The autumn migration and wintering ecology of the Siskin *Carduelis spinus*

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In his excellent review on the types of migration in 'invasion' birds Svärdson (1957) has also dealt with the Siskin. He shows that spruce seed is the most important food of the Siskin in breeding time and suggests that an abundant birch seed crop delays the departure of Siskins in autumn. He concentrated especially on the abnormal abundance of Siskins in Fennoscandia in 1949. He describes the invasion type of the Siskin like this: "The invading birds move mainly westwards (or eastwards) over their potential breeding range, being gradually absorbed by those regions in which food is most abundant. They may or may not leave this region for a period in winter, returning in spring to breed in the region located in autumn. After breeding a new search for the next year's breeding area begins." Svärdson thus agrees with the opinion put forward by Verheyen (1956) that the birds taking part in the 1949 invasion may have come from the east, from the Ural region.

The lack of knowledge about the migration routes of the Siskin at the time is shown by Svärdson's (1957) question: "Why did not the Siskins of 1949 start for a return flight eastwards, into the vast regions of spruce forest of Russia?"

Later the migration of the Siskin has been dealt with in detail only by Bernhoft-Osa (1964), who shows, using material based on recoveries of birds ringed in Norway, that the Siskin populations moving through Southern Norway follow a very regular migration pattern to Western Europe for the winter. This indicates that the Siskin may be a more regular migrant than it has been considered earlier.

Svärdson (1957) demonstrated that the seed crop of trees can be an important factor regulating the migration and wintering of the Siskin. Later Evans (1966) and Eriksson (1970) have been able to show that the movements of the wintering population of the Redpoll depend on the seed crop of trees, particularly of the birch. On this basis it seems appropriate to study the factors influencing migration, wintering and the movements of the breeding population of the Siskin in detail, as well as their dependence on the seed crop of trees.

Material and methods

The material showing the fluctuation of wintering populations of the Siskin 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 winters, the last one being 1968/69. The censuses were carried out between December 25th and January 6th. They are always done along exactly the same routes and normally also by the same persons each year. In recent years the total number of routes has been about 450. For the purpose of the present study the routes were grouped according to zoo-geographical regions (Merikallio 1958). The material was homogenized by leaving out all those routes more than 20 km long. The greatest number of routes is from Lounais-Suomi (LS), i.e. 220; Järvi-Suomi (JS) has some 95 and Pohjanmaa (Pm) about 60. The variables used in the statistical analysis were taken from these three best explored areas. Since the number of participants in each census varies between the regions, the number of birds has been calculated per participant. The mean length of the routes was 11.0 ± 4.5 km, and the mean number of participants 1.92 ± 1.2. The observers were in the field for the entire daylight period, i.e. between 9 a.m. and 3 p.m. Since weather affects the census results, an attempt to avoid this has been made by instructing the observers to carry out their census in good weather, avoiding e.g. strong winds or blizzards. Thus one may assume that the number of participants and the length of the routes are the main causes of error in the census results. These were studied by means of regression analysis by calculating the correlation of the number of birds on each route to the length of the route on the one hand, and to the number of participants on the other. There is almost no correlation between the number of birds and the number of participants ($r = 0.01$) and the correlation between the number of birds and the length of the route is likewise almost nil ($r = 0.02$). Even the total number of birds did not show any correlation to these two variables. Thus we find that random factors determine the occurrence of birds on each route to a greater extent than these systematic errors. On methods of conducting bird censuses see also KOSKIMIES (1966) and HILDÉN & KOSKIMIES (1969).

The meteorological data for an analysis of the factors relating to weather were taken from the Meteorological Yearbook of Finland for the years 1956—67, published by the Finnish Meteorological Institute. The readings for Lounais-Suomi are those of Helsinki (60°14′N; 24°55′E), those for Järvi-Suomi come from Jyväskylä (62°14′N; 25°44′E), and those for Pohjanmaa from Kruununkylä (63°43′N; 23°09′E). The mean temperature (C°), the mean minimum and mean maximum temperatures and the number of days with snow cover in October, November and December were chosen as the actual independent weather variables. These were used separately for each month as well as combined together to form readings for the whole autumn.

The seed crops of trees. The Forest Research Institute has studied the seed crops of the economically important trees, i.e. pine, spruce and birch. The cone crop of the spruce and the pine is studied annually by means of an investigation, where the cone crop is classified into six categories 0—5. The information used in the present paper was obtained from the following issues of Metsälehti: 38/1956, 40/1957, 46/1958, 38/1959, 44/1960, 50/1961, 1—2/1963, 51—52/1963, 2/1965, 2/1967, 50/1967, and 48/1968. The crop figures for the last few years are based on investigations carried out in some 400 localities. To permit statistical treatment the crop figures were also grouped according to the zoo-geographical regions. There were no similar details for the seed crop of the birch, but this has been calculated on the basis of seed readings on the Forest Research Institute sample plots, which are given as the number of seeds shed per square metre. Only three sample plots provide complete figures covering the whole period 1956—68. Corresponding figures for the spruce and the pine have been used to give an idea of the actual variation in seed crops.

The migration of the Siskin is very well shown from the observations at the Signildskär bird observatory. Only those autumns are included, when migration was recorded for the whole of the migration period of the Siskin. The observatory was manned by various observers (in brackets) the following periods: 1.9.—30.11.1956 (P. Linkola); 1.9.—30.11.1957 (P. Linkola); 1.9.—17.11.1959 (P. Linkola); 3.9.—8.10.1960 (M. Rautkari, P. Saurola, J. Rinne and A. Vuorjoki); 31.8.—30.9. and 14.10—12.11.1965 (P. Kalinainen). The material is presented in Table 1. The missing values are estimated on the basis of the others and they are given within parentheses. These include both years of abundant occurrence and wintering and years of minimum occurrence, so they form a good sample of the timing of the migration of the Siskin.

The data on wintering areas and speed of migration are based on recoveries of birds ringed in Finland and Norway, 173 in number. The fluctuation of Siskin populations in Finland and Norway was compared on the basis of the number of birds ringed each year. Since it is obvious that the number of ringed Siskins depends on the total number of birds ringed each year, these figures were made comparable by relating them to the grand total and expressing them as the number of Siskins ringed per 10 000 birds ringed.

