Ornis Fennica 94: 92–100. 2017

Autumn irruptions of Eurasian Jay (*Garrulus glandarius*) in Norway in relation to acorn production and weather

Vidar Selås

Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway. E-mail: vidar.selas@nmbu.no

Received 10 June 2016, accepted 25 March 2017

In Scandinavia, the Eurasian Jay (*Garrulus glandarius*) is a resident forest-dwelling species, which in some years show eruptive movements in the autumn. Such irruptions seem to be related to the variation in seed crops of oaks (*Quercus* spp.). When there has been a high seed crop, termed mast, Jays use hoarded acorns not only during winter, but also as food for their young in the succeeding spring. However, whether this leads to an irruption in a succeeding year may also depend on other factors that affect survival and reproduction. A Jay hunting index (1995–2015) and a Jay irruption index (observations at a coastal ornithological station 1976–2015) from southern Norway peaked in years with mast failure, but there also was a significant negative relationship with mean snow depth in January–February and precipitation in April–May. Much snow is assumed to reduce winter survival, by making hoarded acorns less available, whereas heavy rain in spring is known to have a negative effect on passerine breeding success in general.

1. Introduction

The huge annual variation in seed crops of some forest tree species, termed masting when synchronized within a population, has a profound influence on the associated guild of seed foraging animals and their predators (Petty *et al.* 1995, Ostfeld & Keesing 2000, Koenig 2001, Fox *et al.* 2009). Vertebrates show both numerical and functional responses to mast seeding, and for mobile species like birds, the numerical response may be caused both by migration and reproduction (Bogdziewicz *et al.* 2016). In autumns after a mast year, seed-eating birds are often recorded in high numbers outside their natural range (Koenig & Knops 2001, Newton 2006, Fox *et al.* 2009). The intensity of such irruptions also depends on population abundance (*e.g.* Lindén *et al.* 2011), and should thus be most pronounced if there were high seed crops in the previous year (Koenig & Knops 2001, Newton 2006), accompanied by favourable weather for survival and reproduction. However, except from an apparent negative impact of winter harshness on Pine Siskin (*Spinus pinus*) irruptions in North America (Strong *et al.* 2015), physical conditions have so far not been revealed to play an important role in modulating bird irruptions.

Among masting trees, oaks (*Quercus* spp.) are particularly important, by providing large fruits (acorns) that are utilized by several vertebrate species, including mice, squirrels, deer, wild boar (*Sus scrofa*), pigeons and corvids (Murton *et al.* 1964, Jackson 1980, Kenward & Holm 1993, Schley & Roper 2003, Den Ouden *et al.* 2005). The main disperser of oak seeds in Western Europe is the Eurasian Jay (*Garrulus glandarius*; hereafter Jay), which in mast years hides large numbers of acorns on the ground (Bossema 1979, Gomez 2003, Pons & Pausas 2007). Because Jays use hoarded acorns not only as winter food, but also to feed their nestlings in the succeeding spring (Bossema 1979), mast years should be expected to increase both winter survival and subsequent reproduction. In Scandinavia, the Jay is a resident forest-dwelling species, which shows irruptive movements in some autumns (Harrison 1957, Haftorn 1971, Andrén 1985, 1990).

Observations from Falsterbo Ornithological Station in southern Sweden 1942–1994 suggest that Jay irruptions, which mainly consist of juveniles, occur in autumns with poor acorn production, but that the extent of an irruption depends on the acorn crop of the previous year (Andrén 1985, Karlsson *et al.* 1994). Lack of irruptions, despite mast failure of oaks, was ascribed to mast seeding of European Beech (*Fagus sylvatica*). The Jay also utilizes a large number of other food resources, such as insects, bird eggs and nestlings, small rodents and carrions (Holyoak 1968, Bossema 1979). Of these food resources, small rodents in particular vary considerably in abundance in Fennoscandia. Hence, Andrén (1985) speculated that high numbers of voles improve the breeding success of Jays, resulting in enhanced Jay autumn irruptions when vole peaks occur in years with poor acorn production.

In northern areas, snow conditions during winter may reduce Jay winter survival, by making stored acorns, as well as other food resources, less available. This may be especially so in southern parts of Norway, where the oceanic climate frequently results in snow melting and freezing, making the snow layer compact and difficult to penetrate for the Jay. Weather conditions in the spring may further affect the breeding success and thus autumn population sizes. At least for smaller passerines, heavy rainfall during the incubation and nestling periods seems to be especially negative for nesting success (Veistola *et al.* 1996, Hogstad 2000, Öberg *et al.* 2014).

