


# Bilberry seed production explains spatiotemporal synchronicity in bank vole population fluctuations in Norway

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## Abstract

Population fluctuations of small rodents are often synchronized over larger areas (>100 km) than what could be explained by dispersal, suggesting that the synchronizing factor is weather-related and possibly mediated through changes in food quality. Because bank vole (*Myodes glareolus*) populations usually peak 1 year after peaks in reproduction of the staple winter food plant bilberry (*Vaccinium myrtillus*), we tested for a possible link between food and spatial synchrony by comparing the synchrony in bank vole population indices and bilberry seed production indices between three study areas across about 20,000 km<sup>2</sup> in South Norway during a four decade period (1979–2019). There were subperiods of spatial synchrony and asynchrony between the study areas in the fluctuations of bank vole numbers and bilberry seed production, with the latter part of the study period displaying more pronounced synchrony than the first and middle part. However, with a few marked exceptions, when vole fluctuations were spatially out of phase across study areas so was bilberry seed production. Thus, we conclude that bilberry seed production to a large extent explained the spatiotemporal synchronicity in bank vole population fluctuations. Although bilberry seed production seems to be a causal driver of vole fluctuations, it remains to be seen to what extent the chemical composition of bilberry plants influences vole performance. Finally, certain weather factors may still influence voles directly, or indirectly by triggering bilberry seed production.

## KEYWORDS

*Myodes*, spatial synchrony, *Vaccinium*, weather

## 1 | INTRODUCTION

The high-amplitude multiannual population fluctuations of small rodents in the northern hemisphere are often

synchronized over large geographical areas (Angerbjörn, Tannerfeldt, & Lundberg, 2001; Bjørnstad, Stenseth, & Saitoh, 1999; Christiansen, 1983; Krebs et al., 2002; Myrberget, 1973). Suggested mechanisms for the spatial

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synchrony are dispersal, exogenous factors such as temperature or precipitation, and trophic interactions (Liebhold, Koenig, & Bjørnstad, 2004). The spatiotemporal dynamic may, however, change over time (Bierman et al., 2006). Populations of bank vole (*Myodes glareolus*) in eastern Norway fluctuated in synchrony within a spatial scale of up to 30–40 km during 1990–1994 (Steen, Ims, & Sonerud, 1996), whereas population peaks observed in 2007 and 2014 occurred synchronously in areas situated several hundreds kilometers apart (Andreassen, Johnsen, Joncour, Neby, & Odden, 2020; Selås, 2020; Selås et al., 2011; Wegge & Rolstad, 2018).

Because population peaks of small rodents commonly occur simultaneously over much larger areas than what could be explained by dispersal (Ims & Andreassen, 2005), several authors assume that the synchronizing factor most likely is weather-related (Angerbjörn et al., 2001; Huitu, Laaksonen, Klemola, & Korpimäki, 2008; Koenig, 2002; Krebs et al., 2002). One possible weather effect is high mortality in years with unfavorable winter conditions (Bilodeau, Gauthier, & Berteaux, 2013; Kausrud et al., 2008). Nevertheless, attempts of linking large-scale rodent population dynamics directly to weather have not given any firm conclusions (e.g., Myrberget, 1974; Østbye, Steen, Framstad, & Tveite, 1989; Solonen & Ahola, 2010). Weather may however be an indirect spatially synchronizing factor, by affecting important food resources (e.g., Övergaard, Gemmel, & Karlsson, 2007; Selås, Sønsteby, Heide, & Opstad, 2015).

Bilberry is a staple food plant for *Myodes* voles in winter (Hansson, 1985; Hansson & Larsson, 1978), when food appears to be a limiting factor (Haapakoski & Ylönen, 2013; Johnsen et al., 2017; Ylönen & Eccard, 2004). In Fennoscandia, the autumn population level of *Myodes* voles usually peaks 1 year after peaks in the berry production of bilberry (*Vaccinium myrtillus*) (Laine & Henttonen, 1983; Selås, 2020). A similar berry-vole relationship has been reported from Canada (Krebs, Cowcill, Boonstra, &

Kenney, 2010). Regardless of the causal relationship, spatial synchrony in *Myodes* vole population dynamics may therefore reflect a similar synchrony in bilberry reproduction, determined by weather factors that act during the flowering cycle of this plant species (Selås et al., 2015).