The autumn migration

Timing of migration. — The timing of Siskins' migration is clearly shown in Table 1 giving the distribution of migration observed at the Signildskär bird observatory. It shows that during the five years when the observation period has been long enough to cover the whole of the migration period of the Siskin, the birds have migrated at very much the

TABLE 1. The distribution of migrating Siskins at the Signilskär observatory as a percentage of the total number for each season. (*Signilskärin lintuasemalla viitenä syksynä todettujen muuttavien vihervarpusten jakaantuminen muuttokaudella prosentteina kauden kokonaismäärästä.)*

Year	September *Syyskuu*			October *Lokakuu*			Seasons total
Vuosi	1—10.	11—20.	21—30.	1—10.	11—20.	21—31.	*Kauden summa*
1956	0	8	54	28	7	4	12 904
1957	1	6	50	22	11	11	557
1959	3	14	54	17	8	4	5 683
1960	7	50	11	16	(9)	(6)	3 243
1965	5	37	35	(21)	0	1	957

same time. The greater part seems to migrate very regularly during the last third of September. There are no clear signs of unusually early or late starts to migration. During September 57—77 % of the population has migrated, and none of the figures differs significantly from the whole series ($p>0.30$). However, the different thirds of September show great variation, but this may be attributed to chance because of the nature of the material. Whenever the start or culmination of migration varies between different years, the difference in time is rather short, some 10 days at the most.

Similarly migration seems to end almost completely by the end of October, as observations carried out during the whole of the month of November show that Siskins are seen after the end of October only in sporadic small flocks during the first few days of November. According to the material obtained at the Signildskär observatory it seems that the migration of the Siskin occurs at almost the same time during different years.

The abundance of autumn migrants. — The observation material obtained from different observatories in Fennoscandia is fairly incoherent, so it is difficult to get an idea of fluctuations in the migrating populations of Siskin in the autumn on the basis of those figures. The Siskin is a species which is ringed entirely as adult at the observatories mainly during autumn migration. Thus the ringing records of the observatories give a fairly good idea of fluctuations in the migrating populations. Bird watching activity has shown a tremendous increase in Finland (ERIKSSON 1969). Since the total activity influences the numbers of each individual species ringed, the number of Siskins ringed is also given per 10 000 birds ringed (Table 2). This enables us to compare figures obtained from different parts of Fennoscandia, i.e. Norway and Finland. The introduction of Japanese mist nets in 1959 caused a sudden increase of numbers, so actually comparisons should be restricted to the years 1959—68.

The population of the time of autumn migration in Finland seems to have been especially abundant in 1960, 1965, and 1968. The Siskin seems to have been fairly numerous also in the autumn of 1964 and 1967. In Norway the migrating population seems to have been very abundant in 1961 and 1965. The population also seems to have been more numerous than average during the autumns of 1962, 1964, 1966 and 1968.

TABLE 2. Absolute numbers (A) and relative numbers of Siskins ringed per 10 000 birds ringed (B) in Norway and Finland during the years 1956—68. (*Tutkimuskaudella 1956—68 Norjassa ja Suomessa rengastettujen vihervarpusten absoluuttiset määrät (A) ja suhteelliset määrät 10 000 rengastettua lintua kohti (B).*)

	Year *Vuosi*												
	1956	-57	-58	-59	-60	-61	-62	-63	-64	-65	-66	-67	-68
Norway *Norja*													
A	6	5	7	199	173	651	506	120	604	1480	325	250	396
B	2,1	1,6	2,2	50	64	310	190	41	220	322	95	54	97
Finland *Suomi*													
A	108	13	16	132	1152	586	698	1394	1554	3861	727	2599	3454
B	34,8	3,3	4,7	25	160	64	59	116	130	310	53	190	210

The autumn populations of the Siskin in Norway and Finland seem to fluctuate rather independently of each other. Between the relative ringing records of Norway and Finland there seems to be a slight positive correlation ($r = 0.44$; $df = 12$) but it is clearly not statistically significant. The slight correlation may be caused by the years of abundance, e.g. 1964, 1965 and 1968 occurring simultaneously. An exceptionally strong invasion covering a wide area seems to have taken place in the autumn of 1965, when ringing scores both in Norway and Finland reached their peaks.

Direction of migration and wintering areas. — Fig. 1 summarises all the ringing recoveries of Siskins ringed in Finland and Norway. The ringing material demonstrates convincingly that the Norwegian (Fig. 1A) and Finnish (Fig. 1B) populations of the Siskin differ from each other as to their wintering area in an east-westerly direction. It was possible to demonstrate this statistically by a t-analysis between the E-longitude degrees, which produced a highly significant difference in this respect ($t = 12.4$; $p < 0.001$). The maps show that there are very few Norwegian Siskins recovered in northern Italy and central Europe, where about half of the Finnish birds are recovered. But both populations seem to winter frequently in Belgium and Holland. The difference in wintering areas may be explained by the fact that some of the birds ringed in Finland migrate across Sweden to Western Europe, whereas others migrate via the Baltic states to central and southern Europe. However, there is not enough material to verify this statistically.

The most distant recoveries are distributed at random over various years of ringing and recovery, so there is no clear connection between abundance of population and wintering. Almost every year some Siskins seem to extend their migration to the farthest corners of south-western and southern Europe. In