Here I compare two different Jay indices from Norway with acorn production indices, small rodent indices and selected weather variables. Irruptions are predicted to occur in years with few acorns, but the strength of an irruption is assumed to reflect fluctuations in both current year reproduction and previous winter survival, which both may depend on acorn production in the previous year and weather conditions.

2. Material and methods

2.1 Study area

The study area is Aust-Agder and Vest-Agder Counties (hereafter Agder) situated at the southern coast of Norway. The area is dominated by a mosaic of young, medium-aged and old deciduous, mixed and coniferous forest stands, with scattered lakes, bogs and less than 5% agricultural and developed areas. The dominating tree species are Norway Spruce (*Picea abies*), Scots Pine (*Pinus sylvestris*), Aspen (*Populus tremula*), Downy Birch (*Betula pubescens*) and Silver Birch (*B. pendula*). Sessile Oak (*Quercus petraea*) is common and Pedunculate Oak (*Q. robur*) occurs in the lowland and close to the coast, whereas the European Beech is almost absent. Forests with a timber production high enough for commercial utilisation, and which should also be suitable for the Jay, cover 3,665 km^2 in Aust-Agder and 2,440 km^2 in Vest-Agder.

2.2 Jay hunting index

From 1994 onwards, Statistics Norway (www.ssb.no) estimated the annual hunting bag of small game species, including the Jay, in each county based on report forms submitted by individual hunters. The submission of the report form was voluntary, but more likely from 2000 onwards, due to an extra fee if the report form was not submitted. During 1994–1999, additional questionnaires were sent to a sample of the hunters who did not respond, and Statistics Norway assumes that the change in methodology had marginal impact on their results. In Agder, the number of hunters, i.e. persons who bought a hunting tax card, was rather stable throughout the period, varying from 12,700 (1994, 1998, 2007) to 13,600 (1999). During 2002–2015, the number of hunters who submitted the report varied from 11,420 (2006) to 12,040 (2015), i.e. a variation of ca. 5%. The response rate was 88–92%.

The hunting period for Jays lasts from 10 August to 28/29 February. There are no traditions for utilising Jays as food in Norway. Most hunters kill Jays in Agder because they regard corvids as harmful to grouse and other bird species, and they are not expected to adjust the hunting effort according to Jay abundance. Hunting statistics should therefore be expected to reflect the relative number of Jays present in the study area during the hunting season. This may depend on both previous winter survival and summer reproduction. However, many Jays are killed close to human settlements, where they are attracted by bird feeders. Hence, if Jays seek bird feeders more frequently in acorn-poor years, the hunting statistic may also reflect changes in Jay behaviour. As an example, one hunter killed >30 Jays at his bird feeder in Aust-Agder, ca. 20 km from the coast, in the irruption year 1977.

In the analyses, I used the estimated number of Jays killed from 1995 onwards. The estimate of 4,680 Jays in the first year of statistics, 1994, was omitted as it was a clear outlier, more than twice as high as the highest annual number during 1995–2015, when the estimated number ranged 630–2,140.

2.3 Jay irruption index

As an irruption index, I used the number of Jays observed in autumn at Lista ornithological station in Vest-Agder (58°07’ N, 06°34’ E) during 1977–2015, taken from the Norwegian Species Observation database (artsobservasjoner.no). This station is situated close to the coast, in an open landscape outside the natural habitat for the Jay. The number of Jay observations has fluctuated considerably from year to year, varying from zero in most years to many hundreds in irruption years. Observations from August–January were used, although the majority of the observations (99%) are from September–October.

There is a strong positive trend in the Jay observation data from Lista, due to increased interest for bird watching and species reporting. This escalated in the irruption year 2014, with 8,217 observations, compared to 0–697 for the period 1977–2013. When adjusting for observation effort, Heggøy *et al.* (2015) operated with an observation index for 2014 approximately twice as high as the second highest during 1989–2014. Accordingly, I adjusted the 2014-index to twice the value of the second highest in my time series.

2.4 Acorn production

I used the annual amount of acorns of Sessile Oak exported from Agder to Denmark, provided by the Norwegian Forest Seed Centre (Selås 2016), as an index of acorn production, but with some modifications. Acorns have been exported by Reiersøl/Oveland nursery in Aust-Agder for the entire study period, and by Randesund nursery in Vest-Agder from 1980 onwards, although with small volumes during the first 10–15 years. When the two time series were detrended by using annual change (first difference), they were significantly correlated ($r = 0.81$, $P < 0.001$). I therefore used only the Reiersøl/Oveland series for my analyses. For most years, additional information about the acorn production is given by the Norwegian Forest Seed Centre or the head of Reiersøl/Oveland nursery, gardeners Gunnar Oveland and Torgeir Oveland (Selås 2016).

