



Irruptions of Bohemian Waxwings in relation to population density and food availability

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Abstract

Bird irruptions are thought to be triggered by a combination of lack of food in the regular distribution range and high population density (push factors). Recent studies have also suggested that irruptions may be drawn towards areas with high food availability (pull factor). The Bohemian Waxwing (*Bombycilla garrulus*) is an irruptive species with large annual variation in the numbers reaching southern areas during winter. I used long-term (up to 41 years) data on annual number of waxwings observed during breeding in Finland and Sweden, during winter in Norway, Sweden, Denmark, UK and Poland, and data on their main winter food, Rowanberries (*Sorbus aucuparia*; masting occurs at 2–3 year intervals) from Norway (southern areas) and Finland (overlapping with northern breeding areas) to test the push and pull hypotheses. Winter numbers fluctuated in synchrony over large parts of northern Europe. In years with low food availability in Finland waxwings arrived to southern areas early, and early arrival to southern areas was linked to larger winter numbers in some countries. However, controlling for arrival time to southern areas, numbers were larger when there were more rowanberries in Finland. Thus, irruptions generally occurred with high rowanberry abundance, but sometimes occurred with the combination of low rowanberry abundance and early arrival. There was mixed evidence that irruptions were linked to high breeding population density. There was no support that irruptions were drawn towards high rowanberry abundance in southern areas. In conclusion, waxwing irruptions had complex relationships with food availability, but most irruptions occurred in years with high rowanberry abundance in autumn in northern areas. This is opposite to expectations from the current view that irruptions are triggered by lack of food, but irruptions departing late may still have been triggered by abundant food finally becoming depleted late in winter.

Keywords Migration · *Bombycilla garrulus* · Push and pull dynamics · Rowanberry · *Sorbus aucuparia*

Zusammenfassung

Einflüge von Seidenschwänzen im Verhältnis zu Populationsdichte und Nahrungsangebot

Man nimmt an, dass Vogelirruptionen durch eine Kombination aus Nahrungsmangel im regulären Verbreitungsgebiet und einer hohen Populationsdichte (Push-Faktoren) ausgelöst werden. Neuere Untersuchungen legen aber auch die Möglichkeit nahe, dass Einflüge von Gegenden mit einer hohen Nahrungsverfügbarkeit angezogen werden (Pull-Faktoren). Der Seidenschwanz *Bombycilla garrulus* ist eine irruptive Vogelart, bei der die Anzahl der Tiere, die im Winter in südlichen Gebieten auftauchen, stark variiert. Anhand von Langzeit-Beobachtungsdaten (bis zu 41 Jahren) der jährlichen Anzahl von Seidenschwänzen während der Brutzeit in Finnland und Schweden sowie während des Winters in Norwegen, Schweden, Dänemark, Großbritannien und Polen nebst Daten zu deren Hauptnahrungsquelle, Vogelbeeren (*Sorbus aucuparia*; Mastjahre finden in 2–3-jährigem Abstand statt) aus Norwegen (südliche Bereiche) und Finnland (Überschneidungen mit den nördlichen Brutgebieten) sollten die Push- beziehungsweise Pull-Hypothesen getestet werden. Die Winterzahlen zeigten über weite Teile

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Nordeuropas eine synchrone Fluktuation. In Jahren, in denen es in Finnland wenig Nahrung gab, kamen die Seidenschwänze schon früh im Süden an und eine frühe Ankunft in den südlichen Gebieten stand mit höheren Winterzahlen in manchen Ländern im Zusammenhang. Unter Berücksichtigung der Ankunftszeit in den südlichen Regionen waren die Anzahlen allerdings größer, wenn es in Finnland mehr Vogelbeeren gab. Somit kam es allgemein bei großem Angebot an Vogelbeeren zur Einflügen, manchmal allerdings auch beim Zusammentreffen von einem geringen Vogelbeerenangebot mit früher Ankunft. Es gab keine eindeutigen Hinweise darauf, dass die Einflüge mit einer hohen Brutpopulationsdichte gekoppelt sind. Wir fanden keine Bestätigung dafür, dass Einflüge von einem großen Vogelbeerenangebot in den südlichen Regionen angezogen werden. In der Summe zeigten die Seidenschwanzeinflüge ein komplexes Beziehungsgeflecht mit dem Nahrungsangebot, die meisten Einflüge ereigneten sich jedoch in Jahren mit einem großen herbstlichen Vogelbeerenangebot in den nördlichen Regionen. Dies widerspricht Erwartungen gemäß der gängigen Ansicht, dass Irruptionen durch Nahrungsmangel ausgelöst

werden, allerdings können späte Einflüge dennoch dadurch verursacht werden, dass ein ursprünglich reichhaltiges Nahrungsangebot zum Ende des Winters hin allmählich erschöpft ist.

Introduction

Several bird species in the northern hemisphere, typically owls and seed-eating birds breeding in boreal forests, show large annual variations in the number of individuals wintering in different parts of the distribution range (Newton 2008, 2012). The annual variation is often related to fluctuations in the availability of their main winter food such as rodents or seeds of masting trees (Bock and Lepthien 1976; Koenig and Knops 2001; Newton 2008, 2012). Rodent population cycles often have peaks at 3–5 year intervals (Lack 1954; Cheveau et al. 2004; Newton 2008; Robillard et al. 2016), whereas masting trees normally have very low seed or fruit production after a year with a large crop (Svärdson 1957; Koenig and Knops 2000). Thus, bird species depending on rodents or seeds or fruits from trees are exposed to food shortage in some years, and may then occur irruptively in areas south of their regular wintering range. Years with low food availability often follow years with high food availability when breeding success may have been high. Irruptions may therefore be triggered by a combination of low food availability and high population density (Lack 1954; Svärdson 1957; Bock and Lepthien 1976; Koenig and Knops 2001; Newton 2006, 2008), conforming to a scenario where birds are pushed away from northern areas due to high competition for few resources. On the other hand, recent studies indicate that rich food resources in distant areas (e.g. further south) may sometimes function as a pull factor and influence migration from northern areas, either alone (Dale 2023) or in combination with push factors (Strong et al. 2015; Dale and Sonnerud 2023).