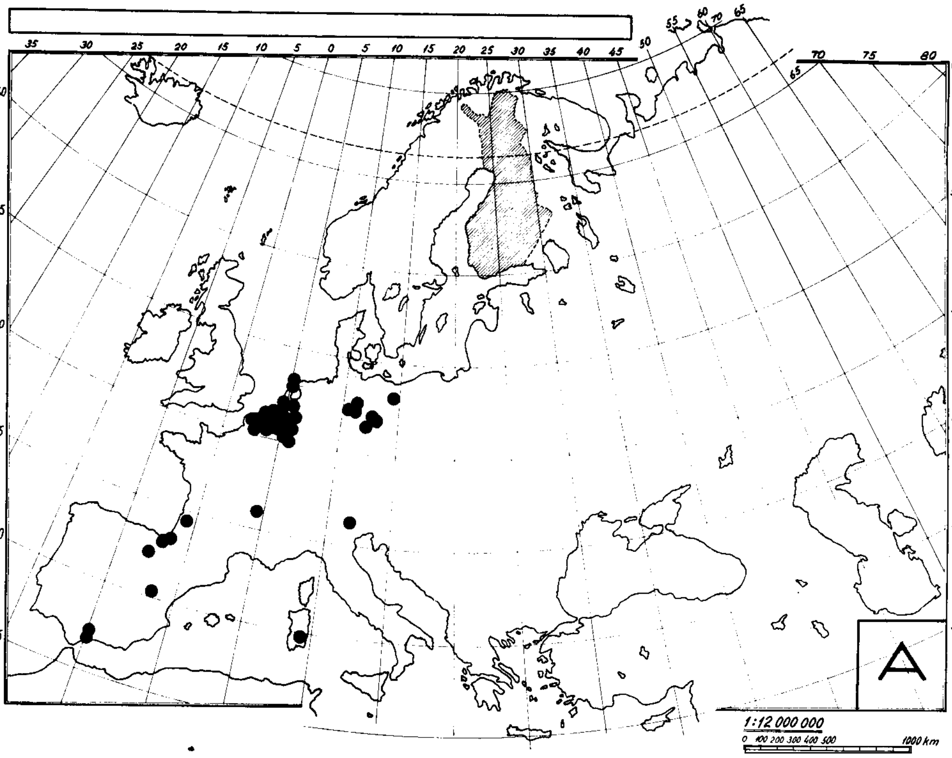
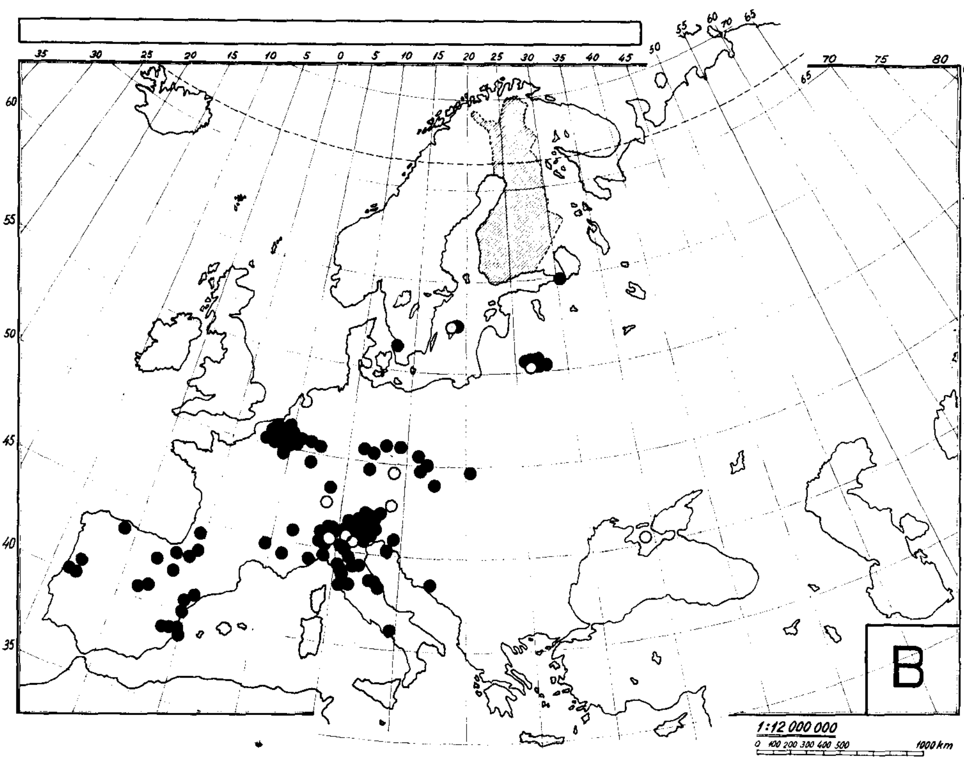


FIG 1. Recoveries of Siskins ringed in Norway (A) and Finland (B) (●) and the recoveries of Siskins ringed in Finland in the winter of 1963/64 (○). (*Norjassa (A) ja Suomessa (B) merkityistä vihervarpusista saadut rengaslöydöt (●) sekä Suomessa merkityistä yksilöistä talvikaudella 1963/64 tulleet löydöt (○).*)

TABLE 3. The number of Siskins ringed in Finland and Norway and recovered at different distance during the winter months. (*Norjassa ja Suomessa merkityistä vihervarpusista eri etäisyyksiltä saatujen löytöjen määrä talvehtimiskaudelta kuukausittain.*)

Distance *Etäisyys*	Month *Kuukausi*							
	IX	X	XI	XII	I	II	III	IV
< 500 km	6	3	1	—	1	—	—	1
500—1000 km	—	2	—	1	—	—	—	—
1000—1500 km	—	10	2	—	—	1	2	2
1500—2000 km	2	21	11	6	5	3	2	—
2000—2500 km	3	20	4	7	2	1	2	—
> 2500 km	—	5	5	3	5	3	1	—



most years the distribution of recoveries of wintering Siskins is coherent. Only the recoveries of the winter 1963/64 (Fig. 1B) have come significantly more from the east than those of other years ($t = 2.48$; $p < 0.05$). In some years the wintering area thus seems to move in an east-westerly direction. The distribution over various distances (Table 3) of recoveries made in different months indicates that the Siskin winters on the average about 2 000 kms away from where it was ringed, i.e. Southern Fennoscandia. The most distant recoveries were made in Spain some 3 000—3 350 kms from the ringing localities.

Speed of migration. — For a physiological background to migration it is important to estimate the speed of migration. Ringing recoveries may be very misleading in this respect. Usually it means that the estimate is too low. This is due to the fact that most of the recoveries are made in the wintering area at a time when the birds may already have spent a considerable time there, long after actual migration flight has finished. Thus it seems appropriate to assume that the recoveries of birds during the migration period which have made the fastest flight over the longest distances give a fairly accurate idea of the speed of migration. This is especially so, when there are several of these birds in the material and their range is fairly narrow. The fastest migration flight was performed by a Siskin which in 20 days flew 1 740 km. Seven other birds have achieved almost similar readings flying some 1 600—2 400 km in a month. These eight birds have a speed range of 65—87 km/day, the average speed being 75.5 km/day.

TABLE 4. The number of Siskins per participant per ten census routes in three zoo-geographical regions during the years 1956—68. *(Tutkimuskautena 1956—68 talvilintulaskennoissa kolmella eläinmaantieteellisellä alueella todettujen vihervarpusten määrä laskijaa kohti kymmenellä reitillä.)*

Zoo-geographical area *Eläinmaantieteellinen alue*	Winter *Talvi* -56 /57	-57 /58	-58 /59	-59 /60	-60 /61	-61 /62	-62 /63	-63 /64	-64 /65	-65 /66	-66 /67	-67 /68	-68 /69
SW-Finland *Lounais-Suomi* (LS)	72	16	9	117	28	8	7	8	312	9	60	65	10
Lake-Finland *Järvi-Suomi* (JS)	16	51	14	42	5	14	7	3	118	4	9	8	2
Ostrobothnia *Pohjanmaa* (Pm)	3	6	2	13	7	8	0	0,3	30	9	9	3	3

Obviously the Siskin performs its migration flight fairly fast over a period of approximately one month. The daily distances seem to be fairly short.

Migration losses. — Calculations based on ringing recoveries show that adult mortality in the Siskin is rather high. During the first three months after the ringing date 42.5 % of the ringed Siskins have been recovered. The respective reading for six months is 61.9 %. During the first year 76.2 % of the population is recovered. Only about 4 % of the population reaches an age of two years. About half of the recoveries are of retrapped birds, which tends to give a higher mortality rate than is actually the case. But the error caused by this factor is less important.