In large parts of Fennoscandia, vole populations have fluctuated with a regular periodicity of 3–4 years (Angelstam, Lindström, & Widén, 1985). These population cycles are usually characterized by a negative autocorrelation at a time lag of 2 years (Hörnfeldt, 1994). Such delayed density dependence has commonly been interpreted as a result of trophic interactions, either between voles and their predators, or between voles and their food plants (Oli, 2019). Here, we use time series from three separate areas in South Norway to test whether any delayed density dependence in bank vole numbers could be linked to bilberry reproduction. Thereafter we examine spatial synchrony of bank voles and bilberry seeding. Our prediction is that the spatial pattern of bank vole synchrony reflects a similar pattern of synchrony in bilberry reproduction.

## 2 | MATERIALS AND METHODS

### 2.1 | Bank vole population index

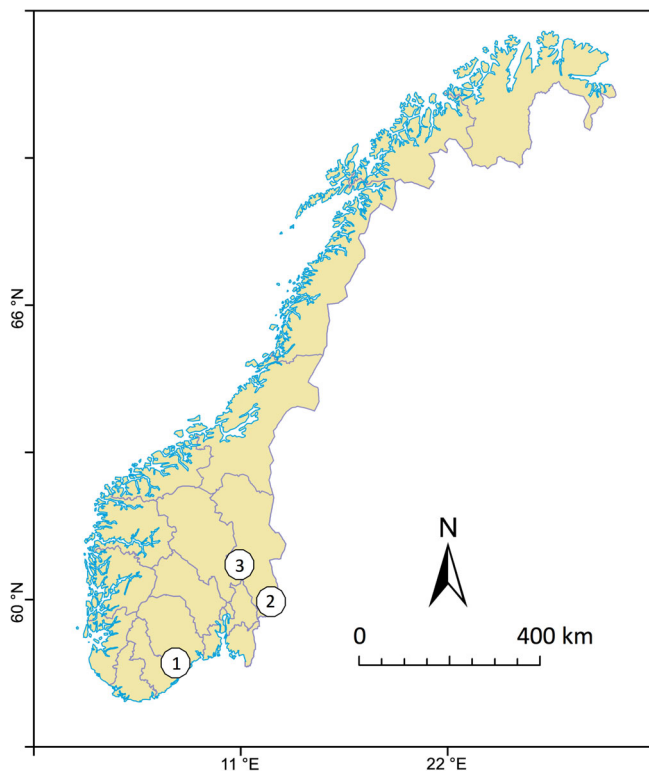
Small rodents were snap trapped in autumn for four decades in three areas within approximately 20,000 km<sup>2</sup> in South Norway; Agder (two sites situated 20 km apart, one in Vegårshei and one in Gjerstad), Varaldskogen and Vangsåsen (Table 1). Varaldskogen and Vangsåsen are situated 120 km apart, while Agder is situated 270 km from Varaldskogen and 280 km from Vangsåsen (Figure 1). Permission to conduct the snap trapping was given by the Norwegian Environment Agency.

Trapping sites in Agder and Varaldskogen were located in mature forest stands with bilberry as a common plant species in the field layer, which is the

**TABLE 1** Information about the study areas and the small rodent trapping protocols

Study area and subsite	Elevation (m)	Trapping period	Trap nights	Trap nights × number of traps		Bait
				Mean	(Range)	
Agder	200	1980–1989	2	395	(383–400)	Raw potato
		1999–2019	4	962	(895–997)	Raw carrot
Gjerstad	375	1988	3	660		Soya-bean oil
		1990–2019	3	1,439	(329–1,500)	Soya-bean oil
Varaldskogen	300	1979–2019	2	136	(44–317)	Raw potato
Vangsåsen	575	1981–2019	4	1,062	(968–1,148)	Coconut fat

Note: Traps of type “Rapp” were set out along transects for 2–4 nights each autumn. Trapped animals were removed every day, and traps were reset and if necessary rebaited.



**FIGURE 1** Map of Norway showing the study areas. 1 = Agder, 2 = Varaldskogen, 3 = Vangsåsen [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

preferred habitat of bank voles in South Norway (Gorini et al., 2011). In Vangsåsen, trap lines were permanent and crossing several patches of different successional stages, so during the four-decade study traps were in both mature forest stands and younger forest succession stages from clear-cuts to medium-aged forest. Because the amplitude of bank vole population fluctuations increases with altitude (Andreassen et al., 2020), most population peaks caused by high berry production in old forest stands would most likely be very apparent also in other habitats in this high-elevation study area.

The population index used was number of bank voles trapped per 100 trap nights. For years with trapping in both subsites in Agder (1988, 1999–2019), we used the mean of the two trapping indices. Due to slightly different trapping protocols among study areas, we present the index as standardized values (Z-scores).

