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Nutcracker irruptions depend more on food abundance than population size

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Irruptive migration is a form of partial migration, where the part of the population that migrates varies significantly between years. The intensity of irruptions has been explained by variation in food availability, breeding success and breeding population size. We investigated factors affecting the irruptions by northern nutcrackers *Nucifraga caryocatactes* (hereafter nutcrackers) in northern Europe. We used long-term monitoring data on nutcrackers autumn migrating in SW Finland (Hanko) and SW Sweden (Falsterbo), the age ratio of nutcrackers in Finland, breeding population size estimates in Sweden, the annual pollen abundance variation of hazel nuts *Corylus avellana* in Finland and Sweden and annual nut crop size variation in SW Finland. Two subspecies of nutcrackers occur in the area: southern breeding birds belong to the nominate subspecies *caryocatactes*, whereas individuals of the *macrorhynchos* subspecies breed further north but also occur in irruptions from the east (Russia). The ringing numbers of the nominate subspecies at Hanko were negatively correlated with the nut crop size, but this connection was not found in *macrorhynchos*. The annual autumn total nutcracker migration numbers in Hanko and Falsterbo were negatively connected with hazel nut crop size and also hazel pollen abundance in Hanko. Proportion of young was positively connected with migration intensity in Hanko. The Swedish adult breeding population size did not show any connection with the migration numbers in Falsterbo. The role of the nut crop size was clearly stronger than the age ratio indicating that the lack of food is the key driver of the irruptions.

1. Introduction

Animal migration is typically caused by fluctuations in the environment, especially seasonality in food availability and weather conditions (Alerstam 1990, Newton 2006). In addition to the fitness value for the individual, migration plays an important role in ecosystem

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functioning, where migratory animals are acting as vectors for other species such seeds of plants, fungal spores, microalgae, and vegetative propagules of lichens (Viana *et al.* 2016, Tesson *et al.* 2018, Johansson *et al.* 2021). In partial migration, one part of the population is migratory and the other part is residents. Irruptive migrants are a special case of partial migration, where a part of the population that is migrating varies substantially between years (Alerstam 1990, Newton 2006). The reasons behind irruption intensity vary between species, but the main causes have been suggested to be variation in food availability, breeding success and breeding population size. Reduced food availability has been suggested to cause increased irruptions for instance in owls, woodpeckers, tits, and crossbills (Alerstam 1990, Newton 2006, Nilsson *et al.* 2006, Summers *et al.* 2024). Alternatively, the irruptions can be caused by increased population density due to high breeding success (Silverin 2003) or a high number of breeding adults (Lindén *et al.* 2011). Irrupting individuals are typically young birds with lower dominance status in the population (Newton 2006). Irruptions have been studied for decades, but the relative role of food availability, breeding success and breeding population size has rarely been investigated in the same study system.

We investigated the role of the three factors on irruptions in northern nutcrackers *Nucifraga caryocatactes* (hereafter nutcrackers) in Northern Europe. Nutcrackers are typically sedentary, but especially young birds can show irruptions. According to Finnish ringing recoveries nutcrackers can move even thousands of km (Valkama *et al.* 2014). However, the movement distances vary between subspecies. Individuals of the eastern *macrorhynchos* subspecies have been shown to move more than 3000 km and birds have often been documented to cross vast stretches of sea, *e.g.* between Finland and Sweden. On the other hand, the nominate subspecies has only rarely been found to move more than 100 km and individuals avoid crossing larger water areas. Despite hundreds of ringed individuals in Southwest Finland, none indicates crossing of the Baltic Sea from Finland westwards to Sweden (Valkama *et al.* 2014). The irruptions of the *macrorhynchos* subspecies breeding mainly in Russia have been shown to link with the crop size of Siberian pine *Pinus sibirica* (Cramp & Perrins 1994). On the other hand, the irruptions of the nutcrackers of the nominate subspecies have been poorly studied. Nuts of hazel *Corylus avellana* and seeds of Arolla pine *Pinus cembra* have been suggested to be key of the main food items for the nominate subspecies during winter (Glutz von Blotzheim 2008). The Arolla pines does not occur in North Europe, but variation in hazel nut crops have been suggested to influence the local movements of nutcrackers in central Switzerland (Rolando & Carisio 1999, Glutz von Blotzheim 2008).