The Bohemian Waxwing (*Bombycilla garrulus*, hereafter called waxwing) has generally been regarded as a typical irruptive bird species (e.g. Glutz von Blotzheim and Bauer

1985). During winter, Rowanberries (*Sorbus aucuparia*) are an important food source for the species in Europe, and has been considered as a critical winter food which may influence winter movements (Cornwallis 1961; Glutz von Blotzheim and Bauer 1985). Siivonen (1941) claimed that moderate eruptions are linked to low food abundance in northern areas, whereas mass eruptions are due to high waxwing population density with no influence of food availability, and occurring in 10-year cycles after build-up in numbers over a few years where good breeding conditions coincide with good wintering conditions. However, most other authors believe that all irruptions are due to a combination of low abundance of rowanberries and high waxwing population density in the northern breeding areas (Svärdson 1957; Hansson and Wallin 1958; Cornwallis 1961; Cornwallis and Townsend 1968; Glutz von Blotzheim and Bauer 1985), and there is no further evidence of a 10-year cycle. If winter food is lacking at a large spatial scale, irruptions are thought to occur earlier in autumn and proceed further south and west (Glutz von Blotzheim and Bauer 1985). Although rowanberries as a pull factor has never been explicitly stated as a potential cause of waxwing irruptions, several previous studies have indicated that waxwing numbers in areas south of the breeding range during winter are positively related to availability of rowanberries (Svärdson 1957; Hansson and Wallin 1958; Kolunen and Vikberg 1978).

However, there is a striking lack of recent studies of waxwing irruptions, and many of the previous evaluations have been based on data from only one or a few irruptions (Svärdson 1957; Hansson and Wallin 1958; Cornwallis 1961; Cornwallis and Townsend 1968). Quantitative analyses based on long-term data on annual variation in waxwing numbers and their main winter food rowanberries have been done for the periods 1895–1940 (Siivonen 1941) and 1960–1975 (Glutz von Blotzheim and Bauer 1985). During recent times, systematic breeding and wintering bird surveys and online citizen data provide larger amounts of data, which may enable better tests of hypotheses. For example, in Fennoscandia systematic surveys of the breeding population density of landbirds is available for Sweden from 1998 (Green et al.

Table 1 Data sets used for analyses of winter numbers of Bohemian Waxwings (*Bombycilla garrulus*) in Europe

Data set	Location	Time period	Years	Type of data	Source
Breeding population density	Finland	1984–2017	34	Monitoring	Väisänen et al. (2018)
	Sweden	1998–2020	23	Monitoring	Green et al. (2021)
Winter numbers	Southern Norway	1980–2020	41	Citizen data	National Biodiversity Information Centre in Norway ^a
	Southern Sweden	1980–2020	41	Citizen data	Swedish Species Observation System ^b
	Denmark	1989–2020	32	Monitoring	Vikstrøm et al. (2022)
	Hampshire, UK	1980–2010	31	Citizen data	Clark (2011)
	Zielona Góra, Poland	1994–2014	21	Author observations	Czechowski and Jędro (2017)
Rowanberry abundance	Finland	1986–2014	29	Citizen data	Gallego Zamorano et al. (2018)
	Norway	1980–2020	41	Monitoring	VIPS project ^c

^awww.artsobservasjoner.no, data extracted for this study

^bwww.artportalen.se, data extracted for this study

^cwww.vips-landbruk.no/applefruitmoth/, same data set as used in Dale (2023)

2021) and for Finland from 1975 (Väisänen et al. 2018). Furthermore, data on masting of rowan is available for Norway from 1979 (Kobro et al. 2003), and for Finland from 1986 (Gallego Zamorano et al. 2018). Thus, waxwing irruptions may be analysed in relation to the main expected influencing factors with larger amounts of data than were available for the previous studies (Siivonen 1941; Glutz von Blotzheim and Bauer 1985).

In the present study, I analyse long-term time series (up to 41 years) of waxwing numbers during the breeding season in northern Fennoscandia, winter numbers in southern Norway, southern Sweden, Denmark, UK and Poland, and rowanberry abundance in Norway and Finland (Table 1). Rowanberry abundance in Norway (southern parts of the country) was used as a proxy of food availability in southern areas, whereas rowanberry abundance in Finland (overlapping with the breeding distribution of waxwings) was used as a proxy for food availability in northern areas where irruptions originate. The following predictions from theories of bird irruptions are tested (Table 2): irruptions are expected to occur due to a combination of (1) lack of rowanberries in northern

areas and (2) high population density (push factors). Furthermore, (3) winter numbers in southern areas are expected to be positively related to rowanberry abundance in southern areas (pull factor). In addition, I tested whether the timing of arrival to southern areas was related to food availability following previous suggestions that if winter food is lacking at a large spatial scale, movements are thought to occur earlier and proceed further south and west.

Materials and methods

Study area and study species

Bohemian Waxwings may occur irruptively to large parts of northern and central Europe (Glutz von Blotzheim and Bauer 1985; Cramp 1988). In addition to using existing time series and published data on waxwing winter numbers (Table 1), citizen data were also collected specifically for the present study from western and southern parts of Norway and from southern Sweden to obtain measures of winter

Table 2 Predictions from and tests of hypotheses for irruptions of Bohemian Waxwings (*Bombycilla garrulus*) in Europe

Hypothesis	Predictions	Tests	Results
High population density (push)	Irruptions are expected to be triggered by high population density in breeding areas	Relationships between breeding population size in Sweden and Finland and winter numbers further south	Mixed evidence
Lack of food in northern areas (push)	Irruptions are expected to be triggered by lack of food in northern breeding areas	Relationships between rowanberry abundance in Finland and winter numbers further south	No support, most often opposite (larger numbers when there was more food in Finland)
Abundant food in southern areas (pull)	Irruptions are expected to be drawn towards abundant food in southern areas	Relationships between rowanberry abundance in southern Norway and winter numbers	No support

number of waxwings in these areas (detailed information about these data sources are given below in the paragraph ‘Waxwing numbers’).

In Norway, the most northern county (Troms and Finnmark) is less affected by irruptions, being also the main breeding area for the species (Solheim 1994). Thus, data on winter numbers were collected for counties south of Troms and Finnmark. Although Nordland is quite far to the north (ca. 65–69° N), the county has no breeding population of waxwings, but is reached by movements with a westerly direction. In Sweden, data were collected for landscapes north to and including Dalarne and Hälsingland (ca. 62° N). Landscapes further north in Sweden have breeding populations of waxwings (Svensson et al. 1999), although commonly only in the far north. The breeding distribution of the waxwing continues north to Troms and Finnmark in Norway (ca. 69–70° N), and the latitudinal breeding distribution range in Finland is ca. 64–70° N (Valkama et al. 2011). The breeding population size of waxwings in Fennoscandia may amount to ca. 40,000–240,000 pairs [Norway: 100–2000 pairs (Shimmings and Øien 2015); Sweden: 20,000–146,800 pairs (Ottosson et al. 2012); Finland: 20,000–90,000 pairs (Valkama et al. 2011)]. Assuming two surviving young per breeding pair, the total autumn population size of the Fennoscandian population may be ca. 160,000–960,000 individuals.