Relation of wintering and breeding of the Siskin to seed crop of trees

Fluctuation of wintering population

Winter bird censuses carried out in 1956—68 give a very good idea of the fluctuations in the wintering populations of the Siskin (Table 4). Wintering Siskins have been particularly numerous in Southern Finland during the autumns of 1959 and 1964. They were also more numerous than average in the autumns of 1966 and 1967. The best Siskin winter was 1964/65, when 312 Siskins were recorded along 10 routes in Lounais-Suomi and 118 along 10 routes in Järvi-Suomi. During the second best winter corresponding readings were 117 and 42.

Siskins have been particularly scarce in the early winter in 1958, 1961, 1962, 1963, 1965 and 1968. In Lounais-Suomi and Järvi-Suomi there have always been some Siskins on some routes in the census even in scant years. In Pohjanmaa no Siskins were found in the winter of 1962/63 even though there were 59 census routes in the region. The maximum extent of the wintering area of the Siskin in Finland is shown in Fig. 2., which gives the figures for the most abudant winter 1964/65. Further north the Siskin has never been recorded in the winter bird censuses. The winter distribution of the Siskin in good years seems to correspond to its regular breeding range in Finland, of which MERIKALLIO (1958) has given a good picture.

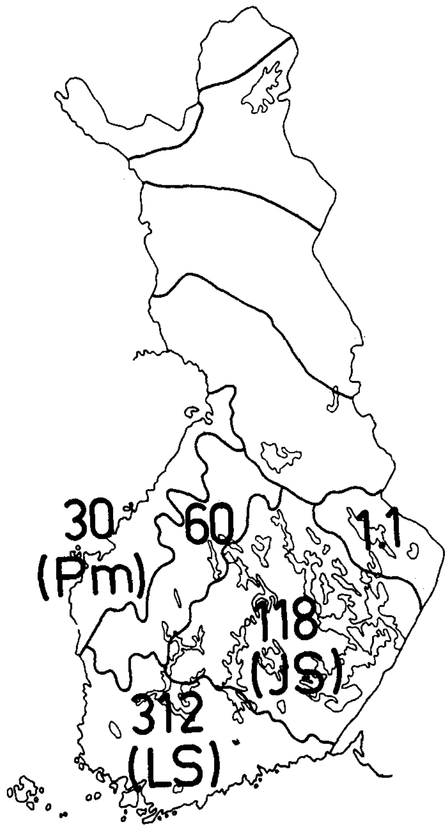


FIG. 2. The number of siskins per participant on ten census routes during the abundant wintering period of 1964/65. (*Vihervarpusten esiintymisarvot talvilintulaskennoissa laskijaa kohti kymmenellä reitillä runsaimpana talvehtimiskautena 1964/65.*)

Wintering success

Some idea of the winter movements of Siskins may be obtained from the control censuses carried out in February—March. More systematic control censuses have been available only since the winter of 1964/65. In that year the wintering population of the Siskin was particularly abundant. The Helsinki routes yielded 2 076 Siskins in the actual census. Two months later the control census on the same routes produced only 145 Siskins or 7 % (HILDÉN 1965). During the exceptionally cold winter of 1965/66 when there also was plenty of snow, only 113 Siskins were recorded on all the census routes (245), dropping to 29 or 25.7 % two months later (HILDÉN & KOSKIMIES 1969). In the winter of 1966/67 the wintering population was fairly numerous. On the Helsinki routes 134 Siskins were recorded in the actual census (HILDÉN & MIKKOLA 1967). The control census produced 114 Siskins or 85 %. Wintering was fairly abundant even in 1967/68 with 481 Siskins on the Helsinki routes in the actual census (HILDÉN & MIKKOLA 1968) but the control census produced only 7 or about 1 % of them.

There are considerable differences between the numbers of Siskin in the actual winter census and in the control census, the percentage varying between 1 and 85 %. The wintering Siskin population was most succesful in the winter of 1966/67, when the birch had a very good seed crop the preceding autumn and even the spruce produced a better than average crop. Even though quite a lot of Siskins remained in Finland in the autumn of 1967, they moved southwards later, as the control census produced only 1 % of the original number. The main cause for the disappearance of the Siskins may have been lack of food. The seed crop of the birch was good, but not as good as in the autumn of 1966. The seed crop of the spruce was average and that of the pine a little better than average. Wintering Siskins seem to survive rather well, as in the very cold winter of 1965/66 the control census produced 26 % of the original number. During that winter the seed crops were worse than average with only the spruce producing a slightly better than average crop, so the wintering population was rather small even in December.

TABLE 5. The cone crop of the spruce during 1956—68 in three zoo-geographical regions according to autumn crop investigations. Categories 0—5. *(Kuusen käpysatoarvot tutkimuskaudella 1956—68 kolmella eläinmaantieteellisellä alueella syksyisten satotiedustelujen perusteella. Asteikko 0—5.)*

Zoo-geographical area *Eläinmaantieteellinen alue*	Year *Vuosi* 1956	-57	-58	-59	-60	-61	-62	-63	-64	-65	-66	-67	-68
SW-Finland *Lounais-Suomi* (LS)	3.1	1.4	1.7	2.1	3.1	2.2	1.6	0.8	4.2	2.2	1.2	4.2	1.3
Lake-Finland *Järvi-Suomi* (JS)	2.7	1.2	2.0	1.5	3.5	2.0	1.3	0.8	2.5	3.2	1.4	3.3	1.3
Ostrobothnia *Pohjanmaa* (Pm)	2.4	1.4	3.0	1.7	2.9	1.9	1.8	1.0	2.3	3.1	2.1	3.7	1.9

Fluctuation of seed crops

For the spruce and the pine the crop details collected by the Forest Research Institute from all over Finland were available. In these the cone crop of conifers, which also is a good indicator of the seed crop, is classified into six categories 0—5. The theoretical mean is 2, so seed crops of more than 2 may be considered better than average, while those below 2 are lower than average. Although the crop figures of the pine have been included in the statistical analysis, it may be unnecessary to deal with them here, since it has no effect on the wintering of the Siskin. Table 5. gives the cone crop of the spruce for the study period in all the zoo-geographical regions concerned. The data show, that the crop doesn't vary very much between different regions during one autumn, but there are considerable differences between the different years. Because of the method of collecting these data, it is never possible to obtain the theoretical minimum even in very bad years nor the maximum in good years. Thus we have to consider figures around 1 as indicators of very bad cone years and correspondingly figures around 3—4 as indicators of a very good crop. The table shows that the spruce had a very scant cone crop in the autumns of 1957, 1962, 1963, 1966 and 1968. A fairly good crop was produced in 1956, 1960, 1964 and 1967.