The acorn export from Reiersøl was intensified in 1984, and at least for some years (possibly all) during 1984–1999, acorns were collected from larger areas, including parts of Vest-Agder. From 2000 onwards, acorns collected in the three municipalities closest to the nursery (the core area) were reported separately, and by using only these data the possible bias caused by increased sample areas in years with moderate acorn production is eliminated. In order to get a comparable index for the entire study period, I used half of the value of the amount exported as an acorn index for the period 1984–1999, when acorns were collected from an area of approximately twice the size of the core area. I then obtained very similar values for the years 1980, 1984, 1995 and 1997, which G. Oveland characterized as extraordinary rich acorn years (Selås 2016).

The general pattern in Agder seems to be that there are either many or almost no acorns. The only intermediate years, according to G. Oveland, were 1988, 1994, 1999 and possibly 1985 (Selås 2016). The relatively high amounts of acorns exported in 1988 and 1999 were due to high demand for acorns in Denmark, combined with a strong ef-

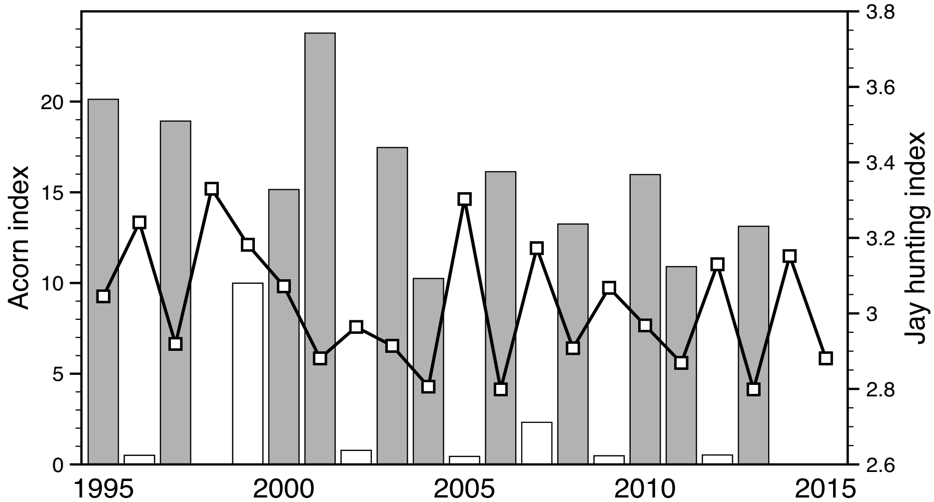

Fig. 1. Seed production indices of Sessile Oak in Aust-Agder (bars) and the log-transformed number of Eurasian Jays killed in Aust-Agder and Vest-Agder (line), southern Norway, 1995–2015. The acorn index is the annual quantity of acorns (metric tons) exported to Denmark, except from the years 1995–1999, when acorns were collected from larger areas and the index thus is the half value of the amount exported. Open bars are used for years with low or intermediate acorn production, and shaded bars for years with high production, according to expert evaluations.

fort in Norway to meet this demand. For 1985, the index is a minimum estimate, because only information about the export to two buyers were given, whereas acorns may have been sold also to 2–3 other traditional buyers. According to G. Oveland, there were "some acorns", but "much less" than in 1984 (Selås 2016).

2.5 Vole index

The vole index was the number of voles, mainly Bank Vole (*Myodes glareolus*), trapped per 100 trap-nights in Aust-Agder County; in Birkenes municipality during 1972–1978, in Vegårshei municipality during 1979–1989 and in Gjerstad municipality during 1990–2015 (see Selås *et al.* 2002, Framstad 2016). The Wood Mouse (*Apodemus sylvaticus*) was not included, because this species is mainly nocturnal and more agile, and thus it is assumed to be less available for the Jay.

2.6 Meteorological data

Mean monthly snow depth (December–April), precipitation (April–May) and temperature (April–May) data were taken from the Norwegian Meteorological Institute (sharki.oslo.dnmi.no). In southern parts of Norway, Jays usually start egg-laying in mid or late April, and the young fledge in early June (Haftorn 1971). I therefore regarded weather conditions in April–May to be most important for the breeding success, and used the weather index (rain or temperature) that gave best fit in the model. Mean monthly snow depth and precipitation data were taken from Mykland Meteorological Station, and temperature data from Bygland Meteorological Station.