During the breeding season, waxwings are mostly insectivorous. However, during autumn and winter waxwings in Europe feed to a large extent on rowanberries, although other fruits and berries are also taken (including from ornamental plants), especially when availability of rowanberries is low (Hansson and Wallin 1958; Cornwallis 1961; Glutz von Blotzheim and Bauer 1985; Cramp 1988). Rowans are distributed over most parts of Fennoscandia, including the breeding range of waxwings, but are most common in mixed forests in southern areas, and also occurs further south in Europe (Räty et al. 2016). Rowan is a typical masting tree and produces large crops at 2–3 year intervals (Kobro et al. 2003; Dale 2023). Annual crop size in rowan in Finland is spatially synchronous at scales up to 1000 km (Gallego Zamorano et al. 2018), and masting in Norway and Finland is also normally synchronous (Kobro et al. 2003). However, for the period 1980–2020, Dale (2023) found that, although mostly synchronous, masting during the period 2008–2013 was asynchronous, i.e. peak years in Finland were years with low rowanberry abundance in Norway and vice versa.

Waxwing numbers

To obtain data on the number of waxwings observed during autumn and winter (called ‘winter’ for short) in each year in southern and western Norway and southern Sweden, I searched the websites of the National Biodiversity

Information Centre in Norway (www.artsobservasjoner.no) and the Swedish Species Observation System (www.artportalen.se) and extracted all waxwing records. These websites are online portals for reporting observations of species, and they are open to the public. Most reports of birds are submitted by members of BirdLife Norway and BirdLife Sweden. Both websites are built on almost identical systems for handling species observations. The unit used for analyses was a ‘record’, i.e. one or more individuals observed in one place at one time (at www.artsobservasjoner.no termed ‘funn’, at www.artportalen.se termed ‘fynd’). Each record had a corresponding number indicating how many individuals the observer had seen. The seasonal number of records was strongly correlated with the number of individuals reported (Norway: $r=0.97$, $n=41$ years, $p<0.001$; Sweden: $r=0.90$, $n=41$ years, $p<0.001$), so the choice of unit will not have substantial influence on the results, and number of records was used in this study. Depending on the type of analysis, separate numbers for Norway and Sweden (analyses of large-scale spatial synchrony of winter numbers), or combined numbers for Norway and Sweden (timing of movements, analyses of causes of irruptions), were used. These time series are hereafter called southern Norway, southern Sweden, and southern Norway and Sweden.

For each year, the number of waxwing records included records from October–December in one year and records from January–March in the following year. For example, 2020 refers to and includes records from the period October 2020–March 2021. Breeding season observations (April–August) were not included, and movements rarely reach southern Fennoscandia before October. Data were collected for the period October 1980–March 2021 to match the period for which data on rowanberries in Norway were available (Table 1).

The number of waxwing records in Norway and Sweden increased over time (log-transformed number of records: $r=0.93$, $n=41$ years, $p<0.001$). This was likely due to increased observation activity or reporting because the total number of records of all bird species also increased over time (log-transformed number of records: $r=0.97$, $n=41$ years, $p<0.001$). Thus, to control for observation effort, I calculated an index of waxwing winter numbers as the proportion of all bird records that were records of waxwings. Data on the total number of bird records were extracted from the online bird portals for the same areas and same time periods that were used for data on waxwings in Norway and Sweden (i.e. excluding northern parts of each country, and excluding April–September each year). For southern Norway and Sweden combined, this index of waxwing abundance varied from 0.0017 to 0.0262, and did not show a significant temporal trend ($r=0.21$, $n=41$ years, $p=0.19$). Dale (2023) performed similar analyses of Pine Grosbeak (*Pinicola enucleator*) irruptions with detrended

numbers (i.e. using residuals from a regression of number of observation records (\log_{10} -transformed) on year). For the waxwing, detrended numbers were significantly correlated with the index described above ($r=0.75$, $n=41$ years, $p<0.001$). However, the index was deemed more suitable than detrended numbers because waxwing breeding numbers in northern Europe have increased over time (Väisänen et al. 2018; Keller et al. 2020; Green et al. 2021).

Data on breeding numbers of waxwings in Sweden and Finland, and winter numbers in Denmark, the UK and Poland were based on monitoring projects and citizen data (Table 1). The time series used in the present study covered 21–41 years. Details of the time series are given in Online Resource 1. Other European time series were also considered for analyses, but had data mainly for a few very large irruptions (Belgium: Jacob 1996; Austria: Teufelbauer and Khil 2005). For Sweden and Finland there are also standardized winter counts (Väisänen and Solonen 1997; Green et al. 2021), but these cover both southern wintering areas and northern areas overlapping with the breeding distribution so they do not clearly reflect numbers in areas affected by irruptions.

In general, the terms irruption and invasion are used in particular for years with exceptionally large number of birds. However, there is no clear definition of how many birds need to be involved in order to apply the term irruption. The present study takes into account waxwing winter number for all years with data available, ranging from years with no birds observed to peak years. The years with the largest numbers observed represent irruptions, but it cannot be specified exactly which years this is because the border between irruption and non-irruption years is a matter of opinion.

Rowanberry indices

Rowanberry indices for southern Norway were taken from the VIPS project (see <https://www.vips-landbruk.no/applefruitmoth/>) run by the Norwegian Institute of Bioeconomy Research (NIBIO) and Norsk Landbruksrådgivning (the Norwegian Agricultural Extension Office). VIPS (Varsling innen PlanteSkadegjørere) monitors the risk of pest species attacks on a number of crop species. To forecast risk of attack by Apple Fruit Moths (*Argyresthia conjugella*) on apple, the moth's alternative host rowan has been monitored at 59 sites in both eastern and western Norway from 1979 (see Kobro et al. 2003 for details). The number of flower clusters was counted on reference rowan trees in the vicinity of apple orchards in May each year. Because of a strong correlation in most years between this rowanberry index based on flower clusters and a Finnish rowanberry index based on actual counts of berries in early autumn (Gallego Zamorano et al. 2018), Dale (2023) argued that flower clusters predict rowanberry abundance well.

Some monitoring sites had shorter time series or several years with missing data. First, only six sites were monitored in 1979 compared to ≥ 27 sites during 1980–2020. Following Dale (2023), the year 1979 was excluded from analyses. Furthermore, 14 sites that had < 30 years of data (mean 18.9) during the period 1980–2020 were excluded. The remaining data used for analyses were from 45 sites [14 from eastern Norway (ca. 58–60° N), 31 from western Norway (ca. 59–62° N)] and had data for 32–41 years (mean 38.0). For both eastern and western Norway the yearly rowanberry index was calculated as the median number of flower clusters across sites. The national index for 1980–2020 was calculated as the mean of the indices from eastern and western Norway so that the two regions were weighted equally. The rowanberry index ranged from 1 to 805 (mean 145, median 94; $n=41$ years). See Dale (2023; Fig. 3) for a plot of annual fluctuations in the index.

