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Facultative migration in two thrush species (Fieldfare and Redwing): Rowanberry abundance is more important than winter weather

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Facultative migration is thought to be influenced by food and weather, with birds remaining in northern areas if food is abundant and weather conditions are benign, but migrating south when food is scarce and weather is harsh. However, the relative importance of these two factors has rarely been tested with long-term data, and effects of weather are poorly documented. Here, I assess whether winter numbers of the Fieldfare (*Turdus pilaris*) and the Redwing (*T. iliacus*) in southern Norway during the period 1980–2020 varied in relation to the abundance of an important source of winter food (rowanberries, *Sorbus aucuparia*) and indices of winter harshness (North Atlantic Oscillation index, temperature, duration of snow cover). Two regions with contrasting winter harshness (western Norway with a maritime climate, eastern Norway with a continental climate) were compared. Winter numbers of Fieldfare in both regions, and Redwing in eastern Norway, were highest in years with high rowanberry abundance. Weather had mixed influence on thrush winter numbers, but interacted with rowanberry abundance in several cases so that small numbers of thrushes occurred with the combination of low rowanberry abundance and harsh weather. Such interactions occurred both in eastern and western Norway, and for both species, including for the Redwing in western Norway. In conclusion, facultative migration was strongly related to food availability with large numbers wintering in years with large rowanberry crops, and with additional effects of harsh weather working in concert with low rowanberry abundance to reduce wintering numbers to low levels in some years.

1. Introduction

Migratory patterns in birds show substantial variation, from obligate migrants with consistent timing of movements between fixed breeding and wintering areas, to facultative migrants in which timing of movements in particular during autumn is variable, dependent on food availability and weather conditions, so that wintering areas may differ between years (Newton 2008, 2012). Facultative migration typically occurs in species utilizing food sources that are spatially and temporally variable such as fluctuating rodent populations or seed crops from masting trees (Newton 2008). Extreme examples of facultative migration are the so-called irruptive species which in some years may occur in large numbers outside their regular ranges (Bock & Lepthien 1976, Koenig & Knops 2001, Newton 2006, 2008, 2012). Facultative migrants also often occur in northern regions so that southward migration may be triggered by severe winter weather (Haila *et al.* 1986, Newton 2008).

Rowanberries (*Sorbus aucuparia*) are an important food resource during autumn and winter for several European bird species, ranging from irruptive species (Bohemian Waxwing *Bombycilla garrulus*, Bullfinch *Pyrrhula pyrrhula*, Pine Grosbeak *Pinicola enucleator*) to facultative migrants (Fieldfare *Turdus pilaris*, Redwing *T. iliacus*). Rowan is a typical masting tree and produces large crops at 2–3 year intervals in northern Europe (Kobro *et al.* 2003, Gallego Zamorano *et al.* 2018, Dale 2023a). Previous studies have shown a wide range of responses to annual variation in rowanberry crop size. Bullfinches occur irruptively in autumn and winter in southern areas when there is crop failure further north (Fox *et al.* 2009), Pine Grosbeaks move south to exploit abundant crops every 2–3 years (Dale 2023a), whereas waxwings show a more complex pattern with southward migration mostly in years with good crops, but sometimes also in years with poor crops (Dale 2023b). In facultative migrants such as the Fieldfare, parts of the populations stay in northern areas when there is high rowanberry availability, but most individuals migrate south in other years (Tyrväinen 1975, Haila *et al.* 1986, Kanerva *et al.* 2020).

However, there is much less knowledge of how species consuming large amounts of rowanberries when they are available ("rowanberry specialists") are affected by weather, and there are also few quantitative studies of how facultative migrants in general respond to weather (Newton 2008). Snow cover may be a smaller disadvantage for species foraging in trees than for species feeding on the ground (Newton 2008), whereas cold spells will increase energy demands and may trigger southward migration and limit wintering in northern areas independent of foraging site (Ulfstrand 1963, Zuckerberg *et al.* 2011). Kanerva *et al.* (2020) found that temperature had little influence on the timing of autumn migration in Finland for a variety of irruptive species and facultative migrants. The study of Kanerva *et al.* (2020) is also one of the few that have assessed the relative importance of crop size and weather, and found that crop size was most important for determining timing of autumn migration, including for all the rowanberry specialist species. Similarly, partial migration in many Finnish landbird species was influenced more by tree seed and berry crops than temperature (Meller *et al.* 2016). Interestingly, weather is in general not considered to be important for movements of irruptive species (Newton 2006). Thus, there is mixed evidence for relationships between harsh weather and large-scale winter distribution of facultative migrants.

Here, I analyse 41-year time series of winter numbers of two facultative migrant birds, the Fieldfare and the Redwing, in relation to rowanberry abundance and indices of winter harshness (North Atlantic Oscillation index [NAO], temperature, duration of snow cover) in two parts of southern Norway. My main aim is to assess the relative importance of food and weather in determining wintering in Northern Europe. In general one would expect both factors to influence winter numbers, but the results from Kanerva *et al.* (2020) suggest that food availability might be more important than weather. Furthermore, I test the importance of weather in more detail by comparing winter numbers in two areas of southern Norway: eastern Norway which has a continental climate with snow cover during most winters, and western Norway which has a milder maritime climate with little snow in the lowlands along the coast. The prediction is that the impact of weather would be more evident in eastern than in western Norway. This prediction also follows from the foraging behaviour of these thrushes, because although rowanberries are important during winter, both species may also supplement their diet by foraging on the ground, and then especially snow cover may have a negative impact (Tyrväinen 1970, 1975, Cramp 1988).

