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Annual change in forest grouse in southern Norway: variation explained by temperatures, bilberry seed production and the lunar nodal phase cycle

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Forage quality is rarely the focus of studies on grouse performance. The plant stress hypothesis predicts that the protein digestibility of a focal food plant for grouse in Norway, the bilberry *Vaccinium myrtillus* should be highest after a peak in seed production. Protein digestibility may also be affected positively by cosmic ray (muon) fluxes, which fluctuate with the 9.3-year lunar nodal phase cycle, and negatively by high temperatures in the preceding summers. The annual change (first difference) in ln-transformed black grouse *Tetrao tetrix* and capercaillie *T. urogallus* hunting statistic indices from southern Norway 1999–2017 was positively related to the mean June temperature, which is assumed to have a direct positive impact on chick survival. In multiple regression models, there was also a positive relationship with the seed production of bilberry in the preceding year, the lunar nodal phase index with a two-year time lag, and a negative relationship with the combined mean June–September temperature of the two preceding years. Small rodent numbers did not contribute significantly in these models. In further monitoring of grouse populations, the seed production of bilberry or other important food plants should also be recorded.

Keywords: bilberry, grouse, herbivore performance, lunar phase, rodent cycles

In the boreal zone of Norway and Sweden, there is a well-known positive relationship between grouse reproduction and vole numbers. So far, this phenomenon has usually been explained solely as a result of prey switching by generalist predators; the alternative prey hypothesis (Hagen 1952). However, the factors that generate annual fluctuations in vole numbers may also act directly on grouse, and thus be the ultimate cause of a synchrony enhanced by predation. Vole and grouse peaks have commonly occurred at intervals of three–four years, and often simultaneously over large areas (Angelstam et al. 1985). A plausible explanation for the spatial synchrony is that herbivores respond to changes in forage quality caused by weather synchronized fluctuations in seed crops of their food plants (Selås 2016).

A focal food plant for both grouse and *Myodes* voles is bilberry *Vaccinium myrtillus* (Kaasa 1959, Hansson 1985, Pulliainen and Tunkkari 1991), and their population levels usually peak one year after a high production of bilberries (Nordhagen 1928, Laine and Henttonen 1983, Selås et al. 2011a). There is often a noticeable temporal variation in the seed crop of this long-lived deciduous dwarf shrub (Myrberget 1982, Langvall and Dahlgren 2016), and at least in some areas and periods, it has peaked at intervals of three–four years (Selås 1997, Selås et al. 2011a). It is, however, also strongly affected by temperatures acting during key stages of the flowering cycle (Selås et al. 2015), and thus by regional weather patterns (Selås 2016).

In southern Norway, a one-year delayed numerical response by the bank vole *Myodes glareolus* to peaks in bilberry seed production is due mainly to increased winter survival (Selås unpubl.). It can thus not be caused by the berries themselves, which disappear during autumn and are not stored by the voles. Selås (1997) suggested that there is a tradeoff between seed production and chemical defence in this plant species. According to the plant stress hypothesis (White 1984), protein and not energy, is usually the limiting factor for herbivores, and in particular for their reproduction and growth. Any stress factor that requires increased metabolic activity in a plant, such as a high seed crop, will force the plant to transfer complex stored proteins, which may serve as herbivore deterrents, to simpler transportable and easily digestive proteins. The resulting change in the ratio between protective and digestive proteins may make

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otherwise inedible plants suitable as food. The effect has been suggested to be strongest if summer temperatures are low prior to or during the seed production (Selås et al. 2011a).

In some grouse populations, there is also an approximately 10-year fluctuation pattern. This is particularly pronounced in Iceland (Nielsen 2008) and North America (Archibald 2014), but it has also been reported from Norway (Hagen 1952). Archibald (1977) suggested that the environmental cue for these '10-year' cycles, including that of the snowshoe hare *Lepus americanus* in Canada, is the 9.3-year lunar nodal phase cycle. A possible explanation for the undeniable correlation between this lunar cycle and hare, grouse and moth time series (Archibald 2014) is that the 9.3-year signature in surface cosmic ray fluxes (muons), caused by the Moon's impact on geomagnetic activity, reflects a regularly fluctuating plant stress factor. As a result, the protein digestibility of some plants may rise and fall around the critical threshold for herbivores in a regular 9.3-year cycle (Selås 2014).

A general shortcoming with many studies on grouse performance is that possible fluctuations in forage quality are not accounted for. There are no simple ways to determine the nutritional quality of grouse food plants, and to my knowledge, such data do not exist for any time series on grouse reproduction or population level. Hence, we are so far restricted to use variables assumed or suggested to affect forage quality in analyses on grouse reproduction or survival. Here, I use indices of bilberry seed production, the lunar nodal phase cycle and previous summer temperatures as proxies for food quality in an analysis of black grouse *Tetrao tetrix* and capercaillie *T. urogallus* hunting statistic from southern Norway. The analyses also included June temperatures, which were assumed to affect the survival of young grouse chicks (Wegge and Rolstad 2017), and small rodent numbers, assumed to buffer against egg and chick predation.

