

Irruption and wintering ecology of the Great Spotted Woodpecker *Dendrocopos major*

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The study is based on winter bird censuses carried out in Finland in the years 1956—68, cone crop figures of the spruce and pine for the same period, and recoveries of Great Spotted Woodpeckers ringed in Finland. It is statistically demonstrated that the density of wintering populations of Great Spotted Woodpeckers depends on the cone crop of the spruce ($r = +0.32$; $p < 0.05$). The irruptive populations of the Great Spotted Woodpecker fluctuate synchronously in Finland and Norway ($r = +0.74$; $p < 0.01$). It is claimed that young birds tend to erupt annually. High population density and early territoriality of the young release a mass emigration, the extent of which is regulated by the cone crops.

Only a few authors have studied the autumnal eruptions of the Great Spotted Woodpecker, which are sometimes exceptionally large. PYNŃÖNEN (1939) reports that Great Spotted Woodpeckers moved along the Southern coast of Finland in greater numbers than usual in August 1930 and 1935. He connects these autumn emigrations with the unusually poor seed crops of the spruce (*Picea abies*) and the pine (*Pinus silvestris*) in those years. SVÄRDSON (1957) in his extensive survey of bird invasions also deals with the Great Spotted Woodpecker, and he states that the influx of this species in Central Europe in the autumn of 1929 led to breeding in the alpine region, where spruce had a good seed crop. The following autumn there was a new invasion which took the birds to Italy. He thus considers the invasions to be emigration leading to the occupation of new breeding areas. In the autumn of 1962 there were very extensive irruption movements in Fennoscandia and the British Isles, which have been studied in detail only in Britain (WILLIAMSON 1963) and on Helgoland (VAUK 1964). WILLIAMSON claims that the weather was a releasing factor for the flight to the British Isles, while VAUK concentrated

on the age and sex ratios among the irrupting birds. The great irruption in Fennoscandia in autumn 1968 was studied in detail by HILDÉN (1969), who claims on the basis of recoveries of birds ringed in Finland that Woodpeckers coming from the east performed a loop movement in Fennoscandia.

However, it is possible to clarify the picture of the wintering and irruption ecology of the Great Spotted Woodpecker on the basis of winter bird censuses carried out in Finland, data about the seed crops of conifers, and Finnish ringing recoveries.

Material and methods

The material showing the fluctuation of wintering populations of the Great Spotted Woodpecker is based on winter bird censuses organized by the Zoological Museum of the University of Helsinki. These have been carried out in various parts of the country since the winter of 1956/57. The present paper deals with the censuses for 13 successive winters, the last one being 1968/69. The censuses were carried out between 25 December and 6 January. They were always made along exactly the same routes and normally also by the same persons each year (see also HILDÉN & KOSKIMIES 1969). In recent years the total number of routes has been about 450. In the present study the routes were grouped according to the zoo-geographical

regions of Finland (MERIKALLIO 1958), and three regions were chosen for consideration because their census scores were the most reliable. The seed crop figures examined were those from the corresponding years and regions. Since the variances of the statistical functions were roughly equal, the figures of all three regions were pooled in the regression analysis. The methods were otherwise the same as those described in detail earlier (ERIKSSON 1970a).

In order to eliminate the effect of weather on the results, the observers were instructed to carry out their census in good weather, e.g. avoiding strong winds or blizzards. It may be assumed therefore that the number of participants per route and the length of the routes are the main causes of error in the census results. Using multiple regression analysis the effect of the length of the route and the number of participants on the number of birds observed was studied. The analysis showed that these errors are very small and of no importance.

Details of the cone crop of the spruce and pine were obtained from the Finnish Forest Research Institute, where the cone crops are annually classified into six categories (0—5) on the basis of inquiries made each autumn in some 400 localities in Finland (see also ERIKSSON 1970a).

The data on migration is based on 35 recoveries of Great Spotted Woodpeckers ringed in Finland before 1 February, 1970. The whole material has been checked and the study includes all but unimportant records, such as short-term local controls, etc. None of the recoveries excluded contradict the results presented.

