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Breeding population size, migration, and wintering of the Eurasian Siskin *Spinus spinus* in relation to seed crop sizes of food trees

Antalet häckande individer, flyttning och övervintring hos grönsiskan Spinus spinus *i förhållande till frösättningen hos födoträd*

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BIRD SPECIES in boreal forests that utilise seed crops from masting trees face large temporal and spatial variation in food availability. Seed crop size is therefore expected to influence breeding population size, migration, and wintering. We analyse ≤ 36-year time series of Eurasian Siskin *Spinus spinus* numbers in Sweden in relation to seed crop sizes of Norway spruce *Picea abies*, Scots pine *Pinus sylvestris*, birch *Betula* spp. and alder *Alnus* spp. Breeding numbers were somewhat positively associated with spruce, birch, and alder seed crop sizes, but peak breeding numbers sometimes also coincided with small crop sizes. Migration was not strongly related to seed crop sizes, but positively associated with breeding population size. Wintering numbers were strongly positively associated with spruce, birch, and alder seed crop sizes. Pine did not affect any Siskin numbers. This suggests that at large spatial and temporal scales, spruce seeds are less important for Siskin breeding than previously thought. Nevertheless, spruce, birch and alder may all have some influence on breeding and were positively associated with wintering numbers, while migration appears to be a density-dependent process rather than a response to lack of food. The results provide a unique insight into how multiple seed crops affect a seed-eating bird.

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Introduction

Boreal forests are characterised by resource pulses that have large influences on the population dynamics of many species. For example, rodents fluctuate with peaks at 3–5-year intervals and rodent-eating raptors have high breeding success in peak years, but may have to emigrate when rodents are scarce (Newton 2008). Similarly, many tree species have variable seed production from year to year. In particular, masting tree species may in some years produce bumper crops followed by years with very poor crops (Silvertown 1980, Kelly 1994, Koenig & Knops 2000). Seed-eating birds in boreal forests therefore face large spatial and temporal variation in food availability. Availability of seeds is known to influence both breeding population size, breeding success, migration and wintering of such birds (Newton 1998, 2008, 2012), and poor seed crops may cause large-scale eruptions (Bock & Lepthien 1976, Koenig & Knops 2001, Newton 2006a, 2008).

In the boreal forests of northern Europe, the Norway spruce *Picea abies* (hereafter spruce) is an important tree species, and has large annual fluctuations in seed production (Lindén *et al.* 2011, Nussbaumer *et al.* 2016, Gallego Zamorano *et al.* 2018). Several species of birds depend on or exploit this large food resource. For example, the Common Crossbill *Loxia curvirostra* is extremely specialised and consumes almost exclusively spruce seeds, and has adapted to the fluctuations in food availability by migrating annually between breeding sites that may be thousands of kilometers apart (Svärdson 1957, Newton 1972, 2006b, Marquiss *et al.* 2012, Dale & Edvardsen 2024). The Eurasian Siskin *Spinus spinus* (hereafter Siskin) is also known to exploit spruce seeds when they are available, and breeding population size has been found to fluctuate in synchrony with spruce seed crop size (Haapanen 1966, Hogstad 1967, Newton 1972, Petty *et al.* 1995, Förschler *et al.* 2006). However, these studies were on small spatial scales and often of short duration, and there is less knowledge about large-scale and long-term synchrony of Siskins and spruce seed crop size. The Siskin is known to be nomadic with low breeding site fidelity (Newton 2006a), and large-scale synchrony would require substantial immigration from distant areas. Svärdson (1957) suggested that an exceptionally large breeding population of Siskins in 1949 over much of Sweden had immigrated the year before from areas further east, possibly even as far away as Ural.

The Siskin exploits seeds from other tree species as well. Newton (1972) reported that during the breeding season Siskins may switch to Scots pine *Pinus sylvestris* (referred to as pine) seeds after spruce seeds have been consumed because pine cones open later than spruce cones. However, there have been no studies of how pine seed crop size influences population dynamics of Siskins. Furthermore, during autumn and winter seeds from birches (*Betula pubescens* and *B. pendula*) and alders (*Alnus incana* and *A. glutinosa*) are important food sources for Siskins wintering in northern Europe (Cramp & Perrins 1994). Good seed crops of birch and alder delay migration (Svärdson 1957, Kanerva *et al.* 2020) and increase numbers wintering (Eriksson 1970, Stolt & Mascher 1971, Meller *et al.* 2016). However, there have been no studies of how seed crop sizes of birch and alder affect breeding population size of Siskins, potentially via an effect on wintering numbers and winter survival, although Stolt and Mascher (1971) noted that a large breeding population followed a winter with good alder and birch seed crops and large numbers of wintering Siskins.

Eriksson (1970), following ideas of Svärdson (1957), suggested that several masting tree species, in particular spruce, birch and alder, often have good seed crop years synchronously over large areas, and that in such years Siskins may have good wintering conditions where they can exploit the birch seed crop in autumn, alder during winter and spruce during late winter and spring. In Finland, Gallego Zamorano *et al.* (2018) showed that seed production of spruce and birch are synchronous at large spatial scales because of large-scale synchronous variations in temperature affecting flowering. Flowering of birch and alder is also known to be synchronous (Ranta & Satri 2007). Thus, wintering numbers of Siskins may be related to the combined effect of seed crop size of several tree species, and this may in turn affect breeding population size.

In the present study, long-term time series (up to 36 years) from Sweden of Siskin breeding population size, migration and wintering were analysed in relation to seed crop sizes of spruce, pine, birch and alder. We predicted that breeding population size of Siskins would be positively related to crop sizes, specifically through the mechanisms that good birch and alder crops would increase winter survival and wintering in the study areas, and that good spruce and pine crops would provide abundant food for Siskins during breeding. Good spruce seed crops may lead to increased reproduction (Furness & Furness 2021). Thus, numbers on migration may be larger in autumns following breeding seasons that coincided with good spruce seed crops. Finally, we predicted that poor crops could lead to increased emigration, whereas good crops, in particular of spruce, birch and alder, would lead to larger numbers wintering. These analyses will provide a unique insight into how seed crop sizes of multiple tree species affect different life stages of a seed-eating bird.

Material and methods

STUDY AREA AND STUDY SPECIES

In this study, time series of Siskin numbers and seed crop sizes from Sweden were used (Table 1, see below for details). The Siskin is a common breeding bird in boreal forest in most parts of Fennoscandia. Spruce, pine, alders and birches are also widespread. The spruce flowers in early summer and the cones open and seeds are shed during late winter the next year (Newton 1972), although seed shedding may sometimes occur in part during autumn. The Siskin is unable to access the seeds before the cones have opened, and therefore exploit spruce seeds mostly during March–May (Newton 1972). The spruce produces few cones after a masting year, and a new good spruce crop in the same area will not be available until at least one year (but usually several years) after the previous crop was shed. The Scots pine has a reproductive cycle of two years (Owens & Blake 1985). After flowering and pollination during spring–early summer in the first growing season, fertilization and seed development takes place during