The above data are lacking in one very important biological aspect. The method used obliterates the actual great variation in the material. In other ways the material corresponds better with the winter bird census results obtained by a similar method. One may get a true idea of the great annual fluctuation in the seed crop of the spruce from the data on seeds shed per square metre. Unfortunately there is only one sample plot from which these data are available for the whole period 1956—68. The great random variation in this material makes it doubtful for a multiple regression analysis, so this has not been carried out. Table 6. shows the crop figures of the spruce for five sample plots in Southern Finland. These data show, that the annual seed crops in different plots are of roughly the same category, but there may be even 1 000-fold differences between different years on the same plot. When comparing the data in Tables 5. and 6., one must remember that the seeds are ripe in the cones in the autumn but they are not shed until the following February—April. This is why the seed crops of 1968 have been compared with the cone crops of 1967. This comparison makes the data coherent.

There are no seed crop figures for the birch covering the whole of Finland, but there are data for the number of seeds shed per square metre on the sample plots. These are complete for the whole period from only three plots. The present material is shown in Table 7. When using the seed crop data of the birch in the multiple regression analysis as independent variables, the data obtained from sample plots had to be used, as is explained elsewhere. The data in Table 7. show that the seed crops of birch also are fairly coherent in different plots in the same year, but there may be very great differences between the years even in one single plot. The seed crop of the birch seems to have been particularly scant in the autumns of 1956, 1958, 1960, 1962, 1963,

TABLE 6. Seed crops of the spruce at five Forest Research Institute sample plots in 1956—68. The figures indicate number of seeds shed/sq. m. (*Kuusen siemensadot viideltä Metsäntutkimuslaitoksen koealalta tutkimuskaudella 1956—68. Luvut ilmoittavat varisseiden siementen määrän/m².*)

Year *Vuosi*	Bromarv Sample plot *koeala 1*	Siilinjärvi Sample plot *koeala 544*	Kuorevesi Sample plot *koeala 35*	Tuusula Sample plot *koeala 30*	Padasjoki Sample plot *koeala 3*
1956	. .	. .	. .	31	3
1957	. .	. .	. .	1187	52
1958	. .	. .	. .	22	15
1959	. .	. .	. .	18	127
1960	. .	. .	. .	58	43
1961	143	291	. .	196	704
1962	4	17	. .	206	12
1963	117	29	. .	39	12
1964	9	3	. .	2	10
1965	500	6	1	671	384
1966	30	1140	216	42	58
1967	103	184	41	56	. .
1968	1034	1057	709	2979	. .

1965, and 1968. Good crop years were 1957, 1959, 1961, 1964, 1966, and 1967.

Even on the basis of this small amount of data it is possible to distinguish a tendency for the seed crops to be synchronous over vast areas. Thus the seed crops of the spruce in different sample plots show on the average a fairly good correlation. ($r = 0.54$; $p < 0.05$; $df = 11$). Correspondingly, there is a slight correlation between the seed crops of the birch in Lapland and Järvi-Suomi ($r = 0.35$; $p < 0.20$), or even a very high correlation ($r = 0.65$; $p < 0.02$) depending on which sample plots one chooses. Between the sample plots in southern Finland the correlation is very high ($r = 0.69$—0.85; $p < 0.01$).

TABLE 7. Seed crops of the birch at three Forest Research Institute sample plots in 1956—68. Number of seeds shed/sq. metre. (*Koivun siemensadot kolmella Metsäntutkimuslaitoksen koe-alalla tutkimuskaudella 1956—68. Luvut ilmoittavat varisseiden siementen määrän/m².*)

	Vilppula Sample plot *koeala 153*	Padasjoki Sample plot *koeala 162*	Rovaniemi Sample plot *koeala 31*
1956	2590	205	1180
1957	44480	3880	20170
1958	1230	3580	630
1959	31155	66950	7820
1960	4990	8030	3607
1961	49495	102000	11990
1962	1346	1885	3557
1963	587	2100	323
1964	24616	58618	11750
1965	5916	3888	520
1966	57037	31300	1374
1967	18421	29902	36560
1968	3290	1805	160

Different species of trees also seem to be somewhat synchronous. Some difficulty in this comparison is presented by the fact that the seeds of different species of trees take different times to ripen and different species shed their seeds at different times of the year. The birch sheds its seeds in July—September, although in good seed years some seeds remain in the trees even in winter. The seed crop of the birch probably correlates well with that of the alder, which sheds its seeds in midwinter. Furthermore, a good seed crop of the birch is usually followed by a good seed crop of the spruce the following year, and this is shed in late winter the year after that. Many grasses and berries also follow the same rhythm, so in years of good seed crops food is available in different plants all through the winter (see SVÄRDSON 1957).

Fluctuation of breeding population

According to HAAPANEN (1966) the breeding population of the Siskin in 1959—63 varied in Lounais- and Järvi-Suomi in spruce stands between 10—40 pairs per square km and in pine stands between 10—30 pairs per square km. According to his study, the Siskin is almost as abundant in pine stands as in spruce stands. In pine stands, however, its density fluctuations do not match the fluctuations in the pine seedcrop, but show the same trend as those in spruce stands.

According to HAAPANEN's results the abundance of breeding Siskin shows an almost linear correlation to the cone crop of the spruce. It is surprising to find that HAAPANEN presents a figure where even with a fairly low seed reading of 1.3 a breeding density of 40 pairs/sq. km, which is the highest recorded density would be reached. That summer (1961) both spruce and pine had only an average crop whereas the birch had a very good seed crop. A particularly small breeding population seems to have been recorded in 1960 and 1963. In the spring of 1960 and 1963 both conifers and the birch had a seed crop close to the minimum. The breeding population was abundant even in 1965. Linkola (in litt.) states that the Siskin that year in the spruce stands of central Finland was, in places, the most abundant species. The Siskin was very abundant in 1965 even in the Helsinki area according to the author's own observations. That spring the spruce had the best seed crop of the whole period, while the seed crop of the pine and the birch was lower than average. In the spring of 1965 the seed crop of the spruce was very good in the whole of Finland, and Siskins seem to have bred further north than usual. According to HIETAKANGAS (1967) the Siskin is an exceptional bird at 67° N (Meltaus Game Research area), being recorded there e.g. in the summer of 1962. In 1965 I found a stationary pair of Siskins in Utsjoki, Karigasniemi, between 29.6.—4.7., and two single birds flying over, probably neihter of the stationary birds. There seem to have been fairly or very abundant breeding populations of Siskins in 1959, 1961 and 1965, years of better than average seed crop of conifers. In such years the Siskin also tends to nest further north. Even SVÄRDSON (1957) mentions some examples of this. Breeding areas may move even over a wider area. Some foreign recoveries of Finnish birds in the breeding season point in this direction. Of birds ringed as adult migrants in Finland in October that year 1967, and so had probably nested in eastern Fennoscandia two were recovered in Southern Norway in the following breeding season. One of them was recovered on 5.6.1968 in Rendahl, Hedmark, the other on 5.7.1968 in the same area. Similarly, one bird ringed in Finland in June 1961 was recovered on 16.7.1963 in Sweden, Småland, Sävsjö.