2. Material and methods

2.1. Study species and study area

Although Fieldfares and Redwings winter in Norway in variable numbers, large parts of the populations, especially of the Redwing, are migratory. Autumn migration of Redwings is mainly during September–October, and they return in April, whereas Fieldfares migrate south mainly during October–November and return during March–April (Haftorn 1971). For birds staying in Norway and other parts of Fennoscandia during winter fruits and berries are important food sources, in particular rowanberries (Tyrväinen 1970, 1975, Haftorn 1971, Cramp 1988). Tyrväinen (1970) reported that winter food of Fieldfares consisted almost exclusively of rowanberries (rowanberries main food in 288 out of 300 observations) in the winter of 1964/65, and the same was the case in the winter of 1969/70 (rowanberries main food in 144 out of 157 observations; Tyrväinen 1975). He reported that minor food sources were mainly apples and berries of juniper (*Juniperus communis*) and hawthorn (*Crataegus* spp.). Quantitative studies of winter food of Redwings is lacking from Fennoscandia. In years with high rowanberry abundance, both species may occur in small–large flocks, whereas in years with few rowanberries birds winter singly or in small flocks (Haftorn 1971, Svorkmo-Lundberg *et al.* 2006).

Rowans are distributed over most parts of Fennoscandia but are most common in mixed forests in southern areas (Räty *et al.* 2016). Rowans are common in all parts of Norway, including both eastern and western Norway (Artsdatabanken 2023). Masting is normally synchronous over large areas, including across Fennoscandia (Kobro *et al.* 2003, Gallego Zamorano *et al.* 2018, Dale 2023a), because flowering is determined by large-scale patterns of temperature (Gallego Zamorano *et al.* 2018).

Data on Fieldfares and Redwings were collected from eastern and western parts of Norway to match data on rowanberries. Eastern Norway consisted of the counties Innlandet, Viken, Oslo, and Vestfold and Telemark (*ca.* 59–62.5˚N, *ca.* 8–12˚E). Western Norway consisted of the counties Rogaland, Vestland, and Møre and Romsdal (*ca.* 58–63.5˚N, *ca.* 5–7˚E). Eastern parts of Norway have cold winters with snow cover except close to the Oslo Fjord, but coastal areas in the west have January temperatures just above zero with little snow cover (Statens kartverk 1996).

2.2. Winter numbers of thrushes

To obtain data on the number of Fieldfares and Redwings observed during each winter, I searched the website of the National Biodiversity Information Centre in Norway (www.artsobservasjoner.no) and extracted all winter records. The website is an online portal for reporting observations of species, and is open to the public. Most reports of birds are submitted by members of BirdLife Norway. The website can summarize both the number of 'records' and the number of individuals observed in specified time periods. A 'record' is one or more individuals observed in one place at one time (at www.artsobservasjoner.no termed 'funn'). The seasonal number of records was positively correlated with the number of individuals recorded (eastern and western Norway combined; Fieldfare: $r = 0.72$, $n = 41$ years, $p < 0.001$; Redwing: $r = 0.97$, $n = 41$ years, $p < 0.001$). The number of individuals was used instead of the number records because the latter may contain many records of a few individuals, whereas the former also includes information that some records were of large flocks with many individuals, thereby better reflecting variation in total numbers of wintering thrushes.

For each year, the number of individuals was based on observations from December in one year and from January to February in the following year. For example, the number for 2020 included the total number of individuals from all observations during the period December 2020–February 2021. Thus, years refer to the beginning of the winter. Data were collected for the period December 1980–February 2021 to match the period for which rowanberry data were available (see below). Winter numbers were extracted separately for eastern and western Norway for each species.

The number of thrush records increased over time (Fieldfare eastern Norway: $r = 0.76$, $n = 41$

years, $p < 0.001$; Fieldfare western Norway: $r = 0.67$, $n = 41$ years, $p < 0.001$; Redwing eastern Norway: $r = 0.46$, $n = 41$ years, $p = 0.003$; Redwing western Norway: $r = 0.69$, $n = 41$ 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 (eastern Norway: $r = 0.86$, $n = 41$ years, $p < 0.001$; western Norway: $r = 0.85$, $n = 41$ years, $p < 0.001$). Thus, to control for observation effort, I calculated annual indices of thrush winter numbers as the total number of thrush individuals recorded divided by the total number of records of all bird species. Annual number of bird records was assumed to reflect observation effort better than annual total number of bird individuals observed, because the latter may be more heavily influenced by fluctuating numbers of other species (*e.g.* irruptive species) or by fluctuating weather conditions which could influence number of birds wintering (Supplementary Material Fig. S1–2; note in general smaller annual fluctuations in number of bird records than in number of bird individuals). Data on the total number of bird records were extracted from the online bird portal for the same areas and same time periods that were used for data on thrushes (*i.e.* for December–February for the eastern and western regions separately). Thrush indices showed relatively weak temporal trends (Fieldfare east: $r = –0.30$, $p = 0.06$, Fieldfare west: $r = –0.15$, $p = 0.36$, Redwing east: $r = –0.20$, $p = 0.20$, Redwing west: $r = 0.31$, $p = 0.047$; Fig. 1).