The fluctuations of the irruptive populations of the Great Spotted Woodpecker were examined by studying the number of birds ringed in Finland and Norway in the years 1956—68. Since the majority of Great Spotted Woodpeckers are ringed when full grown, (the proportion is especially large in irruption years) these figures should give a fairly good idea of the strength of the autumn movements. Since it is obvious that the number of Great Spotted Woodpeckers ringed is connected with the intensity of ringing activity, the figures were made comparable by relating them to the total number of birds ringed each year and expressing them as the number of Woodpeckers per 10 000 birds ringed.

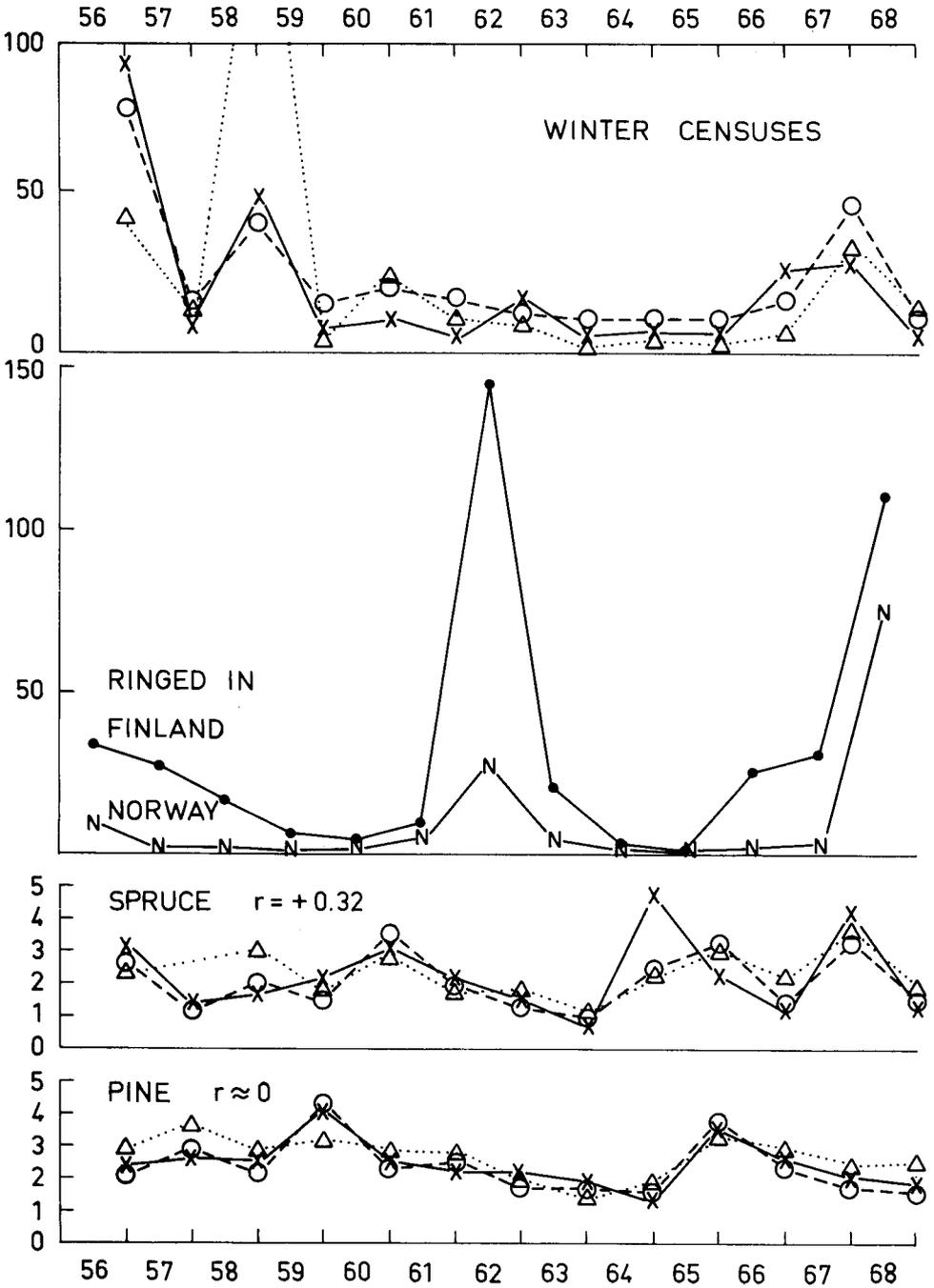
Numbers of wintering population and cone crops

The best-explored parts of Southern Finland, i.e. South-western Finland, Lake-Finland and Ostrobothnia, were taken into consideration. Fig. 1 gives the mean numbers of Woodpeckers per participant and ten census routes for each region in each of the winters of 1956—68. The material indicates clearly that the Great Spotted Woodpecker was most abundant in Finland in the winters of 1956/57, 1958/59 and 1967/68. The greatest autumn eruptions during this period occurred in 1962 and 1968 but in neither year was the number of wintering Woodpeckers above average. In autumn 1967 there was also a clear, although weaker exodus (HILDÉN 1968, 1969), which was followed by abundant wintering.