Dependence of wintering on the seed crop of trees

The dependence of the number of wintering Siskins on the seed crop of trees was studied by means of multiple regression analysis using as dependent variables the number of Siskins per participant per 10 routes each winter in the three zoo-geographical regions (LS, JS and Pm). The seed crop data for the spruce and the pine in the same regions were used as independent variables. In these regions the data from the bird census and the seed crop investigation correspond very well with each other. There are no similar data for the seed crop of the birch, so here the independent variable was the reading of seeds shed per sq. metre on one Forest Research Institute sample plot in each region. Biologically this variable is more correct than the other seed crop data based on investigations, but since it is obtained by a different method it is not as suitable for this purpose.

The number of wintering Siskins seems to be very dependent on the seed crop of the spruce ($r = 0.35$; $p < 0.05$; $df = 35$); the degree of correlation is even higher with the square of the spruce seed crop ($r = 0.41$; $p < 0.05$; $df = 35$). A linear regression model shows the dependence of the number of wintering Siskin (y) on the seed crop of the spruce (x), $y = -7.7 + 10x$, the coefficient being statistically reliable ($t_b = 2.2$; $p < 0.05$; $df = 35$) and the explanation is fairly good, 34.4 %. The model is reproduced in Fig. 3. In fact the dependence must be curvilinear, since the squares of the seed crop figures correlate better with the number of wintering Siskin than the actual seed crop figure. A corresponding model was statistically unreliable because of the great random variation.

The number of wintering Siskins did not correlate in any way with the seed crop of the pine ($r = 0.09$; $p > 0.10$; $df = 35$). On the other hand a correlation with the seed crop of the birch is fairly obvious ($r = 0.28$; $p < 0.10$; $df = 35$), although it is not statistically significant. The different methods used

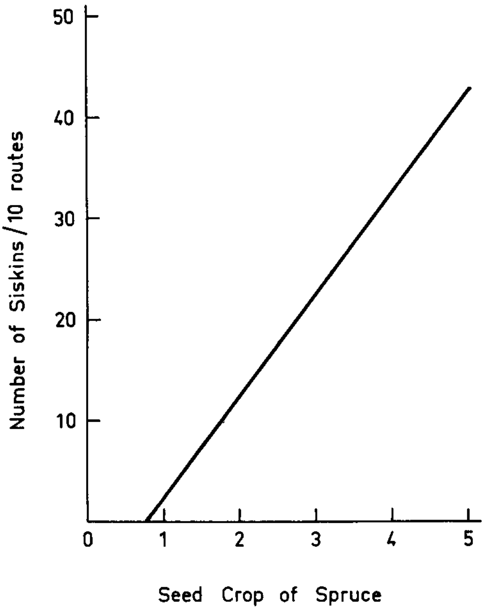


FIG. 3. The dependence of the number of wintering Siskins on the cone crop of the spruce. (*Talvehtivien vihervarpusten määrän riippuvuus kuusen käpysadosta.*)

for obtaining the variables makes the model weaker. Similarly a linear model $y = 8.9 + 0.29x$ is weak, giving only a 25.4 % explanation.

On the basis of the regression models one may deduce, that the number of wintering Siskins is highest during those autumns when both spruce and birch have a good seed crop. This was the case in 1964 and 1967.

Timing of nesting

A survey by v. HAARTMAN (1969) conducted on 39 nests found in southern Finland (60°—62°N) indicates that most clutches are to be found in the middle of May. 16 of the 39 nests found were of the period 11—20.5. The earliest nest found was one from Pori (LS) on 17.4. consisting of 4 unincubated eggs. Clutches have been found as late as 17.7., but according to v. HAARTMAN there are relatively few second broods.

In the spring of 1965 I found the Siskin to be much more abundant than usual in the vicinity of Helsinki. In early April several birds were seen collecting nest material, but since no special attention was paid to this at the time, records on the timing of nesting were only sporadic. But the nest-building activity observed on 3—7.4, and the six nests found on 3—8.5. where the parents were carrying food indicate that the breeding of Siskins that year was about a fortnight earlier than the average.

That very year BJØRNSON-BERGER (1968) reports a nest found further south in Telemark, Norway as early as 19.3.1965 with three eggs. The same author states that there were several nests in the area at that time. GEYR VON SCHWEPPENBURG (1930) has also found Siskins nesting earlier than normal in the spruce stands in Hochgebirge in the spring of 1930. He uses the term winter-nesting. The same author found a nest with three eggs as early as 9.3. During the following days he found four more nests, but was unable to check the number of eggs in them. There were no more than three eggs that year in the nest he found first. He also mentions that the parent birds ate spruce seeds.

These records indicate that the Siskin some years — probably those years when the spruce has a good seed crop as in 1965 tends to nest earlier than usual. The number of eggs in these early nests seems to be very much smaller than average, though the material is scant. According to v. HAARTMAN (1969) the most frequent number of eggs for the Siskin in Finland is 5 (n = 26/39) and the next is 4 (n = 10/39). Nests with three eggs are rare.

In good seed crop years nesting seems to continue later than usual. I observed some nests in the Helsinki area in 1965. On 20—26.7. I still found three nests where the parents were carrying food. Nests with young so late may indicate a second brood.

Dependence of wintering on autumn weather

The dependence of the size of the wintering population of Siskins on the autumn weather was studied by means of multiple regression analysis.

There is a great random variation in the material, but even so it seems obvious that the weather factors have only a marginal effect on the number of wintering birds. The snow cover during the different months had no effect on wintering whatsoever, either separately or combined. Of the temperature variables only the mean maximum temperature of October showed a statistically significant correlation to the number of wintering Siskins ($r = 0.29$; $p < 0.05$; $df = 37$). This seems to indicate that high maximum temperatures in the migration season inhibit the start of migration and influence the number of Siskins which stay for the winter. Since the effect of the weather variables is so slight, there is no need to deal further with the temperature data. It may be mentioned that the three highest mean maximum temperatures were recorded for the Octobers of 1961 (+11.7°C), 1964 (+10.7°C) and 1967 (+11.2°C) as measured in Helsinki. Correspondingly the three coldest Octobers were 1956 (+7.7°C), 1960 (+6.5°C) and 1966 (+8.1°C). When comparing these with the statistics in the wintering table there seems to be only a weak correlation. This correlation is based, however, on the combined readings of the three regions so it may be considered real. On the other hand the variation in temperature readings for different regions is quite different from the variation in their bird populations, which may cause some bias in the model.

