Spring flocking of the Chaffinch *Fringilla coelebs* and the Brambling *F. montifringilla* in northern Finland

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The spring flocking of the Chaffinch and the Brambling was studied at Utajärvi (64°57'N, 26°58'E) in April–May during 6 successive years (1967—1972). The present data cover 12648 individuals from 986 species or mixed flocks and 1233 single Chaffinches and 405 single Bramblings.

Chaffinches arrive significantly earlier in spring than Bramblings. In the observation years, the average migratory period lasted from 17 April till 19 May for the former species and from 2 till 26 May for the latter. The results of this study support the notion that several ultimate and proximate factors together influence the flocking behaviour of birds. In April–May, Chaffinches usually occurred single or in small groups and only seldom in large flocks. In contrast, Bramblings were seldom single, usually occurring in greater groups. The highest numbers of flocks were seen during the peak of the spring migration. The flocks were typically migratory or foraging groups.

Habitat selections by the Chaffinch and the Brambling resemble each other greatly. Migratory flocks of both the species utilized the same habitats in the area, but chiefly at different times of the spring. The mean size of pure Chaffinch flocks was 5.0 (N = 479) and that of Brambling flocks 12.9 (N = 412). If the single birds were included, the mean group size was 2.1 for the Chaffinch and 7.0 for the Brambling. Furthermore, the average size of mixed flocks of the two species was 36.6 individuals (N = 95). Therefore, according to the size and the behaviour of spring flocks in the same environmental conditions, the basic sociability appears clearly more notable among Bramblings than among Chaffinches.

Generally, flocking may facilitate protection from predators and enhance foraging efficiency and social stimulation. The social tendency of the species reflects the flocking behaviour and the development of social organization for the nesting time. Chaffinch males try to secure a breeding site in the familiar area for the future season. Further, the flocking of Bramblings aids in the use of the local food supplies and the synchronization of reproductive activities. For the above reasons, there is a distinct separation between the Chaffinch and the Brambling in social ecology during the prenesting time. Coexistence and competition between the species on a sympatric breeding ground were briefly discussed.

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Introduction

The flocking behaviour of birds varies from species to species (e.g. Miller 1922, Moyniham 1962, Buskirk 1976). The ultimate factors influence the evolution of flocking and the proximate factors govern the dynamics of flocks (e.g. Pulliam 1973, Wilson 1975, Moriarty 1976, Caraco & Pulliam 1980, Wilkinson 1982). The flocking behaviour reflects the sociability of the species (Emlen 1952, Wynne-Edwards 1962, Wilson 1975). There are often changes in social behaviour throughout the year, because several species which feed and form large flocks in winter disperse to nest on their breeding sites in spring (e.g. Crook 1965, Lack 1968, Pulliam & Millikan 1982). However, there is a basic gregariousness which remains also in territorial birds. Darling (1938, 1952) has shown that social attraction may also be an essential element of territorial display in relatively dispersed non-colonial species (see also Kalela 1953, Werth 1960). Furthermore, adapted social organization is very important for the breeding success of the species (e.g. Emlen & Oring 1977, Wiens & Johnston 1977, Oring 1982).

At high latitudes with brief summers and unpredictable breeding environments, birds must often begin to nest very rapidly. Therefore, flocking and dispersal of individuals or changes in social behaviour may take place sensitively according to the local conditions in spring (see Pulliam & Millikan 1982). Thus it is useful to compare related species, in order to gain insight into selection pressures influencing their social organizations during the nesting time and in the annually changing environmental conditions.

The Chaffinch *Fringilla coelebs* and the Brambling *Fringilla montifringilla* are closely related and very common in the southern part of N Finland (e.g. Järvinen & Väisänen 1979, Mikkonen 1983d). They are migratory species which are usually in flocks in winter and territorial at the breeding time (e.g. Palmgren 1932, Bergman 1952, 1953, Marler 1956a, Udvardy 1956), but their strategies of selecting breeding grounds are quite different (Mikkonen 1983a). The former is a highly site-tenacious species, while the latter is not. Further, earlier investigations on Chaffinch and Brambling flocks are very scant (e.g. Bergman 1949, 1966, Marler 1956a, Gruys-Casimir 1965, Newton 1972).

For the above reasons, the Chaffinch and the Brambling provide good opportunities for comparing the flocking behaviour of a southern and a northern migrant in a sympatric breeding ground during the prenesting period. In this work, I therefore examined the intraspecific and interspecific variations in the spring flocking of the two *Fringilla*-species in order to interpret the significance of the flocking and the possible modifying effects of environmental factors on it before true nesting.

Table 1. Different biotopes, habitats and dominant tree species in the study area at Utajärvi, Juorkuna. The habitats were classified according to vegetations (age and tree species composition of the forest).

Biotopes	ha	%
Forest	38	56
Wooded bogs	4.5	7
Bushes or meadows	3.5	5
Open fields or yards	22	32
Total	68	100
Habitats along census line (2.8 km)		**%**
Young pine forest		18
Mature coniferous forest		19
Mixed forest		9
Deciduous forest		14
Open fields and yards		41
Total		101
Tree species		**%**
Pine		68
Spruce		15
Birch		13
Other species		4
Total		100

Note: Wooded bogs and bushes or meadows were included in neighbouring habitats.