The rowanberry index in Norway showed a negative temporal trend during 1980–2020 (\log_{10} -transformed index; $r=-0.38$, $n=41$ years, $p=0.014$) which could be due to either natural factors or temporal changes in study sites, including habitat changes and changes in methodological procedures. Dale (2023) performed analyses of Pine Grosbeak irruptions based on a detrended rowanberry index (i.e. using residuals from a regression of number of flower clusters (\log_{10} -transformed) on year) using the same rowanberry dataset. However, the detrended and the non-detrended rowanberry indices were strongly correlated ($r=0.93$, $n=41$ years, $p<0.001$), and analysis results were similar when using non-detrended indices. Thus, the choice of index is unlikely to influence results, and the non-detrended rowanberry index was used here in line with no detrending of waxwing numbers.

In addition to rowanberry indices from Norway, I used data from Finland (Gallego Zamorano et al. 2018, their Fig. 2). They presented rowanberry indices from 248 sites, mostly in southern Finland, but also northern sites overlapping with the breeding distribution of waxwings. Overall, rowanberry sites were located at ca. 60–69° N. Finnish rowanberry sites were ca. 500–1500 km from rowan sites in southern Norway. During 1986–2014, the number of rowanberries was estimated in early autumn, and classified on a categorical abundance scale. The index ranged from 0.34 to 1.42 (mean 0.93, median 0.92; $n=29$ years). The rowanberry index from Finland did not show a temporal trend ($r=0.05$, $n=29$ years, $p=0.81$).

Timing of waxwing movements

To obtain a measure of the timing of waxwing movements, I calculated an index of the number of waxwing individuals reported during October–December relative to the number of individuals reported during January–March for

each season. The index was the ratio between numbers in October–December and January–March, and was used as a continuous variable in analyses. The index was calculated for the citizen data from southern Norway and Sweden combined to provide an index relevant for much of northern Europe. Based on the mean value of the ratio, years were also classified as having early ($n = 17$ years) or late arrival ($n = 24$ years) to southern Norway and Sweden.

Statistical analyses

Initially, correlation analyses were used to explore the spatial synchrony of winter numbers across regions in Europe, the relationships between waxwing numbers during breeding in northern areas and numbers during winter in southern areas, and the relationships between waxwing numbers in winter and rowanberry indices in different regions. All these analyses took year into account, and partial correlation coefficients when controlling for the effect of year are reported. Analyses used \log_{10} -transformed waxwing indices from Finland (breeding), Sweden (breeding), Denmark (winter) and the UK (winter). The significance level in multiple comparisons of the same hypothesis was adjusted with Bonferroni correction.

The main analyses of the influence of push (breeding density in Sweden and Finland, and rowanberry abundance in Finland) and pull factors (rowanberry abundance in Norway, \log_{10} -transformed) on waxwing winter numbers were conducted with generalized linear models (GLM) with Gaussian error distribution. Timing of movements and year were included as covariates. In addition, the interaction between breeding density and rowanberry abundance in Finland was included, based on the idea that the combination of high breeding density and lack of food could lead to particularly large irruptions. Model fit was assessed with AIC_c . Models with combinations of explanatory variables that had the lowest AIC_c -values ($\Delta AIC_c < 2$ compared to best model) were considered. The best models are shown in the main text with parameter estimates based on centered and scaled predictors to allow comparisons of the relative importance of predictors. Alternative models within $\Delta AIC_c < 2$ are detailed in Online Resource 1, Tables S2 and S3. All statistical analyses were conducted in JMP Pro version 16.

Results

Waxwing winter numbers

During recent years with the largest amount of data, up to 1.35 million waxwing individuals (ca. 27,000 records) were observed during autumn and winter in southern Norway

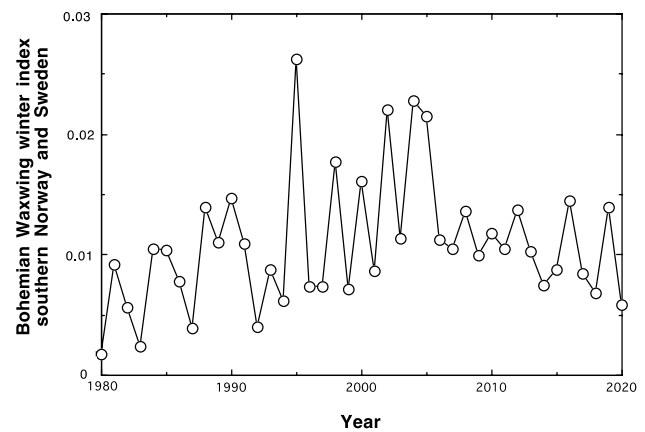


Fig. 1 Bohemian Waxwing (*Bombycilla garrulus*) winter index in southern Norway and Sweden during 1980–2020. The index was the proportion of all bird records submitted to online bird reporting portals that were records of waxwings. The observed range of index values corresponded to waxwing records constituting 0.17–2.62% of all bird records. For each year, the number includes records from October–December and from January–March the following year. Thus, e.g. 2020 includes records from the period October 2020–March 2021

and Sweden. The waxwing abundance index, measured as the percentage of all bird records that were records of waxwings, varied between 0.17% and 2.62% (mean 1.11%, median 1.04%; $n = 41$ years; Fig. 1). The annual fluctuation in abundance had a ratio of up to 5.5 for successive years (mean ratio = 2.0, median = 1.7). There was substantial annual variation in waxwing numbers in Denmark, the UK and Poland also (Online Resource 1, Fig. S1).

Synchrony of winter numbers

Waxwing winter numbers were generally synchronous over large parts of Europe (Table 3; Online Resource 1, Fig. S2). In particular, numbers in southern Scandinavia (Norway, Sweden and Denmark) correlated well with numbers in the UK, but less well with Poland.

Winter numbers and breeding population density

There was evidence that breeding population size in Finland and winter numbers in southern Norway and Sweden, Denmark and Poland, were positively correlated, but there was no evidence that breeding population size in Sweden was related to winter numbers in any country (Online Resource 1, Table S1). Thus, when breeding density in Finland was high, winter numbers in several countries could be both large and small, but large numbers were not recorded when breeding density was low (Online Resource 1, Fig. S3).