Methods

Study area

The grouse data were collected from Aust-Agder County, situated in the southern part of Norway. The county covers 9158 km^2, and range 0–1500 m above sea level. The average spring population level of black grouse and capercaillie has been estimated to 8000 and 4000 individuals, respectively (Bengtson et al. 2009). The majority of the populations of these species are found at 200–900 m elevation, where Scots pine *Pinus sylvestris*, Norway spruce *Picea abies* and downy birch *Betula pubescens* are the dominant tree species. This area consists of ca 2950 km^2 forest, of which ca 70% has a timber production high enough for commercial utilisation, and ca 440 km^2 bogs, of which ca 25% is covered by scattered pine and birch trees (Tomter et al. 2001). Bilberry is a common plant species in the field layer, and dominates at least 20% of the area (Hofsten et al. 2010).

Grouse indices

The grouse indices used were hunting statistic from Aust-Agder County for the period 1999–2017, from which information on bilberry seed production was also available. The hunting season is from 10 September to 23 December. Hunting statistic is provided by Statistics Norway (<www.ssb.no>), and is based upon reports from individual hunters. From 2000 onwards, the hunters had to pay an extra fee if they did not submit the report form. The proportion of hunters that reported was in general high (mean 89.5%, range 88.5–92.1%), but there was a significant decrease in the number of small game hunters, from 2580 in 2001 to 2150 in 2017 (mean 2346).

For the selected period, there was a highly significant positive correlation between the annual number of black grouse and capercaillie killed ($r = 0.93$, $p < 0.0001$, $n = 19$; Fig. 1). The mean number killed was 1700 (range 810–2740) for black grouse and 333 (range 180–460) for capercaillie. For both species, the hunting statistic correlated well with the hunting statistic from the larger neighbouring county in east, Telemark, confirming that there was a strong spatial synchrony in the fluctuation pattern during the selected period (black grouse: $r = 0.90$, $p < 0.0001$; capercaillie: $r = 0.75$, $p = 0.0003$). Also in Telemark, the black grouse was hunted in larger number than the capercaillie.

If grouse hunting indices reflect population levels, they should correlate significantly with count data. In a restricted area in Gjerstad Municipality in eastern Aust-Agder, close to the border of Telemark, members of the local hunter organization have counted grouse along 44–91 km line transects each autumn during 2002–2017 (results available at their home page <www.njff.no/fylkeslag/aust-agder/lokallag/gjerstad>). The mean annual number observed was 104.4 (range 30–165) for black grouse and 6.5 (range 1–18) for capercaillie. Their estimates of number of black grouse per km^2, based on the software 'distance sampling', correlated significantly with the number of black grouse hunted in Telemark ($r = 0.52$, $p = 0.040$), but not in Aust-Agder ($r = 0.36$, $p = 0.170$). However, when omitting the result from the starting year 2002, which seems to have an unrealistic low estimate, the correlation was highly significant for both counties (Telemark: $r = 0.72$, $p = 0.003$; Aust-Agder: $r = 0.68$, $p = 0.005$). I therefore regard the hunting indices to be reliable proxies for population levels.

When analysing for relationships with the selected explanatory variables, I used annual changes (first differences) of the ln-transformed grouse hunting statistics as response variables. This index gives the relative population change, positive or negative, from the previous autumn (year $t-1$) to the current autumn (year t). This index is assumed to reflect mainly current year reproduction (year t), but to some extent also adult survival during the last winter. Use of annual changes reduces the influence of a possible negative trend in the grouse series due to reduced hunting activity.

Bilberry indices

The production of bilberries has been recorded in Vegårshei Municipality, situated in the eastern part of Aust-Agder County, at ca 200 m elevation. During 1999–2017, I counted all bilberries in late July or early August at 15 fixed plots of 2×2 m^2, within an area of approximately 15 km^2. The plots were situated 0.5–5 km apart, all in old forest stands with bilberry as the dominant plant in the field layer. For each plot, the bilberry seed production of each succeeding year is calculated as a proportion of the production