Materials and methods

Study area. The present work was carried out at Utajärvi, Juorkuna (64°57'N, 26°58'E), in the southern part of N Finland during 1967—1972. The study area, about 68 ha, is bordered by the Juorkuna lake in the north and an open bog in the south. It consists of forests, wooded bogs, bushes or meadows, and open fields or yards as shown in Table 1. Most of the forest land consists of young pine *Pinus sylvestris* forests *(Calluna-Vaccinium* site type) and mature pine or pine-spruce forests *(Empetrum-Myrtillus* site type). Part of the more fertile coniferous forests *(Hylocomium-Myrtillus* site type) are moister. Mixed forests are deciduous-dominated (20—80 % birch or aspen, and the rest conifers) woods. Small areas are covered by stands of pure spruce *Picea abies*, birch *Betula* spp. and aspen *Populus tremula*. Around the fields and on the shores, there are also more luxuriant woods. The most important bushes are willows. Furthermore, *Ribes*-bushes grow near the houses. About one third of the field area is cultivated with cereals and potato, and about two thirds with hay, chiefly *Phleum*. On the yards and at the edges of the fields there grow single trees, such as *Betula pubescens, Sorbus aucuparia,* and *Prunus padus*.

Materials. In the study area, observations were recorded on 986 spring flocks, of which Chaffinch flocks accounted for 48.6 % (N_1 = 479) and Brambling flocks for 41.8 % (N_2 = 412), and mixed flocks of both the species for 9.6 % (N_3 = 95). Simultaneously, 1233 single Chaffinches and 405 single Bramblings were seen. So in 1967—1972, the total number of individuals was 12648, of which flocking birds accounted for 87.0 % (N_1 = 11010) and single birds for 13.0 % (N_2 = 1638). Chaffinches accounted for 36.8 % of the total number of both the finches and Bramblings for 63.2 %, respectively. In the observation years, 22—30 pairs of Chaffinches bred annually and 12—16 pairs of Bramblings began to nest in the study area (see Mikkonen 1983a). Altogether 259 adult Chaffinches and 410 adult Bramblings were ringed.

Methods. The field observations were begun in early April each spring and continued throughout the breeding season. They included direct observations, mist-netting and individual marking of birds. All the Chaffinches and Bramblings noted alone, in species flocks and in mixed flocks were counted on a 2.8 km census line in the study area between 6 and 9 o'clock a.m. Furthermore, the behaviour of flocks was observed at other times of the day. Recognition of the species is quite easy. Also flighting individuals can usually be distinguished by their typical undulating flight, specific calls and colour of the rump (see Marler 1956a, Gruys-Casimir 1965).

Using the colour-ringing method, suggestions could be obtained of the flocking behaviour of local adult Chaffinches and Bramblings in spring. The nesting adult birds were marked both with an aluminium ring and with individual combinations of plastic colour-rings (Mikkonen 1983a).

Temperature, cloudiness, wind direction and strength were recorded during the observations. The daily temperatures shown in the figures and the tables have been recorded at the Pelso Meteorological Station, Vaala (see Mikkonen 1981a). The depth of the snow cover was measured at the Särkijärvi Observation Point of the Meteorological Institute, Utajärvi. The abundances of the pine and spruce cone crops, expressed with an arbitrary scale from 0 to 5, were taken from following issues of Metsälehti: 2/1967, 50/1967, 48/1968, 49/1969, 47/1970 and 51—52/1971. These annual reports were based on studies by the Forest Research Institute.

Statistics. The statistical analyses used have been previously described by Mikkonen (1981a, 1981b).

As a measure of habitat breadth (B') I used a weighted version of Levin's measure (Hurlbert 1978, Smith 1982):

$$B' = 1 / \sum_{i=1}^{r} (p_i^2 / q_i),$$

where p_i is the proportion of habitat i used by a given species, and r is the total number of habitats, q_i is the proportion of habitat i available for use. The formula attains its maximum value (1) when the species uses all the habitats exactly in proportion to their presence. The weighting of habitats by habitat availability is important (e.g. Hurlbert 1978, Alatalo 1981; see also Smith 1982).

To express the degree of overlap (C_{xy}) in habitat utilization between the species x and y, I used the percentage similarity (Hurlbert 1978) recommended by Alatalo & Alatalo (1979).

$$C_{xy} = 1 - 1/2 \left(\sum_{i}^{r} | p_{xi} - p_{yi} | \right),$$

where p_{xi} is the relative frequency of individuals of species x in habitat i and, correspondingly, p_{yi} is the frequency for species y, and these are summed over r habitats. The measure takes on values between zero and one (zero if there is no overlap, one if there is complete overlapping). Lawlor (1980) suggested that such similarity indices are important for testing hypotheses on past competitive pressures on an evolutionary time scale.

Definitions of concepts. The stages of the spring migratory period have been defined by Mikkonen (1981a). A flock is defined here as two or more individuals behaving in an integrated fashion (see also Wing 1941). Species flocks consist of individuals of one species only. Mixed flocks include birds of several species gathered together, in this study Chaffinches and Bramblings only. In the Figure 9, the mean sizes of mixed flocks were calculated when the flocks within below 10 % of individuals of the other species were excluded. Small flocks consist of 2—5 individuals, flocks or great flocks of 6—99 individuals and large flocks of over 100 individuals. Social flocks are characterized by highly integrated behaviour of the whole group.