TABLE 1. Data sets used for analyses of breeding population size, autumn migration and wintering of Eurasian Siskins *Spinus spinus* in relation to seed crop size of Norway spruce *Picea abies*, Scots pine *Pinus sylvestris*, birches (*Betula* spp.) and alders (*Alnus* spp.) in Sweden.
– *Tidserier som använts för att analysera förhållandet mellan grönsiskor* Spinus spinus *och frösättningen hos gran* Picea abies*, tall* Pinus sylvestris*, björk (*Betula *spp.) och al (*Alnus *spp.) i Sverige.*

Data set *Data*	Location *Plats*	Time period *Tidsperiod*	Years *År*	Type of data *Typ av data*	Source *Källa*
Eurasian Siskin *Grönsiska*					
Breeding index *Häckningsindex*	Sweden *Sverige*	1998–2021	24	Monitoring *Övervakning*	Swedish Bird Survey[a] *Svensk fågeltaxering*[a]
Breeding numbers *Häckningsantal*	Southern Sweden *Södra Sverige*	2001–2021	21	Citizen data *Medborgardata*	Swedish Species Observation System[b] *Artportalen*[b]
Autumn migration *Höstflyttning*	Falsterbo, Sweden *Falsterbo*	1986–2021	36	Monitoring *Övervakning*	Falsterbo Bird Station[c] *Falsterbo fågelstation*[c]
Winter index *Vinterindex*	Sweden *Sverige*	1986–2020	35	Monitoring *Övervakning*	Swedish Bird Survey[a] *Svensk fågeltaxering*[a]
Seed crop sizes *Frösättningens storlek*					
Spruce and pine *Gran och tall*	Sweden *Sverige*	1986–2021	36	Monitoring *Övervakning*	Forestry Research Institute of Sweden[d] *Skogforsk*[d]
Spruce and pine *Gran och tall*	Southern Sweden *Södra Sverige*	1986–2021	36	Monitoring *Övervakning*	Forestry Research Institute of Sweden[d] *Skogforsk*[d]
Birch and alder *Björk och al*	Southern Sweden *Södra Sverige*	1988–2021	34	Monitoring *Övervakning*	Swedish Museum of Natural History[e] *Naturhistoriska riksmuseet*[e]

[a]www.fageltaxering.lu.se, [b]www.artportalen.se, [c]www.falsterbofagelstation.se, [d]www.skogforsk.se (based on counts of cones *baserat på antalet kottar*), [e]www.pollenrapporten.se (based on pollen counts *baserat på pollenkoncentrationen*)

summer in the second growing season. The seeds are shed in spring and early summer in the year after they ripened (Newton 1972). Scots pine has a more stable seed production than Norway spruce (Lindén *et al.* 2011, Nussbaumer *et al.* 2016). Birch and alder flower in early spring and seeds may be available to Siskins from late summer and through autumn and winter. Availability of birch seeds last mainly through autumn, alder seeds are available from late autumn and through winter, whereas spruce seeds are usually accessible from late winter for the Siskin (Eriksson 1970, Newton 1972). Birch and alder often have peak seed production at two-year intervals (Dahl & Strandhede 1996, Ranta & Satri 2007). During summer, Siskins eat seeds from a large variety of plants, including herbs (Cramp & Perrins 1994).

SISKIN BREEDING AND WINTERING NUMBERS

Data on Siskin breeding numbers for Sweden were taken from the Swedish Bird Survey (www.fageltaxering.lu.se; Green *et al.* 2021). Results were based on 716 fixed routes spread across Sweden and surveyed during the breeding season of birds in general (May–July). Each route was surveyed once in a given year, but individual routes were not always surveyed every year (e.g. 550 routes surveyed in 2020). Routes were 8 km long, and birds were recorded through a combination of point and line transect counts. Surveys were conducted by volunteer birders. Data were available for the period 1998–2021 ($n = 24$ years). Breeding numbers were expressed as an index where 1998 was set to a value of 1.0. The breeding index was on average 1.07 (median 1.03, range 0.62–1.39) and increased over time (Pearson correlation; $r = 0.50$, $p = 0.022$). Although counts could include juvenile Siskins late in the season, the bulk of the data reflect the number of adult breeding birds.

The Swedish Bird Survey also includes winter counts (Green *et al.* 2021). In this case, counts are conducted in areas selected by the observers (volunteer birders), so unlike the breeding bird survey described above, the counts are not spatially representative for the whole of Sweden, and have a strong bias to the southern half of Sweden. Counts were conducted 1–5 times during October–March. A winter count route consisted of 20 points where counting was conducted for 5 min at each point. Data were available for the winters 1986/1987–2020/21 ($n = 35$ years). Numbers were expressed as an index where 1998/1999 was set to a value of 1.0. The winter index was on average 0.39 (median 0.23, range 0.01–1.45) and did not change over time ($r = -0.13$, $p = 0.45$).

Breeding population fluctuations in a more restricted area were also analysed to avoid large-scale asynchrony in numbers. For this purpose the number of records submitted to the Swedish Species Observation System (www.artportalen.se) were extracted. Most reports of birds are submitted by members of BirdLife Sweden and other birders. The unit used for analyses was a 'record', i.e. one or more individuals observed in one place at one time (termed 'fynd'). Records from parts of southern Sweden were used (the regions Värmland, Västmanland, Uppland, Södermanland, Närke, Dalsland, Bohuslän, Halland, Västergötland, Östergötland, and Småland). The choice of regions was based on regions showing similar fluctuations in spruce crop size (below). Records during the main breeding season (May–June) in the period 2001–2021 ($n = 21$ years) were used. There were relatively few records in the years before 2001. The number of records was on average 1,511 (median 1,828, range 264–2,749) and increased over the study period, most likely due to increased reporting frequency by birders over time ($r = 0.91$, $p < 0.001$).

SISKIN MIGRATION DATA

Data on emigration of Siskins from northern Europe during autumn was based on migration counts from Falsterbo bird station at the southwestern tip of Skåne, southernmost Sweden (www.falsterbofagelstation.se). Birds migrating south during autumn head for Denmark and Germany. Daily counts during the period 1 August–20 November were conducted each year (except that they started 11 August until 2000), and data were available for the period 1986–2021 ($n = 36$ years; www.falsterbofagelstation.se/strack/art-alla-ar/). The migration index was on average 52,542 individuals (median 43,265, range 7,318–193,740) and increased over time ($r = 0.56$, $p < 0.001$).

SPRUCE AND PINE SEED CROP SIZE

Seed crop size estimation was conducted by Skogforsk (Forestry Research Institute of Sweden; www.skogforsk.se) by counting the number of cones on sample trees at a large number of sites across the whole country (Riksskogstaxeringen). Each year cones on

c. 2,000 trees (range c. 1,000–3,000) of spruce and similar numbers of pine trees were recorded. Average values across individual trees were reported for each of 31 regions and for each year. Data were available from 1983, but to match Siskin data, the period 1986–2021 was used ($n = 36$ years). Counts were conducted in autumn, and for pine second year cones (mature cones) were counted. As reported by Dale and Edvardsen (2024; same data set used in present study), counts were conducted in two different ways: in interval groups (up to and including 2014) and as exact numbers (from 2011). Thus, there were four years where both methods were used, and in these years counts were strongly correlated (spruce: $r = 0.99$, $n = 111$, $p < 0.001$; pine: $r = 0.99$, $n = 114$, $p < 0.001$). However, interval values were consistently higher than exact counts [mean difference: 7.1 for spruce ($SE = 0.25$) and 16.7 for pine ($SE = 0.69$)], and this was partly because the first interval (0–16 cones) was coded as 8 so that even years with no cones had a value of 8. Thus, exact values for 2015–2021 were adjusted by adding the mean difference. This was preferred over subtracting from interval values because this would have produced a few negative values. For remaining years (1986–2014), interval values were used.

