Ornis Fennica 86:51–60. 2009

Northern Bullfinch *Pyrrhula p. pyrrhula* irruptive behaviour linked to rowanberry *Sorbus aucuparia* abundance

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Received 23 December 2008, revised 15 April 2009, accepted 28 April 2009

Autumn Northern Bullfinch abundance at bird observatories around the Baltic Sea confirmed periodic irruptive behaviour outside of its normal wintering range, but age-ratio data suggested dispersal was not linked to reproductive success. Rowan berries are important food of Fennoscandian Northern Bullfinches and show synchronised masting in annual fruit production over large spatial scales. Norwegian and Finnish annual berry abundance indices from 1972–2004 were used to test the hypothesis that poor rowanberry production in normal wintering areas was responsible for efflux of birds to other areas. Annual Finnish wintering bird surveys and catches at local bird observatories correlated with rowanberry abundance indices, supporting the prediction that highest Bullfinch abundance would occur in normal wintering areas in years with heavy rowanberry crops. Northern Bullfinch autumn abundance at Danish and Swedish bird observatories (outside the normal winter range) showed inverse correlations with Norwegian rowanberry crops, supporting the prediction of highest irruptions in years of lowest rowanberry abundance from the normal wintering range. These data suggest that at large spatial scales, berry masting can have profound effects on the annual distribution and migratory behaviour of birds consuming the crop.

1. Introduction

Arrivals of large numbers of wintering birds outside their normal range (irruptions) are a feature of several northern hemisphere species (Newton 2006a, 2008). This behaviour is especially common among species feeding on seeds or berries of trees and bushes which show greater inter-annual fluctuation in their reproductive investment in seeds and berries than, for example, herbaceous plants (Newton 1972). Unlike regular "obligate" migrants, moving predictably and seasonally between regular breeding and non-breeding quarters (Alerstam 1990), irruptive species are “facultative” migrants, retaining flexibility in their migratory response in the face of fluctuating food supplies. Irruptive species show greater annual variability in proportions of the population that migrate, and greater individual and year-to-year variations in timing, directions and distances of movements. Irruptive behaviour is generally driven by lack of food on the normal wintering grounds, causing birds to be displaced elsewhere. However, this is not always the case, because it may also result from nomadic or irruptive behaviour in relation to breeding conditions (Newton 2006a). For example, nesting Siskin *Carduelis spinus* densities correlated with local spruce-cone abundance (Haapanen 1966) and Common Redpoll *C. flammea flammea* breeding densities with birch *Betula* spp. (Taylor 1954, Enemar 1969) or spruce *Picea* spp. seed stocks (Peiponen 1957, 1962). Many passerines respond to unpredictable local food abundance by nomadic shifts between wintering areas, which are not strictly eruptions from a traditional winter range, for example, Bramblings *Fringilla montifringilla* aggregate in areas with densest beech *Fagus sylvatica* mast cropping (Lithner & Jönsson 2002) and Crossbills (*Loxia* spp.) may traverse continents in response to preferred conifer seed abundance (Reinikainen 1937, Newton 1972, 2006b, Benkman 1992, Adkisson 1996). However, despite many local studies, large scale studies of irruptive migrants remain scarce in the literature, with the notable exception of Koenig & Knops (2001) in North America.

The Bullfinch *Pyrrhula pyrrhula* seems an unlikely irruptive species; median documented recovery distance of British-ringed birds is less than 1 km (Newton 2002), and 67% of individuals ringed in Denmark have been recovered within less than 5 km (Bønløkke *et al.* 2006). Nevertheless, the nominate race, the so-called Northern Bullfinch *P. p. pyrrhula*, is invasive (e.g. Newton 1972, 2006a), showing variable abundance outside of its normal winter range, ranking in the top ten migrants showing greatest annual fluctuations in catches at eastern European ringing stations (Nowakowski & Vähätalo 2003). But is this irruptive behaviour the result of density-dependent dispersal, with birds departing traditional wintering areas when reproductive success has been high relative to the food supply, or simply a response to a lack of winter food supply? Some passerines exhibit density-dependent dispersal (Matthysen 2005, Nilsson *et al.* 2006), especially among juveniles (e.g., Greenwood *et al.* 1979, Nilsson 1989). Could this be the case among Northern Bullfinches? If so, more birds would be expected to appear outside normal wintering areas following summers with high reproductive success (measured by the proportions of young in the caught sample).