Fig. 1. shows that on the average a slightly smaller number of Woodpeckers was recorded in South-western Finland than in the other regions. This is due to the fact that the parts of the routes traversing forest are smaller. Otherwise the population fluctuations in different winters seem to be similar in the different regions. An exception is the astonishing abundance of Great Spotted Woodpeckers in Ostrobothnia in the winter of 1958/59. This winter was a good one for wintering Great Spotted Woodpeckers everywhere in Finland but on the basis of other figures, the expected density figure for Ostrobothnia should have been around 20, whereas in fact it was 168.8, the highest density figure for this region for the whole study period.

Fig. 1. presents the cone crop figures of the spruce and pine for the corre-

FIG. 1. The numbers of wintering Great Spotted Woodpeckers per participant and ten census routes in Finland in three zoo-geographical regions in the winters 1956—68 (upper). The relative numbers of Great Spotted Woodpeckers ringed per 10 000 birds ringed in Norway and Finland (middle). The cone crop of the spruce and pine in respective periods and regions (lower). The regions studied are SW-Finland (×), Lake-Finland (○) and Ostrobothnia (△).



sponding regions during the period 1956—68. The best cone crop of the spruce seems to have been that of autumn 1967. The seed crop records were also better than average in the autumns of 1956, 1958 (especially in Ostrobothnia), 1960, 1964 and 1965. Of these, the only years with abundant wintering Great Spotted Woodpeckers were 1956, 1958 (in Ostrobothnia) and 1967. The cone crop scores of the pine are on average a little higher than those of the spruce. Pine cones were abundant in the autumns of 1959 and 1965, whereas in 1962, 1963, 1964 and 1968 the crops were rather poor.

ERIKSSON (1970a) has earlier presented the numbers of spruce seeds shed per square metre and demonstrated that there are enormous differences between different years in this respect. The mean number of seed/m² is much smaller in the pine than in the spruce and the variation between the years is also smaller. The differences between the years are 10—30-fold in pine, whereas for spruce they may be up to 300-fold.

In the pooled material the numbers of wintering Woodpeckers were found to correlate significantly with the cone crop of the spruce ($r = +0.32$; $p < 0.05$; $df = 37$), but not with the cone crop of the pine ($r = 0.04$). Their dependence on the spruce crop can perhaps be explained by a linear regression model $y = 4.7x + 0.88$, since the coefficient (bx) is statistically nearly significant ($t = 1.8$; $0.05 < p < 0.10$; $df = 36$).

Irruptions in the years 1956—68

An idea of the numbers of irrupting Woodpeckers in the different years in Fennoscandia may be obtained from Fig. 1, which shows the number of Great Spotted Woodpeckers ringed in Finland and Norway. There is a clear and statistically very significant correla-

tion ($r = +0.74$; $p < 0.01$; $df = 12$) between the relative numbers of Woodpeckers ringed in the two countries. The fluctuations in the numbers of Woodpeckers in Finland and Norway are thus synchronous. The mass irruptions of Great Spotted Woodpeckers in 1962 and 1968 appear as clear peaks in the statistics of both countries. Large irruptions seem to have occurred also in the years 1956, 1957 and 1966. HILDÉN (1968) considers the irruption in the year 1967 also to be more abundant than average.