## 2.2 | Field measurements of bilberry seed production

In two of the study areas, the production of bilberries was recorded in the field. Berries were counted in representative plots in old forest stands of similar types as used for rodent trapping, spread out in the study areas. The annual berry

index is the number of berries per  $m^2$ . In Agder (Vegårshei), all berries in 15 fixed plots of  $2 \times 2 m^2$  were counted in late July or early August, that is, at  $60 m^2$  each year, from 1999 onward (Selås, 2020). In Varaldskogen, berries were counted in mid-August in three circles of  $0.5 m^2$  in the same 6–8 forest stands each year, corresponding to 9–12  $m^2$  each year, from 2003 onward. Because we did not use the same plots each year in this area, the number of berries was corrected for the coverage of bilberry plants in each circle. The berries were not subject to further investigations, because major variations in the mean number of seeds per berry were not expected, despite marked annual variations in berry numbers per plot (Jacquemart & Thompson, 1996; Kloet & Cabilio, 1996).

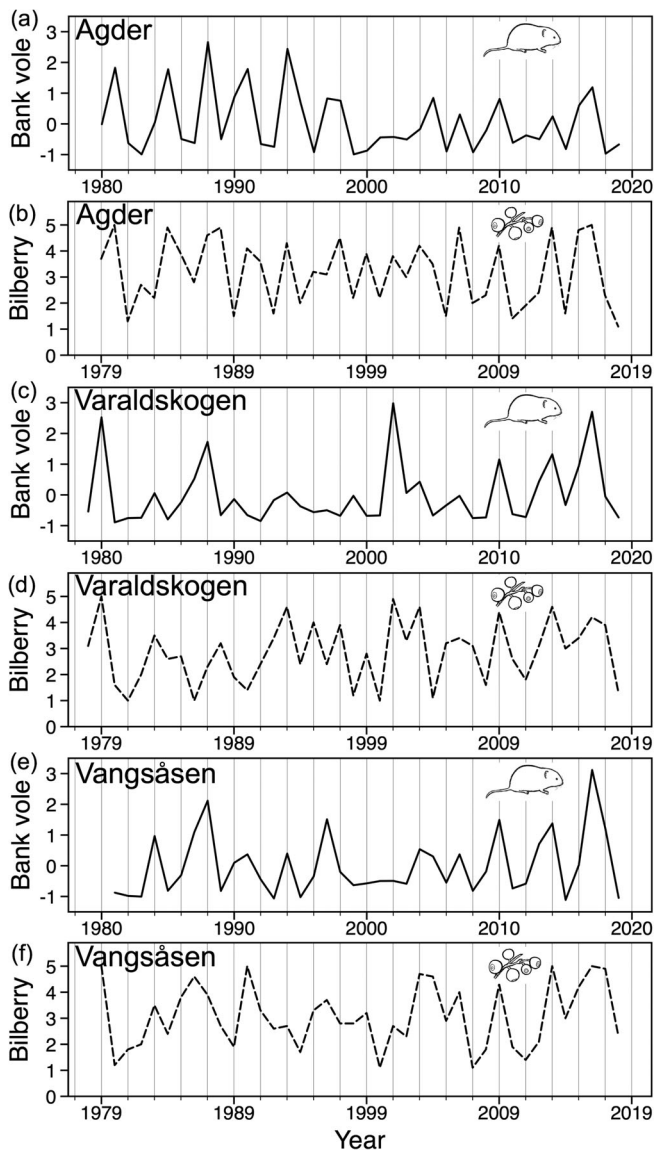
## 2.3 | Bilberry index based on newspaper reports

The bilberry counts covered the latter half of two of the vole time series only. To obtain an index of bilberry seeding for the entire study period from all areas, we searched for reports of bilberry production in all relevant local and regional newspapers, as well as in national newspapers, which sometimes gave information related to one of our regions. All newspapers used are available at the National Library of Norway. Although the quality of newspaper reports may vary, Selås (2019) found a significant positive correlation between a bilberry index obtained from newspaper reports and annual counts of bilberries ( $r = .7$ ). Hence, the method appeared to be appropriate for revealing peak years. Deficiencies in newspaper reports are likely to make it easier to reject the proposed hypothesis. Hence, using newspaper reports should be a conservative approach.

For each region, 10 persons, specific for the region, were asked to evaluate the annual berry production based on newspaper reports, by use of the following scale: 1 = very poor, 2 = poor, below average, 3 = average or normal, 4 = good, above average and 5 = very good, peak year. We then used the mean of their assessments as a bilberry index for each year. All contributors were familiar with bilberry harvesting in Norway. Because a few more newspaper reports than those used by Selås (2019) were later found for Agder, and a longer time period was of interest, the procedure was repeated for this region, with other persons than those asked in Selås (2019). However, for the common period 1999–2017, the result was very similar ( $r = .95$ ).