One could argue that the index described above could mask thrush fluctuations if annual total number of bird records fluctuated more or less in synchrony with thrush numbers. Thus, as an alternative way of calculating thrush numbers,

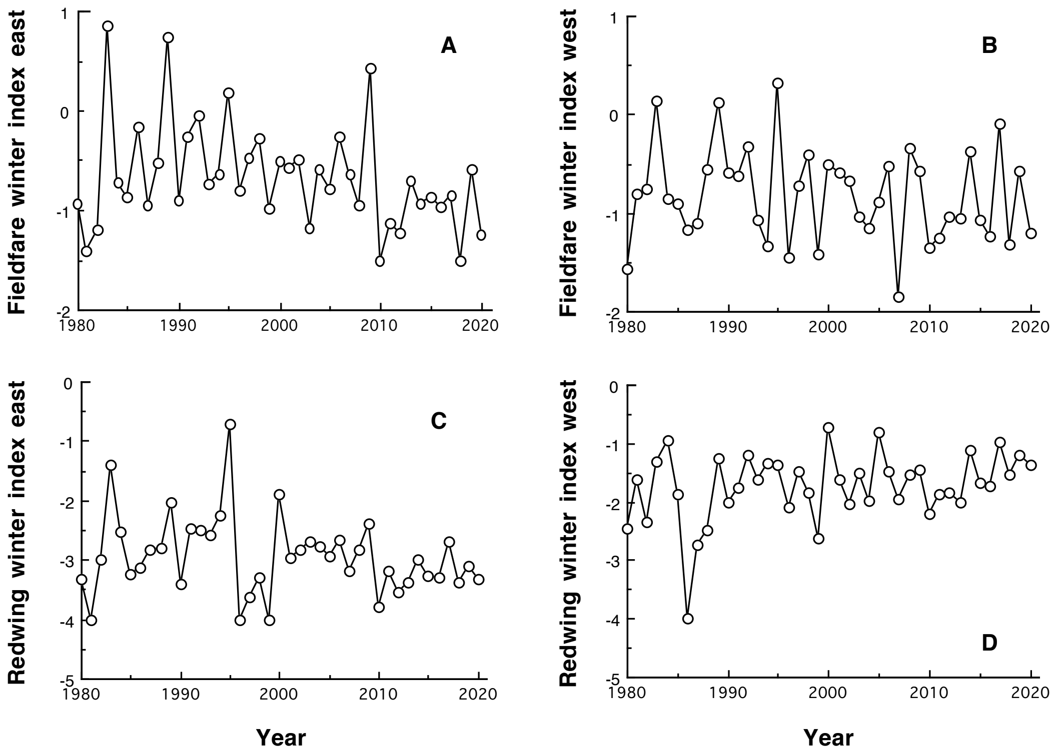

Fig. 1. Annual indices of winter numbers of Fieldfare (*Turdus pilaris*) and Redwing (*T. iliacus*) in eastern and western Norway during 1980–2020. Indices were log-transformed ratios of total number of thrush individuals recorded to total number of records of all bird species (an index of observation effort). For each year, the indices include records from December in one year and from January–February the following year. Thus, for instance, year 2020 includes records from the period December 2020–February 2021.

I also used detrending of the number of thrush individuals recorded. Detrended values were based on residuals from a regression of the number of individuals recorded ($\log_{10}(x)$ for Fieldfare, $\log_{10}(x+1)$ for Redwing) on year. However, note that detrended numbers were strongly correlated to the indices calculated above (Fieldfare east: $r = 0.90$, $p < 0.001$, Fieldfare west: $r = 0.92$, $p < 0.001$, Redwing east: $r = 0.93$, $p < 0.001$, Redwing west: $r = 0.85$, $p < 0.001$), most likely because total number of bird records did not show major fluctuations from year to year (Supplementary Material Fig. S1–2). Because the total number of records of all bird species submitted to the online bird portal has an increase from 2008 when the portal was launched (Supplementary Material Fig. S1–2), the detrended data are likely not as good as the index reported above, and results based on the index are given stronger weight in interpretations than results based on the detrended data.

Neither of the two thrush indices would capture a long-term trend of increasing number of thrushes due to climate warming because the citizen data do not easily reflect absolute numbers. There are no standardized winter counts of wintering birds in Norway. However, Swedish winter counts indicate that the Fieldfare has not had any long-term trend in numbers wintering during the period 1975–2020 (Green *et al.* 2021). Thus, the limited data available do not suggest that climate change has influenced winter numbers of thrushes.

2.3. Rowanberry indices

Rowanberry indices for southern Norway were taken from the "Varsling innen PlanteSkadegjørere" project (VIPS, see www.vips-landbruk.no/applefruitmoth) run by the Norwegian Institute of Bioeconomy Research (NIBIO) and Norsk Landbruksrådgivning (the Norwegian Agricultural Extension Office). VIPS 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 (2023a) 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 (2023a), 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, *ca.* 9–11° E), 31 from western Norway (*ca.* 59–62° N, *ca.* 6–7° E)] 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. Annual rowanberry indices in eastern and western Norway were strongly and positively correlated (log-transformed data; $r = 0.88$, $n = 41$ years, $p < 0.001$).

The rowanberry index in both eastern and western Norway showed negative temporal trends during 1980–2020 (log-transformed indices; $r = -0.33$, $n = 41$ years, $p = 0.036$ and $r = -0.37$, $n = 41$ years, $p = 0.019$, respectively) which could be due to either natural factors or temporal changes in study sites, including habitat changes and changes in methodological procedures. Dale (2023a) 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-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 (Dale 2023a). Thus, the choice of index is unlikely to influence results much, and the non-detrended rowanberry index was used here in line with no detrending of the main index of thrush numbers (based on number of thrush individuals relative to total number of bird records).

2.4. Weather variables

Weather variables included the NAO index, temperature and snow cover. The North Atlantic Oscillation index (NAO) was used as a general indicator of the weather conditions in southern Norway. Indices for November–January were retrieved from the website of the National Weather Service in the US (www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml). In Norway, a high NAO index is associated with mild and moist winds from the west, and a low NAO index colder winds from the east (Store norske leksikon 2018). In addition to using monthly values, the mean value for these three months was also used to assess whether the number of thrushes remaining in Norway during winter was affected by winter weather conditions. The reason for using a time period starting one month earlier than for the bird data, was that conditions during November may have a large influence on the birds' decision to stay or to migrate south. Similarly, conditions during December and January may also affect winter numbers, whereas conditions during February only affects a smaller number of birds, either because most birds have migrated south during December–January or because of mortality.