It is appropriate to study the mass irruptions of 1962 and 1968 in closer detail. During the summer of 1962 the mass movements of Woodpeckers started as early as July. Great Spotted Woodpeckers were found to be exceptionally abundant in the Finnish forests, especially in Lapland, around the middle of July, though no abundance was yet apparent in Southern Finland. PULLIAINEN (1963) states that Great Spotted Woodpeckers began to appear in great numbers in Lake-Finland in August. The Woodpeckers seem to have come from the east along the coniferous zone, arriving first in Northern Finland and then in Northern Norway, where many birds were found around 20 July climbing the steep cliffs of Röst, as Toralf Mikalsen told me the following summer. It was observed that from there the birds continued southwards, scattering in different directions, and arrived in greater numbers than normal in the British Isles and Helgoland, where the first birds belonging to the irruptive northern race were recorded on 15 July (WILLIAMSON 1963, VAUK 1964). A very strong eastward movement was recorded at the Signildskär Bird Observatory in the Åland Sea, where some 130 000 Woodpeckers were recorded during the period 25—27 July (WILLIAMSON 1963), the peak being on 26 July. Records supplied by Pertti Saurola for the morning of 27 July show that between 05.30 and 06.30 a total of 457 Great Spotted Woodpeckers passed the Tvärminne Biological Station on the Hanko-niemi peninsula. The Woodpeckers were migrating eastwards in flocks of 2—12 birds. In the Helsinki region several observers also saw Woodpeckers flying eastwards (although no proper migration watch was kept at that time). Unfortunately further detailed data of the timing and the intensity of flight are not available.

According to PULLIAINEN (1963), the Woodpeckers were most abundant in the forests of Southern Finland in September and

my own observations in the Helsinki region show a similar tendency. WILLIAMSON (1963) states that the Woodpeckers were most numerous at the British observatories (Fair Isle, Isle of May, and Spurn Point) on 11 October. But these observatories were regularly manned only from 19 September. The ringing statistics presented by VAUK (1964) show that some Woodpeckers were also ringed as late as between 14 and 24 October, but he states clearly that the peak was on 21 July and that the irruption was over by the end of October.

The 1968 irruption does not seem to have been as massive as the 1962 one. According to HILDÉN (1969), Woodpeckers were very abundant at the observatories Tauvo and Hailuoto in the Gulf of Bothnia from 15 and 16 August onwards. Of the more southerly observatories only Valassaari was manned in July. No clear migration movements were recorded even though this irruption also continued as far as the west coast of Norway and the British Isles.

The 1967 irruption was clearly weaker than the two irruptions described above; dispersion of the irruption type seems to have started at the beginning of August, as some 300 Woodpeckers were observed in Hailuoto on 7–8 August.

Recoveries of Great Spotted Woodpeckers ringed in Finland

HILDÉN has earlier (1969) presented a map of the recoveries of Great Spotted Woodpeckers ringed in Finland, on the basis of which he assumes that the irrupting birds come from the east and proceed in September–October to Sweden and Norway, returning eastward later in the autumn. However, he has neither studied the times of ringing nor the recoveries in very great detail. The loop movement he described agrees very well with the recoveries in Russia in the autumns of 1962 and 1968 of birds ringed the same autumns. But there are other adult birds ringed in Finland in spring or during the nesting period and recovered far to the east which are also interesting from the point of view of the nature of the irruptions.

1. An adult male ringed at Hauho, Ilmoila (61°12'N; 24°22'E), during breeding time on 23 June, 1957, was recovered on 5 December,

1957, in the USSR, Leningrad (59°57'N; 31°3'E).

2. An adult male ringed at Pori, Musa (61°29'N; 21°32'E) on 10 March, 1959, was recovered in the USSR, Udmurtien (56°15'N; 54°17'E) on 3 May, 1959.

3. An adult male ringed at Helsinki (60°10'N; 25°3'E) on 3 March, 1963, was recovered two years later in the USSR, Gorki (57°57'N; 47°23'E) on May, 1965.

4. An adult male ringed on Signildskär, Eckerö (60°12'N; 19°21'E) on 18 April, 1967, was recovered in the USSR, Tula (54°07'N; 36°30'E) on 21 February, 1968.

Of these recoveries, No. 1 shows that adult birds which have nested in Finland may move eastwards in the autumn. No. 2 shows that adult birds wintering in Fennoscandia may move eastward in spring to nest. Birds Nos. 3 and 4 may have nested in Finland although they were finally recovered in the USSR. All these birds were adult males. The recoveries of Woodpeckers ringed in Finland and the material presented by VAUK (1964) indicate that many birds ringed as eruptive ones at the observatories stayed in the area for several months. The numerous recoveries of birds (some 15) ringed as adults and found 1–2 years later at the ringing site also indicate that they clearly tend to remain in the same locality.