Table 3 Synchrony of Bohemian Waxwing (*Bombycilla garrulus*) winter numbers across different parts of Europe

Region	NO	SE	DK	UK
Southern Norway (NO)	–	–	–	–
Southern Sweden (SE)	0.71 41 < 0.001*	–	–	–
Danish winter count (DK)	0.72 32 < 0.001*	0.59 32 < 0.001*	–	–
Hampshire winter index (UK)	0.65 31 < 0.001*	0.49 31 0.001*	0.44 23 0.005*	–
Zielona Góra winter numbers (PL)	0.33 21 0.035	0.19 21 0.23	0.54 21 < 0.001*	0.09 17 0.60

Synchrony was measured as the partial correlation coefficient between annual waxwing winter numbers in pairs of regions when controlling for the effect of year. For each analysis, the partial correlation coefficient (top), sample size (years, middle), and *p*-value (bottom) are reported. Significant values are shown in bold, those significant also after Bonferroni correction are marked with *

Winter numbers and rowanberries in northern areas

There was no evidence that large numbers in winter were linked to low rowanberry abundance in northern areas (Online Resource 1, Table S1 and Fig. S4). Specifically, there were no significant negative correlations between the rowanberry index in Finland and waxwing winter numbers in different regions of Europe. On the contrary, there were trends that the Finnish rowanberry index was positively related to waxwing numbers in southern Norway and Sweden, and in the UK (Online Resource 1, Table S1 and Fig. S4).

Winter numbers and rowanberries in southern areas

There was no evidence that large winter numbers were linked to high rowanberry abundance in southern areas, as measured by the Norwegian rowanberry indices (Online Resource 1, Table S1 and Fig. S5). Thus, when the rowanberry index in Norway was high, winter numbers in most parts of Europe could be both large and small (Online Resource 1, Fig. S5).

Timing of movements

The timing of arrival to southern Norway and Sweden varied substantially between years. The number of waxwing individuals reported during October–December was up to 8.4 times higher than the numbers during January–March

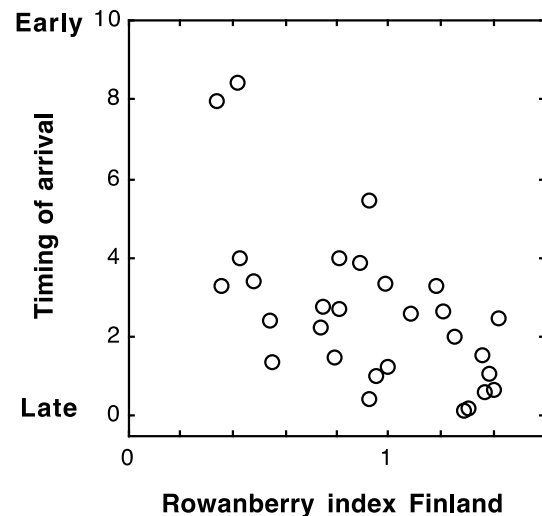


Fig. 2 Timing of Bohemian Waxwing (*Bombycilla garrulus*) arrival to southern Norway and Sweden in relation to rowanberry (*Sorbus aucuparia*) abundance in Finland. Timing was measured as the ratio between number of waxwing individuals reported during October–December and the number of individuals during January–March. A large ratio indicates early arrival, a small ratio indicates late arrival

(early arrival), or could be as low as 13% of the numbers during January–March (late arrival). Early arrival to southern areas was related to low rowanberry abundance in Finland (continuous scale for timing of arrival: partial $r = -0.57$, $n = 29$ years, $p < 0.001$; Fig. 2), and also low rowanberry abundance in Norway (partial $r = -0.38$, $n = 41$ years, $p = 0.017$). Arrival to southern areas was not related to Swedish breeding density (partial $r = -0.13$, $n = 23$ years, $p = 0.41$), but tended to occur earlier at high breeding density in Finland (partial $r = 0.31$, $n = 34$ years, $p = 0.052$).

Early arrival to southern areas was positively and significantly related to winter numbers in Denmark (partial $r = 0.45$, $n = 32$ years, $p = 0.004$) and Poland (partial $r = 0.70$, $n = 21$ years, $p < 0.001$), but not for southern Norway and Sweden (partial $r = 0.21$, $n = 41$ years, $p = 0.19$) or UK (partial $r = 0.03$, $n = 31$ years, $p = 0.84$; Fig. 3).

Multiple factor analyses

GLM analyses of waxwing winter numbers in relation to all putative explanatory factors revealed that winter numbers in southern Norway and Sweden, and in Denmark, were positively related to rowanberry abundance in Finland when also taking timing of arrival to southern areas into account (Table 4; Online Resource 1, Table S2). Furthermore, there were some effects of Finnish breeding density with a significant positive effect on waxwing numbers in Poland (Table 4) and positive effects in some alternative models for southern Norway and Sweden, and for the UK (Online Resource

Fig. 3 Bohemian Waxwing (*Bombycilla garrulus*) annual winter numbers in different parts of Europe in relation to timing of arrival to southern Norway and Sweden. Timing was measured as the ratio between number of waxwing individuals reported during October–December and the number of individuals during January–March. A large ratio indicates early arrival, a small ratio indicates late arrival