2.7 Statistical analyses

I tested for relationships between Jay indices and the selected explanatory variables using generalized linear models (Poisson distribution and log link) accounted for over-dispersion. The software used was JMP®Pro 12.1.0 (SAS Institute, Cary, North Carolina). When log-transforming the time series, there was a significant linear trend in the Jay irruption index but not in the hunting index. To account for this trend, year was included as predictor in the analysis of the irruption index. The other selected explanatory variables used in the presented

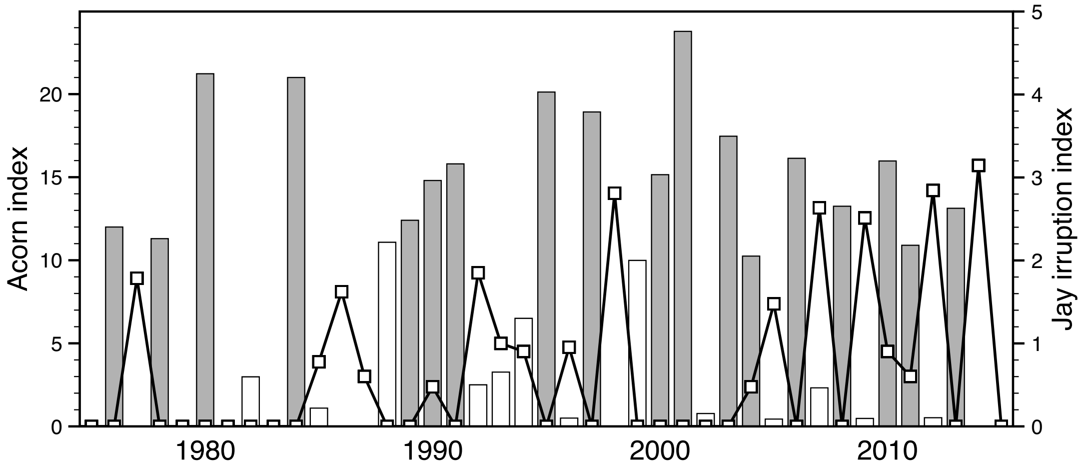

Fig. 2. Seed production indices of Sessile Oak in Aust-Agder (bars) and the log(x+1)-transformed number of Eurasian Jays observed during August–January at Lista Ornithological Station in Vest-Agder (line), southern Norway, 1975–2015. The acorn index is the annual quantity of acorns (metric tons) exported to Denmark, except from the period 1984–1999, when acorns were collected from larger areas and the index thus is the half value of the amount exported. Open bars are used for years with low or intermediate acorn production, and shaded bars for years with high production, according to expert evaluations.

models were (1) the acorn index of the current year, (2) the acorn index of the previous year, (3) mean snow depth in January–February, (4) precipitation in April–May (for the hunting index) or in May (for the irruption index), (5) the vole population index of the current year. Because of a significant negative relationship between temperature and precipitation, temperature was not used. The only significant temporal autocorrelations in the series was a negative one-year lag in the acorn index and a positive three-year lag in the vole index.

3. Results

All peaks in the Jay hunting index (Fig. 1), and almost all in the Jay irruption index (Fig. 2), occurred in a year with few acorns. However, there were no irruptions in 1979, 1981, 1985 and 2002 despite mast failure (Fig. 2). In 2002, there was only a minor peak in the Jay hunting index (Fig. 1).

Assuming that the Jay hunting index is an adequate proxy for population levels, the Jay irruption index for the period 1995–2015 should be well explained by the hunting index and the present year's acorn index, with no need of including previous seed crops or weather variables. In this model, where I accounted for the positive effect of year ($P = 0.011$), there was a significant positive relationship with the hunting index ($P = 0.024$) but only a tendency for a negative relationship with the acorn index ($P = 0.063$). This is presumably because the Jay hunting index overestimates population levels in irruption years, due to increased Jay movements.

In models with all explanatory variables included, the Jay indices were both negatively related to the acorn index of the current year and mean snow depth in January–February (Table 1, Figs. 1–3). For the irruption index, there was also a highly significant negative relationship with precipitation in May (Table 1, Fig. 4), whereas there was a tendency for a negative relationship with precipitation in April–May for the hunting index (Table 1). No significant interactions between acorn and weather variables were found, i.e., snow and precipitation negatively affected the Jay indices regardless of acorn production (Fig. 3 and 4).