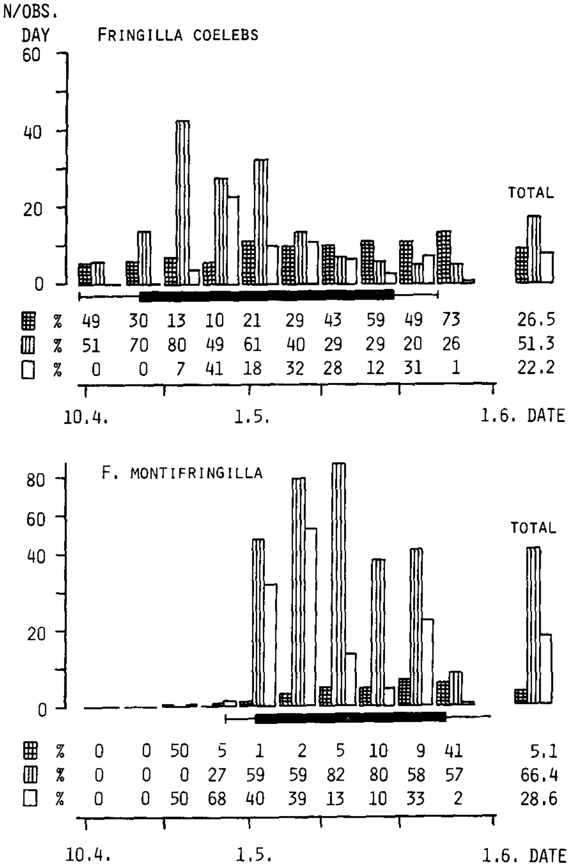

Fig. 1. Numbers and percentages of Chaffinches and Bramblings occurring single (▦) and in species (▥) and mixed flocks (☐) at Utajärvi, Juorkuna, in the springs 1967—1972. The numbers of individuals per observation day were summed in periods of 5 days for the study springs. ▬ = mean migratory period; ⊢—— = range of migratory period.

Results

Occurrence of flocks in spring. In 1967—1972, the first Chaffinches arrived in April about 2 weeks earlier on an average than the first Bramblings. In early spring, Chaffinches usually occurred single or in small groups (Fig. 1, Table 2a). Bramblings, on the other hand, were seldom single, because they were almost all in species flocks or associated with Chaffinch flocks (Fig. 1). At the beginning of the spring migratory period, only males were seen in flocks of both the species, because the first Chaffinch females arrived about 2 weeks and the first Brambling females about 1 week later than the corresponding males (Mikkonen 1981a). In the study area, the numbers of single Chaffinches and Bramblings per observation day increased throughout the migratory season (Fig. 2). The relative numbers were higher for the Chaffinch than for the Brambling (Appendix 3).

Most of the Chaffinches arrived in late April or early May (Table 2a). As to the Bramblings, a majority of the migrants arrived in May (Fig. 1, Table 2b), when there was snow left only in the forests. So the main flocks of both the species occurred at different times with some overlap (C_{xy} = 0.55, Figs 3 and 4). At the peak of the spring migration the mean size of flocks was at its greatest (Table 2 and see Appendix 2). At that time in the study area, only some large species flocks per spring were observed for the Chaffinch, but several per spring for the Brambling. The largest Chaffinch flock (about 350 individuals) was seen on 28 April 1968 and the largest Brambling flock (about 750 individuals) was noted on 8 May 1968. After the peak numbers of migrants had passed the study area, the mean size of the flocks decreased (Tables 2).

Table 2a. Average development of the size of Chaffinch species flocks in periods of 5 days at Utajärvi, Juorkuna, summed for the springs 1967—1972.

Date	Flock size	(number of individuals per flock)							
	2—3 %	4—5 %	6—10 %	11—20 %	21—99 %	>100 %	Total N	$\bar{x}$	SD
6—10 April	66	33	0	0	0	0	3	2.7	1.1
11—15 "	79	21	0	0	0	0	14	2.9	1.1
16—20 "	58	18	15	9	0	0	33	4.5	4.2
21—25 "	42	13	23	13	10	0	71	8.3	9.6
26—30 "	52	23	13	10	2	2	62	7.4	18.9
1— 5 May	57	17	11	13	3	0	118	5.4	5.6
6—10 "	71	5	20	2	2	0	56	4.0	3.9
11—15 "	93	5	2	0	0	0	43	2.3	0.8
16—20 "	97	0	3	0	0	0	36	2.2	1.0
21—25 "	97	3	0	0	0	0	29	2.3	0.7
26—31 "	100	0	0	0	0	0	14	2.3	0.6
Total (N)	66.4 (318)	12.3 (59)	11.5 (55)	7.1 (34)	2.5 (12)	0.2 (1)	100.0 (479)		

However, some great Brambling flocks were occasionally seen even in late May, as in 1968 and 1970. Small groups of both the finches migrating northwards were still seen in late May (Chaffinches) or even early June (Bramblings) in 1968, 1970 and 1971. Furthermore, small groups of local nesting Chaffinches and Bramblings were also seen in the feeding places. So in N Finland, Chaffinch flocks occurred for a longer time in April–May than Brambling flocks.

Annual variations in relative numbers of flocking birds. As a whole, 73.5 % of the Chaffinches (N = 4653) and 94.9 % of the Bramblings (N = 7995) were seen in flocks and all the others were single during April–May in 1967—1972 (Appendix 3). The percentages of flocking individuals varied annually by 25 % (CV) for the Chaffinch (range 38.8—85.8 %) and only by 11 % (CV) for the Brambling (range 70.8—97.9 %). For both the species the percentage was lowest in 1971, when the spring was late and very cold and the snow cover was very thick in forests, but the spruce had a remarkably abundant seed crop. Moreover, the spring migration of both the finches was also late in the study area. The highest percentage was obtained in 1967 for the Chaffinch, when the spring was early and mild, but the spruce seed crop was very scanty, while for the Brambling the maximum percentage was recorded in 1968, when the spring was nearly average, but the pine seed crop was scanty and a very cold and snowy period occurred on 20—24 May.

The relative numbers of flocking Chaffinches and Bramblings were lower in cold springs than in others (Fig. 5, Table 4). Both of them correlated strongly with the daily minimum temperatures on 11 April – 20 May (see the average times of spring migratory periods). According to the partial correlation coefficients, temperature was the most important environmental factor for the Chaffinch, but for the Brambling the seed crop of conifers and the snow cover also had a marked effect on the annual variations of the flocking percentage in spring (Table 5). The air temperature, the abundance of snow and the size of the seed crop of conifers together explained 98.4 % of the annual variations in the relative numbers of flock-

Table 2b. Average development of the size of Brambling species flocks in periods of 5 days at Utajärvi, Juorkuna, summed for the springs 1967—1972.