To assess how specific weather conditions in the eastern and western regions of southern Norway affected thrushes, I retrieved data on temperature and duration of snow cover for the eastern and western regions separately. For each region, data for the largest cities (Oslo and Bergen, respectively) were used both because they were situated roughly in the geographical centres of each region, and because fairly large proportions of the bird data come from within and around these cities due to their large human populations, and, hence, more birders. Data were extracted from the website of the Norwegian Meteorological Institute (www.yr.no) for the period November–January each year. Temperature over these three months (both monthly and mean across each three-month period) and total number of days with snow cover (at least 1 cm; both monthly and sum across each three-month period) were used for analyses. For Bergen, data on snow cover was missing for all months during the two first years, and for November in the third year so that there was data for 38–39 years. Both meteorological stations were in the lowlands (Blindern in Oslo: 94 m a.s.l., Florida in Bergen: 12 m a.s.l.) where the largest numbers of wintering thrushes occur. The term 'harsh winter conditions' is used for a low NAO index, low temperatures, and long duration of snow cover.

2.5. Statistical analyses

Pearson correlations were initially used to explore the relationships between annual indices of the number of thrushes during winter in the two regions, between indices of the two species, between thrush indices and rowanberry indices ($\log_{10}$-transformed), and between thrush indices and weather variables. The Fieldfare index was $\log_{10}$-transformed. The Redwing index had a few zero observations and the index values were small. Thus, the Redwing index was $\log_{10}(x+0.0001)$-transformed. There were no temporal autocorrelations in the thrush time series (one year lag; Fieldfare eastern Norway: $r = –0.11$, $p = 0.45$, Fieldfare western Norway: $r = –0.25$, $p = 0.09$, Redwing eastern Norway: $r = 0.04$, $p = 0.78$, Redwing western Norway: $r = 0.14$, $p = 0.36$). Thus, numbers wintering in one year were not related to numbers wintering the previous year, and yearly values were therefore considered as independent data points.

The main analyses of the relative importance of the influence of rowanberry abundance and weather variables on thrush winter numbers in the two regions of Norway were conducted with GLM with least squares estimation. Three sets of analyses were compared: (1) models with only rowanberry abundance (based on expectations from Kanerva *et al.* 2020, and results of the exploratory analyses), (2) models with rowanberry abundance and weather variables, and (3) models with rowanberry abundance, weather, and interactions between rowanberry abundance and weather. Due to significant correlations between many weather variables (especially positive relationships within and between NAO indices and temperature, but often negative relationships between NAO indices/temperature and duration of snow cover; Supplementary Material Table S1), each model included only one weather variable. Predictors were centred (mean = 0) and scaled (sum of squares = 1) to obtain standardized parameter estimates in order to assess the relative importance of the predictors (rowanberry abundance and weather). Models were compared with AIC_c, and were based on $n=41$ years of data except analyses including duration of snow cover in western Norway where $n=38$ years due to missing data (see above). Analyses were conducted separately for each species and region.

To test for effects of region on the relationships between thrush numbers and weather, data for eastern and western Norway were merged and region was included as a covariate. The prediction that weather should have a larger impact in eastern than in western Norway was tested by including the interaction between region and weather. For each of the two thrush species, analyses were conducted where the weather variables included were based on the best models in the previous analyses.

Because the total number of records of all bird species submitted to the online bird portal increased over time, data from more recent years may be more reliable. Thus, data from the period 2008–2020 (chosen because of larger amounts of data from 2008 after the online portal was launched in that year) were used to evaluate whether analyses based on this period gave similar results as analyses based on the whole 41-year data set. This shorter time period for analyses is likely also less influenced by climate change (see above regarding thrush indices). Results were qualitatively similar despite much smaller sample size ($n=13$ years; Supplementary Material Tables S9–S10). Thus, the main text reports analyses based on the full data set.

Finally, the results from the main analyses were relatively similar when using detrended thrush numbers instead of the main index based on number of thrush individuals relative to total number of bird records (Supplementary Material Table S11). Note, however, that analyses based on the main index were considered to be most reliable. Thus, the main text reports analyses based on the main thrush index. All statistical analyses were conducted in JMP Pro version 16 (SAS 2021).

3. Results

3.1. Thrush winter numbers

The number of Fieldfare individuals recorded each winter during 1980–2020 in southern Norway constituted on average 2.0% of all bird individuals recorded (median = 1.1%, range = 0.3–13.2%, $n=41$ years). In total, 507,232 Fieldfare individuals were recorded, of which 63.1% were from eastern Norway and 36.9% from western Norway. The number of Redwing individuals constituted on average 0.11% of all bird individuals recorded (median = 0.06%, range = 0.002–0.67%, $n=41$ years). In total, 34,861 Redwing individuals were recorded, of which 6.1% were from eastern Norway and 93.9% from western Norway.

The annual thrush indices (log-transformed ratios of total number of thrush individuals recorded to total number of records of all bird species [an index of observation effort]) for eastern and western Norway showed pronounced variation from year to year (Fig. 1), and were positively and significantly related between the two regions in both species (Fieldfare: $r=0.62$, $n=41$ years, $p<0.001$; Redwing: $r=0.40$, $n=41$ years, $p=0.010$; Supplementary Material Fig. S3). The Fieldfare indices were also positively and significantly related to the Redwing indices (eastern Norway: $r=0.69$, $n=41$ years, $p<0.001$; western Norway: $r=0.45$, $n=41$ years, $p=0.003$; Supplementary Material Fig. S4).

3.2. Thrush numbers and rowanberry abundance

The Fieldfare indices were positively and significantly related to the rowanberry indices (eastern Norway: $r=0.61$, $n=41$ years, $p<0.001$; western Norway: $r=0.49$, $n=41$ years, $p=0.001$; Fig. 2a,b). The relationship for western Norway was also significant without an outlier (left hand data point in Fig. 2b; $r=0.52$, $n=40$ years, $p<0.001$).