Much of the Northern Bullfinch range (e.g., Fennoscandia) lies beyond the present range of many plant species exploited for food at lower latitudes – such as the “keys” or seeds of ash *Fraxinus excelsior* and the berries of blackberries *Rubus* spp. – and winter snow cover precludes feeding on herbaceous weed seeds, the staple diet of smaller most southerly distributed races (Newton 1967). As a result, rowanberry *Sorbus aucuparia* seeds (an important food item for Bullfinches throughout their distribution) attain particular significance in the northern part of the range, where they dominate the autumn diet of *P. p. pyrrhula* and are also taken in large amounts in winter (Erkamo 1948, Pulliainen 1978, Snow & Snow 1988, Raspé *et al.* 2000).

Rowans rarely fruit heavily (Ahlberg 1927), and recent Norwegian studies have shown that the rowan is a classic “masting” species, with large variations in berry production across years, highly synchronised at large spatial scales (Kobro *et al.* 2003, Satake *et al.* 2004). It is tempting to speculate, therefore, on whether the autumn irruptions of Northern Bullfinches, witnessed outside of Fennoscandia, coincide with years of poor rowanberry cropping there.

Because of the level of cropping synchrony throughout the Nordic countries, we here use the time series of fruit setting in the rowan from Finland and Norway to test the hypothesis that Fennoscandian Northern Bullfinches are eruptive, departing their normal short migration wintering areas in seasons when the rowan crop fails.

We test three specific predictions:

1. At bird observatories outside the normal range of the Northern Bullfinch population, the species’ abundance should show wider annual

variations compared to more regular migrant species, consistent with an irruptive migratory pattern.
2. Years with heavy rowanberry masting should coincide with high densities of Northern Bullfinches remaining in Fennoscandia, as shown by comparing winter bird abundance in Finland with indices of rowanberry abundance there.
3. In years of poor rowanberry production, unusually large numbers of Northern Bullfinches should be witnessed migrating outside of Fennoscandia, consistent with an eruption, with few residual birds in remaining in core winter areas because of lack of food there.

We use winter bird count data and ringing totals as measures of efflux of Northern Bullfinches from Fennoscandia during their passage at four different bird observatories around the Baltic to test predictions about how the birds should distribute themselves in relation to rowanberry abundance in each year.

2. Material and methods

2.1. Measures of annual berry abundance

In Fennoscandia, rowan is a common tree, varying in size from tall shrubs (1–2 m) to full-sized trees more than 3 m high (Lid 1979). Clusters of early summer white flowers give rise to conspicuous autumn red berries. Flower and berry production on individual trees varies greatly between 0 to >100,000 between years in a spatially synchronous manner in classic masting behaviour (Sperens 1997a, b, Kobro *et al.* 2003). Because of its importance as a food resource for the larvae of the apple fruit moth *Argyresthia conjugella* Zeller, the most significant insect pest of apple in Fennoscandia (Ahlberg 1927), agricultural advisers count berry numbers on reference branches of trees in the vicinity of orchards. Data were available from 60 Norwegian sites (including those listed in Kobro *et al.* 2003) from 1972 to 2004, converted to means as an index of annual berry production (see Kobro *et al.* 2003 for full details).