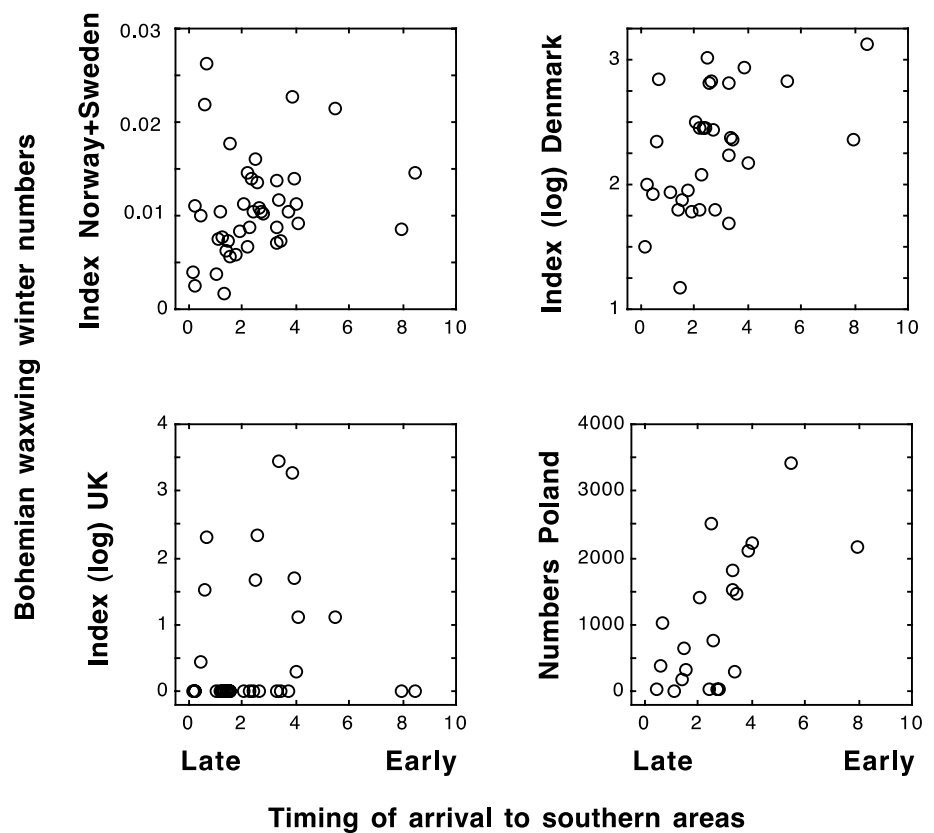


Table 4 GLM analyses of Bohemian Waxwing (*Bombycilla garrulus*) winter numbers in different parts of Europe in relation to push (breeding density in Finland, rowanberry abundance in Finland, including the interaction between these two factors) and pull factors (rowanberry abundance in Norway), timing of movements, with year included as a covariate

Region	Estimate	SE	<i>p</i>
Southern Norway and Sweden (<i>n</i> =29 years)			
Rowanberries Finland	0.021	0.006	<0.001
Timing of movements	0.017	0.006	0.005
Denmark (<i>n</i> =26 years)			
Rowanberries Finland	1.71	0.47	<0.001
Timing of movements	2.24	0.47	<0.001
UK (<i>n</i> =25 years)			
Rowanberries Finland	4.10	1.45	0.005
Rowanberries Norway	−3.07	1.48	0.038
Year	1.86	0.95	0.051
Poland (<i>n</i> =21 years)			
Breeding density Finland	2970.9	916.2	0.001
Timing of movements	2301.9	634.1	<0.001
Year	−3455.1	883.8	<0.001

Results are from the best GLM models based on AIC_c-values (Online Resource 1, Table S2) and show parameter estimates for centered and scaled predictors

1, Table S2). There were no positive effects of rowanberry abundance in Norway (Table 4).

In southern Norway and Sweden, winter numbers were positively related to the Finnish rowanberry index both during years with early arrival and during years with late arrival (Table 4, Fig. 4a). As stated above, early arrival occurred in particular when rowanberry abundance was low. Thus, of the 6 years with largest waxwing numbers, two occurred with early arrival and moderate rowanberry abundance in Finland and four occurred with late arrival and high rowanberry abundance in Finland (Fig. 4a).

Similarly, in Denmark winter numbers were positively related to Finnish rowanberry abundance at the same time as winter numbers were larger for early arrival than for late arrival for a given rowanberry index from Finland (Table 4, Fig. 4b). In this case, the eight years with the largest numbers occurred both with the combinations of early arrival and low or moderate rowanberry abundance in Finland, early arrival and high rowanberry abundance, and late arrival and high rowanberry abundance (Fig. 4b). Interestingly, numbers in the UK were positively related to Finnish rowanberry abundance, but were lower when rowanberries were abundant in Norway (Table 4, Fig. 5). Larger numbers in Poland occurred when migration was early and when breeding density in Finland was high (Table 4).

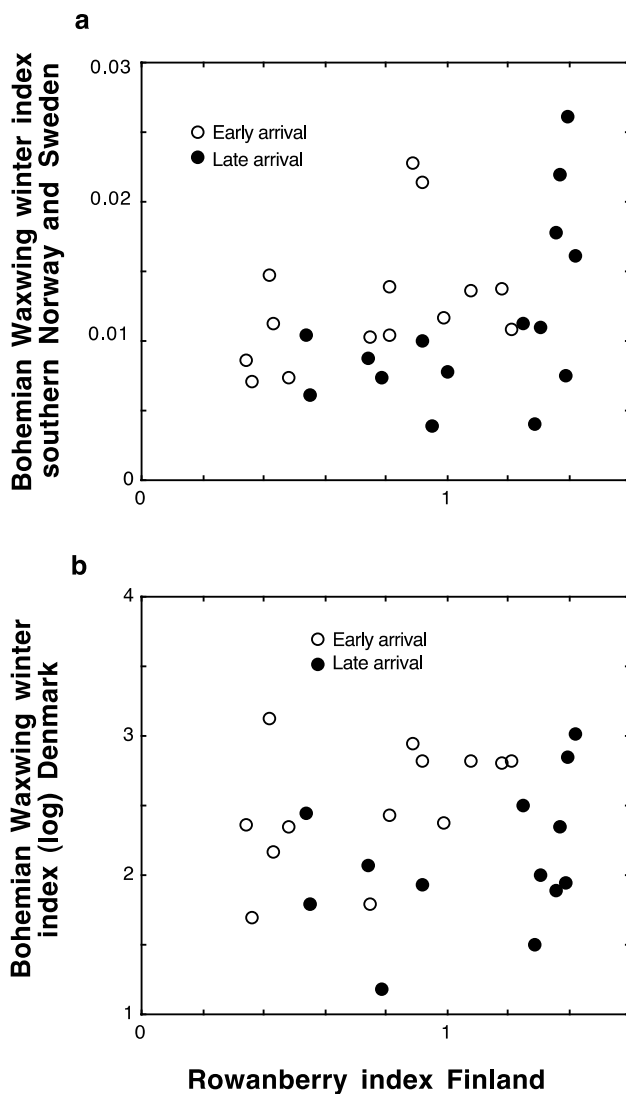


Fig. 4 Bohemian Waxwing (*Bombycilla garrulus*) annual winter index in **a** southern Norway and Sweden, and **b** Denmark in relation to rowanberry (*Sorbus aucuparia*) abundance in Finland. Different symbols separate years with early or late arrival to southern Norway and Sweden

These findings were similar when analyses used the Swedish indices for breeding density (Online Resource 1, Tables S3–S4). Swedish breeding density had little or no relationship to winter numbers (no effect in best models, positive effects in some alternative models for Poland; Online Resource 1, Tables S3–S4). However, these analyses were based on substantially shorter time series than the analyses presented above with the Finnish breeding density indices.