4. Discussion

The Jay indices were negatively related to the acorn index, as all peaks or irruptions were associated with mast failure. Acorn production of the previous year did not contribute significantly in

Table 1. Results from generalized linear models (Poisson error distribution and a log link, corrected for over-dispersion) with the annual number of Eurasian Jays shot in Vest-Agder and Aust-Agder in August–February (year *t* – *t*+1) or observed at Lista Ornithological Station in Vest-Agder in August–January (year *t* – *t*+1) as response variables.

Explanatory variable	Estimate	SE	χ^2	*P*
Jay hunting index 1995–2015				
Intercept	7.7333	0.3262		
Acorn index, year *t*	–0.0205	0.0092	5.10	0.024
Acorn index, year *t*–1	0.0074	0.0095	0.61	0.434
Snow January–February, year *t*	–0.0089	0.0037	5.77	0.016
Precipitation April–May, year *t*	–0.0025	0.0015	2.81	0.094
Vole index, year *t*	0.0012	0.0256	<0.01	0.961
Jay irruption index 1977–2015				
Intercept	–228.6054	47.4677		
Year	0.1181	0.0237	40.25	<0.001
Acorn index, year *t*	–0.5108	0.1677	57.58	<0.001
Acorn index, year *t*–1	0.0340	0.0461	0.54	0.464
Snow January–February, year *t*	–0.0133	0.0070	4.04	0.044
Precipitation May, year *t*	–0.0390	0.0074	52.12	<0.001
Vole index, year *t*	0.0121	0.0511	0.06	0.812

the models, i.e., my analyses did not support the hypothesis of enhanced irruptions after high seed crops. This suggests that there usually were enough young surplus birds present in autumn to give an irruption when the acorn production failed, regardless of the food supply of the previous year. Many Jays observed at Lista are likely to come from larger areas than Agder (Løfaldli 1983), but this is probably a minor source of error because there usually is at least a regional synchrony in acorn production.

Former oak mast years in Agder, according to the acorn export, were 1950, 1954, 1958–60, 1964, 1966, 1968, 1970–71 and 1974 (Selås 2016). Jay irruptions were reported from Lista or Western Norway only in the mast failure years 1955 (Harrison 1957), 1972 (Holgersen 1973) and 1975 (Byrkjeland & Overvoll 2003). In Sweden, pronounced irruptions were observed in 1955, 1961, 1972, 1977 and 1981 (Karlsson *et al.* 1994). These years were mast failure years of oak both in Sweden and Norway.

Although Jay population peaks and irruptions certainly depend on acorn production, the Jay indices from Agder also showed a strong relationship with weather conditions assumed to affect survival or reproduction. There were no irruptions in 1979, 1981 and 2002, despite mast failure. This could be due to heavy rains in spring, resulting in poor breeding success. During his 33-year study of Bramblings (*Fringilla montifringilla*) in Central Norway, Hogstad (2000) regarded the low breeding success in 1978, 1979 and 1981 to be caused by extremely cold and rainy weather. There may, however, have been a small peak in Jay numbers in Agder in 1981, because at Revtangen Ornitological Station, in the neighbouring county Rogaland, western Norway, ca. 20 Jays were recorded in October 1981, compared to only 3 and 2 in 1979 and 1980, respectively (Runde 1979, 1980, 1981).

Also snow depth in January–February turned out to be a good predictor in the Jay models. For the hunting index, only the lack of a marked peak in 2002 may not be explained by snow conditions, but rather by precipitation in spring. A thick snow cover may be negative both by making the forage on stored acorns and other food resources more time-consuming, and by making the Jays more vulnerable to predation during foraging. The Jay's ability to penetrate a snow layer when trying to access hoarded food items on the ground may also depend on the consistency of the snow, but it was not possible to adjust for this in the analyses.