## 2.4 | Statistical analyses

Although there is a functional relationship between vole generations in 1 year and the next, there is considerable



**FIGURE 2** Standardized (*Z*-scores) autumn snap trapping indices of bank vole (number trapped per 100 trap nights) and bilberry indices based on newspaper reports (for method, see text) in three areas in Norway. Note that the x-axis for the bilberry series is moved 1 year to the right, because of the expected 1-year time lag between berries and voles

variation in the vole indices from year to year (Figure 2). There were only a few cases of significant positive autocorrelations for the data sets: at lag 3 years for the bank vole index from Agder, and at lag 4 years for the bilberry newspaper index from Varaldskogen. There were no significant autocorrelations at lag 1 year. Hence, we did not use any adjustments when testing for relationships between voles and berries.

Spectral density and autocorrelation were used to analyze for periodicity in the bank vole series (Hörnfeldt, 1994), and cross-correlation to test for time lags between berries and voles in each area. Thereafter we used the

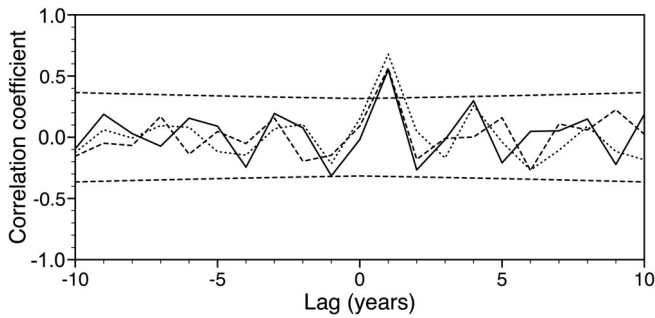
bank vole number trapped (not the trapping index) as response variable in generalized linear models (GLM) with Poisson distribution and log link function, and the log-transformed number of trap nights as offset. For each model, the degree of overdispersion was estimated in a post-model fit, and then controlled for by including an overdispersion parameter. Explanatory variables were previous population level and berry production, with time lags identified by the autocorrelation and cross-correlation analyses, respectively.

When testing for temporal relationships between vole indices, between bilberry indices, and between vole indices and bilberry indices, we used Spearman rank correlation, which is a conservative test statistic. We used a sliding window approach, with a “window” of 10 years moved over the time series, 1 year at a time, computing the correlation coefficient for each 10-year period. With a time series of 40 years, 30 correlation coefficients with associated confidence intervals were calculated. The software used for all analyses was JMP<sup>®</sup> Pro 15.0.0 (SAS Institute, Cary, NC).

### 3 | RESULTS

In all study areas, there was a strong multiannual fluctuation in both bank vole indices and bilberry newspaper indices (Figure 2a–f), but the bank vole showed some temporal variations with regard to peak levels. In Agder and Vangsåsen, there were no marked peaks during a 6-year period in the early 2000s (Figure 2a,e), and in Agder, later peaks were in general lower than peaks during 1980–1995 (Figure 2a). In Varaldskogen, there was a 12-year period with low-amplitude fluctuation centered in the 1990s (Figure 2c). Spectral density analyses showed a significant periodicity only in bank vole indices from Vangsåsen, with a cycle period of 3.3 years (Fisher's  $Kappa = 6.08$ ,  $p = .018$ ). There was a negative autocorrelation at time lag 2 years in all areas, but significantly so only in Agder ( $r = -.35$ ,  $p = .031$ ) and Vangsåsen ( $r = -.40$ ,  $p = .015$ ), and not in Varaldskogen ( $r = -.14$ ,  $p = .412$ ). No other significant negative autocorrelations in the bank vole series were found.

In cross-correlation analyses, the only significant correlation between vole indices and corresponding bilberry newspaper indices was at time lag 1 year (Figure 3). There was a significant correlation between the bilberry newspaper index and the bilberry count index in Agder 1999–2018 (Figure 4a), and marginally nonsignificant correlation at Varaldskogen 2003–2018 (Figure 4b). The bank vole index was significantly related to the two bilberry indices, with a 1-year time lag, both in Agder 2000–2019 (berry count index:  $r_s = .60$ ,  $n = 20$ ,  $p = .005$ ;