We investigated (i) how much the hazel nut crop size varies between years and (ii) if the annual autumn irruption numbers of nutcrackers is linked with the annual crop size of hazel nuts, annual breeding population size and annual breeding success. We expected that irruption numbers of the nutcrackers, especially in case of the nominate subspecies, would be negatively linked with hazel nut crop size, but the irruption numbers of eastern *macrorhynchos* subspecies would not show such a connection. We also expected that increased breeding success *i.e.* higher proportion of young in the population and a large breeding population size would increase the number of migrants. We also investigated the spatial synchrony in hazel reproduction using pollen data and spatial synchrony of the irruption numbers by comparing the autumn migration numbers of nutcrackers in two migratory bottlenecks, the Hanko Bird Observatory Southwest Finland, and the Falsterbo Bird Observatory, Southwest Sweden. These sites are situated over 700 km from each other and are separated by the Baltic Sea (Fig. 1). If the annual numbers were positively correlated, it would indicate a large spatial synchrony.

2. Materials and methods

2.1. Hazel data

We used two measures of the potential hazel nut crop: hazel pollen abundance in the spring and local hazel nut crop at the end of the summer. The hazel pollen has been monitored for health

Fig. 1. Breeding distribution of the northern nutcrackers *Nucifraga caryotactes* in North Europe in 50 km x 50 km grids based on European Breeding Bird Atlas (Keller *et al.* 2020). "A" is the sampling location of nut crop (Karjaa) and age ratio (Lohja) of nutcrackers (more detailed in text). The four hazel pollen sampling sites from Sweden are shown with p1-4. "T" is the Turku pollen monitoring site in Finland. "H" and "F" are the locations of the Hanko and Falsterbo Bird Observatories, respectively.

(pollen allergy) reasons, but it is not known how well pollen abundance reflects the actual production of the nuts later in the season. We used hazel pollen data from four Swedish sites: Bräkne-Hoby, Eskilstuna, Norrköping and Stockholm and one Finnish site: Turku, which are all situated in the core area of the hazel (Fig. 1). Airborne *Corylus* pollen abundance was monitored with Hirst-type samplers situated at the height of 4–18 m above the ground. The pollen counts were converted to daily averages per cubic metre of air. The sampling method, slide preparation and data interpretation were performed according to the standard methodology following the principles of the European Aeroallergen Network (2024).

The four Swedish sites showed strong spatial autocorrelation in annual pollen abundance during 1992–2025 (mean r = 0.58, range 0.41–0.80). Because of this we used the annual mean pollen abundance of all four sites (available from 1992 onwards) as a proxy of Swedish pollen abundance. The pollen abundances were log-transformed before analyses (Table S1).

Hazel nut crops were studied in Karjaa, Raasepori, SW Finland (60.06°N, 23.69°E; Fig. 1) in 2009–2025. Each year the same 26 branches of four hazel nut bushes, situated 60–200m meters apart, were surveyed by AL and the number of hazel nuts were counted at the end of July–early August, before animals (*e.g.* nutcrackers, and red squirrels *Sciurus vulgaris*) had started eating and hoarding them in larger

numbers. The log-transformed total count of the survey was used as an annual proxy of the hazel nut crop (see Table S1). We are not aware of any other hazel nut crop data from the two countries.

2.2. Nutcracker data

Nutcrackers are relatively uncommon breeding species in both Finland and Sweden with estimated population sizes of 2000 (Valkama *et al.* 2011) and 10 000 pairs (Ottosson *et al.* 2025), respectively. Both subspecies breed in both countries. In Finland, the nominate subspecies breeds in southwest Finland and the expanding breeding population *macrorhynchos* breeds in Central Finland (Valkama *et al.* 2011). In Sweden, most of the breeding population belongs to the nominate subspecies and occur in the southern half of the country, with a smaller breeding population of *macrorhynchos* (1000–2000 pairs) in northeast Sweden (Ottosson *et al.* 2025). Furthermore, *macrorhynchos* individuals of eastern Russian origin are irrupting in larger numbers in some years (*e.g.* Hilden 1969, Valkama *et al.* 2014).

