national scale, we estimated the correlation between the interspecies correlations and overlap index. Further, at regional and county level, we 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 region, 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. 2008). To investigate the effect of habitat overlap index on interspecific synchrony, we 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 the county level, a two-step approach was used to assess the spatial scaling of the synchrony. First, we estimated the

correlation between bootstrapped (see next paragraph) intraspecific correlations and the distance between counties to achieve a robust estimate on the relationship between synchrony and distance. Thereafter, to describe the relationship visually, we analysed the relationship between synchrony and distance with a generalized additive model (GAM) using the 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 a lack of statistical independence of intraspecific pairwise cross-correlations, we calculated median cross-correlation coefficients and confidence limits with a bootstrap procedure (Ranta et al. 1995; Cattadori et al. 2000; Kerlin et al. 2007) in R (R Development Core Team 2006). Pairwise cross-correlation coefficients were sampled with replacement to generate 10000 matrices of sampled coefficients. 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.

Results

Interspecific synchrony

Capercaillie and black grouse ($r = 0.768$, $P < 0.01$), willow ptarmigan and rock ptarmigan ($r = 0.668$, $P < 0.01$) and black grouse and willow ptarmigan ($r = 0.515$, $P = 0.01$) fluctuated in synchrony at the national scale (Fig. 2). Willow ptarmigan and caper-

Fig. 2 Fluctuations in rate of change in hunting bags of Norwegian tetraonids in the period 1982/1983–2005/2006

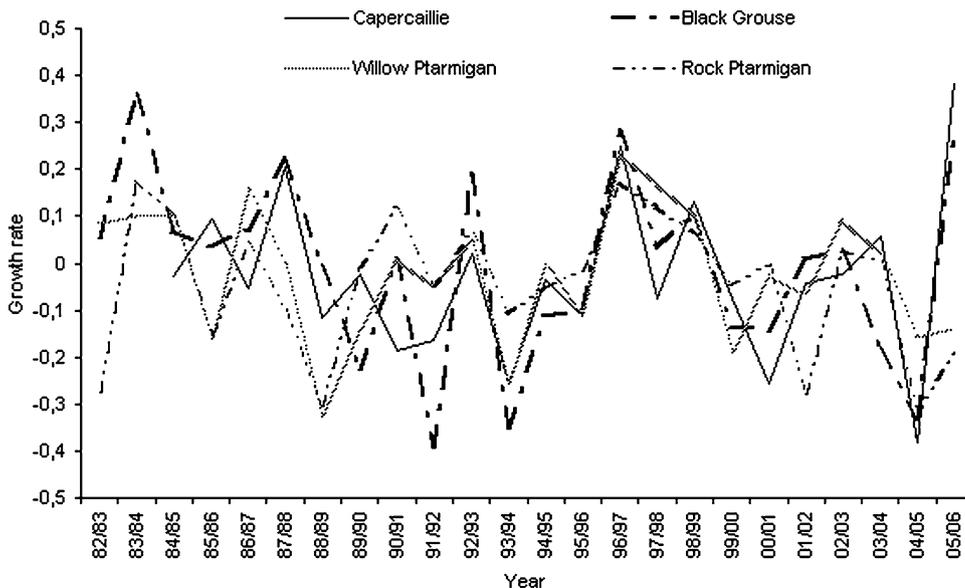


Table 1 Pairwise interspecific correlation coefficients at national scale and mean correlation with max and min values for regional and county scale

	Norway	Region			County		
	<i>r</i>	Mean <i>r</i>	Max	Min	Mean <i>r</i>	Max	Min
Capercaillie versus black grouse	0.768	0.595	0.852	0.079	0.478	0.919	0.190
Capercaillie versus willow ptarmigan	0.341	0.282	0.607	-0.028	0.241	0.769	-0.290
Capercaillie versus rock ptarmigan	0.095	0.154	0.341	-0.049	0.216	0.665	-0.361
Black grouse versus willow ptarmigan	0.515	0.360	0.730	0.019	0.338	0.705	-0.077
Black grouse versus rock ptarmigan	0.325	0.386	0.658	0.203	0.313	0.702	-0.272
Willow ptarmigan versus rock ptarmigan	0.668	0.731	0.827	0.586	0.581	0.779	0.278