For the national index for Sweden, values were averaged across regions. However, spruce data from three regions (northern Dalarna, Malmöhus, Gotland) were excluded because of low number of sampled trees (<10) in many years. Seven years from the remaining 28 regions were also excluded for the same reason. For pine, two regions (Malmöhus, Blekinge) were excluded together with 24 years from the remaining 29 regions. Thus, analyses were based on 1,001 data points for spruce and 1,020 for pine. Yearly crop size indices for Sweden did not show temporal trends (spruce: $r = 0.13$, $p = 0.46$, pine: $r = 0.19$, $p = 0.27$).

Spruce crop sizes across Sweden often fluctuated in synchrony, but in some years in particular northern parts of Sweden and the southernmost nemoral areas differed from south-central parts (Dale & Edvardsen 2024). To provide data for a more restricted area where spruce crop size fluctuated relatively synchronously, a subset of the data based on regions in southern Sweden were used (the regions Värmland, Västmanland, Uppland, Södermanland, Närke, Dalsland, Bohuslän, Halland, Västergötland, Östergötland, and Småland). Although there were less clear regional patterns in crop size of pine, an index based on the same regions was also used for pine. Yearly crop size indices for southern Sweden did not show temporal trends (spruce: $r = 0.21$, $p = 0.22$, pine: $r = 0.10$, $p = 0.57$).

BIRCH AND ALDER SEED CROP SIZE

As a measure of flowering of birches and alders, and hence seed crop size, we used annual pollen integrals from pollen counts conducted by the Swedish Museum of Natural History and collaborators (www.pollenrapporten.se; Lind *et al.* 2016). Pollen counts have in recent years been conducted at 22 stations spread over much of Sweden, but with the majority in the southern half of the country. Counts started in 1973 in Stockholm, and more stations were added over years. We included stations with long-term and uninterrupted time series. Eight stations had data from the whole period 1988–2021, of which three stations started in 1987–1988 and five during 1973–1979. Only one station was in the northern part of Sweden (Umeå) and was therefore excluded. The remaining seven stations (Eskilstuna, Göteborg, Jönköping, Malmö, Norrköping, Stockholm, Västervik) were from the southern half of Sweden. There was some spatial bias towards stations situated in east-central Sweden (from Jönköping to Stockholm). However, an index based on the average of all seven stations was strongly correlated with an index where two outlying stations (Göteborg in western Sweden and Malmö in southern Sweden) were weighted with a factor of two (birch: $r = 0.989$, $p < 0.001$; alder: $r = 0.996$, $p < 0.001$). Furthermore, counts from Umeå were strongly correlated to the average index from southern Sweden (birch: $r = 0.83$, $p < 0.001$; alder: $r = 0.68$, $p < 0.001$), and pair-wise correlations between the eight stations were in all cases strongly significant (birch: $r = 0.40–0.90$, all p-values < 0.013, alder: $r = 0.63–0.94$, all p-values < 0.001). Thus, the index based on the average of the seven southern stations was used and considered to be representative for large parts of Sweden. Yearly crop size indices for southern Sweden increased over time, but significantly only for alder (birch: $r = 0.18$, $p = 0.31$, alder: $r = 0.52$, $p = 0.002$; see also Lind *et al.* 2016).

STATISTICAL ANALYSES

Analyses of the influence of seed crop sizes on Siskin breeding numbers, migration and wintering were conducted with partial correlation analyses (r_p) that controlled for the effect of year because several variables had significant temporal trends. Breeding numbers were analysed in relation to crop sizes in the previous year because these crops are available to Siskins from autumn until next spring depending on tree species. Analyses of breeding numbers were also conducted with Siskin winter numbers replacing crop sizes based on the idea that winter numbers could reflect overall food availability during winter.

Siskin numbers on migration during autumn were analysed in relation to crop sizes in the same year. Siskin autumn migration was also analysed in relation to breeding numbers in the same year. Finally, winter numbers were analysed in relation to crop sizes from the previous growing season. Thus, winter numbers during e.g. 1998/1999 were analysed in relation to crop sizes from 1998. Analyses used $\log_{10}$-transformed numbers for number of Siskins on migration and during winter.

In the data material used, indices of seed crop sizes of spruce, birch and alder were in general positively correlated (Table 2). Thus, multiple regressions to evaluate the relative importance of each tree species were not conducted. Furthermore, some of the hypotheses (Eriksson 1970) were rather based on additive effects of seed crop sizes. Thus, in addition to the singular effect of each tree species, we also evaluated the combined effect of spruce (all of Sweden), birch and alder crop sizes on Siskin breeding, migration and wintering. The combined effect was based on the sum of standardised values (mean = 0, SD = 1) of seed crop sizes of each tree species. Positive values represent above-average crop sizes and negative values below-average crop sizes. This variable did not have a significant temporal trend ($r = 0.29$, $p = 0.11$).

However, due to the correlations between seed crop sizes of several tree species, the above analyses do not provide direct information of the relative importance of all crop types. To gain more insight into how large breeding and wintering numbers were related to individual crop sizes, we investigated the crop conditions present during peak years for breeding and wintering of Siskins. Peak years were defined as years where numbers were larger than both the year before and the year after, and numbers were above average. Crop sizes of each tree species were defined as small, moderate or large (one third of all years in each group). The number of peak years that coincided with large crop sizes of at least two tree species were compared to the number of peak years coinciding with only one or no large crop sizes. We used χ^2-tests to assess whether these numbers differed from random. With crop sizes of four tree species having a one third chance of being large in any given year, there is a 41% chance of observing 2–4 crop types being large, and a 59% chance of 0–1 crop types being large in each year.

When presenting relationships between variables in figures, variables that had significant temporal trends (Siskin breeding index both in the whole of Sweden and southern Sweden, Siskin migration index, alder crop size index) were detrended (i.e. using residuals from regressions of the focal variable on year). All statistical analyses were conducted in JMP Pro version 17.