Discussion

The start and timing of autumn migration of the Siskin depends on the seed crop of the birch according to SVÄRDSON (1957). He presents a large amount of migration material collected at the Ottenby observatory in 1947—55. According to him migration in the good birch seed crop year 1954 started very late, only towards the end of September. Correspondingly in bad seed crop years for the birch, like 1949 and 1955, migration started in early September. The culmination of migration in late September is in accordance with the results presented here. But it was not possible to demonstrate statistically any significant differences between the years in the Signildskär migration material. Neither does the material presented by BERNHOFT-OSA (1964) from the Revtangen observatory in Norway fully agree with SVÄRDSON's (1957) material. Common to all three sets of material is the fact that when the migrating population has been a small one, migration seems to have started late. In years of abundant populations migration seems to have started earlier. It may be possible that the population is heterogeneous as to the timing of migration, and the birds migrating early are easier to observe in years of abundance, which may cause some bias in the material. The apparent regularity of the start of migration in Finland leads us to believe that a part of the Siskin population regularly tends to migrate annually at the same time.

The size of the Siskin population observed at the observatories in different years seems to vary very much. This is in accordance with earlier studies (SVÄRDSON 1957, BERNHOFT-OSA 1964). As may be seen even in the material presented by SVÄRDSON (1957), the migrating populations are small in those years when the birch has a poor seed crop. The results in the present paper show that this rule cannot be generalised. The breeding population of the Siskin seems to depend very much on the seed crop of the spruce (see HAAPANEN 1966), so it would be natural to assume that migrating birds are abundant in those years, when the breeding population has been a strong one.

SVÄRDSON (1957) also refers to the inhibiting effect of weather on the start of migration. The results of the present study indicate that the maximum temperatures of October show a positive correlation to the number of wintering Siskins. This indicates that exceptionally good weather during the migration season may cause a complete inhibition of migration.

After the winter bird censuses at Christmas time the numbers of Siskin seem to decrease in January and February. HILDÉN & KOSKIMIES (1969) consider this a kind of migration: "They are physiologically prepared for migration throughout the winter and move from one place to another as food becomes scarce." The results of the present study show that a great part of the Siskin population regularly migrates in a relatively short period of time, about a month, to central and southern Europe. The daily distances are fairly short as with the Redpoll (see ERIKSSON 1970), which may be due to the fact that the Siskin, like the Redpoll (EVANS 1966), does not accumulate any fat deposits. This may mean, that when the days grow shorter in autumn acquiring the necessary energy becomes more difficult and actual migration flight becomes impossible. ABS (1964) has weighed migrating Siskins in Germany. His extensive material reveals that the Siskins are at their heaviest ($\overline{X} = 13.5 \pm 0.2$ g) in December and they are significantly heavier then than in October ($\overline{X} = 12.8 \pm 0.1$ g). This may be caused by the fact, suggested by EVANS (1966) for the Lesser Redpoll, that during the short winter day the bird collects more food in a given time, which makes the weight increase during the day greater than in autumn. This is possible only in very good seed crop years.

The results of the present study indicate that the wintering of the Siskin depends on the seed crop of the birch and the spruce. The dependence is statistically strong. A stronger correlation to the exponential function of the seed crops indicates that the models are in fact curvilinear and rise steeply. This means that although a small number of Siskins try to winter every year the number of wintering Siskins rises only when the seed crop is better than average. A similar correlation to the seed crop of the birch has been demontsrated for the Redpoll (ERIKSSON 1970).

The Siskin (SVÄRDSON 1957, HAAPANEN 1966), as well as the Redpoll (PEIPONEN 1967) have been shown to nest abundantly in areas with a good seed crop of the spruce. The material presented here completes the suggestion put forward by SVÄRDSON (1957) that the Siskin moves its breeding areas in accordance with seed crops and it may thus breed further north than usual. The movement of the breeding range has been demonstrated even by ringing recoveries. HOLSTEIN (1934) also found the Siskin nesting in Denmark in 1934 after a period of abundant wintering. A clear movement during the breeding season, as demonstrated for the Redpoll (PEIPONEN 1957), has not been shown to exist in the Siskin. But the results indicate that in years with a good seed crop of the spruce the Siskin may start nesting earlier and finish later than in other years. Such a lengthening of the breeding season is common with other seedeaters as well (NEWTON 1967) and it has been shown to exist in the Redpoll (HILDÉN 1969).

Ringing recoveries show that the wintering areas of the Finnish and Norwegian populations of Siskin are partly separate, although they have a common wintering area in Belgium and Holland. Both populations seem to follow their direction of migration very closely. In some years birds ringed in Finland seem to winter further east than usual. This may result from the fact that part of the Finnish population of Siskins migrates across Sweden to western Europe and another part east of the Baltic states to southern Europe. In some years the main part of the Finnish population seems to fly along the eastern route which takes them more to the east for the winter.

The timing of the autumn migration of the Siskin and its dependence on seed crops is very similar to that of the Redpoll (ERIKSSON 1970). Both these species have a short life-span and great mortality during migration and wintering according to ringing recoveries. Thus it seems natural to assume that in exceptionally good seed crop years it is advantageous to winter in the breeding area. Because of physiological factors relating to supply of energy the Siskin is able to resort to this method only when an abundant supply of seed is guaranteed for the whole winter. This condition is best filled when the trees with an abundant supply of seed, i.e. the birch and the spruce, have a simultaneous maximum crop. An exceptionally good crop from either one of these trees naturally diminishes the importance of the other, so the trees may partly compensate each other in this respect. A rational biological basis for this is provided by the tremendous annual differences in seed crops. For the same reason the great variations in the density of the breeding population of the Siskin and the changes in breeding areas are accounted for by the food economy of the population.

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Summary

The material on wintering Siskins was obtained from winter bird censuses carried out during the period 1956—68. To homogenize the material, census routes exceeding 20 km in length were left out. The census results were grouped according to zoogeographical regions, but for the statistical analysis only Lounais-Suomi, Järvi-Suomi and Pohjanmaa were used. By means of multiple regression analysis it was found that neither the length of the route nor the number of participants in each census had any significant effect on the results. Minimum, maximum and mean temperatures for September, October and November and the number of days with snow cover were used as independent variables. Furthermore, wintering was explained by the seed crop records for the spruce and the birch. Migration routes were studied on the basis of recoveries of birds ringed in Finland and Norway and the fluctuations in the migrating population were estimated on the basis of migration records at the Signilskär bird observatory during five autumns and by the number of Siskins ringed in Finland and Norway.

It was shown, that the migration of the Siskin regularly reaches its peak at the end of September, and there were no statistically significant differences between different years in this respect.

The material indicates that the migrating populations of Siskins in the autumn in Finland and Norway fluctuate indepently of each other, although there was one common peak in 1965. Annual differences in the size of the migrating population are fairly large.

Ringing recoveries show that Finnish and Norwegian Siskins differ from each other as to their wintering areas. The Norwegian populations winter further west than the Finnish ones. Finnish Siskins seem to migrate along two routes.