Age and sex ratio

VAUK (1964) in his study of the 1962 irruption states that of the 47 birds captured only 6 were adults, that is some 12%. Similarly HILDÉN (1969) reports that of the 1050 birds ringed at the observatories in 1968 only about 9% were adults. He did not study the sex ratio among the birds. VAUK (1964) also determined the sex of 14 birds; of these one was an adult male, 5 adult females, 4 young males and 4 young females. Although this material is not sufficient for a statistical test, it suggests that very few adult males take part in the irruption movements.

Discussion

A comparison of the figures of winter bird censuses and the seed crops of conifers shows that the density of a wintering population of Great Spotted Woodpeckers is to some extent dependent on the cone crop of the spruce. The results do not show any dependence of the wintering population level on the cone crop of the pine. Nevertheless, the cone crop of the pine may be a more or less important factor in the food ecology of Great Spotted Woodpeckers. It is generally considered that poor cone crops of the spruce and pine release an eruption of Great Spotted Woodpeckers (PYNNÖNEN 1939, VOOUS 1947, PULLIAINEN 1963, and HAAPANEN 1966). Pynnönen mentions that the eruptions in 1935 were caused by unusually poor cone crops. Unfortunately, more recent estimates of fluctuations in the breeding population are not available. According to the results, the eruptions seem to start in late July (PYNNÖNEN 1939, WILLIAMSON 1963, VAUK 1964, HILDÉN 1968 and 1969), coinciding with the time when the young birds begin to move about. According to JOHANSEN (1955), young Great Spotted Woodpeckers head for western Siberia in late June or early July. PYNNÖNEN (1943) has noted that, at that time of the year, the Woodpeckers still feed mainly on various insects and plants. Not until the end of September do the seeds of conifers begin to form the main part of their diet. Pynnönen also observed that the Woodpeckers seem to be very versatile in their choice of food at the end of July, when the culmination of eruption usually occurs. This makes it hard to believe that the primary releasing factor of the emigrations is lack of food.

It has been demonstrated with a group that is ecologically closely related, namely the Tits, that the releasing factor of eruption is the density of population and that food supply only

controls the extent of the exodus (KLUIJVER 1951, ULFSTRAND 1962). It is mainly young Tits which take part in these eruptions. A similar eruption mechanism has been found to exist in the Nuthatch *Sitta europaea*, where a growth of population leads to the emigration of young birds, which causes an abrupt drop in population density (BERNDT & DANCKER 1960, ERIKSSON 1970b). So it seems reasonable to assume that regular eruption movements are part of the normal behaviour of young Great Spotted Woodpeckers too. The denser the population, the greater is the proportion participating in the emigrations, the extent and the duration of which seem to be regulated by the availability of food.

This assumption agrees with the finding of PULLIAINEN (1963) that young Woodpeckers demonstrate clear, territorial aggressive behaviour and try to occupy their territories as early as August. He also states that the territories are larger in areas where food is scarce. They also seem to be larger in pine forest than in spruce forest, which is due to the differences in the amounts of seed of these trees. Further, the predominance of young birds in the age ratio (VAUK 1964, HILDÉN 1968) probably reflects high population density during eruption. PYNNÖNEN's (1939) study shows that the breeding population was rather large before the eruption of 1935 but dropped abruptly after the emigration. This is typical of species such as Tits and Nuthatches, whose eruptions are caused by high population density. SVÄRDSON (1957) has already suggested that the emigrations of the Great Spotted Woodpecker lead to the occupation of new breeding areas.

HAAPANEN (1966) states that the nesting populations of this species fluctuated relatively little during his study period 1960—1964 in Southern Finland. This may be due to the fact that

adult birds mainly tend to stay in their territories. On the basis of ringing recoveries and the study of VAUK (1964), it seems that adult males are the most territorial ones, while young birds show a strong urge to erupt. The assumption that population density, is the primary cause of eruption explains the apparently contradictory findings that in the autums of 1956 and 1967 with good cone crops there were clear eruptions from Fennoscandia, whereas in the very poor cone crop autumns of 1963 and 1966 there were only weak eruptions. The lack of seeds may cause some eruptive movements in September—October when the birds settle down in their final winter territory since, as noted by PULLIAINEN (1963), the settling down is regulated by the cone crop. Such representatives of the floating population appear at the observatories fairly often in September—October.