There was no relationship between Jay irruptions and vole numbers. Jays certainly know how to handle dead voles (pers. obs.), but they are probably not efficient vole hunters themselves. Nonetheless, improved breeding success in vole peak

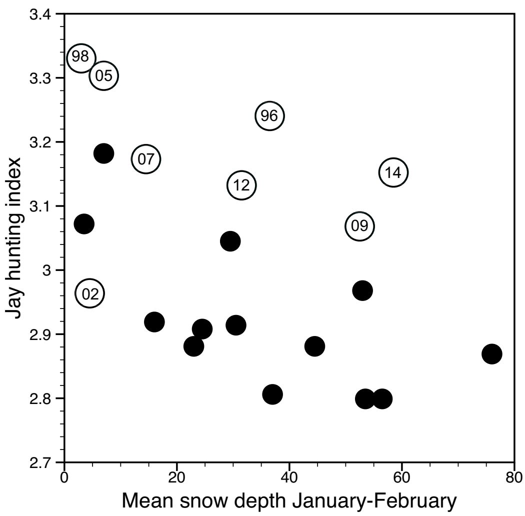

Fig. 3. The log(x+1)-transformed number of Eurasian Jays killed in Aust-Agder and Vest-Agder, southern Norway, 1995–2015, in relation to mean snow depth in January–February in the previous winter. Open enlarged symbols with year refer to the peak years shown in Fig. 1.

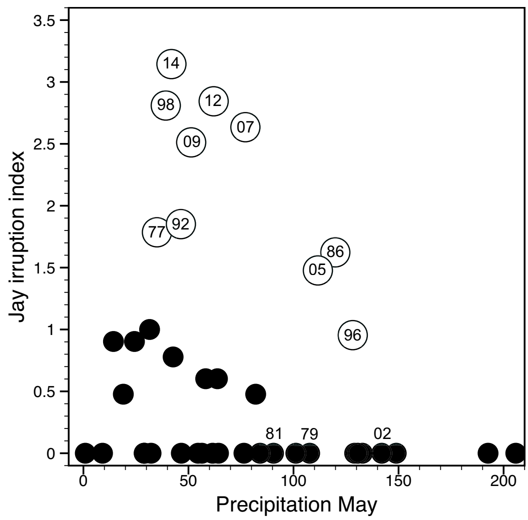

Fig. 4. The log(x+1)-transformed number of Eurasian Jays observed during August–January at Lista Ornithological Station in Vest-Agder, southern Norway, 1975–2015, in relation to the total amount of precipitation in May. Open enlarged symbols with year refer to the peak years with low acorn production shown in Fig. 2. Three years without Jay observations (1979, 1981, 2002) are also shown, because peaks were predicted based on the acorn index alone.

years has been observed for smaller passerines, which obviously do not eat voles (Veistola 1996, Selås & Steel 1998). Whether this is caused mainly by reduced predation risk (Järvinen 1985) or increased numbers of herbivorous insects (Selås *et al.* 2013), such effects seemed not to be important for Jay numbers in Agder.

The annual hunting bag of 600–1,000 Jays in Agder had apparently a minor impact on the breeding population in this area, and the number shot was independent of the number shot in the previous year (no significant autocorrelations). The population size of Jays is difficult to assess in the breeding season, but based on a minimum estimate of 1,000–2,000 pairs in Aust-Agder (Bengtson *et al.* 2009), there are probably at least 2500 pairs in Agder. Assuming, however, that the home range of a Jay in the breeding season is usually less than 1 km^2 (Andrén 1990, Grahn 1990), and that most of the total productive forest area of 6,000 km^2 in Agder is suitable habitat for the Jay, the breeding population may in fact be much higher, at least in years with autumn irruptions.

This study supports that population peaks and irruptions of Jay in Norway are related to acorn production and to weather conditions affecting survival or reproduction. Both snow depth in winter and precipitation in spring appeared to affect Jay numbers negatively, regardless of acorn production.

Acknowledgements. I am grateful to Ingvar Fystro, Tore Wetlesen and Jan Ulitzsch at the Norwegian Forest Seed Centre for kindly providing information about acorn production and export, to Thrond Haugen and Leif Egil Loe for statistical advice, and to Eduardo J. Belda, Veli-Matti Pakanen, Andreas Lindén and an anonymous referee for valuable comments on the manuscript.

Tammenterhotuotannon ja säätekijöiden vaikutukset närhen (*Garrulus glandarius*) syysvaellusten esiintymiseen Etelä-Norjassa

Närhi (*Garrulus glandarius*) on metsässä pesivä paikkalintu. Joinakin syksyinä esiintyy voimakkaita närhien vaelluksia. Vaellukset näyttävät olevan yhteydessä eri tammilajien (*Quercus*) siementuotannossa (terhojen) esiintyvään vaihteluun.

Tammenterhojen massatuotantovuosina närhet käyttävät varastoimiaan terhoja talven lisäksi myös seuraavana pesimäkautena ruokkiessaan poikasiaan. Massatuotantovuotta seuraavan kesän jälkeen saattaakin syntyä vaelluksia. Vaelluksen syntymiseen vaikuttavat kuitenkin myös muut eloonjäävyyteen ja lisääntymiseen vaikuttavat tekijät.