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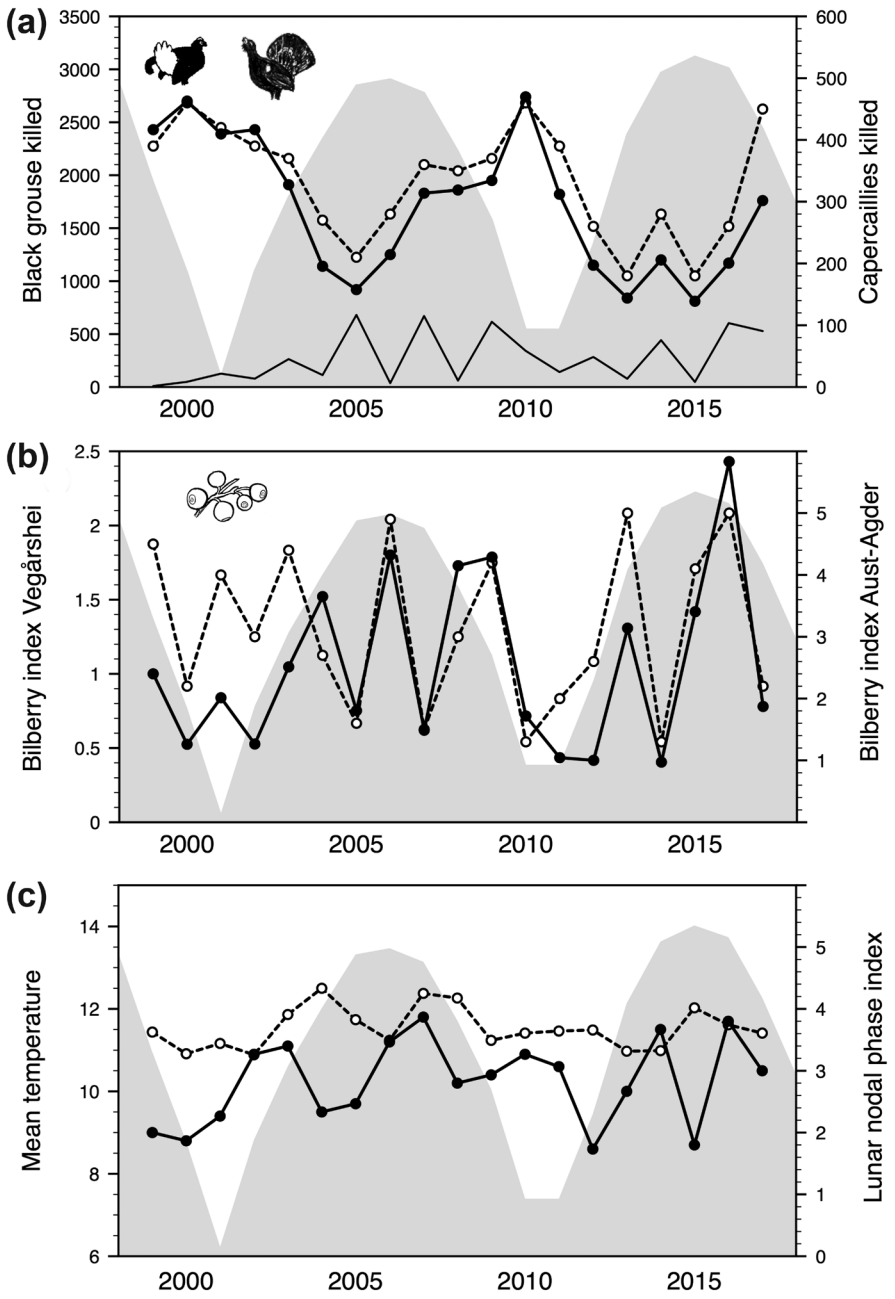


Figure 1. (a) Annual number of black grouse (solid line, filled symbols) and capercaillie (dotted line, open symbols) killed in Aust-Agder County 1999–2017, and an index of small rodent abundance, ranging 0.3–22.7 rodents trapped per 100 trap nights (thin solid line, no symbols, axis not shown). (b) Seed production of bilberry in Vegårshei Municipality (solid line, filled symbols) and Aust-Agder County (dotted line, open symbols) 1999–2017. (c) Mean temperature in June (solid line, filled symbols) and summarized for June–September the two preceding years (dotted line, open symbols) 1999–2017. The lunar nodal phase index is given as shaded area in each panel, with axis in panel c.

in 1999. The annual bilberry seed production indices are thus the mean of all 15 plots.

For all study years except 2005 and 2015, I found one or more statements about the bilberry seed production in 'Agderposten', a regional newspaper for Aust-Agder County. Except from two of these years, the editor of a weekly nature-page, nature photograph Paul Mjaaland, was responsible for one of the statements given. I supplemented the information from Agderposten with statements from some other sources, mainly local newspapers covering parts of Aust-Agder or nearby areas. The mean annual number of statements found was 2.5 (range 2–4). I presented these statements to 10 of my colleagues, who were all unfamiliar with the study area and the grouse data. They were asked to use the statements to evaluate the annual bilberry seed production on the following scale: 1 = very poor, 2 = poor, below average, 3 = average or normal, 4 = good, above average and 5 = very good, peak year. I then used the mean of their evaluations as a bilberry index for Aust-Agder County (Fig. 1).

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Small rodent indices

In the bilberry study area in Vegårshei, the population level of small rodents has been estimated by snap trapping, with ca 1000 trap nights each autumn, permitted by the Norwegian Environment Agency. The dominating rodent species was the bank vole, but also the wood mouse *Apodemus sylvaticus* was common. The indices used were the number of small rodents trapped per 100 trap nights, after having subtracted 0.5 trap nights for each capture of another species.