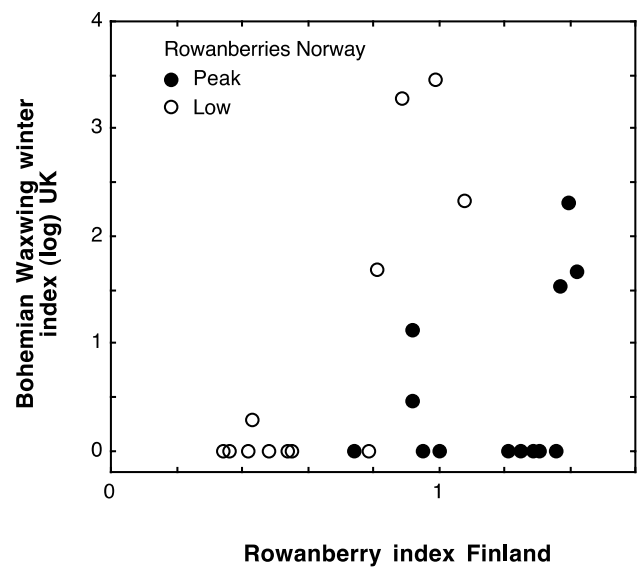


Fig. 5 Bohemian Waxwing (*Bombycilla garrulus*) annual winter index in the UK in relation to rowanberry (*Sorbus aucuparia*) abundance in Finland. Different symbols separate years with below average and years with above average rowanberry abundance in Norway

Discussion

Synchrony of waxwing winter numbers in Europe

In line with previous reports (Siivonen 1941; Glutz von Blotzheim and Bauer 1985), this study found that waxwing winter numbers to northern Europe were in general synchronous over large areas. Annual numbers in southern Norway and Sweden were strongly correlated, and these numbers were also strongly correlated with numbers in Denmark and the UK. However, numbers in Poland were less synchronous with southern Scandinavia and the UK. This may be related to a mainly southwestern migration direction during autumn (Glutz von Blotzheim and Bauer 1985), so that Poland may receive migrants from more eastern populations than western Europe which may be reached by northern Fennoscandian populations (Cramp 1988; Franks et al. 2022). Ring recoveries show that many waxwings in northern UK have migrated from Norway (Bakken et al. 2006). In the present study, this was mirrored by the finding that numbers in the UK were largest when there was low rowanberry abundance in Norway (Fig. 5), most likely because waxwings stopped migration and stayed in Norway when food was abundant, but migrated further when food was scarce.

The waxwing index for southern Norway and Sweden had the two highest values during the winters 1995/96 and 2004/05. These peak years have also been noted in many parts of Europe, including countries not represented with time series analysed in the present study [1995/96: Belgium (Jacob 1996), Germany (Trepte 2021); 2004/05:

nearly all countries in northern and central Europe (Fouarge and VandeVondele 2005)]. The 2004/05 irruption was even noted in Georgia (Abuladze 2016). Other lesser peaks in the index from southern Norway and Sweden match peaks in several other countries, including that a peak in 2016/17 was also noted in Iran (Khaleghizadeh 2019). The waxwing index for southern Norway and Sweden had a generally higher level in the middle of the study period than before or after, and this high level is also reflected in the winter counts covering the whole of Sweden (both south and north; Green et al. 2021).

In some countries, such as the UK, waxwing numbers fluctuated strongly with more or less absence during some winters, and large numbers in a few years (Online Resource 1, Fig. S1). This pattern is also seen in other southern countries such as Belgium and Austria (Jacob 1996; Teufelbauer and Khil 2005). In more northern areas, such as southern Scandinavia, the waxwing occurs during winter every year, but still with large fluctuations. The index for winter abundance of waxwings in southern Norway and Sweden calculated in the present study, showed that numbers in subsequent years often differed by a factor of 2–3 (Fig. 1).

Waxwing winter numbers and breeding population density

Many authors have suggested that waxwing irruptions are triggered by high population density in the breeding range (Siivonen 1941; Svärdsön 1957; Hansson and Wallin 1958; Cornwallis 1961; Cornwallis and Townsend 1968; Glutz von Blotzheim and Bauer 1985). In this study, breeding density indices from northern Sweden and Finland were used to test this hypothesis. Swedish breeding density indices were not related to winter numbers in most analyses. In single factor analyses, the Finnish breeding density indices were positively related to winter numbers in all southern regions (Online Resource 1, Table S1), and two correlations were significant. In GLM analyses that also included other factors, the Finnish breeding density was included in the best model only for Poland, although positive effects were found in alternative models for several countries (Online Resource 1, Table S2). Thus, the results of the present study provided mixed support for an effect of Fennoscandian breeding population density on winter numbers, and this factor likely explains only a moderate proportion of the annual variation in winter numbers.

Depending on how many waxwing irruptions that originate from breeding areas further east than Fennoscandia (Glutz von Blotzheim and Bauer 1985 suggested irruptions come mainly from Russia), there remains a possibility that breeding population size fluctuations in eastern waxwing populations could contribute to variation in winter numbers in northern and western Europe, but this could not be tested

in the present study. Several authors have suggested that waxwing irruptions to Europe may involve, in addition to northern Fennoscandian birds, populations from further east (Svärdsön 1957; Hansson and Wallin 1958), perhaps as far away as Ural (Glutz von Blotzheim and Bauer 1985; Cramp 1988). The origin of irruptive birds from northern boreal forests has been debated repeatedly. For example, irruptions of Northern Hawk-owls (*Surnia ulula*) to southern Fennoscandia have been claimed to come from Russia (Holgersen 1951; Edberg 1955; Mikkola 1983; Cramp 1985), but analyses have indicated that a northern Fennoscandian origin is more likely, at least during the irruptions investigated in detail (Hagen 1956; Dale 2017). Similarly, irruptions of Pine Grosbeaks have also been suggested to come from Russia (e.g. Cramp and Perrins 1994), but a Fennoscandian origin has been suggested in several cases (Sundberg 2001; Nilsson 2019; Dale 2023). At the moment, there is too little information on the actual origin of waxwing irruptions, and a lack of data on annual variations in population size of waxwings from eastern regions, to allow conclusive tests of the hypothesis that waxwing irruptions are related to high breeding density, but the present study indicated that breeding density in at least northern Fennoscandia had only limited importance.

Waxwing winter numbers and lack of food

Waxwing irruptions have in general also been assumed to be triggered by lack of food in the regular northern distribution range (Svärdsön 1957; Hansson and Wallin 1958; Cornwallis 1961; Cornwallis and Townsend 1968; Glutz von Blotzheim and Bauer 1985), although Siivonen (1941) claimed that large irruptions were only due to high breeding density. In the present study, two findings would appear to imply that lack of food led to larger winter numbers. Firstly, low rowanberry abundance in Finland was linked to early migration to southern areas, and, secondly, early arrival to southern areas was linked to larger winter numbers in some countries. However, despite these findings, the analyses revealed that there were significant and strong positive, not negative, relationships between rowanberry abundance in Finland and winter numbers further south. Thus, contrary to theoretical expectations, waxwing winter numbers in southern areas were larger when rowanberry crops in northern areas were large.