Systematic counts of autumn migratory birds have been conducted at the Hanko Bird Observatory, SW Finland (59.80°N, 22.89°E) and Falsterbo Bird Observatory, SW Sweden (55.39°N, 12.85°E) (Fig. 1) since 1979 and 1973, respectively (Lehikoinen & Jaatinen 2011, Lindén *et al.* 2011, Kjellén 2019). In Hanko the main survey period is 25th July–5th November, whereas in Falsterbo it is 1 August–20 November (Lehikoinen & Jaatinen 2011, Lindén *et al.* 2011, Kjellén 2019). The Hanko migration data is available at https://halias.fi/tutkimus-ja-aineisto/ and Falsterbo statistics at https://www.falsterbofagelstation.se/?lang=en. The count periods match well with the peak irruption timing of the nutcrackers from late August to early October (Lehikoinen & Vähätalo 2000). Furthermore, nutcrackers have been trapped at the Hanko Bird Observatory and the ringers have often identified the subspecies based on the bill shape and tail patterns according to Svensson (1992). Both subspecies have been relatively often ringed at Hanko and the nominate subspecies are typically ringed earlier in autumn than the individuals of *macrorhynchos* (Valkama *et al.* 2014).

Nutcrackers have been ringed and recovered at the breeding areas in SW Finland in Lohja next to Raasepori (60.14°N, 23.93°E, Fig. 1) in the late autumn and early winter from the same feeding site in 2009–2024 by a local bird ringer Esa Aaltonen. The September–December captures of nutcrackers varied between 5 and 56 (mean 35). The age of the birds first year bird or older was identified based on Svensson (1992). The age ratio (first year birds / all trapped birds) of the trapped birds was used as proxy of the breeding success.

The nutcracker is such a scarce breeder in Finland that the annual breeding population size cannot be monitored through the national common bird monitoring (Lehikoinen & Väisänen 2023). The species is very secretive in early June during the survey season.

In Sweden the species is common enough to allow annual population size indices to be calculated, although the number of birds counted each year is still low (Green *et al.* 2025). We used data from the 716 Fixed routes in Sweden, a system of 2 x 2 km line transects that cover all of Sweden in a habitat representative way (Lehikoinen *et al.* 2014, Green *et al.* 2025).

2.3. Statistical analyses

To test the link between nutcracker numbers at the bird observatories and the continuous explanatory variables nuts (log-transformed), pollen (log-transformed), year, age ratio and population size, we used generalised linear models with Poisson distribution using function ‘glm’ in R. When analysing the Hanko data, the annual ringed numbers of nominate and *macrorhynchos* nutcrackers as well as annual migration numbers were dependent variables. These were tested against crop size of nuts, pollen abundance, year and age ratio. In the Falsterbo analyses, the annual number of migrants was the dependent variable and tested against nuts, pollen, year and breeding population size index. Pairwise collinearity tests between all predictor variables were low $|r| < 0.31$, except between year and pollen abundance in Finland

(r = 0.53). Therefore, we used detrended pollen abundance in the Finnish analyses (residuals of a linear fit). All the explanatory variables were scaled before analyses using scale an R function 'scale'.

We tested the correlation between hazel pollen abundance in Turku and hazel nut crop in Karjaa (both in Finland; Fig. 1) using Pearson correlation (an R function cor.test; R version 4.4.2., R Core Team 2024). Furthermore, we tested the correlation between migration numbers in Hanko and Falsterbo using Pearson correlation. The coefficient of determination of the GLM models was calculated using function "pR2" from pscl-package in R (Jackman *et al.* 2024).

We tested the synchrony in the log-transformed (log (n+1)) crops of four different hazel nut bushes using Pearson correlation. We also calculated the temporal autocorrelation of one year lag in the total sum of hazel nut crop size using Pearson correlation. The autocorrelation tests were done for both raw and log-transformed crop values.