In Finland, annual abundance estimates were made of rowanberries during 1956–1996 as part of an assessment of annual game statistics carried out by the Finnish Game and Fisheries Research Institute amongst game wardens and hunters, generating some 500 responses annually (Wallenius 1999). Observers assessed relative annual abundance as average (score 2), or above (3) or below average (1), with zeros entered for areas where the species did not occur and for crop failure; average scores were used to generate an abundance index (AI) for the entire country in each year. Here, we use the data presented in Wallenius (1999) for the province of North Karelia, representative of Finland as a whole. Such scores (in contrast to systematic counting) likely overestimate abundance in inter-mast years, since flowers and berries in abundance are conspicuous, but sparse fruiting is more easily overlooked. Although this introduces some bias, the measures nevertheless provide a good measure of those years of greatest and poorest abundance.

2.2. Measures of irruptive bird abundance

Long-term changes of the abundance of different bird species have been monitored in Finland since the winter 1956/1957, based upon fixed route counts, where all observed birds are registered. Here, we use the index of Northern Bullfinch abundance (birds encountered per 10 km) generated from the mid-winter data from this project based upon ca. 5,000 km of transects sampled annually (Väisänen & Solonen 1997).

The island of Christiansø (55°19’ N, 15°11’ E) lies 20 km NE of the island of Bornholm in the Baltic, 40 km SE of the south coast of Sweden. It receives only migrant Northern Bullfinches during spring and autumn passage, and ringing recoveries show that the birds originate from western Norway across to eastern Finland and continue to winter in eastern Denmark and northern Germany (Lausten & Lyngs 2004, Bønløkke *et al.* 2006). Annual numbers passing through Christiansø were assessed from autumn ringing totals, based on constant ringing effort, available from 1976 to 1998 and in 2004 (less catch effort was expended during 1999–2003 after the ringing station closed) and from numbers of birds observed daily according to constant effort protocols during 1976–2004 (Lausten & Lyngs 2004).

Birds have been caught systematically in the Lighthouse Garden at Falsterbo (55°23' N, 12°49' E) each autumn between 21 July and 10 November under the standardised trapping programme (Karlsson *et al.* 2002). Data have been made available on the internet for the years 1980–2004 and consist of annual ringing totals for each season.

Birds have been caught in Heligoland traps and ringed at the ringing station at Kabli on the Baltic coast of Estonia (58º01' N, 24º27' E; see Leivits 1998 for details of catching techniques and habitats). Data were available in the form of annual ringing totals on the internet at the time of writing for the years 1976 to 2003.

At Hanko, on the southernmost point of the Finnish mainland (59º 49' N, 22º 54' E) standardised daily migratory-bird counts were carried out between 20 July and 31 December from 1979 to 2005, and the number of observed Bullfinch records summed for each season (Lehikoinen & Vähätalo 2000). The Bullfinch has increased as a breeding bird in Finland during 1983–2005 (Väisänen 2006), as reflected in an increase in this Hanko migration index over time (Lehikoinen *et al.* 2008).

Hence we fitted a log-linear regression model to the annual index values, measuring the back-transformed residuals from the model as an index of relative abundance correcting for the general increase in overall number with time. We used these residuals to test for a correlation between Hanko Bullfinch relative abundance and the berry crop in Finland. Hanko records also suggested that Bullfinches were less irruptive than at other Baltic observatories, so we also tested whether Bullfinches appeared earlier in the season at Hanko in years of poor rowanberry crops compared to those with abundant berries. Annual phases of migration were defined as the Julian dates when the season's cumulative bird sum reached 5%, 50% and 95% of the total number of birds counted by 5 November in each year. We then tested for correlations between these autumn migration dates and the berry crops in Norway and Finland. The annual percentage of young amongst the catch of the Northern Bullfinches at Hanko was used as an index of reproductive output in the population.