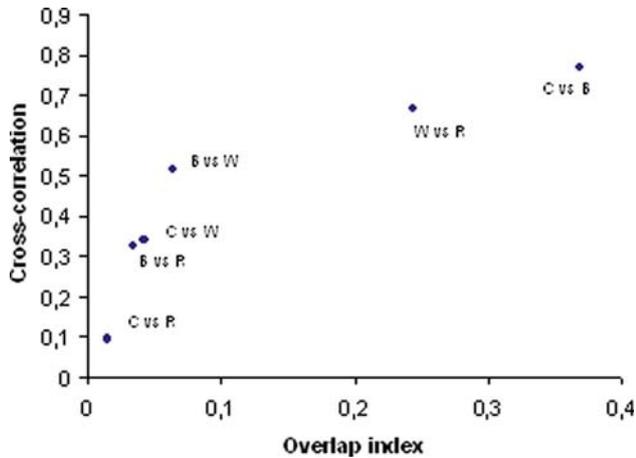


Fig. 3 Synchrony plotted against overlap index between tetraonid species in Norway. *C* Capercaillie, *BG* black grouse, *WP* willow ptarmigan, *RP* rock ptarmigan

caillie ($r = 0.341$, $P = 0.10$), and rock ptarmigan and black grouse showed weak synchrony ($r = 0.325$, $P = 0.12$), and the two most different species, rock ptarmigan and capercaillie, showed no synchrony at all on the national level ($r = 0.095$, $P = 0.67$) (Table 1). Also at the region and county scale, ecologically related pairs of species (capercaillie and black grouse, and willow ptarmigan and rock ptarmigan) fluctuated in rather close synchrony, while black grouse showed weak and capercaillie no synchrony with neither willow nor rock ptarmigan (Table 1). When comparing correlations at the different scales, there was a tendency, however, but not a significant one. The mean synchrony was stronger at the national level than at the county level (Table 1; sign test; $P = 0.22$).

There was a strong, positive relationship between the synchrony and the overlap index at the national scale ($r = 0.888$, $P = 0.02$, Fig 3). At the region and county scale, a mixed-effect model fitted with habitat overlap index 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 (region; $b = 1.567$, $t = 3.671$, $P < 0.01$, county; $b = 0.923$, $t = 4.896$, $P < 0.01$). The variance decomposition analysis further revealed that on both scales,

Table 2 Amount of variation in interspecific synchrony attributed to area (county and region) and species pairs at county and region scale

Variance components (%)	A (%)	B (%)
County scale		
County	27	30
Species pair	21	5
Residual	52	65
Region scale		
Region	27	26
Species pair	33	5
Residual	40	69

Model A is fitted with only random effects whereas model B is fitted with overlap index as a fixed effect. At both spatial scales there is a significant effect of species overlap fitted as fixed effect

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 ~27 and ~52% of the variation in synchrony at county and region scales, respectively. Best linear unbiased predictions (BLUP) from the region scale mixed model indicates an overall stronger interspecific synchrony in west and centre than in east and north (in ranking order) when spatial overlap is fitted as fixed effect (Fig. 4).

Intraspecific synchrony

Different spatial patterns were observed within the species. Bootstrapped cross-correlation between counties indicated overall weak synchrony in capercaillie (median correlation, [2.5, 97.5% percentiles]: 0.09 [0.05, 0.13]) and rock ptarmigan (0.12 [0.07, 0.16]), stronger, but still low in black grouse (0.19 [0.15, 0.24]) and willow ptarmigan (0.21 [0.16, 0.27]).

Synchrony in willow ptarmigan, rock ptarmigan and capercaillie are negatively correlated with distance (bootstrapped correlation [2.5, 97.5% percentiles]:

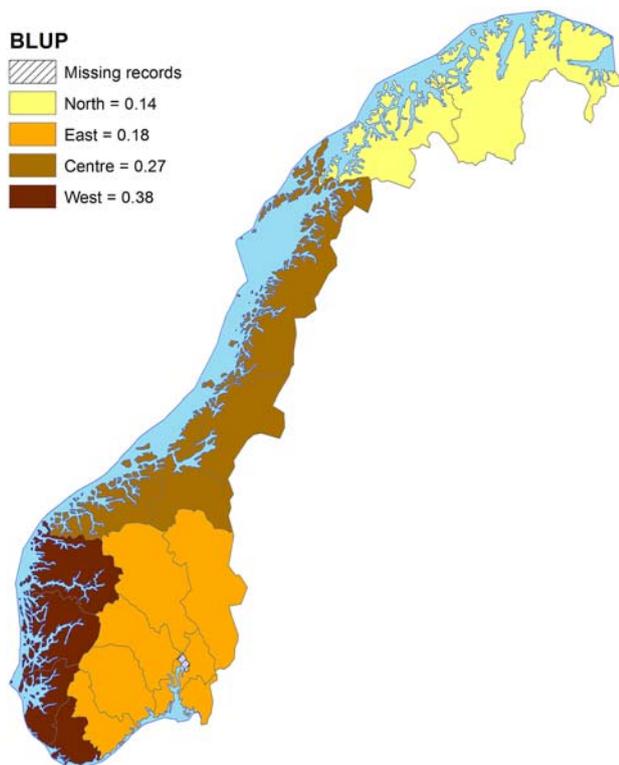


Fig. 4 Best linear unbiased predictions (*BLUP*)—predicted (random) intercepts at the region level. Based on the mixed-effects model. The value indicates the strength of the synchrony between all species pairs in the region