TABLE 2. Synchrony of seed crop sizes of Norway spruce *Picea abies*, Scots pine *Pinus sylvestris*, birches (*Betula* spp.) and alders (*Alnus* spp.) in Sweden. Partial correlation coefficients controlling for year are shown (significant results in bold). SE = Sweden, SS = Southern Sweden, *Spruce = gran, pine = tall, birch = björk, alder = al*
– Synkronicitet i frösättningen hos gran Picea abies*, tall* Pinus sylvestris*, björk (*Betula *spp.) och al (*Alnus *spp.) i Sverige. Partiella korrelationskoefficienter med kontroll av effekten av år (signifikanta resultat i fetstil). SE = Sverige, SS = södra Sverige, Spruce = gran, pine = tall, birch = björk, alder = al.*

Variables *Variabler*	n	Part.	p
Spruce (SE) versus spruce (SS)	36	**0.95**	**< 0.001**
Pine (SE) versus pine (SS)	36	**0.84**	**< 0.001**
Spruce (SE) versus pine (SE)	36	0.28	0.11
Spruce (SS) versus pine (SS)	36	**0.45**	**0.006**
Spruce (SE) versus birch (SS)	34	**0.36**	**0.033**
Spruce (SS) versus birch (SS)	34	**0.40**	**0.018**
Spruce (SE) versus alder (SS)	34	**0.47**	**0.004**
Spruce (SS) versus alder (SS)	34	**0.47**	**0.004**
Pine (SE) versus birch (SS)	34	−0.04	0.80
Pine (SS) versus birch (SS)	34	0.17	0.34
Pine (SE) versus alder (SS)	34	−0.06	0.75
Pine (SS) versus alder (SS)	34	0.31	0.07
Birch (SS) versus alder (SS)	34	**0.58**	**< 0.001**

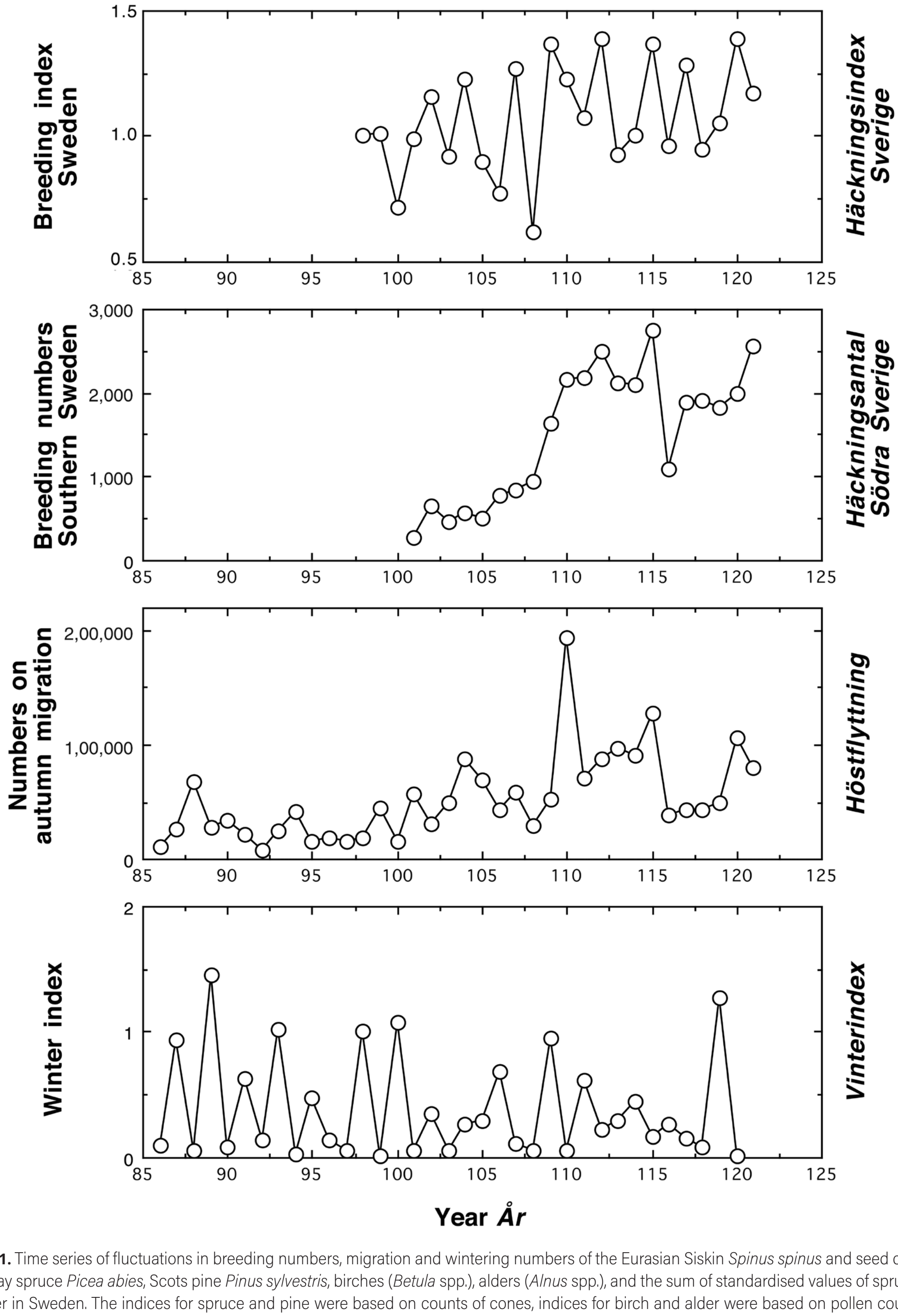

FIGURE 1. Time series of fluctuations in breeding numbers, migration and wintering numbers of the Eurasian Siskin *Spinus spinus* and seed crop sizes of Norway spruce *Picea abies*, Scots pine *Pinus sylvestris*, birches (*Betula* spp.), alders (*Alnus* spp.), and the sum of standardised values of spruce, birch and alder in Sweden. The indices for spruce and pine were based on counts of cones, indices for birch and alder were based on pollen counts. Year 85 = 1985.
– *Tidserier som visar variation i antalet häckande, flyttande och övervintrande individer av grönsiska* Spinus spinus *samt frösättningens storlek hos gran* Picea abies*, tall* Pinus sylvestris*, björk (*Betula *spp.) och al (*Alnus *spp.) i Sverige. Indexen som gäller gran och tall baserades på antal kottar, medan indexen för björk och al baserades på pollenkoncentrationen. År 85 = 1985.*