We used the coefficient of variation (*cv*, calculated by dividing the standard deviation σ of annual autumn ringing or census numbers by the mean μ, $cv = \sigma / \mu$) to assess the degree to which the Northern Bullfinch showed eruptive behaviour at each of the bird observatories. This dimensionless measure of variation is considered to be low variance below 0.7, but very high variance when $cv > 1$, the latter indicating large between-measure fluctuations in numbers.

In all the analyses described below, we have used natural logarithm transformation of the mean numbers of rowanberries recorded from all stations in Norway in a given year, but the Finnish rowanberry abundance index (based as it is on an ordinal score) has not been transformed.

3. Results

3.1. Is the Northern Bullfinch irruptive at Baltic bird observatories?

On Christiansø, the *cv* of the Bullfinch for the years 1976–1998 was 0.93, that at Falsterbo, the *cv* of Bullfinch for the years 1980 to 2005 was 1.10, this compares with 0.45 and 0.59 for greenfinch *Carduelis chloris* and chaffinch *Fringilla coelebs* (similar short distance granivorous non-irruptive migrants) and 0.52 and 0.67 for blackcap *Sylvia atricapilla* and garden warbler *S. borin* (as longer distance migrants). At Kabli (Estonia), the *cv* for Bullfinch was 0.96. At Hanko (Finland), it was 1.12, but accounting for the 7% per annum increase in numbers over the period 1979 to 2005, the *cv* of the residuals after accounting for the increase was 0.19, suggesting that the species is not especially irruptive at this site. Note that there was no sign of similar increasing numbers with time amongst the time-series data from any of the other sites. These results suggest that the Northern Bullfinch shows patterns of irruptive occurrence at all sites, excluding Hanko.

3.2. Do irruption years follow seasons of high reproductive output?

The annual autumn catch of Northern Bullfinches at the bird observatories of Falsterbø, Christiansø, Kabli and Hanko were not significantly correlated with the annual percentage of young amongst the catch ($r^2 = 0.01$, P = 0.70; $r^2 = 0.06$, P = 0.31, $r^2 =$

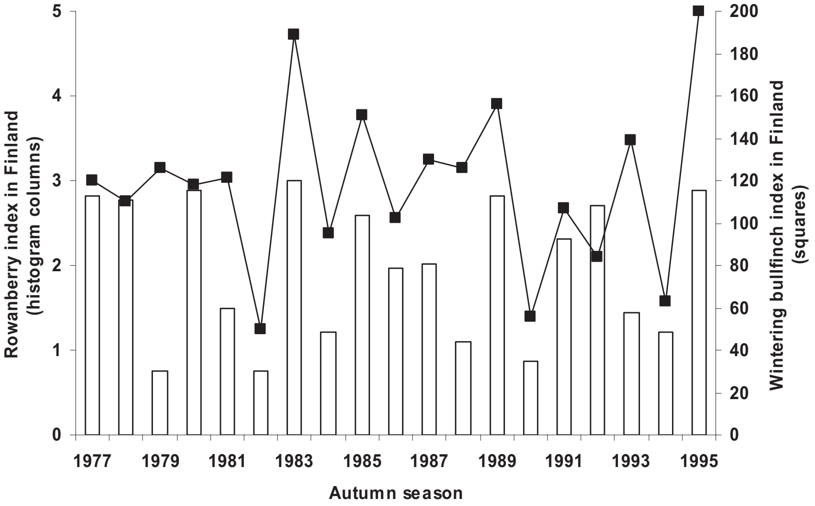

Fig. 1. Annual rowanberry abundance indices for North Karelia, Finland, published in Wallenius (1999; histogram columns) compared with the annual Finnish winter bird count index for Northern Bullfinch during 1977–1995 (Väisänen & Solonen 1997; linked filled squares).

0.01, P = 0.63 and r^2 = 0.12, P = 0.09, respectively after arc sine square root transformations of proportion young data).