3. Results

The annual abundance of hazel pollen and nut crop size showed no correlation (r_p = -0.18, df = 15, P = 0.495). The annual crop sizes of four hazel nut bushes were strongly synchronous (mean r_p = 0.71, range 0.58–0.81; Table S2). The hazel nuts showed strong annual variation

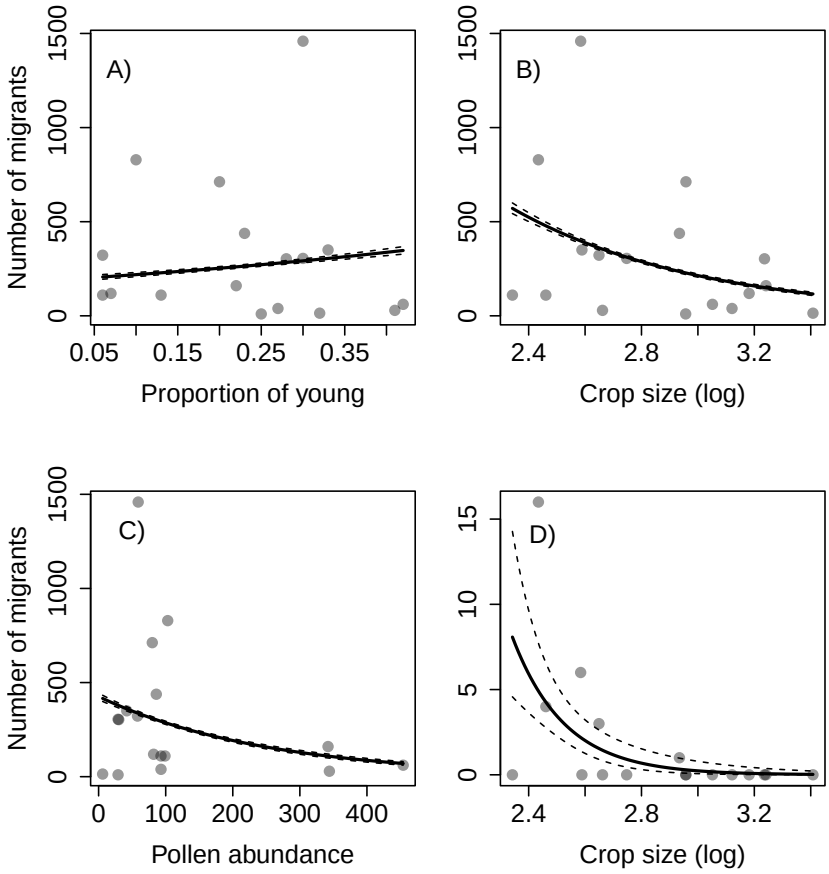

Fig. 2. Number of migrating nutcrackers in Hanko (A-C) and Falsterbo (D) Bird Observatories (see locations in Fig. 1) in relation to proportion of young birds (age ratio) (A) log-transformed crop sizes of hazel nuts (B and D), and pollen abundance (C).

Table 1. Parameter estimates, standard errors, z-values and P-values of models explaining the annual numbers ringed of nominate (left) and *macrorhynchos* (right) nutcrackers at Hanko, Finland in 2009–2024. The nut crop is the annual crop size estimate of hazel nuts, year is the study year, age ratio is the ratio of young birds in autumn traps at the breeding site in Lohja, Finland and Pollen is hazel pollen from Turku, Finland. The R^2 values of models were 0.23 and 0.02 for the nominate and *macrorhynchos* subspecies models, respectively. Significant coefficients are bolded.