$-0.69 \pm [-0.74, -0.64]$, $-0.34 \pm [-0.44, -0.24]$, $-0.14 \pm [-0.23, -0.05]$, respectively) while synchrony in black grouse is unrelated to distance ($-0.09 \pm [-0.18, 0.02]$). Similarly, the GAMs indicate a negative relationship between distance and synchrony in all species except black grouse (Fig. 5). Willow ptarmigan populations were mainly positively correlated at distances less than 750 km, beyond that the populations were mainly negatively correlated before a positive trend began around 1200 km. Both capercaillie and rock ptarmigan showed a weak, negative linear relationship with distance. In capercaillie, black grouse and rock ptarmigan there was much variation in the cross correlations also at smaller spatial scales, indicating that also neighbouring populations often were out of phase (Fig. 5).

Mean interspecific correlation between counties within precipitation-defined regions was stronger than between all counties (mean r , [max, min]; capercaillie 0.17 [0.72, -0.54], black grouse 0.31 [0.81, -0.37], willow ptarmigan 0.43 [0.74, 0.13] and rock ptarmigan 0.16 [0.61, -0.22]) (Table 1; sign test: $P = 0.03$).

Discussion

Using long-term, large-scale hunting bag data, we have examined interspecific and intraspecific synchrony in

four Norwegian tetraonids. As in other studies (North America: Butler 1953; Sweden: Small et al. 1993; Finland: Ranta et al. 1995; Italy: Cattadori et al. 2000), ecologically related species were highly synchronous across Norway, and the synchrony was closely correlated with the habitat overlap index. Also, within weather regions and within counties, we found strong mean synchrony between ecologically related species with a high habitat overlap index. There was, however, much variation between regions and counties. The synchrony observed at county level corresponded to what Ranta et al. (1995) found in capercaillie, black grouse and hazel grouse (*Bonasa bonasia*), at the county level in Finland.

Species with overlapping distributions were strongly synchronous in their population dynamics. When accounting for distribution overlap in the linear mixed-effects models, more of the remaining variation was attributed to differences between areas than to differences between pairs of species. Thus, species living in close proximity often shared common dynamics, and this spatial proximity appears to be more important than differences between species in life histories and body size. This pattern corresponds to what should be expected if the different species in the tetraonid community are affected by the same environmental factors. The interspecific synchrony varied, however, between regions, and the two regions that showed an overall stronger interspecific synchrony (Centre and West) have long coastlines and short distances between shore and inland, whereas the two regions with least interspecific synchrony (North and East) have shorter coastlines and include more continental/inland areas. This might suggest that local and regional environmental factors are important and that they work differently among regions or counties, and have strong local influence on the dynamics in tetraonid populations.

Low intraspecific synchrony at the national scale and a weak relationship with distance in most species (except willow ptarmigan) suggest that although the synchronizing force(s) are correlated in space, large variation even at short distances indicates that local factors may be predominant (Tavecchia et al. 2008). If dispersal was the main synchronizing factor, it could be expected that species with the greatest dispersal distances should have the highest mean synchrony (Paradis et al. 1999); this was, however, not a clear pattern. Further, modelling studies predict that dispersal-induced synchrony causes a stronger negative relationship between synchrony and distance than synchrony caused by stochastic events (Lindstrom et al. 1996). However, in our study, there was a strong decline in synchrony with distance only in willow ptarmigan. The strong interspecific synchrony contra weaker intraspecific synchrony in our results, suggest that extrinsic factors are more important than dispersal in causing synchrony at the spatial scales studied here.

The strong synchrony between species inhabiting areas in close proximity indicates that the same envi-