3.3. Correlations between berry and Finnish wintering Bullfinch abundances

There was a strong correspondence between the rowanberry index in Finland and the abundance of Bullfinches recorded in 19 mid-winters in Finland (Fig. 1). The Finnish rowanberry AI (x) explained a significant amount of the variance in the winter Bullfinch index in Finland (Fig. 2, y = 28.0 x + 62.7, r^2 = 0.34, $F_{1,17}$ = 8.8, $P < 0.001$) as did the rowanberry AI in Norway (y = –30.1 ln(x) + 34.6, r^2 = 0.57, $F_{1,17}$ = 22.1, $P < 0.001$). There was a significant correlation between the Finnish and Norwegian AI values for the years 1977–1995, (r^2 = 0.62, $F_{1,17}$ = 14.5, $P < 0.005$) with distinct crop failures in both countries in 1984, 1990, 1994 and 1996 (Wallenius 1999, Kobro *et al.* 2003).

3.4 Correlations between berry abundance and migration intensity at bird observatories

Rowanberry AI (x) in Norway explained a significant amount of the variation in numbers of Bullfinches captured each autumn on Christiansø (Fig. 3; y = –103.9 ln(x) + 699.2, r^2 = 0.45, $F_{1,22}$ = 18.3, $P < 0.001$). A model predicting the daily counts of Bullfinches on the island corrected for effort in each autumn from rowanberry abundance in Norway was also highly statistically significant, with less explanatory power (y = –4.36 ln(x) + 30.4, r^2 = 0.21, $F_{1,27}$ = 7.9, $P < 0.01$). Rowanberry abundance in Norway explained a significant amount of the variation in numbers of Bullfinches captured each autumn on Falsterbo (Fig. 4; y = –38.2 ln(x) + 256.2, r^2 = 0.27, $F_{1,23}$ = 8.6, $P < 0.01$). At Kabli, Estonia, there was a positive correlation between rowanberry abundance in Norway and the catch of Northern Bullfinches (y = 45.5 ln(x) – 152.3, r^2 = 0.45, $F_{1,26}$ = 21.6, $P < 0.001$).

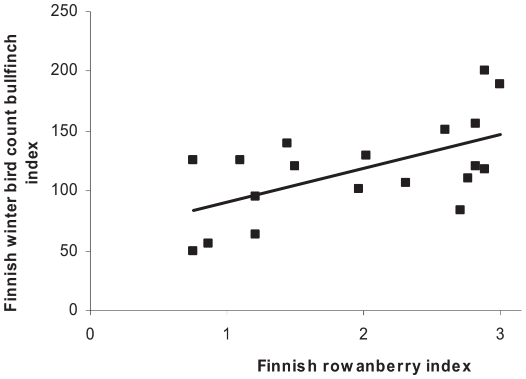

Fig. 2. Annual rowanberry indices for North Karelia, Finland, plotted against annual variation in the Finnish winter bird count index for Northern Bullfinch from Väisänen & Solonen (1997) during 1977–1995. See text for details of model fitting.

The annual numbers of Northern Bullfinches

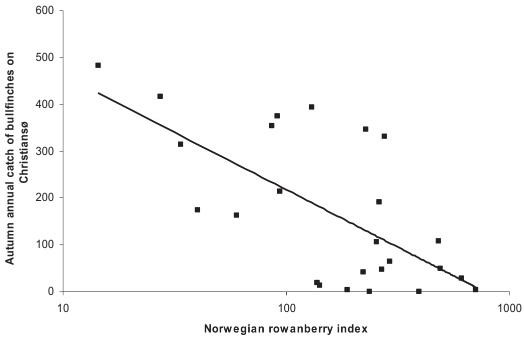

Fig. 3. Annual rowanberry indices from Norway (note logarithmic scale) plotted against annual autumn catches of Northern Bullfinches at the Christiansø Bird Observatory, Denmark, during 1976–2001 and 2004. See text for details of model fitting.