The lunar index

The plane of the Moon's orbit around the Earth, which is tilted by 5° in relation to the plane of the Earth's orbit around the Sun (the ecliptic), rotates because of gravity from the Sun. Twice during a full 360° rotation, i.e. at 9.3-year intervals, the Moon will pass close to the straight line from the Sun to the Earth in midwinter and midsummer. At these times, the magnetic fields of the Sun and the Earth are not parallel, so the magnetic connection is weak. The effect of the Moon, as a physical object, is to strengthen this connection and thus increase the geomagnetic activity, which is a measure of the amount of charged solar energetic particles that hits the Earth's magnetic field. The associated temperature increase leads to an expansion of the outer atmosphere. As a consequence, more ionizing muons, which are secondary cosmic rays created by collisions between high-energetic galactic cosmic ray particles and air molecules, decay before they reach the Earth's surface. Ionizing radiation is known to induce protein mobilization in plants (Selås 2014).

The lunar index used was the absolute value of the difference between maximum lunar declination in September and the tilt angle between the ecliptic and the equatorial plane (Archibald 2014). The index ranges between approximately 0–5, with the lowest value when the Moon is suggested to have strongest impact on geomagnetic activity (Selås 2014). When I compared a 27-year time series on rock ptarmigan *Lagopus mutus* from Iceland (Nielsen 2008) with this index, I found a positive correlation without time lag. Also a 62-year time series on ruffed grouse *Bonasa umbellus* from Minnesota (Archibald 2014) correlates positively with this lunar index, but with a one-year lag. This may be because the latter area is situated farther from the auroral oval, where the protection against cosmic rays is lowest. Also Norway is situated farther from the auroral oval than Iceland, so some time lag between the lunar index and the grouse indices may be expected.

Temperatures

Mean temperatures from each of the months June–September for the region 'Sørlandet' is provided by the Norwegian Meteorological Institute (<www.yr.no>). Weather conditions during the first weeks after hatching are known to be very important for chick survival (Wegge and Rolstad 2017). I therefore used the mean temperatures in June as an explanatory variable. In an analysis of grouse population data from Aust-Agder 1921 to 1977, there was a negative relationship with the combined mean temperature in June–September of the two preceding years (Selås et al. 2011a), so this index was used also in the present analyses. The index was originally chosen because foresters in Norway have applied it for evaluation of growth and seed production of forest trees.

Statistical analyses

I used cross correlation to test for significant time lags between the grouse indices and the lunar index. Thereafter normalized values of the bilberry index of the previous year and the lunar index, with time lag revealed by the cross correlation, were used as explanatory variables in multiple regression models. Additional explanatory variables were normalized small rodent indices, and normalized temperature indices. The residuals of all regression models presented satisfied the criteria for linear regression. Model selection was based on ΔAIC_c. In the selected models, the partial regression coefficient is given for each variable. The software used was JMP Pro ver. 12.1.0 (SAS Inst.).

Results

In the cross-correlation analyses, both grouse indices (annual changes of ln-transformed hunting statistics) were significantly related to the lunar index with a two-year time lag (Fig. 2, 3). With a one-year lag, the relationship was significant only for the black grouse (Fig. 2). The grouse indices were positively related to the previous year's bilberry index from Vegårshei (Table 1, Fig. 3) and Aust-Agder (Table 1), as well as the mean June temperature (Table 1). There also was a tendency for a relationship with the small rodent index, whereas the predicted negative relationship with previous summer temperatures was not significant (Table 1).

The two bilberry indices (Vegårshei and Aust-Agder) fluctuated considerably between years (Fig. 1), but were significantly correlated (Table 1). The main difference was that the peak around 2003–2004 appeared to occur a year later in Vegårshei than in the county in general, and that the Aust-Agder index distinguished less between peak levels (Fig. 1). Most of the explanatory variables were not significantly inter-correlated, but the bilberry index from Vegårshei was positively related to the lunar index and almost so to the June temperature index (Table 1).

The best multiple regression model for both grouse species included four explanatory variables: the mean June temperature, the mean June–September temperature of the two preceding years, the lunar index with a two-year time lag, and the Aust-Agder bilberry index of the preceding year (Table 2, 3, Fig. 4). The explanatory power was reduced if the Aust-Agder bilberry index was substituted by the bilberry index from Vegårshei or the small rodent index (Table 2, 3). The bilberry index from Vegårshei was, however, a significant (capercaillie: $p = 0.045$) or almost significant (black grouse: $p = 0.064$) explanatory variable if the lunar index was used with a time lag of one year instead of two. All other explanatory variables remained significant in these models.