The Redwing indices were positively and significantly related to the rowanberry indices for eastern Norway ($r=0.48$, $n=41$ years, $p=0.001$; Fig. 2c), but not for western Norway ($r=0.10$, $n=41$ years, $p=0.53$; Fig. 2d). The relationship for western Norway was also not significant

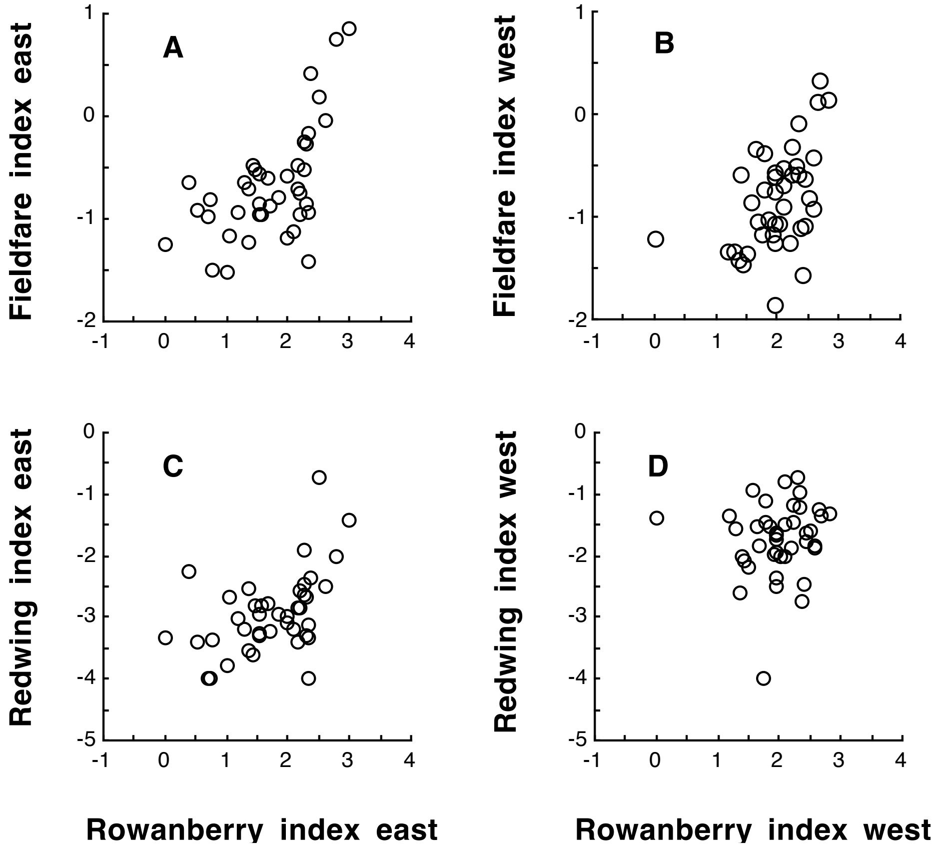

Fig. 2. Annual indices of winter numbers of Fieldfare (*Turdus pilaris*) and Redwing (*T. iliacus*) in eastern and western Norway during 1980–2020 in relation to rowanberry (*Sorbus aucuparia*) abundance in corresponding parts of Norway. Thrush indices were log-transformed ratios of total number of thrush individuals recorded to total number of records of all bird species (an index of observation effort).

without two outliers (left hand and bottom data points in Fig. 2d; $r = 0.17$, $n = 39$ years, $p = 0.30$).

3.3. Thrush numbers and weather

There were no significant relationships between any weather variables and Fieldfare and Redwing indices in simple correlation analyses, not even without correction for multiple testing (Supplementary Material Table S2). The strongest relationships (uncorrected $p \leq 0.10$) were for negative relationships between the NAO index in November and December and the Fieldfare index in western and eastern Norway, respectively (mild weather, fewer Fieldfares), and between duration of snow cover in December and the Fieldfare index in eastern Norway (longer duration of snow cover, fewer Fieldfares; Supplementary Material Table S2).

3.4. Multiple factor analyses: Fieldfare

3.4.1. Eastern Norway

All GLM analyses indicated that the Fieldfare index in eastern Norway was strongly and positively related to the rowanberry index (Supplementary Material Tables S4–5). Weather variables had mixed influence (Supplementary Material Tables S4–5). The best model

Table 1. Parameter estimates for best models explaining winter numbers of Fieldfare (*Turdus pilaris*) and Redwing (*T. iliacus*) in eastern and western Norway during 1980–2020 in relation to rowanberry abundance, weather variables and the interaction between rowanberries and weather.

Thrush indices were log-transformed ratios of total number of thrush individuals recorded to total number of records of all bird species (an index of observation effort). Parameter estimates are for centered and scaled predictors.

Model/variables	Estimate	SE	p
Fieldfare, eastern Norway			
Rowanberry abundance	1.88	0.39	<0.001
NAO index December	–0.85	0.38	0.026
Rowan * NAO	–1.15	0.39	0.003
Fieldfare, western Norway			
Rowanberry abundance	1.70	0.45	<0.001
NAO index November	–0.60	0.43	0.16
Rowan * NAO	–1.02	0.44	0.021
Redwing, eastern Norway			
Rowanberry abundance	1.77	0.51	<0.001
NAO index December	–0.62	0.51	0.23
Rowan * NAO	–1.89	0.51	<0.001
Redwing, western Norway			
Rowanberry abundance	0.85	0.59	0.15
Duration of snow cover December	–0.49	0.59	0.41
Rowan * Snow	1.37	0.61	0.026

(Supplementary Material Table S3) indicated that winter numbers of Fieldfare were also negatively related to the NAO index in December, and with a significant interaction between rowanberry abundance and the NAO index in December (Table 1). The interaction showed that in mild winters rowanberries had small influence on Fieldfare numbers whereas in harsh winters Fieldfare numbers were very small when there were few rowanberries, but large when there was a large rowanberry crop (Fig. 3a).