Nominate subspecies				*macrorhynchos* subspecies			
Variable	B ± SE	z-value	P-value	Variable	B ± SE	z-value	P-value
(Intercept)	0.06 ± 0.26	0.24	0.807	(Intercept)	-0.57 ± 0.33	-1.73	0.083
Nut crop	**-0.88 ± 0.27**	**-3.20**	**0.001**	Nut crop	0.28 ± 0.36	0.78	0.435
Year	**-0.61 ± 0.24**	**-2.51**	**0.012**	Year	0.03 ± 0.36	0.08	0.935
Age ratio	0.33 ± 0.26	1.23	0.216	Age ratio	-0.02 ± 0.37	-0.05	0.958
Pollen	-0.12 ± 0.25	-0.50	0.615	Pollen	-0.05 ± 0.33	-0.16	0.869

between years with a coefficient of variation of 71.8% (Fig. 2). The crop sizes showed a significant strong negative autocorrelation with one year lag (r_p = -0.42 and r_p = -0.49 for raw and log-transformed crop values, respectively; Table S2). Thus, a good year was followed by a poor year, and *vice versa*.

Of the ringed nutcrackers at Hanko bird observatory in 2009–2024, 27 (0–8 per year) and 10 (0–4) were of the nominate and *macrorhynchos* subspecies, respectively. Despite the low number of trapped birds, the annual ringing numbers of the nominate subspecies were significantly negatively correlated with the annual hazel nut crop and year, but such a relationship was not found for the *macrorhynchos* subspecies (Table 1). The age ratio at the breeding grounds showed no connection with the annual ringing numbers in either of the subspecies (Table 1).

The annual migration numbers of nutcrackers varied in Hanko between 2 and 10887 (mean 554) and in Falsterbo between 0 and 1763 (mean 84) in 1979–2025, with a strong peak in 1995 (Table S1). The annual nutcracker migration numbers in Falsterbo and Hanko were significantly positively correlated during 1979–2025 (r_p = 0.87, df = 45, P < 0.001). The annual migration numbers at Hanko were significantly negatively connected with the hazel nut crop size and pollen abundance and year and significantly positively connected with the age ratio (Table 2) in 2009–2025. Also at Falsterbo the annual migration numbers in 2009–2025 were significantly negatively correlated to the hazel nut crop size. However, pollen abundance, year or the Swedish breeding population size did not show any significant correlations (Table 2).

4. Discussion

The hazel nut crop size varied substantially from year to year, but the studied hazel nut bushes were highly synchronous in their annual crop. The annual crop sizes explained a significant part of the variation in annual migration numbers of nutcrackers both in Hanko and Falsterbo. Age ratio also explained a part of the variation in migration numbers in Hanko, but the Swedish population size did not seem to explain the numbers migrating at Falsterbo.

4.1. Role of hazel nut crop on irruptions

The hazel nut crop from SW Finland showed a negative correlation with ringing numbers of the nominate subspecies in Hanko as well as migration numbers of Hanko and Falsterbo. A negative connection in hazel pollen abundance was only detected among Hanko migrants. The negative connection between nuts and nutcrackers suggests a classical food resources related irruption, where birds are leaving their breeding grounds in the autumn to look for better

Table 2. Parameter estimates, standard errors, z-values and P-values of models explaining the annual migration numbers of nutcrackers in Hanko (left) and Falsterbo (right) 2009–2024. Nut crop is the annual hazel nut crop size, year is year, the age ratio is the ratio of young birds in autumn traps at the breeding site in Lohja, Finland, Pop size is the annual Swedish population size index and Pollen is the annual hazel pollen abundance from Finland (Hanko) and Sweden (Falsterbo). The R^2 values of models were 0.18 and 0.45 for Hanko and Falsterbo, respectively. Significant coefficients are bolded.

Hanko Bird Observatory				Falsterbo Bird Observatory			
Variable	B ± SE	z-value	P-value	Variable	B ± SE	z-value	P-value
(Intercept)	**5.65 ± 0.02**	**371.00**	**<0.001**	(Intercept)	-0.68 ± 0.45	-1.50	0.134
Nut crop	**-0.51 ± 0.02**	**-30.41**	**<0.001**	**Nut crop**	**-1.70 ± 0.36**	**-4.66**	**<0.001**
Year	**-0.10 ± 0.01**	**-6.54**	**<0.001**	Year	0.02 ± 0.17	0.14	0.886
Age ratio	**0.08 ± 0.02**	**5.22**	**<0.001**	Pop size	-0.58 ± 0.32	-1.80	0.072
Pollen	**-0.18 ± 0.02**	**-11.31**	**<0.001**	Pollen	0.31 ± 0.25	1.21	0.225