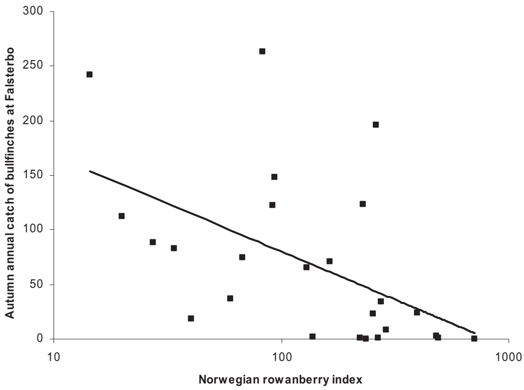

Fig. 4. Annual rowanberry indices from Norway (note logarithmic scale) plotted against annual autumn catches of Northern Bullfinches at the Falsterbo Bird Observatory, Sweden, during 1980–2004. See text for details of model fitting.

observed at Hanko increased during 1979–2005 ($r^2 = 0.27, F_{1,25} = 9.41, P = 0.005$; Lehikoinen *et al.* 2008). There was a positive correlation between rowanberry abundance index in Finland and modelled residuals from the annual model predicting numbers of Bullfinches counted each autumn on Hanko (Fig. 5; $y = 1055.4x–1327.3, r^2 = 0.23, F_{1,17} = 4.88, P = 0.04$), i.e., there was a positive relationship between local abundance (corrected for increase in the population during the period) and the Finnish rowanberry crop. There were also significant positive relationships between the annual Julian dates that marked the observation of 5% and 50% of the total autumn count of Bullfinches at Hanko and the Finnish rowanberry index (Fig. 6; $y = 6.789x + 269.6$, $r^2 = 0.76$, $F_{1,17} = 49.9$, $P < 0.001$; $y = 3.719x + 288.1, r^2 = 0.46, F_{1,17} = 13.8$, $P = 0.002$, respectively). However, the relationships between the Julian dates of 95% arrival and Finnish berries was not significant (Fig. 6; $y = 1.492x + 303.2, r^2 = 0.20, F_{1,17} = 3.90, P = 0.07$). Hence, in years with fewest rowanberries, 50% of Bullfinches had been observed by 13 October compared to two weeks later in years with the greatest abundance of rowans, and an almost 3 week difference between mean dates for the arrival of the first 5% of each annual total.

4. Discussion

The high coefficient of variation of annual Bullfinch abundance at Christiansø, Falsterbo and Kabli shows that this species is irruptive at these sites, but there was no link between breeding success and the autumn catch at the various observatories which would be expected if Bullfinch irruptions were preceded by good breeding seasons.

Finnish winter Bullfinch abundance correlated with indices of rowanberries in both Finland and Norway. In years with abundant berries, Bullfinches remained in Finland and dispersed later in greater numbers locally (supported by the size and

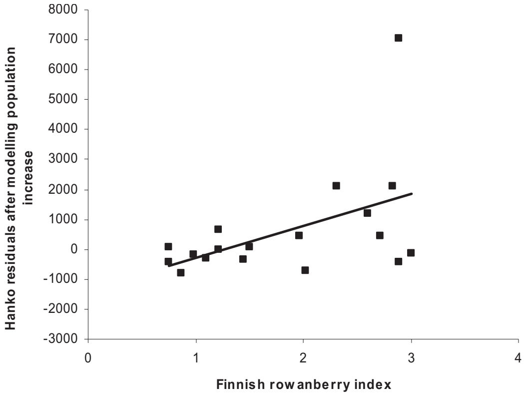

Fig. 5. Annual rowanberry indices from North Karelia, Finland, plotted against the annual autumn residual values after removing the variance accounted for by the increase in numbers in Northern Bullfinch observations at the Hanko Bird Observatory, Finland, during 1979–1996. See text for details of model fitting.