3.4.2. Western Norway

Rowanberry abundance had strong positive relationships with Fieldfare numbers also in western Norway (Supplementary Material Tables S4–5). Again, weather variables had mixed influence (Supplementary Material Tables S4–5). The best model (Supplementary Material Table S3) indicated that a significant interaction between rowanberry abundance and the NAO index in November also influenced Fieldfare numbers (Table 1). This interaction was very similar to the one for eastern Norway reported above, so that Fieldfare numbers were lowest with the combination of low NAO index (harsh weather) and few rowanberries, and highest with the combination of harsh weather and large rowanberry crop (Fig. 3b). Other models that were within $\Delta AIC_c < 2$ replaced the NAO index with December instead of November, or replaced the NAO index with temperature in November or snow in December, or did not include interactions, or only included rowan (Supplementary Material Table S3).

3.5. Multiple factor analyses: Redwing

3.5.1. Eastern Norway

All GLM analyses indicated that the Redwing index in eastern Norway was strongly and positively related to the rowanberry index (Supplementary Material Tables S6–7). Weather variables had mixed influence (Supplementary Material Tables S6–7). The best model (Supplementary Material Table S3) indicated that a significant interaction between rowanberry abundance and the NAO index in December also influenced Redwing numbers (Table 1).

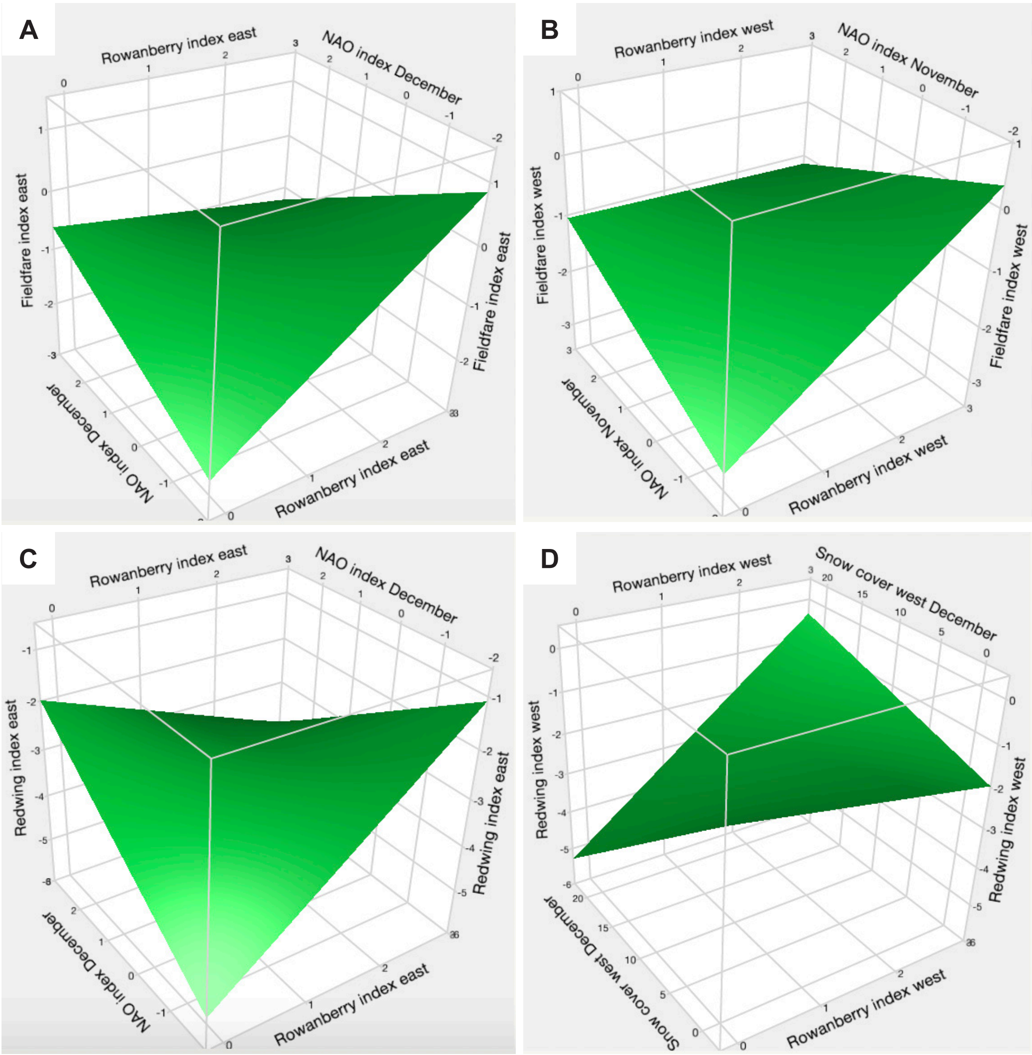

Fig. 3. Influence of the interactions between rowanberry (*Sorbus aucuparia*) abundance and weather variables on annual indices of winter numbers of Fieldfare (*Turdus pilaris*) and Redwing (*T. iliacus*) in eastern and western Norway during 1980–2020. A: Fieldfare eastern Norway; B: Fieldfare western Norway; C: Redwing eastern Norway; D: Redwing western Norway. Thrush indices were log-transformed ratios of total number of thrush individuals recorded to total number of records of all bird species (an index of observation effort).

This interaction was similar to those found for the Fieldfare: Redwing numbers were lowest with the combination of low NAO index (harsh weather) and few rowanberries, but low numbers were also found with the combination of high NAO index (benign weather) and large rowanberry crop (Fig. 3c).