Date	Flock size	(number of individuals per flock)							
	2—3 %	4—5 %	6—10 %	11—20 %	21—99 %	>100 %	Total N	$\bar{x}$	SD
21—25 April	0	0	0	0	0	0	0		
26—30 "	50	0	50	0	0	0	2	5.9	—
1— 5 May	18	19	25	21	17	0	72	13.1	13.8
6—10 "	36	19	20	12	7	5	80	16.5	36.5
11—15 "	31	13	17	17	20	3	111	14.9	22.3
16—20 "	48	13	19	13	4	1	67	9.7	24.9
21—25 "	49	12	21	12	6	1	68	9.9	25.3
26—31 "	75	8	0	17	0	0	12	4.8	5.4
Total (N)	36.7 (151)	14.8 (61)	19.7 (81)	15.3 (63)	11.4 (47)	2.2 (9)	100.1 (412)		

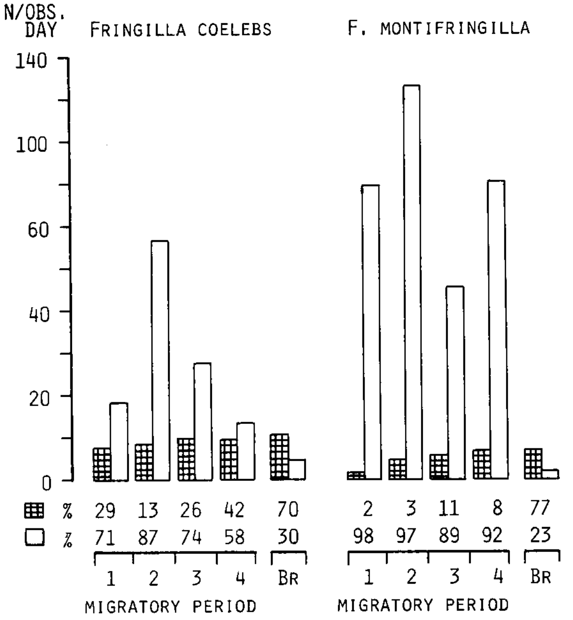

Fig. 2. Numbers and percentages of Chaffinches and Bramblings occurring single (▦) and in flocks (☐) during the spring migratory period and the breeding time (Br) at Utajärvi, Juorkuna, in the springs 1967—1972. The whole length of the spring migratory period per year was divided into four parts and numbers of individuals were summed in subperiods for the study years.

ing Chaffinches (using multiple correlation coefficient R^2, $R_{1.234} = 0.9920$, see Tables 4 and 5). The corresponding figure for the Brambling was 99.5 % ($R_{1.234} = 0.9975$).

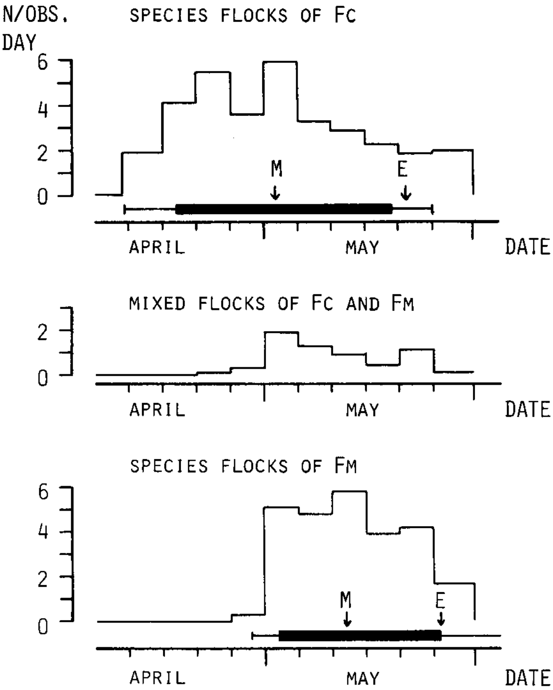

Fig. 3. Numbers of the species and mixed flocks of the Chaffinch (Fc) and the Brambling (Fm) at Utajärvi, Juorkuna, in the springs 1967—1972. The numbers of flocks per observation day were calculated in periods of 5 days for the study years. ■ = mean migratory period; ⊢—— = range of migratory period; M = the mean date of the median of spring migration; E = the starting date of egg-laying for the first clutch in the spring. The occurrence overlap coefficient of both the species flocks was $C_{xy}=0.55$.

Size of spring flocks. The pure species flocks accounted for 83 % of all the Chaffinch flocks and 81 % of all the Brambling flocks, respectively (Table 3). The others were mixed flocks of the two finch species. In April—May, most of the Chaffinch flocks were small in size (Fig. 6). 79 % of the species flocks were below 5 individuals per flock, and only 2.7 % of them were over 20 individuals per flock (Table 2a, see Appendix 4). On the other hand, 52 % of the Brambling species flocks were below 5 individuals in size (Table 2b). The over 20 birds groups accounted for 14 % and the large (over 100 birds) groups for 2.2 % of the total number of Brambling species flocks.

Table 2c. Average development of the size of Chaffinch and Brambling mixed flocks in periods of 5 days at Utajärvi, Juorkuna, summed for the springs 1967—1972.