Tässä työssä tutkin vaelluksen esiintymistä suhteessa eri ympäristötekijöihin Etelä-Norjan metsästäjiltä kerätyn närhisaalis-indeksin (1995–2015) ja ornitologiselta asemalta kerätyn vaellusindeksin (havainnot 1975–2015) avulla. Molemmat indeksit olivat korkeita vuosina jolloin terhojen tuotanto oli heikko. Tammi–helmikuun suuri lumensyvyys ja huhti–toukokuun korkea sademäärä heikensivät vaelluksen todennäköisyyttä seuraavana syksynä. Syvä lumikerros saattaa heikentää lintujen eloonjäävyyttä vaikeuttamalla terhovarastojen saatavuutta kun taas voimakkaiden kevätsateiden tiedetään yleisesti heikentävän varpuslintujen poikastuottoa.

References

Andrén, H. 1985: Nötskrikans *Garrulus glandarius* invasionsflyttningar. — Vår Fågelvärld 44: 261–268. (In Swedish, with English summary)

Andrén, H. 1990: Despotic distribution, unequal reproductive success, and population regulation in the jay *Garrulus glandarius* L. — Ecology 71: 1796–1803.

Bengtson, R., Johnsen, A., Selås, K.O. & Steel, C. 2009: Hekkefuglatlas for Aust-Agder 1995–2004. — Fugler i Aust-Agder Supplement nr. 1 2009. Norsk Ornitologisk Forening avdeling Aust-Agder, Arendal. 485 pp. (In Norwegian, with English summary)

Bogdziewicz, M., Zwolak, R. & Crone, E.E. 2016: How do vertebrates respond to mast seeding? — Oikos 125: 300–307.

Bossema, I. 1979: Jays and oaks: an eco-ecological study of a symbiosis. — Behaviour 70: 1–117.

Byrkjeland, S. & Overvoll, O. 2003: Viltet i Austrheim. Kartlegging av viktige viltområde og status for viltartane. — Astrheim kommune og Fylkesmannen i Hordaland. MVA-rapport 8/2003. (In Norwegian)

Den Ouden, J., Jansen, P.A. & Smit, R. 2005: Jays, mice and oaks: predation and dispersal of *Quercus robur* and *Q. petraea* in North-western Europe. — In Seed fate: predation, dispersal and seedling establishment (ed. Forget, P.M., Lambert, J., Hulme, P.E. & Vander Wall, S.B.): 223–240. CABI, Wallingford.

Fox, A.D., Kobro, S., Lehikoinen, A., Lyngs, P. & Väisänen, R.A. 2009: Northern Bullfinch *Pyrrhula p. pyrrhula* irruptive behaviour linked to rowanberry *Sorbus aucuparia* abundance. — Ornis Fennica 86: 51–60.

Framstad, E. (ed.) 2016: Terrestrial Ecosystems Monitoring in 2015: Ground vegetation, small mammals and birds. Summary of results. — NINA Report 1279. 112 pp. (In Norwegian, with English abstract)

Gomez, J.M. 2003: Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. — Ecography 26: 573–584.

Grahn, M. 1990: Seasonal changes in ranging behaviour and territoriality in the European Jay *Garrulus glandarius*. — Ornis Scandinavica 21: 195–201.

Haftorn, S. 1971. Norges fugler. — Universitetsforlaget, Oslo. (In Norwegian)

Harrison, C.J.O. 1957: Ornithological observations from Lista 1955. — Sterna 2: 101–136.

Heggøy, O., Røer, J.E., Nordsteien, O., Garzía, A.L. & Bjørnstad, O.K. 2015: Bestandsovervåking ved Jomfruland og Lista fuglestasjoner i 2014. — NOF Rapport 6–2015. 46 pp. (In Norwegian)

Hogstad, O. 2000. Fluctuation of a breeding population of Bramling *Fringilla montifringilla* during 33 years in a subalpine birch forest. — Ornis Fennica 77: 97–103.

Holgersen, H. 1973: Fra Revtangen Ornitologiske Stasjon 1971–1972. — Stavanger Museum Årbok 83: 101–116. (In Norwegian, with English summary)

Holyoak, D. 1968: A comparative study of the food of some British Corvidae. — Bird Study 15: 147–153.

Järvinen, A. 1985: Predation causing extended low densities in microtine cycles: implications from predation on hole-nesting passerines. — Oikos 45: 157–158.