3.5.2. Western Norway

In western Norway, Redwing numbers were not directly influenced by rowanberry abundance, and the NAO index and temperature had no influence (Supplementary Material Tables S6–7). However, the best model (Supplementary Material Table S3) included an effect of the interaction between snow cover in December and rowanberry abundance (Table 1). Thus, rowanberry abundance had a positive effect when snow cover in December lasted longer (Fig. 3d). However, this model was only marginally better than a model with only intercept (Supplementary Material Table S3).

3.6. Interactions between region and weather

There were no significant interactions between region and weather in analyses comparing eastern and western Norway (Supplementary Material Table S8).

4. Discussion

4.1. Influence of rowanberries on thrush numbers

I found that numbers of Fieldfares and Redwings during winter in southern Norway were strongly related to rowanberry abundance, except for Redwings in western Norway. However, in western Norway an interaction between rowanberry abundance and snow cover indicated that rowanberries had a positive influence on Redwing numbers when there was snow cover lasting for longer periods, whereas rowanberries did not influence Redwing numbers when there was little snow. These results are in line with those of Kanerva *et al.* (2020) who found that large crop size of several tree species delayed autumn migration of a number of facultative migrants and irruptive species. This included how Rowan affected, for instance, Fieldfare and Redwing, as well as how crop sizes of birches (*Betula spp.*) and Norway spruce (*Picea abies*) affected other bird species (Kanerva *et al.* 2020). Delayed autumn migration is likely to result in larger numbers of these species remaining for winter, so these are alternative ways of analysing facultative migration.

Rowanberry abundance usually varies in synchrony over large areas in Fennoscandia (Kobro *et al.* 2003, Gallego Zamorano *et al.* 2018, Dale 2023a). This may explain synchronous variation in winter numbers of both thrush species between eastern and western Norway, and between the species within each region. This suggests that facultative migration is influenced by yearly variation in food availability at large spatial scales. Thus, thrushes breeding across Fennoscandia may obtain information at an early time (already during summer) that availability of rowanberries will be high in a specific year, and thereby 'know' that staying in northern areas may be possible the coming winter.

4.2. Influence of weather on thrush numbers

Kanerva *et al.* (2020) did not find any influence of weather on timing of autumn migration, and weather is not thought to affect movements of irruptive species (Newton 2006). Similarly, there were few direct relationships between weather and winter numbers of Fieldfares and Redwings in the present study. However, more detailed analyses, in particular including the interactions between rowanberry abundance and weather variables, revealed that weather affected both species, and in both eastern and western Norway, in some years. The most common interaction effect was that thrush numbers were particularly low when there were combinations of harsh weather and low rowanberry abundance, but high when there was harsh weather and high rowanberry abundance. This suggests that high availability of rowanberries may buffer against the negative effects of harsh weather.

The mechanistic relationships between NAO indices and thrush numbers are difficult to assess because the NAO index reflects overall weather patterns. However, the analyses of specific weather variables suggested that weather effects may operate through the duration of snow cover as suggested by the interaction for Redwings in western Norway. For the Fieldfare, some models included significant effects of snow (Supplementary Material Table S5), although these models were not the best based on AIC_c. In years with long-lasting snow cover during early winter (*e.g.* November–December), access to food on the ground may be more or less blocked, and if rowanberry abundance is low the thrushes may have no other option than to leave the northern wintering areas and migrate further south. Snow cover has a large impact on many bird species foraging on the ground, such as on arable land (Golawski & Kasprzykowski 2010, Bosco *et al.* 2022).

The analyses suggested that thrush numbers were mostly influenced by weather indices from December. Thrush indices were based on total numbers for the period December–February, and weather in December may therefore have a stronger impact than in January simply because weather later in winter affects only parts of the data material included in the indices. However, it is likely that snowfalls and cold spells in January may also affect those individuals that are still present.

Although thrush numbers were influenced by harsh weather in negative ways according to several analyses (see above), there were also some analyses suggesting a different pattern. First, the NAO index often had negative effects (Fieldfares, Tables S4–S5), and, hence, lower thrush numbers were sometimes associated with mild winters with many rowanberries (Fig. 3a,c). Wintering thrushes in Norway may also originate from northeastern populations such as Sweden, Finland and perhaps also Russia (Haftorn 1971, Franks *et al.* 2022). Because Rowan masting is synchronous over large areas in Fennoscandia (Kobro *et al.* 2003, Gallego Zamorano *et al.* 2018, Dale 2023a), a high NAO index, in particular combined with a high rowanberry index, could mean that fewer thrushes arrive to winter in Norway because they can remain in Sweden or Finland for a longer time through the winter (Tyrväinen 1970, 1975).

Second, the largest number of thrushes sometimes occurred with the combination of harsh weather and high rowanberry abundance (Fig. 3). In addition to a likely relationship with the spatial distribution of thrushes across Fennoscandia discussed above, this may to some degree also be a methodological effect because snow and cold weather may drive thrushes into urban areas (Tyrväinen 1975) where they are more easily recorded by birders. However, the strong effect of rowanberry abundance on thrush numbers suggests that the combination of harsh weather and high rowanberry abundance was associated with larger numbers of wintering thrushes than the combination of benign weather and low rowanberry abundance.

There was in general little support for the prediction that weather should have an influence mainly in eastern Norway where the climate is more continental. There were weather effects on both species in both regions. Overall, however, it appears that thrush winter numbers is governed to a large degree by food availability, with numbers modulated by weather to a lesser degree, mainly when food availability is low. The conclusion of a larger importance of food than weather was based on 1) the univariate analyses which showed significant effects of rowanberry abundance (except for Redwing in western Norway), but not of weather variables, 2) the multivariate analyses which generally showed significant main effects of rowanberry abundance and non-significant main effects of weather, and interactions between rowanberry abundance and weather having variable effects, 3) that centred and scaled parameter estimates in multivariate analyses indicated larger effect sizes of rowanberry abundance than of weather variables or most interactions, and 4) no interaction between region (eastern and western Norway) and weather on thrush numbers.