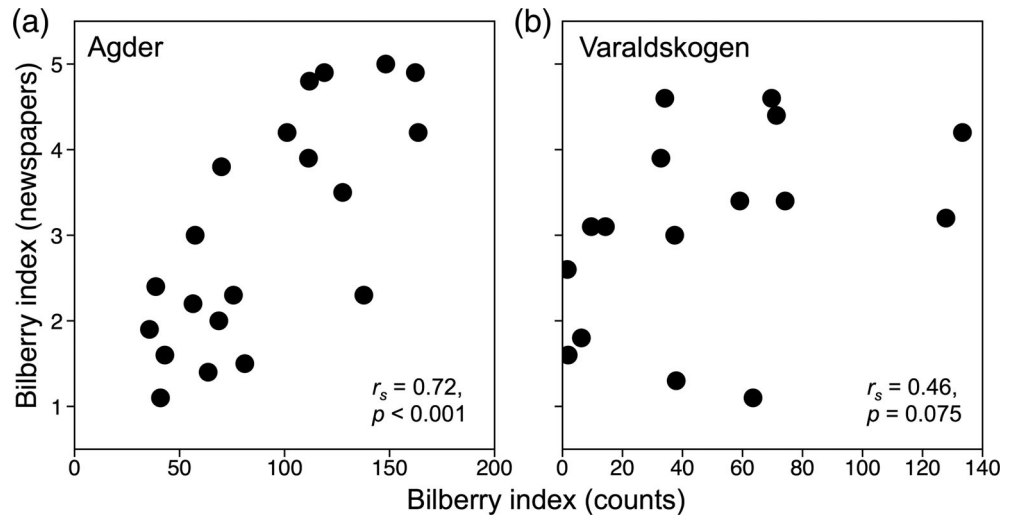
**FIGURE 3** Cross-correlation coefficients calculated between the vole index and the bilberry index in each study area, given in Figure 2. Hatched horizontal lines show the 95% confidence limit. Solid graph line = Agder, hatched = Varaldskogen, dotted = Vangsåsen

newspaper index:  $r_s = .71$ ,  $n = 20$ ,  $p < .001$ ), and Varaldskogen 2004–2019 (berry count index:  $r_s = .55$ ,  $n = 16$ ,  $p = .026$ ; newspaper index:  $r_s = .80$ ,  $n = 16$ ,  $p < .001$ ).

The GLM-models showed that the bank vole index was positively related to the bilberry newspaper index of the previous year in all areas (Table 2). Only in Vangsåsen was there a significant contributing effect of the population level 2 years earlier. If only the bilberry newspaper index was used as explanatory variable, there was no significant autocorrelation at lag 2 years in the residuals (Agder:  $r = -.13$ ,  $p = .43$ ; Varaldskogen:  $r = -.06$ ,  $p = .73$ ; Vangsåsen:  $r = -.25$ ,  $p = .12$ ).

For 10-year sliding-window periods, there was a significant positive correlation between all vole series

**FIGURE 4** Bilberry indices based on newspaper reports compared to indices based on berry counts in (a) Agder 1999–2018 ( $n = 20$ ) and (b) Varaldskogen 2003–2018 ( $n = 16$ )

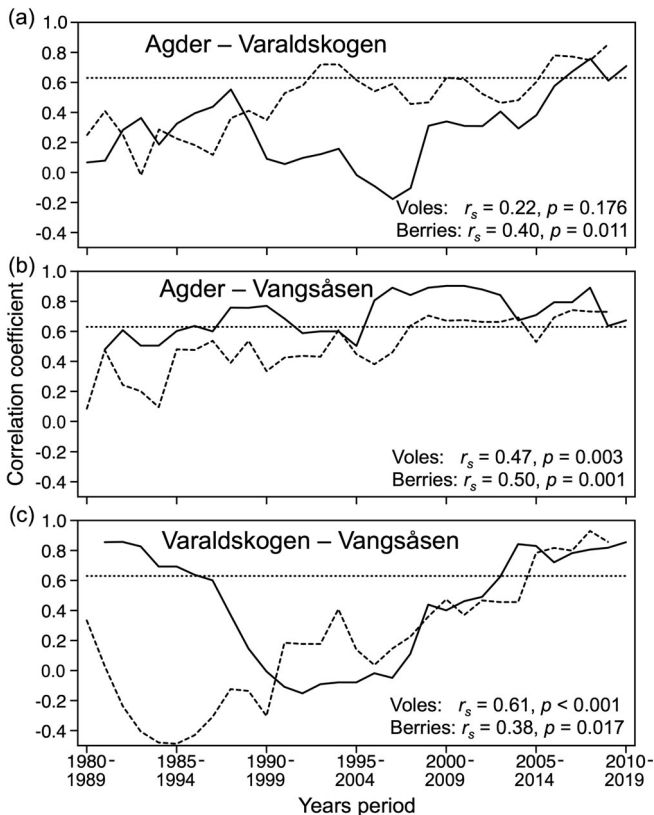


**TABLE 2** Generalized linear models (Poisson distribution and log link, corrected for overdispersion) with the total number of bank vole trapped year  $t$  as response variable and the log-transformed number of trap nights as offset