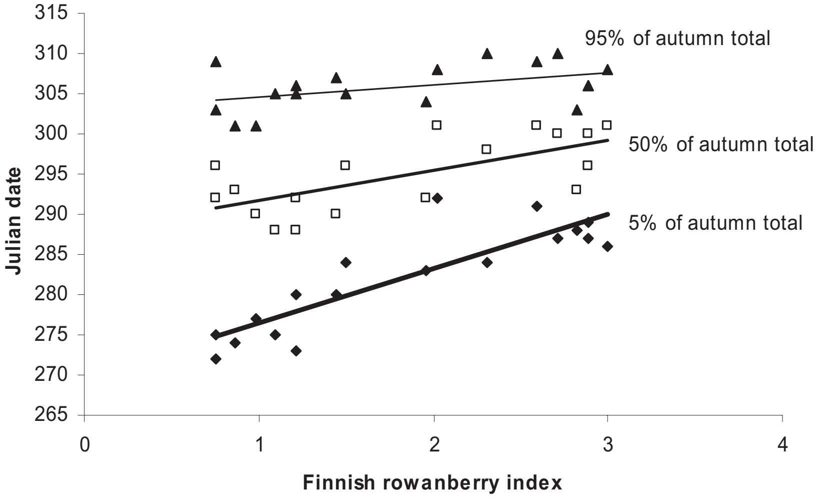

Fig. 6. Annual rowanberry indices from North Karelia, Finland (untransformed scale, 1979–1996) plotted against the Julian date when 5%, 50% and 95% of the annual autumn northern bullfinch total (counted until 5 November) was achieved for each autumn at the Hanko Bird Observatory, Finland. See text for details of model fitting.

phenology of Hanko autumn counts). Winter feeding of birds (including Bullfinches) is common (and long established) in Finland (Väisänen 2008), more so than in neighbouring Estonia and Russia (Ellermaa 2001), a practice which may affect local abundance and contribute to overall increases over time. The later appearance in larger numbers at Hanko in years with abundant berry crops may also explain the positive relationship between overall Bullfinch abundance and the size of the berry crop demonstrated amongst the Kabli data. In years with few berries, Bullfinches departed from core winter areas, as demonstrated for e.g. Fieldfare (Tyrväinen 1975).

Greater numbers of Northern Bullfinches were caught at southern Baltic bird observatories in years with poor rowanberry crops in Norway, regression models explained 27–45% of the variance in the relationship. High berry numbers always coincided with few birds at Christiansø and Falsterbo, strongly supportive of the importance of the crop to the irruptive nature of the population, but there was much greater variance in low berry years, perhaps suggesting a capacity to switch to other food items or resort to other areas. Catch data from Kabli and Hanko were strongly positively correlated with the annual Norwegian and Finnish berry crop indices, respectively. As expected, these areas (within the normal breeding range of the Northern Bullfinch) retained more birds locally in autumn seasons with an abundant berry crop.

Irruptive migration is difficult to study. The avian species involved are making apparently unpredictable changes to their traditional migration patterns and winter quarters, making it difficult to design studies, which can investigate these patterns, especially at appropriate large spatial scales. Many studies have been constrained by small scale (Lensink *et al.* 1989) or relatively sparse ringing recoveries (Troy 1983), so it is rare to find descriptive studies over larger spatial scales (but see Hochachka *et al.* 1999, Koenig & Knops 2001). The present study showed observations of Northern Bullfinches at two major bird observatories on the edge of the normal winter range shows the population is periodically eruptive. Historical time series showed that Finnish birds remain in Finland when rowanberries are abundant, but do not do so (or do so in fewer numbers) when there is little or no berry crop. It would appear that the Northern Bullfinch has a normal wintering range, but the extent to which this is exploited varies with food availability there. Thus in years of greatest berry abundance, birds are numerous and very few birds appear outside this range. However, in years of low rowanberry abundance, variable numbers remain, with fewest in years of very poor berry production, suggesting other food resources are exploited in normal wintering areas before a substantial efflux occurs.