areas for overwintering (Newton 2006). Similar connections have been found in several other irruptive bird species and their diet including carnivorous (rodents) and frugivorous (berries and seeds) foraging species from owls, woodpeckers, waxwings to finches (Alerstam 1990, Newton 2006, Nilsson *et al.* 2006, Lindén *et al.* 2011, Summers *et al.* 2024). The explanatory power of nuts was clearly larger than the coefficient of pollen, which is not surprising as nut is the food source of the nutcrackers, not the pollen. Surprisingly, the annual hazel pollen abundance and nut crop sizes were not correlated based on the Finnish data. However, because both showed significant negative connection in the migration numbers in Hanko, both variables probably together complement the information on the general hazel nut crop situation. Both hazel data sources have their own weaknesses. Pollen is not necessarily a clear proxy of the abundance of nuts. If a significant part of yearly pollen is from more southern origin (long-range transported), it might arrive in the monitoring area before the female flowers have become receptive. The weakness of the nut crop data is, that it is unfortunately available only from a very small area.

As expected, the ringing numbers of the eastern subspecies *macrorhynchos* did not show a significant connection with the nut crop as the origin of the migrants is likely from much further east. However, it was slightly surprising that also the Falsterbo migration numbers related to the local hazel nut crop variation measured over 800 km away. It is unlikely, that poor hazel nut crop in Finland would have caused nutcracker irruptions from Finland that have reached southern Sweden, as nominate nutcrackers do not tend to cross larger waterbodies (Valkama *et al.* 2014). Despite that migration intensity was very different in Hanko and Falsterbo, the annual numbers were strongly positively correlated. Slightly unexpectedly, the nut crop size showed higher coefficient and R^2 values on migration numbers in Falsterbo than in Hanko although the nut crop size was measured much closer to Hanko. This could be because migrants in Hanko are more likely a mixed population of both the nominate and the *macrorhynchos* subspecies, whereas in Falsterbo the migrants are mainly belonging to the nominate subspecies, which are affected by the nut crop. The hazel pollen abundance was not significantly correlated with the ringing numbers, which could be also due to larger uncertainty in analyses due to small ringing sample sizes compared to the number of migrants in Hanko.

The results indicate that the annual variation in hazel nut crops is not only locally synchronous, but potentially largely synchronous over larger areas as also indicated by the strong correlation in Swedish pollen data between sites. This could be due to spatially similar weather conditions (*e.g.* Gallego-Zamorano *et al.* 2018).

Similar synchrony in masting has been found e.g. in rowanberries *Sorbus aucuparia* and Norway spruce *Picea abies*, where the local crop statistics show spatially strong autocorrelation over 500 km in Finland (Gallego-Zamorano *et al*. 2018). Thus, the most parsimonious explanation for the synchronous irruptions in nutcracker irruptions in southern Finland and southern Sweden is similar fluctuations in nut crops in both areas.

The common masting tree species, rowanberry, Norway spruce and birches *Betula spp*. also show interspecific synchrony, where all tree species are masting typically in the same years (Gallego-Zamorano *et al.* 2018). Interestingly, the masting and crop failure years of hazel nuts were not occurring at the same time as in rowanberry and Norway spruce in 2009–2014 (data from Gallego-Zamorano *et al.* 2018) suggesting that drivers of the crop sizes vary between these species.

4.2. Role of age ratio and population size on irruptions

The age ratio in Lohja, Finland showed a positive correlation with the irruption numbers in Hanko, which indicates that increased breeding success also increases the volume of the irruptions. This is logical, because c. 99 % of the ringed migrants have been young birds at Hanko (Valkama *et al.* 2014). But based on the standardized parameter estimates of the explanatory variables, the estimate of the nuts was six times higher than the age ratio. This suggests that variation in the crop size likely has much higher importance on irruptions than the breeding success.