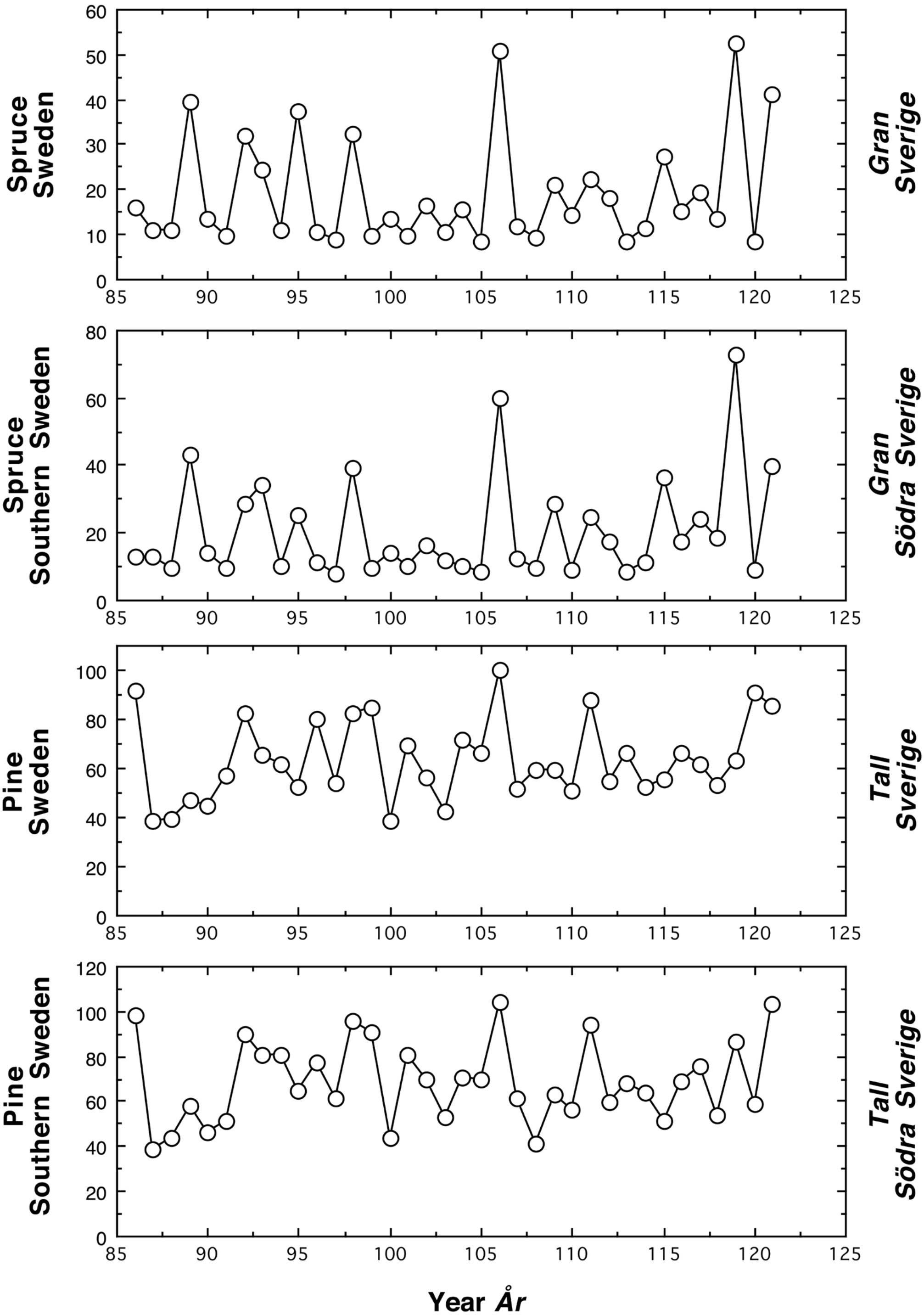

FIGURE 1 continued *fortsatt.*

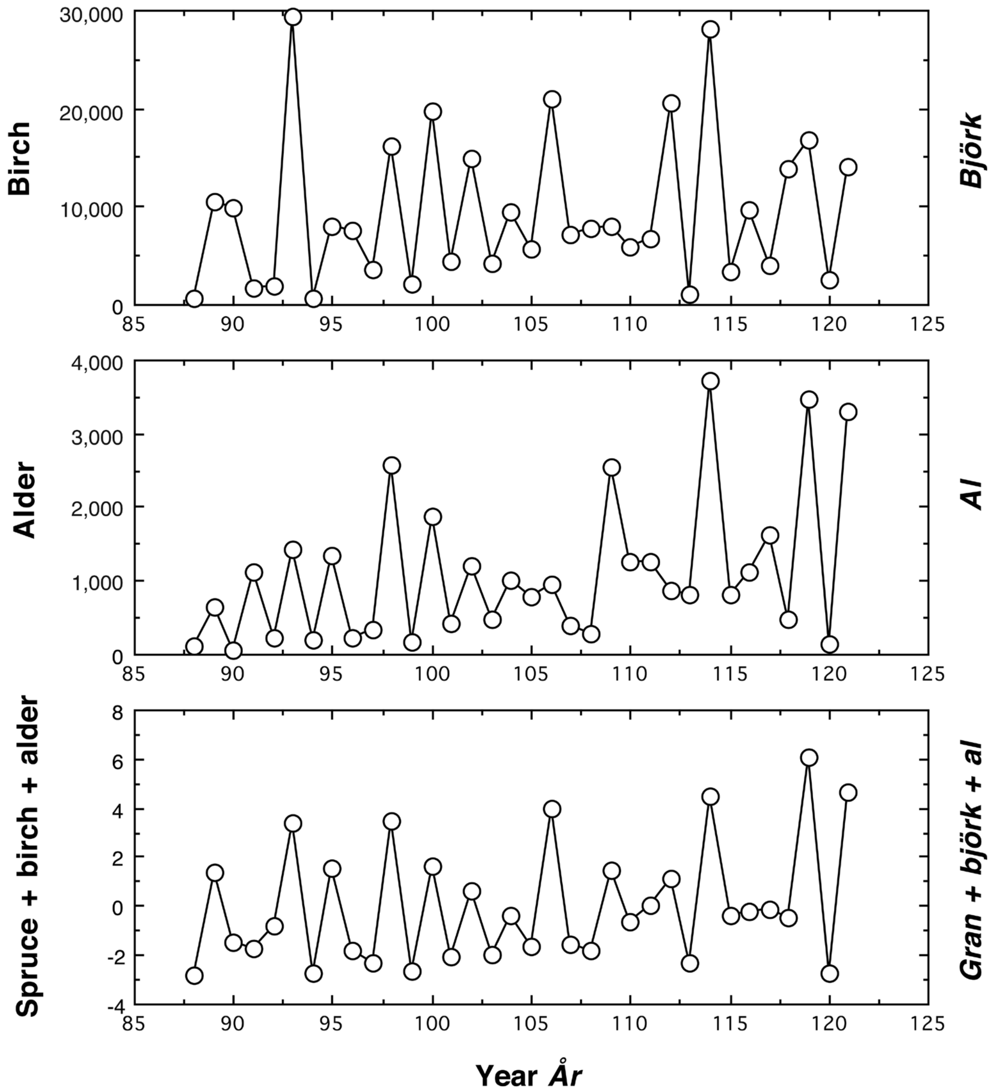

FIGURE 1 continued *fortsatt.*

Results

FLUCTUATIONS IN SISKIN NUMBERS AND SEED CROP SIZE

There were substantial annual fluctuations in Siskin breeding numbers, migration and wintering numbers as well as in seed crop sizes (Figure 1). Furthermore, annual seed crop sizes of spruce, birch and alder were in general positively correlated, whereas seed crop size of pine was mostly weakly correlated with other tree species (Table 2).