Explanatory variable	Estimate	SE	df	$\chi^2$	p value
Agder 1980–2019					
Intercept	−4.706	0.448	1		
Population index, year $t-2$	−0.037	0.039	1	0.92	.337
Bilberries, year $t-1$	0.454	0.102	1	21.27	<.001
Varaldskogen 1979–2019					
Intercept	−4.150	0.589	1		
Population index, year $t-2$	−0.010	0.019	1	0.29	.590
Bilberries, year $t-1$	0.530	0.160	1	11.54	<.001
Vangsåsen 1981–2019					
Intercept	−4.159	0.360	1		
Population index, year $t-2$	−0.065	0.030	1	5.20	.023
Bilberries, year $t-1$	0.424	0.082	1	29.36	<.001

Note: Explanatory variables are the population level index 2 years earlier and the bilberry newspaper index of the previous year.





**FIGURE 5** Ten years period sliding window correlation (Spearman's rank) between bank vole indices (solid line) and bilberry indices (dashed line) from three study areas in Norway. In these graphs, each plot represents the result of a correlation analysis with  $n = 10$ . Horizontal dotted line indicates the critical correlation coefficient value for  $p = .05$  when  $n = 10$ . The correlation for the whole period is given in the lower right corner of each panel

during the last 13–16 years of the 40-year study period (Figure 5a–c). The vole populations in Agder and Varaldskogen fluctuated in synchrony only during this last period (Figure 5a), whereas in Agder and Vangsåsen, they fluctuated more or less in synchrony from the late 1980s onward (Figure 5b). For Varaldskogen and Vangsåsen, there was a close synchrony at the start and the end of the study period (Figure 5c). Notably, the two first vole peaks in Agder were lagging 1 year after Varaldskogen and Vangsåsen (Table 3). For the whole study period, the vole index from Agder correlated significantly with the vole index from Vangsåsen (Figure 5b), but not with the vole index from Varaldskogen (Figure 5a). Despite a marked mid-period of asynchrony, the overall correlation between the vole index of Varaldskogen and that of Vangsåsen was still statistically significant (Figure 5c).

The bilberry newspaper index also varied considerably between years, although the multiannual fluctuations

were less regular than for voles (Figure 2b,d,f). In general, the spatial synchrony among study areas increased gradually throughout the period, with sliding window correlations between all areas being significant only during the last 13–14 years (Figure 5a–c). The most striking deviations from the vole series were a high degree of synchrony between Agder and Varaldskogen during the midperiod (Figure 5a), and a lack of synchrony between Varaldskogen and Vangsåsen in the 1980s (Figure 5c). Notably, similar to the vole index, the two first bilberry peaks in Agder were lagging 1 year after Varaldskogen and Vangsåsen (Table 3). For the entire study period, the bilberry newspaper index correlated significantly between all three study areas (Figure 5a–c).

The sliding window correlation between voles and bilberries based on newspaper reports was weak during the first half of the study period in Agder (Figure 6a) and in particular in Varaldskogen (Figure 6b), but strong throughout the study period in Vangsåsen (Figure 6c). Still, the correlation between voles and berries with a 1-year time lag was significant in all areas when all years were included in the analyses (Figure 6a–c).

Most vole peaks occurred after a year with a bilberry index above average (Table 3). Exceptions were a peak in Agder in 1997, a peak in Varaldskogen in 1988 and a peak in Vangsåsen in 1994. For Agder, it should be noticed, however, that the population actually peaked in summer 1998, with a trapping index much higher than the autumn indices of 1997 and 1998 (Selås, Framstad, & Spidsø, 2002).