The reason for these apparently contradictory findings regarding winter numbers in relation to rowanberry abundance in Finland was that, although winter numbers were larger for early than for late arrival to southern areas at a given level of rowanberry abundance, early arrival occurred mainly at low rowanberry abundances. On the other hand, late arrival was associated with high rowanberry abundance, and movements occurring late could thereby still lead to

as large as or larger numbers than early movements due to the positive relationship between rowanberry abundance and winter numbers (Fig. 4). A simplified interpretation is that in years with high food availability in northern areas, waxwings stay in the north during autumn to exploit the rowanberry crop, but when the crop has been depleted the waxwings move south during winter and large numbers may be seen late in southern areas.

However, because Fennoscandian breeding density did not strongly influence winter numbers, this leaves open the question why these late movements were particularly large. One possible explanation is that the large rowanberry crop in Finland had attracted waxwings with more eastern origin (Svårdson 1957; Hansson and Wallin 1958), and when the rowanberry crop in Finland had been depleted, large numbers involving the combination of Fennoscandian and eastern waxwing populations moved to southern Scandinavia and sometimes even further to e.g. the UK.

The complex interaction between rowanberry abundance and timing of movements resulted in large numbers occurring in a mix of situations. The largest numbers occurred both with the combinations of early arrival and low or moderate rowanberry abundance in Finland, early arrival and high rowanberry abundance, and late arrival and high rowanberry abundance (Fig. 4). But the overriding pattern was that large waxwing numbers occurred in years with high rowanberry abundance in Finland, as shown by the positive, not negative, relationships found between rowanberry abundance in Finland and winter numbers (Table 4). Thus, the findings of the present study provided only weak support for the predictions from the push hypotheses for waxwing irruptions: high breeding density had mixed effect and lack of food was not related to large numbers of waxwings in southern areas during winter (Table 2).

However, it should be remembered that this conclusion is based on analyses where food availability was quantified at the beginning of each autumn. In years with high rowanberry abundance in autumn, there could still be large movements south, only that such movements occurred late (during winter) when rowanberries probably had been depleted. Rowanberries rarely last through the whole winter, so in a sense waxwings face food shortage every winter. Thus, waxwings likely perform migrations every year in search of winter food, but timing and distance of movements depend both on initial rowanberry abundance and at what time they are depleted.

Rowanberries as a pull factor

Rowanberry abundance could potentially also function as a pull factor for waxwing irruptions, as suggested by recent studies of other species (Strong et al. 2015; Dale 2023; Dale and Sonerud 2023). In line with this, some previous studies

have found that waxwing winter numbers are positively correlated with rowanberry abundance (Svårdson 1957; Hansson and Wallin 1958; Kolunen and Vikberg 1978), and the present study indicated that waxwings remained in Norway, instead of migrating to the UK, when rowanberries were abundant in Norway (Fig. 5). However, there was no evidence for an independent positive effect of rowanberry abundance in southern areas (as measured by the index from Norway) on waxwing winter numbers in the models where rowanberry abundance in Finland was also taken into account. This is likely related to the fact that rowanberry abundance is usually synchronous over large parts of Fennoscandia (Kobro et al. 2003; Gallego Zamorano et al. 2018; Dale 2023). However, Dale (2023) found that rowan masting during the period 2008–2013 was asynchronous, but the present analyses did not provide evidence that years with asynchrony (in particular low rowanberry abundance in Finland, but high abundance in Norway) resulted in large winter numbers. On the contrary, during these 6 years, waxwing winter numbers in southern Norway and Sweden were largest when the Finnish rowanberry index was highest (and the Norwegian index was lowest).

The finding that rowanberry abundance in southern areas did not function as a pull factor for waxwings provides an interesting contrast to another northern species. Winter irruptions of Pine Grosbeaks are strongly linked to rowanberries, and Dale (2023) found that irruptions were triggered by high rowanberry abundance in Finland. Because of the large-scale spatial synchrony of rowanberry masting, most irruptions to southern Norway and Sweden therefore coincided with high rowanberry abundance in Norway. During irruptions, Pine Grosbeaks consumed mostly rowanberries, and the birds returned north during winter (January–February), after rowanberry supplies had been exhausted. Irruptions of waxwings sometimes occurred in years with high rowanberry abundance in southern areas, but just as often occurred when there were few rowanberries in southern areas (Online Resource 1, Fig S5). Furthermore, during movements occurring late, waxwings likely have limited access to rowanberries even in masting years, because competition from other bird species eating rowanberries usually mean that rowanberry supplies can be depleted already during autumn or early winter (Suhonen and Jokimäki 2015), although supplies sometimes last until mid-winter (January–February; Tyrväinen 1970, 1975). One possible reason for waxwing winter numbers being relatively unrelated to rowanberry abundance in southern areas is that the waxwing has a more varied winter diet than the Pine Grosbeak, and may switch to other food types if rowanberries are scarce, including that they continue their migrations further south if rowanberries and other food has been depleted (Glutz von Blotzheim and Bauer 1985; Cramp 1988).

Conclusions

Using long-term time series of both waxwing breeding numbers, waxwing winter numbers, and rowanberry abundance, this study could test the main predictions from current hypotheses for bird irruptions. Surprisingly, none of the major hypotheses were clearly supported. There was only mixed evidence that large winter numbers in Europe occurred due to high breeding density, there was no evidence that lack of food in the breeding areas in northern Fennoscandia were related to large winter numbers in the south, and waxwings were not drawn towards abundant food in southern areas. Instead, the main finding was that winter numbers were positively related to food availability in autumn in northern areas.

There remains a possibility that the population dynamics in this part of Europe (Finland, Sweden, Norway, Denmark, UK, Poland) could be influenced by waxwing population dynamics further east (Svårdson 1957; Hansson and Wallin 1958). Thus, one may speculate that Russian waxwings move west when there is lack of food there, and may encounter better food conditions in Finland. This is a possible scenario considering that rowan masting may be synchronous in Fennoscandia and western Russia, but asynchronous as compared with areas further east (Gallego Zamorano et al. 2018). Next, depending on waxwing numbers relative to food availability, large movements may proceed further southwest in certain years to produce early or late irruptions as documented in the present study. If so, waxwing irruptions at very large scales may occur due to a combination of pull (eastern waxwings attracted to high rowanberry abundance in Finland) and push factors (emigration from Russia due to low food availability, emigration from Finland when food supplies have been depleted, whether early or late in winter), but the analyses of the data from western and northern Europe did not provide clear evidence for such processes. Detailed field data from northern parts of Russia, at least east to the Ural Mountains, are needed to resolve this issue. Alternatively, isotopic studies of the geographical origin of waxwings from different irruption years could be attempted, similar to studies of the origin of crossbill irruptions to Europe (Marquiss et al. 2012).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10336-023-02083-7>.

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Availability of data Data are available from the author on request.

Declarations

Conflict of interest The author has no conflicts of interest to declare.

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