Owing to the poor cone crops in the summers of 1962 and 1968, the irruptive birds did not remain in Scandinavia, but performed a loop movement and returned to the east (HILDÉN 1969). The irruptions are always first observed in the north (HILDÉN 1968, 1969). This may be caused by the fact that the Great Spotted Woodpeckers arrive from the east along the coniferous zone and are thus oriented north-west. It has been found that all the irruptions of the Siberian Nuthatch (ERIKSSON 1970b) have a similar orientation. After this the irruption moves southwards dispersing in various directions, e.g. the British Isles, Denmark and across the Åland Sea and Southern Finland to the east. A very large proportion of the birds remain somewhere along this route as indicated by ringing recoveries. The settling in new areas is in accordance with the emigratory nature of the irruption (SVÄRDSON 1957), which means that young birds try to nest in the wintering area. This has been demon-

strated also with Tits and Nuthatches (KLUIJVER 1951, SVÄRDSON 1957, ULFSTRAND 1962 and ERIKSSON 1970b).

A detailed analysis of ringing recoveries shows that, contrary to the opinion expressed by HILDÉN (1969), even birds which have nested in Fennoscandia may move eastwards. On the other hand, adult males that have wintered in Fennoscandia may move eastwards in the following spring, apparently returning to their earlier nesting places, which indicates a tendency to true migration. This may also explain the regular though small spring movement of Great Spotted Woodpeckers noted at bird observatories (HILDÉN 1968; 1969).

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Selostus: Käpytikkojen vaellus- ja talvehtimisekologiasta.

Käpytikan talvehtivien populaatioiden vuotuisista ja alueellisista runsaudentvaihteluista esitettyt luvut perustuvat vuosina 1956—69 suoritettuihin talvilintulaskentoihin. Mukaan on otettu parhaiten tutkitut alueet: Lounais-Suomi, Järvi-Suomi ja Pohjanmaa. Vastaavalta ajalta ja samoilta alueilta on esitetty myös Metsäntutkimuslaitoksen kokoamat tiedot kuusen ja männyn käpysadoista. Syksyisin vaeltaneiden käpytikkojen runsautta on tutkittu vertailemalla Norjassa ja Suomessa merkittyjen käpytikkojen suhteellisia lukumääriä. Edellä esitettyt tiedot on koottu kuvaan 1.

Käpytikkojen talvinen kanta on ollut erityisen runsas talvina 1956/57, 1958/59 ja 1967/68. Joitakin runsaita vaellussyksyjä ja seurannut niukka talvehtiminen. Talvehtivan kannan runsaus näyttää korreloivan positiivisesti kuusen ($r = +0.32$; $p < 0.05$), mutta ei männyn ($r = 0.04$) käpysatoon. Näin siitä huolimatta, että mänty on lajin käyttämä ravintokasvi. Männyn ja kuusen siemensatojen absoluuttisissa määrissä on kuitenkin suuri ero siten, että kuusen siemenmäärä on huo-

noinakin siemenvuosina yleensä paljon suurempi kuin männyllä.

Vaelluksen voimakkuuden vaihtelut Norjassa ja Suomessa korreloivat positiivisesti ($r = +0.74$; $p < 0.01$). Erityisen runsaita massavaelluksia on ollut vuosina 1962 ja 1968, mutta runsasta esiintymistä on ollut myös 1956, 1957, 1966 ja 1967. Vaellusten runsaus huippu näyttää hyvin säännöllisesti sattuvan heinä—elokuun vaihteeseen.

Suomessa merkityistä käpytikoista tulleet rengaslöydöt osoittavat, että Suomessa pesineetkin vanhat linnut voivat vaeltaa kauas itään ja vastaavasti Suomessa talvehtineet voivat vasta keväällä muuttaa itään pesimääjäksi. Vaellustikoista tehdyt iän ja sukupuolen määritykset osoittavat, että vain noin 10 % yksilöistä on vanhoja ja niistä enemmistöä ovat vanhat naaraat. Tutkimuksessa tarkastellaan vaellusten laukaisevia tekijöitä ja arvellaan nuorten lintujen loppukesäisen territoriaalisen käyttäytymisen olevan laukaisevana tekijänä yhdessä populaatiotiheyden kanssa. Vaellukset olisivat tällöin emigraatioita, joiden ulottuvuutta siemensadot säätelevät.

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