To test whether the two grouse species differed in their response to any of the explanatory variables, I built a combined model with species as categorical variable, and with interaction effects of species and the four explanatory variables used in the models presented in Fig. 4. All original

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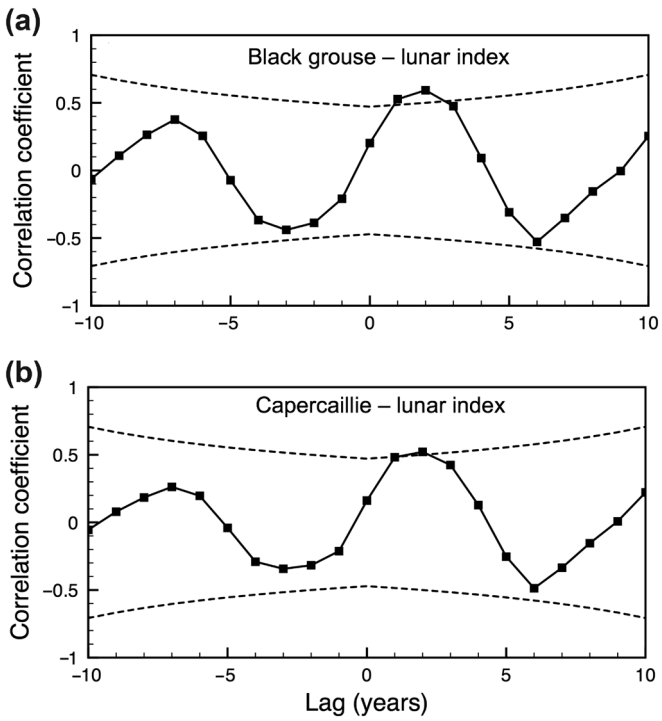


Figure 2. Cross-correlation coefficients calculated between the lunar nodal phase index and the annual change (first difference) of the ln-transformed number of (a) black grouse and (b) capercaillie killed in Aust-Agder County, southern Norway, 1999–2017. The 95% confidence limits are given as dotted lines.

explanatory variables remained highly significant in this model, whereas there was no significant effect of species ($p = 0.56$) or the interaction between species and any of the four predictors ($p > 0.4$).

Discussion

The grouse hunting indices from Aust-Agder showed a strong positive correlation with the mean temperature in June, presumably because cold weather is detrimental for young chicks, and may even make them more vulnerable to predation (Wegge and Kastdalen 2007). This is in concordance with the conclusion of Wegge and Rolstad (2017), i.e. that high spring or early summer temperatures are advantageous for the breeding success of boreal forest grouse. However, as also stated by Wegge and Rolstad (2017), this should not lead to the general conclusion that warmer climate will result in increased population sizes of forest grouse (see also Ludwig et al. 2006). Despite increased breeding success of both black grouse and capercaillie during 1979–2016, the population of black grouse declined during 1979–2008 (Wegge and Rolstad 2011).

Although there was no significant relationship between grouse indices and previous summer temperatures in univariate tests, summer temperatures contributed with a negative effect in the multivariate models. The suggested explanation is that warm summers decrease forage quality, or reduce the recovery period of the plants after a high seed production (Selås et al. 2011a). Low numbers or performance in warm periods has also been reported for other herbivores (Johnson et al. 2010, Yan et al. 2013). Wegge and Rolstad (2017) did not find a similar relationship for forest grouse in eastern Norway, but this question may need to be revisited, in analyses where effects of other factors are accounted for.

The grouse hunting indices from Aust-Agder correlated positively with the bilberry indices of the preceding year, in accordance with the suggested increase in protein digestibility in bilberry plants after a high seed crop (White 1984, Selås 1997). Lower explanatory power than for June temperature and the lunar index may not reflect lower biological impact, but rather that it is difficult, with limited resources, to obtain a bilberry index that is representative for a whole county. The one-year time lag between bilberries and grouse indices suggests that the causal relationship is changes in forage quality rather than nutrients provided by berries. Plant chemical defence is a complex issue, but recent studies support the hypothesis of a tradeoff between reproduction and defence in bilberry (Benevenuto et al. 2018, 2019).

There was also a tendency for a positive relationship with the small rodent index, as expected both from the alternative prey hypothesis and the general relationship between *Myodes* voles and bilberry seed production (Laine and Henttonen 1983, Selås et al. 2011a). Several studies suggest that there is a link between the body condition of grouse hens and the vole cycle (Myrberget 1986, Storaas et al. 2000), i.e. that the grouse–vole correlation is not due solely to predation. In Norway, even the mean annual reproduction of moose *Alces alces*, which also feed on bilberry plants, has varied in synchrony with bank vole numbers, despite lack of common predators (Selås et al. 2011b).