Jackson, J. 1980: The annual diet of the roe deer (*Capreolus capreolus*) in the New Forest, Hampshire, as determined by rumen content analysis. — Journal of Zoology 192: 71–83.

Karlsson, L., Ehnbom, S. & Walinder, G. 1994: Invasionen av nötskrika *Garrulus glandarius* vid Falsterbo hösten 1994. — Meddelande nr. 175 från Falsterbo fågelstation. (In Swedish, with English summary)

Kenward, R.E. & Holm, J.L. 1993: On the replacement of the red squirrel in Britain: a phytotoxic explanation. — Proceedings of the Royal Society of London B 251: 187–194.

Koenig, W.D. 2001: Synchrony and periodicity of eruptions by boreal birds. — Condor 103: 725–735.

Koenig, W.D. & Knops, J.M.H. 2001: Seed-crop size and eruptions of North American boreal seed-eating birds. — Journal of Animal Ecology 70: 609–620.

Løfaldli, L. 1983: Nøtteskrikas forekomst på Vestlandet. — Vår Fuglefauna 6: 183–189. (In Norwegian, with English summary)

Lindén, A., Lehikoinen, A., Hokkanen, T. & Väisänen, R.A. 2011. Modelling irruptions and population dynamics of the great spotted woodpecker – joint effects of density and cone crops. — Oikos 120: 1065–1075.

Murton, R.K., Westwood, N.J. & Isaacson, A.J. 1964: The feeding habits of the woodpigeon *Columba palumbus*,

stock dove *C. oenas* and turtle dove *Streptopelia turtur*. — Ibis 106: 174–188.
Newton, I. 2006: Advances in the study of irruptive migration. — Ardea 94: 433–460.
Öberg, M., Arlt, D. Pärt, T., Laugen, A.T., Eggers, S. & Low, M. 2014: Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. — Ecology and Evolution 5: 345–356.
Ostfeld, R.S. & Keesing, F. 2000: Pulsed resources and community dynamics of consumers in terrestrial ecosystems. — Trends in Ecology and Evolution 15: 232–237.
Petty, S.J., Patterson, I.J., Anderson, D.I.K., Little, B. & Davison, M. 1995: Numbers, breeding performance, and diet of the sparrowhawk *Accipiter nisus* and merlin *Falco columbarius* in relation to cone crops and seed-eating finches. — Forest Ecology and Management 79: 133–146.
Pons, J. & Pausas, J.G. 2007: Acorn dispersal estimated by radio-tracking. — Oecologia 153: 903–911.
Runde, O.J. 1979: Fra Revtangen Ornitologiske Stasjon 1979. — Stavanger Museum Årbok 89: 168–182. (In Norwegian, with English summary)
Runde, O.J. 1980: Fra Revtangen Ornitologiske Stasjon 1980. — Stavanger Museum Årbok 90: 41–51. (In Norwegian, with English summary)
Runde, O.J. 1981: Fra Revtangen Ornitologiske Stasjon 1981. — Stavanger Museum Årbok 91: 169–177. (In Norwegian, with English summary)
Schley, L. & Roper, T.J. 2003: Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. — Mammal Review 33: 43–56.
Selås, V. 2016: Seventy-five years of masting and rodent population peaks in Norway: Why do wood mice not follow the rules? — Integrative Zoology 11: 388–402.
Selås, V., Framstad, E. & Spidsø, T.K. 2002: Effects of seed masting of bilberry, oak and spruce on sympatric populations of bank vole (*Clethrionomys glareolus*) and wood mouse (*Apodemus sylvaticus*) in southern Norway. — Journal of Zoology 258: 459–468.
Selås, V., Kobro, S. & Sonerud, G.A. 2013: Population fluctuations of moths and small rodents in relation to plant reproduction indices in southern Norway. — Ecosphere 4: 123.
Selås, V. & Steel, C. 1998: Large brood sizes of pied flycatcher, sparrowhawk and goshawk in peak microtine years: support for the mast depression hypothesis. — Oecologia 116: 449–455.
Strong, C., Zuckerberg, B., Betancourt, J.L. & Koenig, W.D. 2015: Climatic dipoles drive two principal modes of North American boreal bird irruption. — Proceedings of the National Academy of Sciences of the United States of America 112: E2795–E2802.
Veistola, S., Lehikoinen, E., Eeva, T. & Iso-Iivari, L. 1996. The breeding biology of the Redstart *Phoenicurus phoenicurus* in a marginal area of Finland. — Bird Study 43: 351–355.