BREEDING NUMBERS

Siskin breeding numbers were in general not strongly related to seed crop sizes of individual tree species, although there were nearly significant positive relationships between the national breeding index for Sweden and spruce, birch and alder seed crop sizes (Table 3). However, the national breeding index was significantly and positively related to the combined crop sizes of spruce, birch and alder (Figure 2, Table 3). Large seed crops were often related to large

TABLE 3. Partial correlation analyses of annual fluctuations in breeding numbers, autumn migration and wintering numbers of the Eurasian Siskin *Spinus spinus*) in Sweden in relation to seed crop size of Norway spruce *Picea abies*, Scots pine *Pinus sylvestris*, birches (*Betula* spp.) and alders (*Alnus* spp.) in the previous year (breeding numbers) or in the same year (migration and wintering). Analyses controlled for the effect of year. Siskin numbers on migration and during winter were log-transformed for analyses. Significant results (without correction for multiple testing) are shown in bold. The data sources are monitoring (Breeding Sweden = breeding index; Migration = number of individuals, log-transformed; Wintering = winter index, log-transformed) and citizen data (Breeding Southern Sweden = number of records).
– Sambandet mellan häckningspopulationens storlek, antalet flyttande och antalet övervintrande individer av grönsiska Spinus spinus *i Sverige och frösättningens storlek hos gran* Picea abies*, tall* Pinus sylvestris*, björk (*Betula *spp.) och al (*Alnus *spp.) under föregående år (häckning) eller under innevarande år (flyttning och övervintring). Partiell korrelationsanalys med kontroll av årseffekter. Antalen av flyttande individer och av övervintrande individer logtransformerades före analysen. Signifikanta resultat (utan korrigering för multipla analyser) anges i fetstil. Datakällorna är övervakning (häckning Sverige = häckningsindex; flyttning = antalet individer, log-transformerat; övervintring = vinterindex, log-transformerat) och medborgardata (häckning södra Sverige = antalet observationer).*

	Breeding Sweden *Häckning Sverige*			Breeding Southern Sweden *Häckning Södra Sverige*			Migration *Flyttning*			Wintering *Övervintring*		
Seed crop *Frösättning*	r_p	n	p	r_p	n	p	r_p	n	p	r_p	n	p
Spruce *Gran*												
Sweden	0.30	24	0.09	–			–0.28	36	0.11	**0.58**	**35**	**< 0.001**
Southern Sweden	–			–0.28	21	0.11	–0.27	36	0.11	**0.60**	**35**	**< 0.001**
Pine *Tall*												
Sweden	0.15	24	0.39	–			–0.25	36	0.15	–0.11	35	0.52
Southern Sweden	–			0.05	21	0.76	–0.27	36	0.12	0.10	35	0.56
Birch *Björk*	0.30	24	0.08	0.12	21	0.48	–0.19	34	0.27	**0.59**	**33**	**< 0.001**
Alder *Al*	0.33	24	0.056	0.27	21	0.12	–0.19	34	0.28	**0.74**	**33**	**< 0.001**
Spruce + birch + alder[a] *Gran + björk + al*[a]	**0.37**	**24**	**0.028**	0.06	21	0.73	–0.27	34	0.11	**0.80**	**33**	**< 0.001**

[a]Sum of standardised values of seed crop sizes of spruce (Sweden), birch and alder *Summan av standardiserade värden för frösättningens storlek hos gran (Sverige), björk och al*

breeding numbers, whereas breeding numbers could be both low and high when seed crops were small (Figure 2). Breeding numbers were not related to preceding wintering numbers (breeding index Sweden: $r_p = 0.24$, n = 24, p = 0.16; breeding numbers southern Sweden: $r_p = 0.06$, n = 21, p = 0.73).

Peak breeding years of Siskins coincided with large crop sizes produced the previous year of the four tree species in 2–3 out of 8 peak years (Table 4a). There were two peak Siskin years coinciding with three large crop sizes and two peak years coinciding with two large crop sizes. On the other hand, four peak Siskin years coincided with 0–1 large crop sizes. The distribution (2–4 versus 0–1 large crop sizes) did not differ from random ($\chi^2 = 0.28$, p = 0.59).

MIGRATION

Analyses of Siskin autumn migration in relation to seed crop sizes did not reveal any significant relationships, although there were consistently negative correlations (Table 3). However, there were strong positive relationships between migration and breeding numbers earlier in the same year (breeding index Sweden: $r_p = 0.51$, n = 24, p = 0.002, Figure 3; breeding numbers southern Sweden: $r_p = 0.69$, n = 21, p < 0.001). There was no evidence that large Siskin emigration was related to high competition for food (competition = breeding numbers/sum of spruce, birch and alder crops: $r_p = 0.07$, n = 24, p = 0.71).

WINTERING NUMBERS

Siskin wintering numbers were strongly and positively related to seed crop sizes of spruce, birch and alder, but not to seed crop size of pine (Figure 4, Table 3). The number of Siskins wintering in Sweden was not related to the numbers emigrating from Sweden in autumn ($r_p = -0.22$, n = 35, p = 0.21) nor to previous breeding numbers (breeding index Sweden: $r_p = -0.14$, n = 24, p = 0.41; breeding numbers southern Sweden: $r_p = 0.15$, n = 21, p = 0.38).

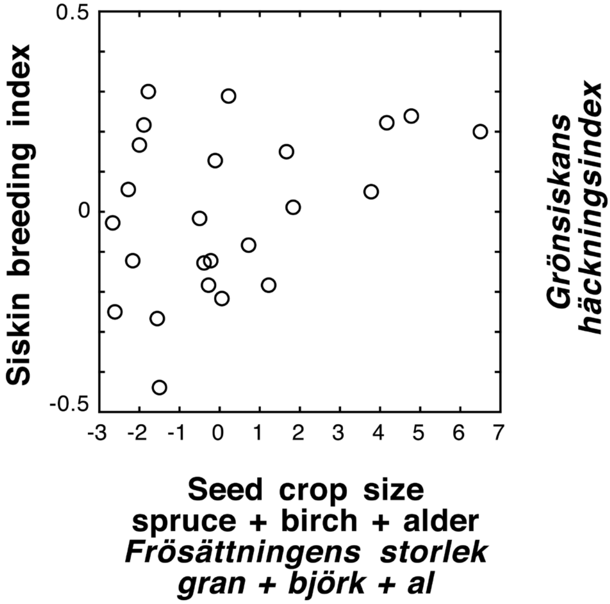

FIGURE 2. Breeding index of the Eurasian Siskin *Spinus spinus* in Sweden in relation to the sum of the standardised seed crop sizes of Norway spruce *Picea abies*, birches (*Betula* spp.) and alders (*Alnus* spp.) in Sweden produced in the previous year. The Siskin breeding index was detrended. – *Häckningsindex hos grönsiska* Spinus spinus *i förhållande till standardiserade värden för frösättningens storlek under föregående år hos gran* Picea abies, *björk (*Betula *spp.) och al (*Alnus *spp.) i Sverige. Tidstrenden togs bort från grönsiskans häckningsindex.*

Peak wintering years of Siskins coincided with large crop sizes produced the previous growing season of spruce, birch and alder in 8–10 out of 12 peak years, whereas only 4 peak years coincided with large crop size of pine (Table 4b). There were two peak Siskin years coinciding with four large crop sizes, three peak years coinciding with three large crop sizes, and six peak years coinciding with two large crop sizes. On the other hand, only one peak Siskin wintering year coincided with one large crop size, and none with no large crops. Thus, peak wintering years of Siskins coincided with two or more large crop sizes much more often than expected by chance (2–4 vs 0–1 large crop sizes; $\chi^2 = 12.89$, $p < 0.001$).

Discussion

BREEDING NUMBERS

Contrary to many previous studies (references in Introduction), we did not find strong relationships between spruce crop size and Siskin breeding numbers in our analyses of long-term data on large spatial scales. Furthermore, seed crop sizes of other tree species were also not strongly related to breeding numbers. In fact, half of the years with peak breeding numbers were not preceded by large crops of any of the four tree species. It is possible that local-scale analyses may sometimes show such relationships better whereas large-scale analyses may be affected by regionally asynchronous seed crop dynamics. Eriksson (1970) suggested that the largest numbers of Siskins winter when these tree species have synchronous crop size peaks and therefore provide abundant food resources through the whole winter. Large Siskin numbers, perhaps in combination with high survival, may then contribute to a large breeding population. However, it is important to note that in our data set there were no significant relationships between Siskin winter numbers and breeding numbers. Thus, peak breeding years of Siskins in Sweden are therefore likely to be related to other factors, e.g. survival during winter in continental Europe, or immigration from other parts of the breeding range (Svärdson 1957).