We did not find any significant connection with the breeding population size index of Swedish nutcrackers and the irruption numbers in Falsterbo. However, we must stress that the species is relatively uncommon and the sample sizes in both migrants of Falsterbo and breeding bird surveys are small. The highest count in both sites was observed in 1995 when the eastern subspecies had a very strong irruption (Pynnönen 1996). In the Swedish fixed routes, on average 11 individuals are observed in the surveys per year (Green *et al.* 2025). This can increase the uncertainty in the annual variation in irruption intensity and breeding abundance index estimates and decrease the chances to detect the connection between the variables.

Overall, our results suggest that irruptions of nutcrackers are synchronous over a large area in Fennoscandia. The irruptions of the nominate subspecies are mainly connected with variation in crop size of hazel nuts although variation in breeding success may also have a small role. We did not found evidence that the variation in breeding population size would have had a major importance on irruptions.

Pähkinähakkien vaelluksen voimakkuuden vaihtelua selittää enemmän pähkinäsadon vaihtelu kuin pähkinähakkipopulaation koko

Vaelluskäyttäyminen on yksi osittaismuuttamisen muodoista, jossa muuttava osuus populaatiosta vaihtelee voimakkaasti vuodesta toiseen. Vaellusten voimakkuuden vaihtelua on selitetty ravinnon määrän, pesimämenestyksen ja pesimäpopulaation koon vaihtelulla. Tutkimme pähkinähakkien Nucifraga caryocatactes syysvaellusten voimakkuuden vaihtelua Pohjois-Euroopassa. Käytimme aineistona pitkäaikaista vuosittaista seuranta-aineistoa pähkinähakkien muutosta Hangon (Lounais-Suomi) ja Falsterbon (Lounais-Ruotsi) lintuasemilta, pähkinähakkien ikäjakaumasta Etelä-Suomesta, pesimäpopulaation koosta Ruotsissa sekä pähkinäpensaan Corylus avellana siitepölyrunsautta Suomesta ja Ruotsista ja pähkinäsatorunsautta Etelä-Suomesta. Tutkimusalueella esiintyy kahta pähkinähakin alalajia: eteläiset pesivät linnut kuuluvat nimialalajiin caryocatactes, kun taas pohjoiset ja idästä vaeltavat linnut kuuluvat ohuempinokkaiseen macrorhynchos -alalajiin. Nimialalajin vuosittaiset rengastusmäärät Hangossa korreloivat merkitsevästi negatiivisesti pähkinäsadon kanssa, mutta tällaista yhteyttä ei löydetty macrorhynchos alalajilla. Hangon ja Falsterbon pähkinähakkien muuttajamäärät korreloivat positiivisesti keskenään eli vaellukset ovat synkronisia laajemmalla alueella. Hangon ja Falsterbon vuosittaiset muuttajamäärät korreloivat merkitsevästi negatiivisesti Suomen pähkinäsadon kanssa. Hangon muuttajamäärien vaihtelua selitti merkitsevästi negatiivisesti myös

pähkinäpensaiden siitepölyn määrä Suomessa sekä positiivisesti nuorten lintujen osuus eteläsuomalaisessa paikallispopulaatiossa. Ruotsin pesimäkannan koon vaihtelu ei selittänyt Falsterbon vuosittaista vaihtelua muuttajamäärissä. Pähkinäsadon merkitys pähkinähakin vaellusten selittäjänä oli huomattavasti suurempi kuin poikastuotosta kertova nuorten lintujen osuus. Tämä tukee käsitystä, että etenkin ravinnon vähyys ajaa pähkinähakit vaellukselle.

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Conflict of interest. The authors report no conflicts of interest.

Author contributions. AL: Conceptualization, Investigation, Data analyses, Writing - original draft, Writing - review & editing. ÅL: Writing - review & editing. AE: Data providing, Writing - review & editing. AS: Data providing, Writing - review & editing.

Ethics statement. The ringed birds were measured under Finnish national bird ringing licenses.

Data availability. The used data in the analyses is available in Tables S1 and S2 in the supplementary material.

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Online supplementary material

Supplementary material available in the online version of the article includes Tables S1–S2.