This analysis underlines the importance of long-term systematic collection of data on large geographical scales to understanding of pattern and process in natural systems. Although the material presented here is correlative, it has provided the opportunity to better understand how a facultative avian migrant responds on a large geographical scale to fluctuations in the availability of its favoured food item. The causes of rowan masting remain a matter of debate (Sperens 1997a, Kobro *et al.* 2003, Pias & Guitian 2006), but whatever the cause, the net effect is an unpredictable autumn/winter food supply for the Northern Bullfinch, since the decision to migrate (or not) in a given autumn correlates with berry abundance. Food shortage may be the main proximate factor stimulating migration amongst Fennoscandian Bullfinches to other areas not regularly used when food is more abundant. In contrast to regular migrants, where endogenous rhythms (e.g., triggered by day length) enable departure from an area in anticipation of food shortages (e.g., where winter food is completely absent), the Northern Bullfinch has to maintain flexibility of response, moving from its regular wintering range only in response to food shortages there to peripheral areas where the food supply is not necessarily better. In the case of the Jay *Garrulus glandarius*, large numbers erupted into western Europe in 1983, to areas with no acorns as staple food supply (John & Roskell 1985), hence such efflux may carry a survival penalty, which may play a role in the population dynamics of the species.

In the case of the Fieldfare in Norway, the abundance of rowanberries (and hence the numbers of fieldfares wintering there) gave a positive contribution to a multivariate model predicting the size of the breeding population the following spring (Hogstad *et al.* 2003). In this way, the extent of Northern Bullfinch eruptions from Fennoscandia has the potential to affect breeding population size in the subsequent spring, both as a direct result of over-winter survival, but also potentially as a result of emigration. These population level effects following such irruption years would repay further investigation.

Acknowledgements. We are deeply grateful to the many observers who have contributed to data collection upon which this analysis was based, especially contributors of bird count and trapping and rowanberry count data, as well as the far-sighted people who started and maintained these monitoring programmes and made them available for common use. Thanks to Ian Newton and two anonymous referees for comments on an earlier draft. This is report no. 74 from the Hanko Bird Observatory.

Punatulkun (*Pyrrhyla p. pyrrhula*) pohjoisen alalajin vaellukset ovat yhteydessä pihlajanmarjojen runsauteen

Punatulkun pohjoisen alalajin (*Pyrrhula p. pyrrhula*) syksyinen runsaus vaihtelee jyrkästi Itämeren lintuasemilla ja riippuu runsauden muutoksista lajin normaalilla talvehtimisalueella, mutta ikäjakauma-aineistojen perusteella ei välttämättä riipu lisääntymismenestyksestä. Pihlaja on merkittävä Fennoskandian punatulkkujen ravinnonlähde. Sen marjasato vaihtelee samassa tahdissa laajoilla maantieteellisillä alueilla. Pihlajan Suomen ja Norjan satoarvioita ajalta 1972–2004 käytettiin tutkittaessa, selittääkö heikko sato normaalilla talvehtimisalueella punatulkun massavaelluksen uusille alueille.

Suomen talvilintulaskenta- ja lintuasema-aineistoissa punatulkun runsaus korreloi pihlajanmarjaindeksien kanssa, joten punatulkkumäärät ovat korkeimmillaan normaaleilla talvehtimisalueilla hyvinä pihlajanmarjavuosina. Tanskan ja Ruotsin lintuasemilla – normaalin talvehtimisalueen ulkopuolella – punatulkkumäärä korreloi negatiivisesti Norjan pihlajanmarjasadon kanssa, mikä viittaa siihen että suurimmat normaalin talvehtimisalueen ulkopuolelle suuntautuvat liikehdinnät johtuvat heikosta pihlajanmarjasadosta. Marjasato voi siis vaikuttaa suuressa mittakaavassa sitä hyödyntävän lajin vuotuiseen runsauteen ja muuttokäyttäytymiseen.

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