Actual migration seems to take place in a fairly short period of time, approximately one month. The daily distances are on the average some 75 km. Adult mortality during migration is great, since about 62 % of the population is recovered during the first six months after ringing. During the first year about 76 % are recovered.

Exceptionally few Siskins wintered in Finland during the autumns of 1958, 1961, 1962, 1963, 1965 and 1968, whereas the wintering population in 1956, 1959, 1964, 1966 and 1967 was larger than usual. The wintering populations seem to survive well.

It is shown that there are enormous annual

fluctuations in the seed crop in the birch an the spruce. It was found that the seed crops of trees in different regions fluctuate synchronously and that the seed crops even of different species of trees are synchronous. This means that in good seed years food is available throughout the winter as the birch sheds its seeds in the autumn, the alder in winter and the spruce in spring. It was shown that the number of wintering Siskins is linearly correlated with the seed crop of both the birch and the spruce, thus the number of wintering birds begins to rise significantly only when the seed crop is very much better than average. It was also found that there exists a positive correlation between the maximum temperature of the migration season, i.e. October and the number of wintering Siskins.

It was found that during good seed crop years the Siskin may nest further north and earlier than usual. It was claimed that a good seed crop inhibits migration for some Siskins but the majority of the population follows a regular migration pattern. Wintering areas may vary a little although the Siskins migrate very regularly in the same direction. Nesting areas may also change from year to year.

Selostus: **Vihervarpusen** *Carduelis spinus* **syysmuuton ja talvehtimisen ekologiasta**

Talvehtivien vihervarpuskantojen vaihteluita kuvaava aineisto on saatu tutkimuskaudella 1956—68 suoritetuista talvilintulaskennoista. Reittien yhdenmukaistamiseksi on yli 20 km:n reitit jätetty aineiston ulkopuolelle. Reittitulokset on ryhmitelty eläinmaantieteellisen aluejaon mukaan, mutta tilastollisiin tarkasteluihin on otettu vain parhaiten tutkitut alueet Lounais-Suomi, Järvi-Suomi ja Pohjanmaa. Regressioanalyysillä todettiin, ettei reitin pituuden tai osanottajamäärien vaihteluilla ole merkittävää vaikutusta tuloksiin. Syksyn säätilaa käytettiin myös talvehtimisen selittämisessä. Niinikään selitettiin talvehtimista käyttäen hyväksi Metsäntutkimuslaitoksen satotiedusteluista ja koealoilta saatuja kuusen ja koivun siemensatotietoja. Muuttoreiteistä saatiin käsitys Suomessa ja Norjassa merkityistä linnuista tulleiden rengaslöytöjen avulla ja muuttavan kannan vaihteluita on arvioitu Signilskärin lintuasemalla viitenä syksynä tehtyjen muuttohavaintojen perusteella sekä laskemalla Suomessa ja Norjassa merkittyjen vihervarpusten määrä 10 000 rengastettua lintua kohti.

On osoitettu, että vihervarpusten muuton kulminaatio sattuu vuosittain hyvin täsmällisesti syyskuun lopulle eikä tässä ole eri vuosien välillä tilastollisesti merkitseviä eroja. Ei myöskään muuton alkamisajankohtien välillä voi todeta tilastollisia eroja.

Aineisto osoittaa, että Norjan ja Suomen syksyiset muuttavat vihervarpuspopulaatiot vaihtelevat runsaudeltaan toisistaan riippumattomasti, vaikka yhtäaikainen huippu sattuu vuodelle 1965. Vuotuiset erot muuttavan kannan suuruudessa ovat melkoiset. Rengaslöytöaineisto osoittaa, että Suomessa ja Norjassa merkityillä vihervarpusilla on merkitsevästi toisistaan poikkeavat talvehtimisalueet. Norjan populaatiot talvehtivat lännempänä kuin Suomessa merkityt. Suomessa merkityt linnut näyttävät muuttavan kahta reittiä, toisaalta Skandinavian eteläosien kautta Belgiaan ja Hollantiin ja toisaalta Baltian kautta Keski-Eurooppaan ja Pohjois-Italiaan. Joinakin vuosina itäinen reitti on ainoa käytetty ja johtaa silloin merkitsevästi eriävään, itäisempään talvehtimispaikkaan. Varsinainen muutto näyttää tapahtuvan verraten lyhyessä ajassa, noin kuukaudessa. Päivittäiset matkat näyttävät olevan keskimäärin noin 75 km. Kuolevuus on muuttoaikana suuri, sillä noin 62 % populaatiosta tavataan ensimmäisten kuuden merkinnän jälkeisen kuukauden aikana. Ensimmäisen vuoden aikana löytyy noin 76 %.

Erityisen niukasti on vihervarpusia talvehtinut tutkimuskaudella syksyinä 1958, 1961, 1962, 1963, 1965 ja 1968 kun taas syksyinä 1956, 1959, 1964, 1966 ja 1967 on lintuja jäänyt talvehtimaan keskimääräistä enemmän. Talvehtivat kannat näyttävät yleensä menestyvän hyvin, vaikka kevään tarkistuslaskennoissa tavataan lintuja vähemmän kuin joululaskennassa. Lintujen arvellaan, enää varsinaisesti muuttamatta, siirtyvän etelämmäksi siementen talvella vähentyessä.

Osoitetaan siemensatotietojen avulla, että eri vuosien välillä on sekä koivun että kuusen siemenrunsaudessa suunnattomat erot. Todetaan eri alueiden seuraavan synkronisesti toisiaan ja että synkronisuutta esiintyy myös eri puulajien välillä. Tämä merkitsee, että hyvinä siemenvuosina on ravintoa koko talveksi koivun karistaessa siemenensä syksyllä, lepän talvella ja kuusen keväällä. On osoitettu talvehtivien vihervarpusten määrän riippuvan lineaarisesti sekä kuusen että koivun siemensadon määrästä niin, että talvehtijoiden määrä alkaa merkittävästi kohota vasta kun siemensato on huomattavasti keskinkertaista parempi. Runsaimmin on talvehtijoita silloin kun molemmat puulajit ovat maksimisadossa, vaikka puut epäilemättä voivat jossakin määrin korvata toisensa. Todetaan myös muuttoajan, lokakuun maksimilämpötilan olevan positiivisesse korrelaatiossa talvehtijoiden määrän kanssa.

Todetaan lajin voivan hyvinä siemenvuosina pesiä tavallista pohjoisempana ja myös tavallista aikaisemmin keväällä. On esitetty näkemys, että metsäpuiden runsas siemensato estää syysmuuton tapahtumisen osalla vihervarpusista kun taas osa populaatiosta muuttaa säännöllisesti. Talvehtimisalueet voivat jonkin verran vaihdella vaikka laji näyttää erittäin uskollisesti noudattavan samaa muuttosuuntaa. Myös pesimäalueet voivat vaihdella vuodesta toiseen.

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