The relationship with the lunar index is difficult to explain by other mechanisms than fluctuating fluxes of cosmic rays acting through forage quality, possibly of both

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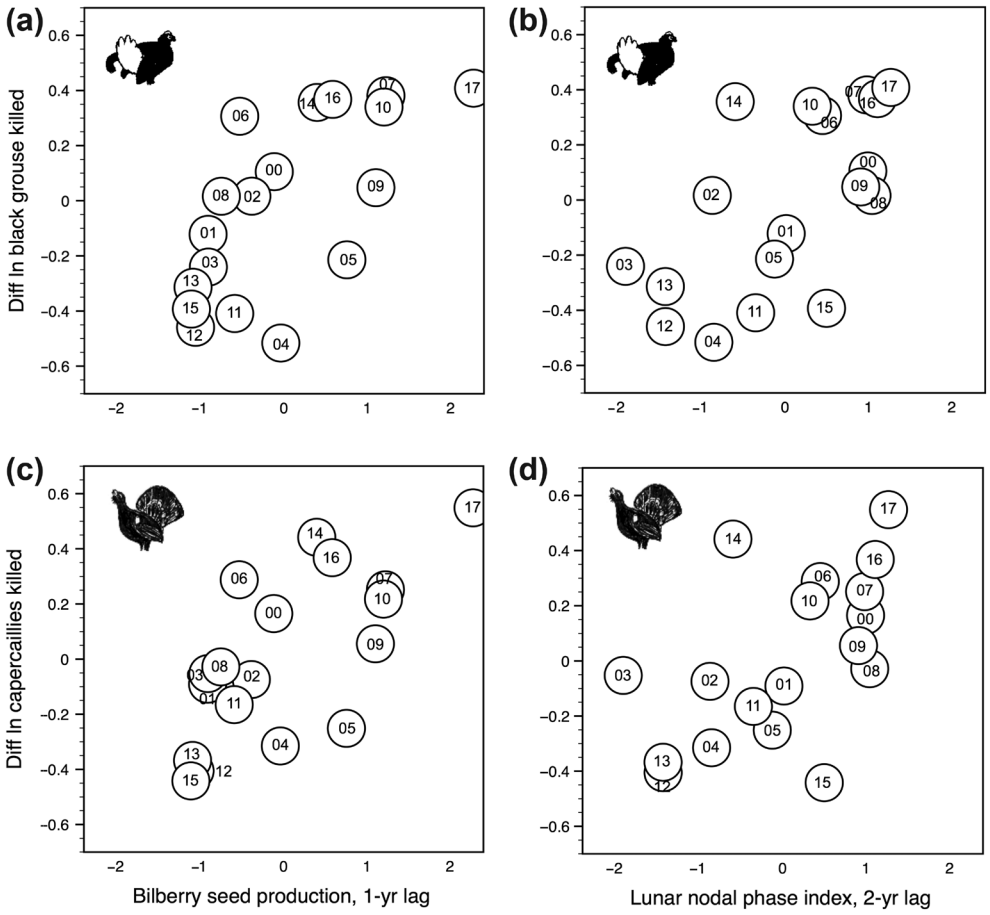


Figure 3. Annual change (first difference) of the ln-transformed number of grouse killed in Aust-Agder County, southern Norway, 1999–2017, in relation to standardized values of the Vegårshei bilberry index with a one-year time lag and the lunar nodal phase index with a two-year time lag. (a) black grouse and the bilberry index, (b) black grouse and the lunar index, (c) capercaillie and the bilberry index, (d) capercaillie and the lunar index. The number given for each plot is abbreviation for year.

bilberry plants and forest trees utilized in winter. Unfortunately, few ecologists are familiar with astrophysics, and both Klemola et al. (2016) and Myers (2018) rejected the cosmic ray hypothesis without evaluating the proposed mechanism, and the lunar–herbivore relationship (Archibald 2014) was just ignored. Feldhamer et al. (2015) suggested that herbivore cycles according to the cosmic ray hypothesis should be synchronized among boreal forests. However, the prediction is rather that population increases should appear first in areas with low magnetospheric or atmospheric protection against cosmic rays (Selås 2014). Also Krebs et al. (2018) miss this point when they state that the delay in snowshoe hare cycles from central parts of Canada (where cosmic ray fluxes are highest) towards east is a challenge for future generations of biologists. A similar pattern is observed for the ruffed grouse – the cycles begin in the north and progress southward and southeastward (RGS 2019).

Table 1. Coefficients (upper right) and p-values (lower left) from correlation analyses of grouse indices (BG = ln black grouse hunting statistic, year t – (t – 1); CA = ln capercaillie hunting statistic year t – (t – 1)) and explanatory variables used in the regression models in Table 2, 3. June = June temperature year t, JJAS = June–September temperature year (t – 1) + (t – 2), Lunar1 and Lunar2 = the lunar nodal phase index year t – 1 and t – 2, respectively, Bil-V and Bil-A, a bilberry index year t – 1 for Vegårshei and Aust-Agder, respectively, Rodents = a snap trapping index of small rodents year t.