## 4 | DISCUSSION

Both bank vole numbers and bilberry seed production varied with subperiods of spatial synchrony and asynchrony among study areas, with the latter part of the study period displaying more pronounced synchrony than the first and middle part. However, with a few notable exceptions, vole peaks lagged 1 year behind peaks in bilberry production, and the delayed density dependence present in two of the vole series was well explained by the berry indices. Thus, much of the synchrony and asynchrony in bank vole numbers could be explained by corresponding synchrony and asynchrony in berry production. The bilberry index based on newspaper reports may be subject to some errors, but analyses based on berry counts in Agder and Varaldskogen confirmed that bank vole fluctuations were related to bilberry seed crops of the previous year in the respective areas and periods. Attempts of linking spatial synchrony in bank vole population dynamics to weather variables should thus focus not only on factors that affect vole performance, but also

**TABLE 3** Years with peak in the bank vole index in three study areas in Norway

Peak No.	Agder		Varaldskogen		Vangsåsen	
	Berries	Voles	Berries	Voles	Berries	Voles
1			1979	1980	1979	—*
	1980	1981				
2			1983	1984	1983	1984
	1984	1985				
3	1987	1988		1988	1987	1988
4	1990	1991			1990	1991
5	1993	1994	1993	1994		1994
6		1997			1996	1997
	1997	1998				
7			2001	2002		
8			2003	2004	2003	2004
	2004	2005			2004	2005
9	2006	2007	2006	2007	2006	2007
10	2009	2010	2009	2010	2009	2010
11	2013	2014	2013	2014	2013	2014
12	2016	2017	2016	2017	2016	2017

Note: Minor peaks are included if they could be related to a high bilberry index of the previous year. The previous year is listed in the berries column if the berry index was above average. Voles were not trapped in Vangsåsen in 1980. Data taken from Figure 2.

\*In 1980, voles were abundant in large parts of eastern Norway (Wegge, Storaas, Larsen, & Bø, 1981), and trapping 150 km north of Vangsåsen in summer revealed a relatively high population level of bank vole (Sonerud, 1982).

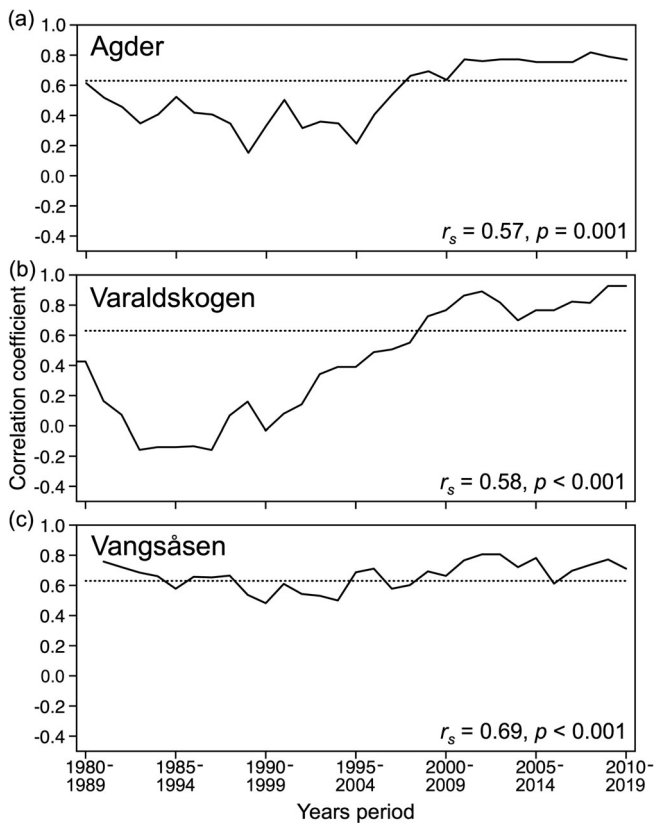
on factors that affect the reproduction of bilberry plants, that is, 1–2 years prior to current population levels.

The most striking difference between the vole and bilberry series was the discrepancy observed between Varaldskogen and Vangsåsen in the 1980s and early 1990s. In this c. 15-year period, there was no correlation between the bilberry series from the two areas, but a rather good correlation between the vole series. In both areas, bank vole populations increased in 1987 and peaked in 1988, in accordance with high bilberry indices for Vangsåsen, but despite low berry indices for Varaldskogen. Two other possible contributing factors in all study areas in 1987 could be the high seed crop (mast) of Norway spruce (*Picea abies*) (Selås et al., 2002), and low summer temperatures (data from the Norwegian Meteorological Institute: klima.no). Spruce seeds are frequently eaten by bank voles (Myllymäki & Paasikallio, 1972), whereas low temperatures may have a positive impact on forage quality (Laine & Henttonen, 1987) and thus vole abundance (Gouveia et al., 2015).