Date	Flock size (number of individuals per flock)								
	2—3 %	4—5 %	6—10 %	11—20 %	21—99 %	>100 %	Total N	x̄	SD
21—25 April	0	0	0	0	100	0	1	50	—
26—30 "	0	0	0	0	50	50	2	205	—
1— 5 May	4	4	12	31	46	4	26	34.4	65.5
6—10 "	0	23	18	5	36	18	22	52.9	86.9
11—15 "	0	22	33	28	11	6	18	19.5	33.4
16—20 "	0	14	29	29	29	0	7	15.6	12.6
21—25 "	6	11	28	28	22	6	18	27.4	37.6
26—31 "	100	0	0	0	0	0	1	3	—
Total (N)	3.2 (3)	13.7 (13)	21.1 (20)	22.1 (21)	36.1 (30)	8.4 (8)	100.1 (95)		

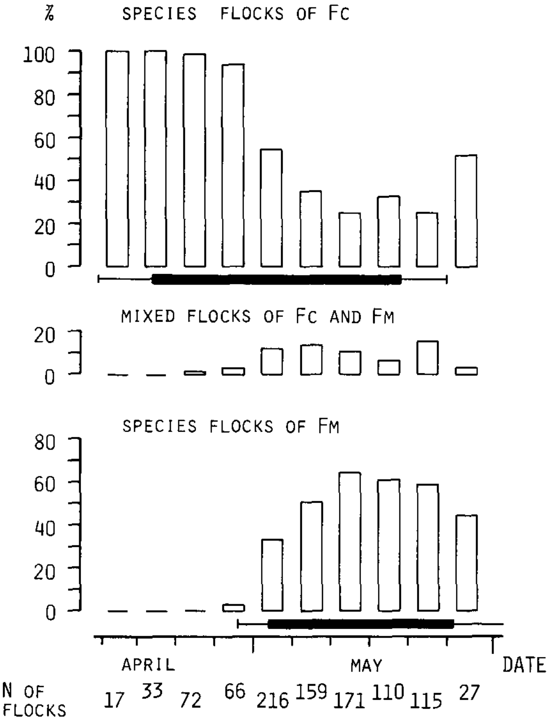

Fig. 4. Relative numbers of Chaffinch (Fc) and Brambling (Fm) flocks in periods of 5 days at Utajärvi, Juorkuna, in the springs 1967—1972. The numbers of flocks summed in periods of 5 days for the study years. ■ = mean migratory period; |—— = range of migratory period.

Bramblings formed clearly greater groups than Chaffinches (Fig. 7). Mean size of the Chaffinch species flocks was 5.0±0.4 (SE), and that of the Brambling species flocks 12.9±1.2 (SE) in April–May (Table 3). When the single birds were included, the mean group size was 2.1 for the Chaffinch and 7.0 for the Brambling. For both the finches the mean size of the species flocks was greater in the springs when the migratory period began early than in the springs when it began late (Fig. 8, see Fig. 5). Further, small Chaffinch flocks were relatively more numerous in the springs when the snow was abundant (see Table 6). On the other hand, the numbers of small Brambling flocks correlated strongly with the temperature and the seed supplies in spring (Table 6).

Mixed flocks of Chaffinches and Bramblings were quite common (Appendix 4, Table 2c), accounting for 16 % of all the Chaffinch flocks and 19 % of all the Brambling flocks (Table 3, see Fig. 9). In the study area in 1967—1972, both the species were relatively the least numerous in mixed flocks in the cold and snowy spring 1971, when the seed crop of the spruce was superabundant, and relatively the most numerous in 1968, when also a return-winter occurred in late May (Appendix 3). Furthermore, there were more Bramblings in mixed flocks than Chaffinches.

Individuals of both the species aggregated in clearly greater groups in mixed flocks than in species flocks (Figs 7 and 9; P<0.001 for both species). Most (84 %) of the individuals of all

Table 3. Mean sizes of Chaffinch and Brambling flocks and the relative proportions of their species and mixed flocks at Utajärvi, Juorkuna in the springs 1967—1972.

		Spring						
Flocks	1967	1968	1969	1970	1971	1972	Total	
Species flocks of *Fringilla coelebs*								
x̄	5.3	5.4	3.5	3.9	3.1	8.3	5.0	
SD	5.6	6.4	3.6	4.5	4.6	19.0	8.6	
CV %	106	119	103	115	148	229	172	
N	41	157	59	118	39	65	479	
Species flocks of *F. montifringilla*								
x̄	20.8	14.4	14.2	9.5	5.2	12.2	12.9	
SD	27.8	27.2	28.9	24.1	6.0	21.6	25.3	
CV %	134	189	204	254	115	177	196	
N	23	179	42	76	26	66	412	
Mixed flocks of *F. coelebs* and *F. montifringilla*								
x̄	59.5	34.8	41.4	32.1	9.0	46.6	36.6	
SD	62.1	66.9	62.5	42.3	—	107.5	67.8	
CV %	104	192	151	132	—	231	185	
N	4	63	5	11	2	10	95	
Flocks of *F. coelebs*								
Species %	91	71	92	91	95	87	83.4	1.5 (SE)
Mixed %	9	29	8	9	5	13	16.6	1.5 (SE)
Flocks of *F. montifringilla*								
Species %	85	74	89	87	93	87	81.3	1.7 (SE)
Mixed %	15	26	11	13	7	13	18.7	1.7 (SE)

Table 4. Simple correlation coefficients between the flocking percentages of Chaffinches and Bramblings and selected factors at Utajärvi, Juorkuna, in the springs 1967—1972. The coefficients were calculated from the data shown in the Appendices 1, 2, and 3. * denotes P<0.05, ** P<0.01, *** P<0.001, ° P<0.10.