Variable	BG	CA	June	JJAS	Lunar1	Lunar2	Bil-V	Bil-A	Rodents
BG		0.94	0.69	−0.23	0.53	0.63	0.67	0.57	0.44
CA	<0.001		0.68	−0.23	0.49	0.56	0.69	0.61	0.43
June	0.002	0.002		−0.01	0.23	0.13	0.43	0.38	0.43
JJAS	0.354	0.364	0.977		0.37	0.12	0.04	−0.08	0.14
Lunar1	0.023	0.041	0.366	0.136		0.73	0.47	0.18	0.39
Lunar2	0.006	0.016	0.596	0.644	<0.001		0.56	0.17	0.30
Bil-V	0.002	0.002	0.078	0.871	0.051	0.037		0.70	0.77
Bil-A	0.014	0.007	0.115	0.759	0.469	0.506	0.001		0.47
Rodents	0.065	0.074	0.076	0.573	0.109	0.226	<0.001	0.051	

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Table 2. Results from multiple linear regression models with the annual change (first difference) of the ln-transformed number of black grouse hunted in year t during 1999–2017 as response variable (n = 18), and factors (standardized indices) assumed to affect adult mortality or breeding success as predictors. The two best models based on ΔAIC_c are presented, together with two models where the bilberry index from Aust-Agder is substituted by the bilberry index from Vegårshei and a small rodent index, respectively.

Explanatory variable	Estimate	SE	df	F	p
Model 1, adjusted $R^2 = 0.85$, $\Delta AIC_c = 0$					
Intercept	−0.018	0.030	1		
June temperature, t	0.160	0.033	1	23.12	<0.001
June–Sept temp, (t − 1) + (t − 2)	−0.089	0.031	1	8.14	0.014
Lunar nodal phase, t − 2	0.178	0.031	1	32.08	<0.001
Bilberries Aust-Agder, t − 1	0.087	0.034	1	6.64	0.023
Model 2, adjusted $R^2 = 0.79$, $\Delta AIC_c = 2.79$					
Intercept	−0.018	0.035	1		
June temperature, t	0.192	0.037	1	27.44	<0.001
June–Sept temp, (t − 1)+(t − 2)	−0.096	0.037	1	6.94	0.020
Lunar nodal phase, t − 2	0.190	0.040	1	26.32	<0.001
Model 3, adjusted $R^2 = 0.80$, $\Delta AIC_c = 5.18$					
Intercept	−0.018	0.034	1		
June temperature, t	0.170	0.040	1	18.46	<0.001
June–Sept temp, (t − 1)+(t − 2)	−0.095	0.036	1	7.15	0.019
Lunar nodal phase, t − 2	0.158	0.043	1	13.19	0.003
Bilberries Vegårshei, t − 1	0.062	0.047	1	1.73	0.211
Model 4, adjusted $R^2 = 0.78$, $\Delta AIC_c = 6.94$					
Intercept	−0.018	0.036	1		
June temperature, t	0.182	0.041	1	19.40	<0.001
June–Sept temp, (t − 1)+(t − 2)	−0.099	0.038	1	6.92	0.021
Lunar nodal phase, t − 2	0.183	0.039	1	21.98	<0.001
Small rodents, t	0.026	0.043	1	0.36	0.560

There are also other factors that may affect the timing of the predicted increases in forage quality, and thus spatial synchrony in herbivore fluctuations. Surface muon fluxes are inversely related to air pressure and temperature, and the relative impact of the 9.3-year lunar cycle and the 11-year solar cycle is hypothesised to depend on the general magnetospheric and atmospheric protection against cosmic rays (Selås 2014). Furthermore, the reproduction of many perennial plant species, including bilberry, is controlled by weather variables that may have stronger impact in some areas and periods than in others. In Sweden, the annual seed production of bilberry in Södra Norrland corresponded well with that in Svealand during 2010–2016, but not during 2003–2009 (Langvall and Dahlgren 2016). For bank vole

Table 3. Results from multiple linear regression models with the annual change (first difference) of the ln-transformed number of capercaillie hunted in year t during 1999–2017 as response variable (n = 18), and factors (standardized indices) assumed to affect adult mortality or breeding success as predictors. The two best models based on ΔAIC_c are presented, together with two models where the bilberry index from Aust-Agder is substituted by the bilberry index from Vegårshei and a small rodent index, respectively.