TABLE 4. Peak breeding and wintering years of Eurasian Siskins *Spinus spinus* in relation to seed crop sizes (small, moderate or **large**) of Norway spruce *Picea abies*, Scots pine *Pinus sylvestris*, birches (*Betula* spp.) and alders (*Alnus* spp.) in Sweden.
– Toppår för häckning och övervintring av grönsiskor Spinus spinus *i förhållande till frösättningens storlek—liten (small), måttlig (moderate) eller stor (**large**)—hos gran* Picea abies*, tall* Pinus sylvestris*, björk (*Betula *spp.) och al (*Alnus *spp.) i Sverige.*

Year *År*	Spruce *Gran*	Pine *Tall*	Birch *Björk*	Alder *Al*
(a) Peak breeding years (n = 8) *Toppår för häckning*				
2002	Small	**Large**	Moderate	Small
2004	Small	Small	Small	Small
2007	**Large**	**Large**	**Large**	Moderate
2009	Small	Moderate	Moderate	Small
2012	**Large**	**Large**	Moderate	Moderate
2015	Small	Small	**Large**	**Large**
2017	Moderate	Moderate	Moderate	Moderate
2020	**Large**	Moderate	**Large**	**Large**
Large crop size *Stor frösättning*	3/8	3/8	3/8	2/8
(b) Peak wintering years (n = 12) *Toppår för övervintring*				
1989/1990	**Large**	Small	**Large**	**Large**
1991/1992	Small	Moderate	Small	**Large**
1993/1994	**Large**	**Large**	**Large**	**Large**
1995/1996	**Large**	Moderate	Moderate	**Large**
1998/1999	**Large**	**Large**	**Large**	**Large**
2000/2001	Moderate	Small	**Large**	**Large**
2002/2003	Moderate	Moderate	**Large**	**Large**
2006/2007	**Large**	**Large**	**Large**	Moderate
2009/2010	**Large**	Moderate	Moderate	**Large**
2011/2012	**Large**	**Large**	Moderate	Moderate
2014/2015	Small	Small	**Large**	**Large**
2019/2020	**Large**	Moderate	**Large**	**Large**
Large crop size *Stor frösättning*	8/12	4/12	8/12	10/12

MIGRATION

We did not find clear evidence in favour of the ideas that seed crop failure should lead to large emigration of Siskins from Sweden, or that large crop sizes should lead to little emigration. Numbers of Siskins on autumn migration at Falsterbo were not significantly related to seed crop sizes of any of the tree species, although there were consistently negative correlations. However, there was a strong positive relationship between breeding numbers and migration. Thus, it appears that emigration from Sweden is mainly a density-dependent process where numbers on migration simply reflect a combination of breeding population size and reproductive success. Note also that some authors (Haftorn 1971) consider that most of the Siskin population migrates in all years, so that the number of Siskins that choose to stay in Fennoscandia during winter in case of large seed crop sizes is in any case relatively small and may not affect migration numbers to a large degree.

WINTERING NUMBERS

Wintering numbers were strongly related to seed crop sizes of both spruce, birch and alder. We also found that crop sizes of these three tree species were synchronous. Thus, in some winters all these tree species, or at least two of them, provide abundant food leading to particularly large numbers wintering as suggested by Eriksson

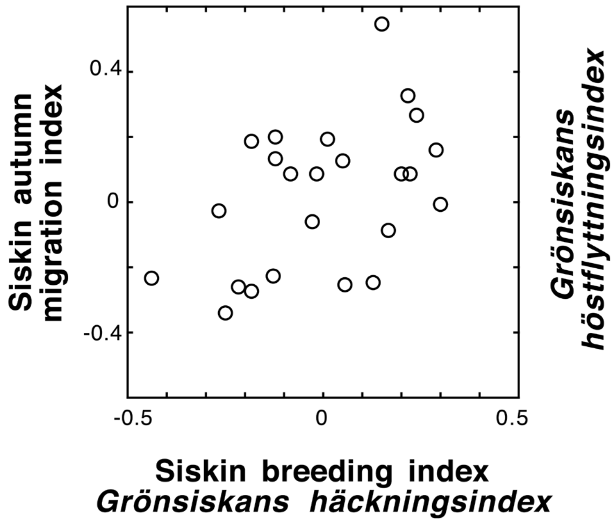

FIGURE 3. Autumn migration of the Eurasian Siskin *Spinus spinus* at Falsterbo, southern Sweden, in relation to the breeding index in Sweden earlier in the same year. Both variables were detrended (detrending of log-transformed numbers for migration).
– *Höstflyttning hos grönsiska* Spinus spinus *vid Falsterbo, södra Sverige, i förhållande till häckningsstorlek tidigare samma år. Tidstrenden togs bort från båda variablerna (i fallet flyttning, togs trenden bort från logtransformerade värden).*

(1970). Note that large crop sizes of only spruce cannot help Siskins to winter because spruce seeds are normally not available to Siskins before February. In order to exploit large spruce crops, Siskins may benefit from synchronous crops of birches and alders to sustain them through autumn and in particular early winter when other food is scarce or absent.

The finding that seed crops of several tree species were associated with large numbers of wintering Siskins in the same years does not necessarily mean that all the crops are equally important for the Siskins. Synchronous flowering of different tree species could lead to spurious correlations with Siskin numbers. Our analyses (Table 3–4) suggested that spruce, birch and alder were about equally important. However, detailed observations of diet selection during different periods of the winter, and survival consequences of lack of particular seed crops would be needed to fully understand the relative importance of each seed crop.

FLUCTUATIONS OF SEED-EATERS IN BOREAL FORESTS

Because many tree species in boreal forests have large variations in seed crop size from year to year, in particular typical masting tree species, seed-eaters in such areas face large variations in food supply. Food supply fluctuations are exaggerated by the fact that masting of several tree species are temporally synchronous over large areas. Thus, the feeding conditions in boreal forests for seed-eaters, especially during winter when other food sources are unavailable, can vary enormously from years with almost no food available to bonanza years when several seed types are abundant. The Siskins illustrate this by their dependence on three seed crops (spruce, birch and alder) which can help them survive the whole winter more easily and also contribute food during breeding (spruce). The Redpoll *Acanthis flammea* is similar although winter food is mostly seeds from birch and spruce so that peak breeding years may occur when good crops of these two tree species coincide (Peiponen 1957, Haftorn 1971, Dale 2021a).