Factors	Temperature	Snow cover	Cone crop	Rain-fall	Migra-tion	Ind./ obs.day
Snow cover	—0.86*					
Cone crop	—0.60	+0.39				
Rainfall	+0.89*	—0.66	—0.55			
Fringilla coelebs						
Migration$^{1)}$	—0.77°	+0.93**	+0.14	—0.55		
Ind./obs.day	+0.50	—0.74°	—0.22	+0.57	—0.62	
Flocking-%	+0.988***	—0.87*	—0.64	+0.88*	—0.73	+0.54
F. montifringilla						
Migration$^{2)}$	—0.90*	+0.66	+0.55	—0.92**		
Ind./obs.day	—0.64	—0.66	—0.42	+0.81°	—0.67	
Flocking-%	+0.94**	—0.86*	—0.78°	+0.81°	—0.79°	+0.68
No. of years	6	6	6	6	6	6

Note: 1) = the median date of the spring migratory period of the Chaffinch. 2) = the beginning date of the spring migratory period of the Brambling.

the mixed flocks were in groups of over 20 birds. For that reason the mixed flocks were considerably greater in size than the pure species flocks of either species (Table 3). 17 % of the total number of mixed flocks consisted of less than 5 individuals and 40 % of more than 20 individuals (Table 2c, see Fig. 6). The mean size of the mixed flocks was 36.6±7.0 (SE) individuals, which was 7.3 times greater than the mean size of the species flocks for the Chaffinch (t-test, P<0.001) and 2.8 times greater than for the Brambling (t-test, P<0.001) (see also Fig. 9). A majority of the mixed flocks of the two species occurred on the feeding sites at the peak migration times or during return-winters (e.g. in 1968). There were no statistical difference in flock size between the different years (Table 3).

Habitat selection in spring. In the study area, Chaffinches used habitats slightly more widely than Bramblings in spring (Table 7). During April–May, both the species changed their habitat utilization to some degree. The annual variation in habitat breadth (B') was 10.6 % (CV) for the Chaffinch and 6.1 % (CV) for the Brambling.

In April, when the snow was abundant, the first Chaffinches (males) preferred mixed and coniferous woods to other habitats (Fig. 10). They fed on abundant conifer seeds on the snow. Chaffinches (single or in flocks) foraged soon after their arrival in those woods or at snowless spots around the buildings. Later in spring, when snowless patches increased rapidly, the flocks usually stayed at the edges of woods and fields. The first Bramblings also arrived in coniferous woods and entered the fields in late April or early May (Fig. 10). The well integrated migratory flocks of both the species typically foraged a lot on open fields. In the study area, their characteristic habitat was open stubble, ploughland or meadow, not far from trees and bushes. Further, local Chaffinches and Bramblings also visited good communal feeding sites, especially at the beginning of breeding, and migrating flocks occasionally aggregated there.

Long cold spells in April–May may be a critical time for both of the species. At that time, local

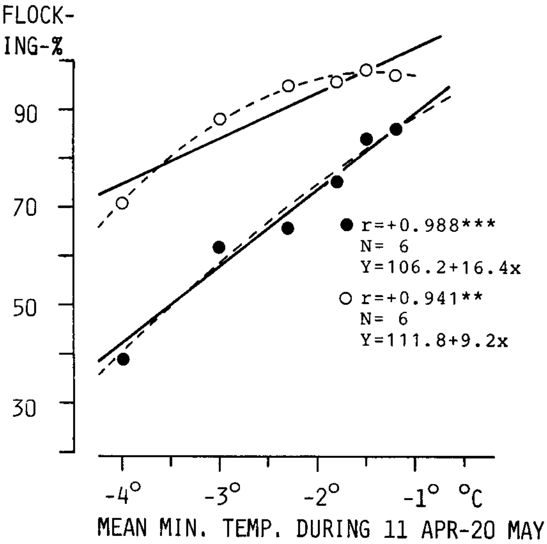

Fig. 5. Linear correlation and regression between the flocking percentages of the Chaffinch (●) and the Brambling (○) and the air temperature at Utajärvi, Juorkuna, in the springs 1967—1972. The data used are shown in the Appendices 1 and 3. The broken line is the parabolic regression line. The parabolic correlation coefficient and regression equation for the Chaffinch are $r = +0.988$, $P<0.01$, $Y = 101.7+12.3x—0.8x^2$, and those for the Brambling are $r = +0.997$, $P<0.001$, $Y = 88.5—11.8x—4.1x^2$.

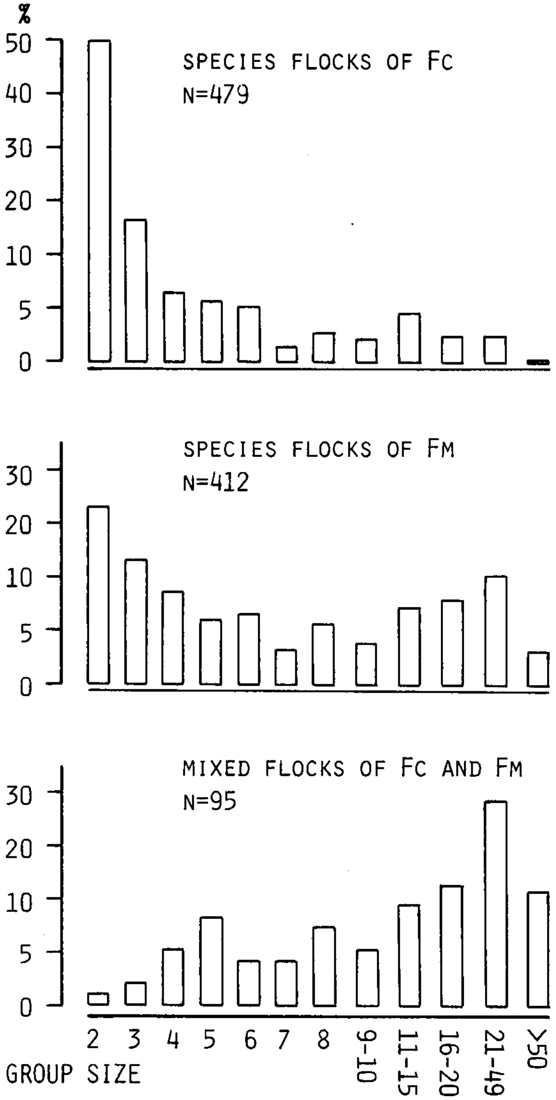

Fig. 6. Frequency distribution (%) of Chaffinch (Fc) and Brambling (Fm) flocks into different group sizes at Utajärvi, Juorkuna, in the springs 1967—1972.