My study confirms previous findings that food availability is more important than weather (Kanerva *et al.* 2020), but in contrast to the latter study, I found that weather had some impact. My study and Kanerva *et al.* (2020) are among the few studies that have evaluated the relative importance of food and weather for facultative migration, although other studies have investigated food or weather separately (Newton 2008).

4.3. Why was food more important than weather?

Although both the Fieldfare and the Redwing forage extensively on the ground, especially in the summer season, fruits and berries in trees and bushes, in particular rowanberries, are important food sources during autumn and winter (Tyrväinen 1970, 1975, Haftorn 1971, Haila *et al.* 1986, Cramp 1988, Kanerva *et al.* 2020). Rowanberries are accessible also after snowfalls when food on the ground has become covered. Thus, compared to bird species that forage mostly on the ground, snow cover may have little influence on wintering Fieldfares and Redwings provided that rowanberries are available. In line with this, harsh weather affected these two species negatively mainly when rowanberry abundance was low. Furthermore, unlike some food types thrushes utilize when foraging on the ground, such as earthworms, rowanberry availability is not affected by frost. The thrushes consume rowanberries even when the berries are frozen. As an example, the 1995/96 winter had one of the highest Fieldfare indices in eastern Norway, and the highest for the Redwing (Fig. 1a,c), yet the mean temperature in Oslo in December that year was –6.4 °C (only three other years had lower temperature in December) and only a few days had maximum temperatures above 0 °C. Finally, feathers have high insulating capacity (Herreid & Kessel 1967) so that temperature in itself may not be a problem as long as the birds have reliable access to enough food.

For bird species relying on rowanberries during winter, the decision to stay in northern areas may be based on a simple and easily assessed cue: rowanberry abundance can be monitored directly on trees through the autumn months. However, because rowanberries are consumed by a number of different bird species (see Introduction) from early autumn, availability declines progressively. Rowanberry supplies may in some years, at least locally, be depleted as early as in November–December (Suhonen & Jokimäki 2015, Suhonen *et al.* 2017), whereas in other years the supplies may last to January–February (Tyrväinen 1970, 1975). This suggests that wintering should be flexibly adjusted not only to initial size of the rowanberry crop, but also to how much of the crop remains at any time. Thus, migratory movements, at least of the Fieldfare, are known to occur also during winter months when rowanberries have disappeared (Tyrväinen 1975). Yet, it seems likely that food availability for rowanberry specialists is more predictable than the weather conditions in specific winters, and facultative migration related to food availability may be the rule for rowanberry specialists and for other species utilizing seed and fruit crops in trees. For species foraging mainly on the ground, I speculate that weather may be more important. Such species may face sudden periods of food shortage, for instance, due to snowfalls, that may trigger migration to warmer regions (Newton 2008, Golawski & Kasprzykowski 2010, Resano-Mayor *et al.* 2020). Thus, the relative importance of food and weather depends not only on the amount of food available or on weather by themselves, but also on how food availability interacts with weather in determining how much food is accessible for facultative migrants.

Kahden rastaslajin, räkättirastaan ja punakylkirastaan, fakultatiivinen muutto: pihlajanmarjojen runsaus on tärkeämpää kuin talvisää

Fakultatiivista muuttoa ohjaavat yleensä ruoan ja sään vaikutukset. Linnut pysyvät pohjoisilla alueilla, jos ruokaa on runsaasti ja sääolot ovat suotuisat, mutta muuttavat etelään silloin kun ruokaa on niukasti ja sää on ankara. Näiden kahden ympäristötekijän suhteellista merkitystä on harvoin testattu pitkillä aikasarjoilla, ja myös sään vaikutuksia on dokumentoitu vähän. Tässä tutkimuksessa arvioin, vaikuttaako talviruoan runsaus (pihlajanmarja, *Sorbus aucuparia*) ja/tai talven ankaruus (NAO-indeksi, lämpötila, lumipeitteen kesto) räkättirastaiden (*Turdus pilaris*) ja punakylkirastaiden (*T. iliacus*) määriin talvella. Tutkimusaineisto on kerätty Etelä-Norjassa vuosina 1980–2020 ja vertailun kohteena on kaksi aluetta, joissa talven ankaruus eroaa toisistaan: läntisellä tutkimusaluella on lauhkeampi meri-ilmasto ja itäisemmällä tutkimusalueella on vaihtelevampi mannerilmasto.

Talvehtivien räkättirastaiden määrä molemmilla alueilla ja punakylkirastaiden määrä itäisessä Norjassa olivat korkeimpia vuosina, jolloin pihlajanmarjoja oli paljon. Sää vaikutti vaihtelevasti rastaiden määriin, mutta havaitsin sään ja pihlajanmarjojen välillä vuorovaikutusta: rastaita oli vähän silloin, kun sääolosuhteet olivat ankarat ja pihlajanmarjoja vähän. Vastaava ilmiö esiintyi molemmilla tutkimusalueilla ja molemmilla rastaslajeilla.

Yhteenvetona voidaan todeta, että fakultatiivinen muutto liittyi vahvasti ruoan saatavuuteen. Enemmän rastaita talvehtii hyvinä pihlajanmarjasatovuosina. Ankarilla talvilla oli eniten negatiivisia vaikutuksia talvehtivien rastaiden määriin silloin, kun myös pihlajanmarjasadot olivat huonoja.

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Online supplementary material

Supplementary material available in the online version includes Figs. S1–S4 and Tables S1–S11.