On the other hand, other seed-eaters rely mostly on one seed crop type. Crossbills (*Loxia* spp.) are in general specialised on one conifer species each, but because of their unique bill shape they are able to access conifer seeds earlier and for a much longer period than e.g. the Siskin. Crossbills can therefore utilise spruce and pine seeds from the summer the cones ripen until next spring when seeds are shed (Newton 1972, 2008). Thus, in northern Europe Common Crossbills

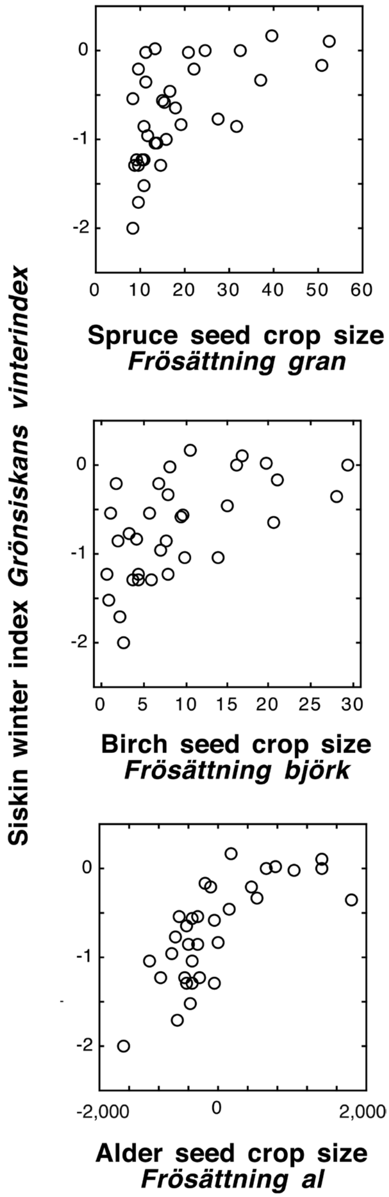

FIGURE 4. Winter index (log-transformed) of the Eurasian Siskin *Spinus spinus* in Sweden in relation to seed crop sizes of (**a**) Norway spruce *Picea abies*, (**b**) birches (*Betula* spp.) and (**c**) alders (*Alnus* spp.) in Sweden produced in the previous growing season. The index for spruce was based on counts of cones, indices for birch and alder were based on pollen counts (for birch divided here by 1,000, alder was detrended).
– *Vinterindex (logtransformerade värden) hos grönsiska* Spinus spinus *i förhållande till frösättningens storlek under föregående säsong hos (**a**) gran* Picea abies*, (**b**) björk (*Betula *spp.) och (**c**) al (*Alnus *spp.). Indexen som gäller gran baserades på antal kottar, medan indexen för björk och al baserades på antal registrerade pollen (för björk delades antalet med 1000 medan tidstrenden togs bort från de data som gäller al).*

rely mostly on seeds from spruce (Reinikainen 1937, Dale & Edvardsen 2024). However, other crossbill species may be more flexible and can be affected by multiple conifer species. The Parrot Crossbill *L. pytyopsittacus* is specialised on cones of Scots pine, but may use spruce as an alternative food source (Dale & Edvardsen 2024), and Two-barred Crossbills *L. leucoptera* may breed based on spruce in Fennoscandia although they rely on Siberian Larch *Larix sibirica* in their main breeding range (Dale 2021b).

In addition to different bird species specializing on different crops, several seed-eating bird species can also utilise the same food resources. Thus, synchronous peak crop years of several tree species can lead to peak years for several seed-eaters at the same time. In southeastern Norway, the 2019/2020 winter and the 2020 breeding season were exceptional due to large seed crops of several tree species produced in 2019 (Figure 1), including spruce, birch and Rowanberries *Sorbus aucuparia*. These crops were exploited by large numbers of both Eurasian Siskins, Common Redpolls, Common Crossbills, Two-barred Crossbills and Pine Grosbeaks *Pinicola enucleator* (Dale 2021a,b, 2023, Dale & Edvardsen 2024). On the other hand, during the next winter almost no seed-eaters were present because no tree species had produced large seed crops in 2020 (Figure 1; Dale 2023, Dale & Edvardsen 2024). Numbers of seed-eating birds may in turn affect raptors (Petty *et al.* 1995). Seed crops also affect populations of many other animals, including rodents and other herbivores (Selås 1997, Selås *et al.* 2002). The relationships between tree seed crop sizes and the population dynamics of seed-eaters in boreal forests provide a good example of how fluctuations in resource abundance have cascading effects through the food web and affect ecosystems. This study has illustrated how multiple seed crops affect different stages of the yearly life cycle of one seed-eater, the Eurasian Siskin, including the possible importance of synchronous peaks of spruce, birch or alder seed crops.

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Svensk sammanfattning

Flera trädarter i boreala skogar sätter olika många frön olika år (figur 1). Det innebär att fåglar som grönsiskan *Spinus spinus*, som är beroende av frön, inte alltid har lika mycket att äta. I den här studien har vi sett att antalet häckande individer, antalet som flyttar och antalet som övervintrar varierar påtagligt mellan olika år (figur 1). Vi har frågat oss vad detta har för samband med den varierande frösättningen hos gran, tall, björk och al. Underlaget är långa tidsserier från Svensk Fågeltaxering, Artportalen, Falsterbo fågelstation, Skogforsk och Naturhistoriska Riksmuseet (tabell 1).

Frösättningen hos gran *Picea abies*, björk (*Betula* spp.) och al (*Alnus* spp.) varierar synkront (tabell 2), och det fanns ett positivt samband med antalet häckande grönsiskor (figur 2, tabell 3). Det har dock förekommit tillfällen då antalet grönsiskor som häckat uppnått toppnivåer, även när dessa tre trädarter haft en svag fröproduktion (figur 2, tabell 4a). Den häckande populationens storlek kan ha påverkats av andra faktorer, till exempel av hur många som överlevt vintern på den europeiska kontinenten, eller att fåglar invandrat från avlägsna områden. Tallens *Pinus sylvestris* fröproduktion varierade inte alls i samklang med de andra träden (tabell 2) och inte heller med hur många grönsiskor som häckade (tabell 3).

Antalet fåglar som flyttade från Sverige under hösten påverkades inte alls av trädens fröproduktion, men däremot av storleken av den häckande populationen (figur 3). Flyttning tycks alltså vara en täthetsberoende process, snarare än att styras av tillgången på föda. Att den regionala mängden frön inte spelar så stor roll beror sannolikt på att många grönsiskor övervintrar söder om landet varje år.

Antalet övervintrande fåglar hade ett starkt och positivt samband med hur mycket frön som gran, björk och al producerat, men däremot inte med mängden tallfrön (figur 4, tabell 3). De högsta antalen övervintrande fåglar sammanföll med att det fanns mycket frön från minst två trädarter samtidigt (tabell 4b), vilket stöder Erikssons (1970) uppfattning att övervintring hos grönsiska gynnas av kraftig frösättning hos gran, björk och al. Björken står för födan under hösten, alen under vintern och granen under senvinter och vår.

Sammanfattningsvis tyder våra resultat på att storskalig variation av mängden granfrön i tid och rum inte är så viktig för grönsiskans häckning som man tidigare trott. Däremot förefaller mängden tillgängliga gran-, björk- och alfrön ha betydelse för hur många av siskorna som övervintrar, medan flyttningens omfattning inte påverkas av fröproduktionens storlek hos något träd. Resultaten ger en unik insikt i hur varierande frösättning i boreala skogar påverkar olika faser i livet hos en fröätande fågel, för vilken tillgången på föda svänger dramatiskt mellan olika år.

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