and migratory Chaffinches and Bramblings searched for suitable feeding sites and shelters, sometimes moving over large areas. This affected the habitat utilization by the birds. In adverse conditions the finches occasionally concentrated in large flocks probably on the best feeding sites. During the late cold spell in 1968, habitat overlapping (C_{xy}) between Chaffinches and Bramblings was higher than before or after that (Table 8). After the spring migration and the return-winter the social tendency soon declined and the flocks dispersed rapidly. The diet of the individuals changed (see also Dolnik 1982), and the foraging on fields clearly decreased. The flocking tendency of nesting individuals was small. At this stage, Chaffinches favoured mixed and deciduous woods and Bramblings coniferous and mixed woods in the study area (Fig. 10).

Table 5. Partial correlation coefficients between the flocking percentages of Chaffinches and Bramblings and external factors at Utajärvi, Juorkuna, in the springs 1967—1972. The variables in the correlations were: 1 = flocking-%, 2 = temperature, 3 = snowiness, 4 = size of the cone crop of the pine and the spruce, 5 = rain, 6 = migration time as shown in Table 4, 7 = ind./obs.day. For further explanations, see the text for Table 4.

External factors		Flocking-% of individuals	
		F. coelebs	*F. montifringilla*
Temperature . . .	$r_{12.3}$	+0.952*	+0.77
	$r_{12.4}$	+0.981**	+0.940*
	$r_{12.5}$	+0.944*	+0.83°
	$r_{12.6}$	+0.976**	+0.86°
	$r_{12.7}$	+0.985**	+0.90*
Snow	$r_{13.2}$	−0.24	−0.32
	$r_{13.4}$	−0.87°	−0.969**
	$r_{13.5}$	−0.80	−0.74
	$r_{13.6}$	−0.77	−0.74
	$r_{13.7}$	−0.82°	−0.75
Cone crop	$r_{14.2}$	−0.34	−0.78
	$r_{14.3}$	−0.66	−0.952*
	$r_{14.5}$	−0.39	−0.68
	$r_{14.6}$	−0.79	−0.67
	$r_{14.7}$	−0.63	−0.74
Rain	$r_{15.2}$	−0.01	−0.20
	$r_{15.3}$	+0.82°	+0.62
	$r_{15.4}$	+0.82°	+0.72
	$r_{15.6}$	+0.83°	+0.34
	$r_{15.7}$	+0.83°	+0.60
Migration	$r_{16.2}$	+0.29	+0.40
	$r_{16.3}$	+0.47	−0.57
	$r_{16.4}$	−0.84°	−0.68
	$r_{16.5}$	−0.60	−0.19
	$r_{16.7}$	−0.59	−0.61
Ind./obs.day . . .	$r_{17.2}$	+0.37	+0.29
	$r_{17.3}$	−0.28	+0.27
	$r_{17.4}$	+0.54	+0.61
	$r_{17.5}$	+0.12	+0.06
	$r_{17.6}$	+0.17	+0.33
No. of years		6	6

As a whole, the modes of habitat selection by Chaffinches and Bramblings were largely similar during April—May (Fig. 10, Tables 7 and 8). Habitat overlap (C_{xy}) between them was more notable during the return-winter and the migratory period than at the beginning of the breeding time. However, there were also some important interspecific differences, especially in relation to the time scale for the habitat utilization by spring flocks (see Table 8).

Some aspects of flocking behaviour. Chaffinches and Bramblings migrated in flocks or single. Particularly early in spring, Chaffinch males also migrated in loose integrated flocks with individuals

Table 6. Partial correlation coefficients between the relative proportions of small (2—5 birds) Chaffinch and Brambling species flocks and external factors at Utajärvi, Juorkuna, in the springs 1967—1972. The variables 2—7, data and further explanations were as in Tables 4 and 5. The variable 1 = % of small species flocks.

External factors		% of small species flocks	
		F. coelebs	*F. montifringilla*
Temperature . . .	$r_{12.3}$	+0.81°	—0.934*
	$r_{12.4}$	—0.79	—0.982**
	$r_{12.5}$	—0.63	—0.78
	$r_{12.6}$	+0.02	—0.79
	$r_{12.7}$	—0.62	—0.923*
Snow	$r_{13.2}$	+0.977**	—0.60
	$r_{13.4}$	+0.993***	+0.74
	$r_{13.5}$	+0.965**	+0.39
	$r_{13.6}$	+0.71	+0.39
	$r_{13.7}$	+0.930*	+0.54
Cone crop	$r_{14.2}$	—0.49	+0.933*
	$r_{14.3}$	—0.88*	+0.82°
	$r_{14.5}$	—0.18	+0.80
	$r_{14.6}$	+0.12	+0.78
	$r_{14.7}$	—0.02	+0.76
Rain	$r_{15.2}$	+0.32	—0.17
	$r_{15.3}$	+0.51	—0.76
	$r_{15.4}$	—0.54	—0.87°
	$r_{15.6}$	—0.06	—0.39
	$r_{15.7}$	—0.18	—0.83°
Migration	$r_{16.2}$	+0.89	+0.06
	$r_{16.3}$	+0.51	+0.74
	$r_{16.4}$	+0.949*	+0.84°
	$r_{16.5}$	+0.929*	+0.32
	$r_{16.7}$	+0.957*	+0.78
Ind./obs.day . . .	$r_{17.2}$	—0.72	+0.06
	$r_{17.3}$	—0.48	—0.22
	$r_{17.4}$	—0.79	—0.47
	$r_{17.5}$	—0.70	+0.39
	$r_{17.6}$	—0.83°	—0.05
No. of years		6	6

separated by distances of a few meters to over 50 meters. Mutual calling between members of the flocks was abundant. In the study area, Bramblings were not seen to form loose flocks of this kind. Early in the morning, finches often flew high in sunny weather. In cloudy weather and later in the day they flew lower and in denser groups. According to the field observations, calls by other individuals attracted well single and small groups to join the greater flocks throughout the day. Well integrated flocks of Chaffinches and Bramblings were most common during the favourable time of the spring migration.