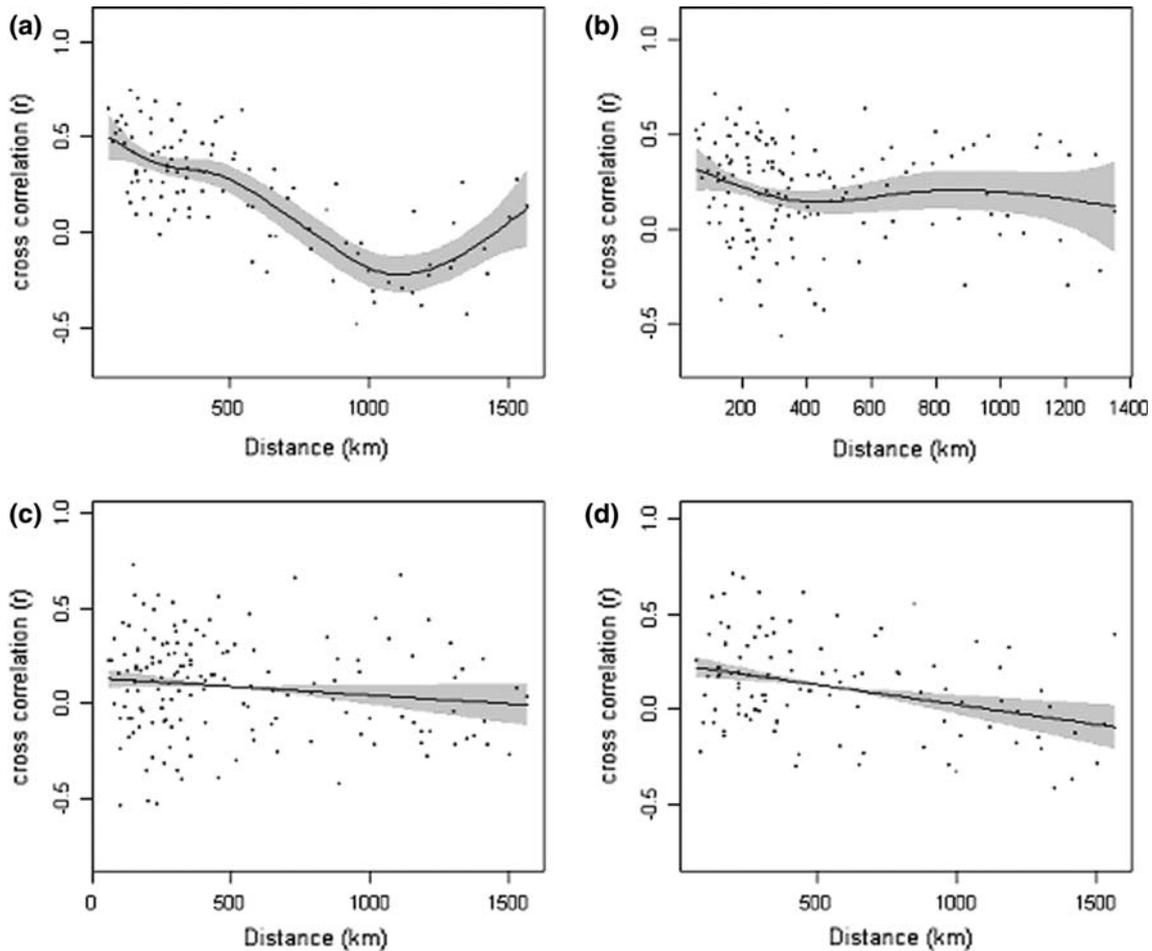


Fig. 5 The relationship between distance and cross-correlation for willow ptarmigan (a), black grouse (b), capercaillie (c) and rock ptarmigan (d), based on GAM non-parametric regression. *Black points* are cross-correlations plotted against distance. *Shaded area* is

the 95% point-wise confidence limit. Estimated degrees of freedom (i.e. edf) for the different slopes: willow ptarmigan (edf = 3.489), black grouse (edf = 3.199), capercaillie (edf = 1) and rock ptarmigan (edf = 1)

ronmental forces affect the tetraonids similarly. Few studies document direct effects of weather on tetraonids, most likely because the birds are well adapted to small deviations from the mean weather conditions (Myrberget 1988; Steen et al. 1988). However, extreme climatic events might affect chick survival either directly or by predisposing the chicks to predation (Erikstad and Andersen 1983; Wegge and Kastdalen 2007). As temporal variation in chick mortality is expected to contribute substantially to variation in population growth rates in tetraonids (Myrberget 1988; Steen and Erikstad 1996; Wegge and Kastdalen 2007), such extreme weather events could be capable of synchronizing tetraonid populations (Cattadori et al. 2000). Another potential effect of climate is mediated through its effects on the community dynamics. For instance, if densities of alternative prey or predator species are affected by climatic conditions, this will also affect the predation pressure on the tetraonid community (Kausrud et al. 2008). The strong synchrony between species with high overlap index also indicates that a shared predator-guild

affecting all species might play a key role in shaping the dynamics.

In this study, we have found answers to the questions stated in the introduction. Ecologically related species fluctuated in synchrony at national, region and county levels, but the strength of the correlations varied strongly between regions/counties. Furthermore, the intraspecific synchrony was generally weak in all species (willow ptarmigan the strongest) and only willow ptarmigan showed a clear decrease in the correlations with distance. Our results suggest that environmental conditions are affecting the tetraonid species similarly and cause the observed patterns of synchrony, and that local conditions are very important and cause the intraspecific synchrony to be variable also for populations in relative close proximity.

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