Explanatory variable	Estimate	SE	df	F	p
Model 1, adjusted $R^2 = 0.80$, $\Delta AIC_c = 0$					
Intercept	0.008	0.032	1		
June temperature, t	0.148	0.036	1	17.10	0.001
June–Sept temp, (t − 1)+(t − 2)	−0.077	0.033	1	5.35	0.038
Lunar nodal phase, t − 2	0.142	0.034	1	17.88	<0.001
Bilberries Aust-Agder, t − 1	0.097	0.036	1	7.28	0.018
Model 2, adjusted $R^2 = 0.74$, $\Delta AIC_c = 1.56$					
Intercept	0.008	0.037	1		
June temperature, t	0.146	0.041	1	12.84	0.003
Lunar nodal phase, t − 2	0.132	0.038	1	11.97	0.004
Bilberries Aust-Agder, t − 1	0.105	0.041	1	8.58	0.022
Model 3, adjusted $R^2 = 0.74$, $\Delta AIC_c = 4.58$					
Intercept	0.008	0.036	1		
June temperature, t	0.154	0.041	1	13.66	0.003
June–Sept temp, (t − 1)+(t − 2)	−0.084	0.038	1	5.03	0.043
Lunar nodal phase, t − 2	0.113	0.046	1	6.11	0.029
Bilberries Vegårshei, t − 1	0.082	0.050	1	2.72	0.123
Model 4, adjusted $R^2 = 0.69$, $\Delta AIC_c = 6.60$					
Intercept	0.008	0.039	1		
June temperature, t	0.174	0.045	1	14.87	0.002
June–Sept temp, (t − 1)+(t − 2)	−0.088	0.041	1	4.58	0.052
Lunar nodal phase, t − 2	0.150	0.043	1	12.25	0.004
Small rodents, t	0.024	0.047	1	0.25	0.626

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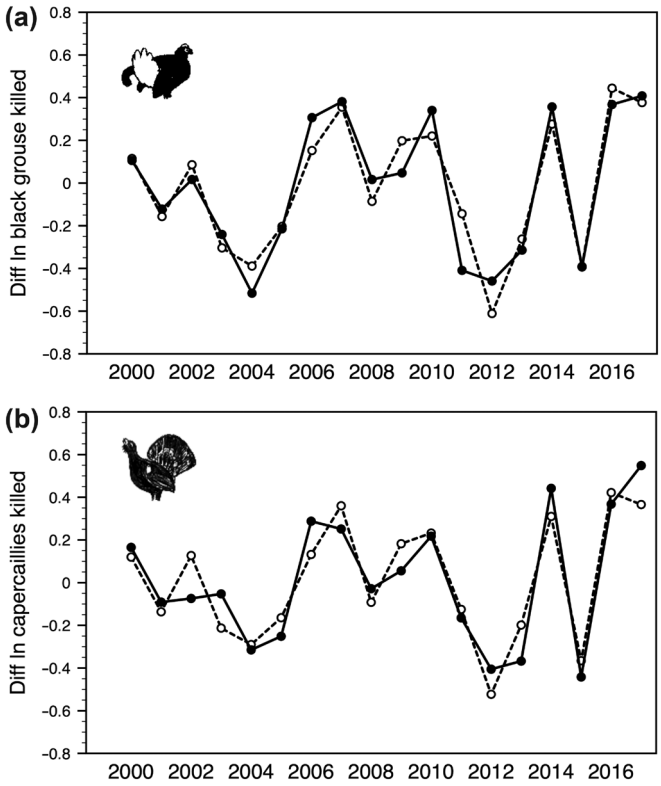


Figure 4. Annual change (first difference) of the ln-transformed number of (a) black grouse and (b) capercaillie killed in Aust-Agder County, southern Norway, 1999–2017 (solid line, filled symbols) compared with the values predicted by the first regression model in Table 2, 3, respectively (dotted line, open symbols).

populations in Norway, there was a high degree of spatial synchrony in the 1970s (Christiansen 1983), but less in the early 1990s (Steen et al. 1996, Selås et al. 2011b).

Even if food quality is a main generator of fluctuations in grouse numbers, predation is likely to be an important contributor (Kämmerle and Storch 2019). Grouse, and chicks in particular, are likely to become more vulnerable to predation in years with low forage quality, not only because they have to spend more time searching for food then, but also because birds in poor body condition are easier to capture for predators (Kenward 1978). If grouse hens have to leave their nests more often and for longer periods for feeding (Erikstad 1986), nests may be easier to detect for egg predators, and the hens themselves may become more vulnerable to predation by goshawks *Accipiter gentilis* (Selås 2003). Tornberg et al. (2011) suggested that the negative relationship between vole numbers and goshawk predation on grouse hens in spring is a result of 'predator facilitation', i.e. vole predators will increase their hunting activity and more often flush grouse hens when voles are scarce, so that the hens are easier to detect for the goshawks. However, they only found a positive relationship between goshawk predation on black grouse hens in summer and the abundance index of stoat *Mustela erminea*, a species that hardly count as grouse nest predator (Jahren 2017). The relationship with the much more important red fox *Vulpes vulpes* was actually negative.

Uncertainty associated with the population trends of grouse populations (Ludwig et al. 2006, Jahren et al. 2016) emphasizes the value of continued annual monitoring of different phases of the breeding cycle and autumn population sizes. If possible, also the body condition of the birds should be monitored on an annual basis (Stenkewitz et al. 2016). As long as we lack simple methods for measuring forage quality, grouse population studies should also include monitoring of the seed production of bilberry or other important food plants, in order to test the generality of the results reported here.

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