Also, some weather variables that affect small rodents directly may act over large areas, and thus contribute to a better synchrony among vole series than among berry series. Very low temperatures in combination with almost snow-free ground in December 1995 were

suggested to have caused high mortality and thus lack of rodent outbreaks in Agder in 1996 (Selås, 2016). This explanation may be valid also for the low vole index from Varaldskogen in 1996, despite a relatively high berry index in 1995. However, adverse weather conditions or other negative factors may also disrupt larger scale spatial synchrony in bank voles if they operate at local scales (Moshkin et al., 2000). In both Agder and Varaldskogen, there was a rather high berry index in 1997 and 2001, but in 1998, voles were abundant only in Agder, and in 2002 only in Varaldskogen. The suggested negative factor for small rodents in Agder in 2002 was low temperatures prior to the first snowfall (Selås, 2020), whereas at Varaldskogen the ground was already well covered with snow prior to the cold spell.

In the effort to explain vole cycles, there has been a strong focus on the role of small mustelids (Oli, 2019), but also the impact of birds of prey has been addressed (Huitu, Laaksonen, Norrdahl, & Korpimäki, 2005). There is no doubt that predators affect prey abundance, but in our view, their contribution is most likely to enhance or dampen population cycles, depending on type of predator (specialist or generalist) and the availability of alternative prey. Temporal asynchrony in the fluctuation pattern of sympatric rodent species is not unusual (Framstad, 2020;



**FIGURE 6** Ten years period sliding window correlation (Spearman's rank) between bank vole indices of the current year and bilberry indices of the previous year within each of three study areas in Norway. In these graphs, each plot represents the result of a correlation analysis with  $n = 10$ . Horizontal dotted line indicates the critical correlation coefficient value for  $p = .05$  when  $n = 10$ . The correlation for the whole period is given in the lower right corner of each panel

Hörnfeldt, 1994; Krebs, Boonstra, Gilbert, Kenney, & Boutin, 2019; Selås, 2020), a pattern not in accordance with the specialist predation hypothesis. Also the fact that rodent cycles exist in the absence of small mustelids (Graham & Lambin, 2002; Krebs et al., 2002; Menyushina, Ehrlich, Henden, Ims, & Ovsyanikov, 2012) refutes predation as a universal explanation (Oli, 2019). It has been argued that predation may still be the cause of rodent cycles in Fennoscandia (Korpimäki et al., 2005), but as questioned by Lambin, Bretagnolle and Yoccoz (2006): "Is there a need for different explanations for single pattern?"

The proposed mechanism for the berry-vole relationship is that a high berry production increases forage quality (Selås, 2020), or that an external factor affects both berry production and the plants' chemical composition (Selås, Holand, & Ohlson, 2011). Grazing induced defense is not regarded as important, but apparently there is a trade-off between reproduction and defense

(Benevenuto et al., 2018, 2019). High berry crops do not seem to affect total nitrogen content or in vitro digestibility of bilberry shoots (Selås, Holand, & Ohlson, 2011). However, the availability of proteins to herbivores may depend on how proteins are stored (Wallis, Nicolle, & Foley, 2010). According to White (1984), stress factors that require protein mobilization force plants to allocate stored proteins, possibly acting as feeding deterrents (Wittstock & Gershenson, 2002), to transportable nitrogen compounds that are easily digested by herbivores. Hence, the consequence of a high production of berries may be that the protein digestibility of bilberry plants per time unit increases above the critical threshold for bank voles. If so, the result will be a strong temporary increase in carrying capacity.

Temperature, which usually acts synchronously over large areas, is probably the main synchronizing factor for bilberry reproduction, by affecting flower bud induction and resource storage in the year prior to flowering, as well as flowering in spring (Selås et al., 2015). On the other hand, other factors, such as protective snow cover during winter, and precipitation during flowering and berry ripening, may have more local impact, thereby interrupting the spatial synchrony.

In accordance with studies on field vole (*Microtus agrestis*) (Bierman et al., 2006), we found that the spatiotemporal dynamic in bank vole fluctuations varied over time. Notably, we found evidence for similar variations in bilberry seeding. Thus, our prediction, that the regional spatial pattern of bank vole synchrony should reflect a similar pattern of synchrony in the previous year's bilberry reproduction, was confirmed. This adds support to the hypothesis that bilberry reproduction plays a major role in explaining the spatiotemporal dynamics in bank vole abundance. Although it remains to be seen to what extent the chemical composition of bilberry plants affects vole performance (Selås, Holand, & Ohlson, 2011), the ultimate cause of the observed pattern seems to be similar to that of large-scale synchrony in rodent populations that primarily respond to masts of forest trees (e.g., Haynes et al., 2009; Turkia et al., 2020), that is, a weather-driven spatial synchrony in seed production. There are few studies on annual variations in seed crops of important food plants for strictly herbivorous rodents, such as *Microtus* voles and lemmings, so further investigations here are highly needed.

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## CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

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