Especially in snowy areas, Brambling flocks, but also Chaffinch flocks, were seen to continue their migratory flight northwards in the morning, but return during the day southwards to the area with several snowless spots. Brambling flocks were observed to behave in this way even in snowless areas in late May (see Mikkonen 1981a). The accidental influence of a heavy snowfall is described

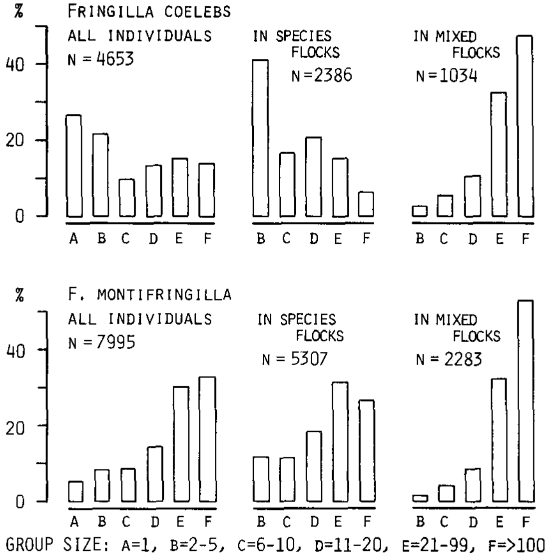

Fig. 7. Frequency distribution (%) of Chaffinches and Bramblings into different group sizes at Utajärvi, Juorkuna, in the springs 1967—1972. The interspecific difference in group size selection between the species was $X^2 = 33.4$, $P<0.001$, df = 5 for all individuals, $X^2 = 35.6$, $P<0.001$, df = 4 for species flocks, and $X^2 = 1.0$, P = 0.92, df = 4 for mixed flocks. The corresponding similarity (C_{xy}) in their group size selection was 0.64 for all individuals, 0.63 for species flocks, and 0.95 for mixed flocks.

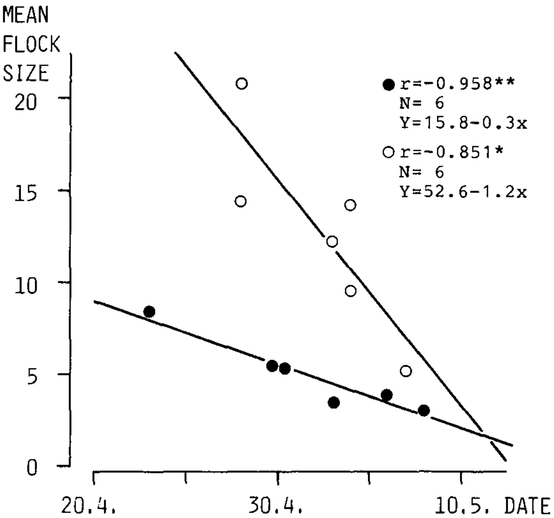

Fig. 8. Linear correlation and regression between the annual mean size of Chaffinch (●) and Brambling (○) flocks and the spring migration time at Utajärvi, Juorkuna, in 1967—1972. The data used are shown in Table 3 and Appendix 2.

Note: The spring migration times were the median dates of the spring migratory period for the Chaffinch and the beginning dates of the spring migratory period for the Brambling.

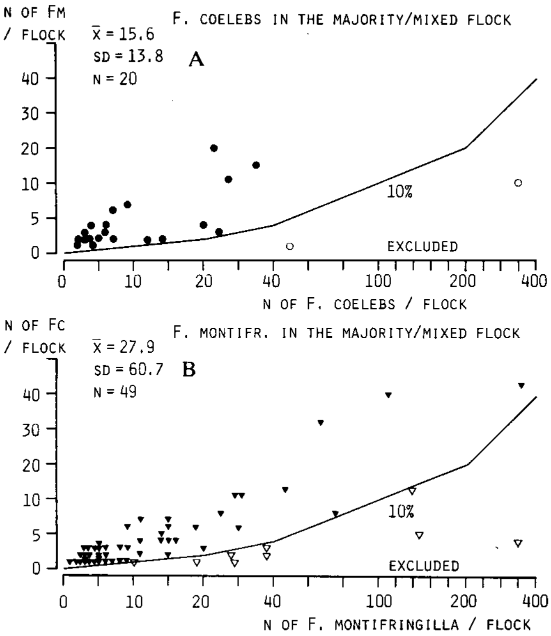

Fig. 9. Relationships between Chaffinches and Bramblings in different mixed flocks at Utajärvi, Juorkuna, in the springs 1967—1972. ● = mixed flocks with Chaffinches in the majority (○ excluded); ▼ = mixed flocks with Bramblings in the majority (▽ excluded); —— = 10 %-curve by which from the mixed flocks excluded those within below 10 % of other species. In (A.) the mean size of subgroups was 10.8 (SD = 9.8) for the Chaffinch and 4.8 (SD = 5.0) for the Brambling. In (B.) the corresponding sizes were 5.7 (SD = 9.0) for the Chaffinch and 22.1 (SD = 53.0) for the Brambling, respectively. As a whole, the mean size of the mixed flocks was 24.3 (SD = 51.8, N = 69), where the mean size of Chaffinch groups was 7.2 (SD = 9.5) and the mean size of Brambling groups was 17.1 (SD = 45.3).

by the following observation on 23 April 1967. The observation time was 06.15—08.40 o'clock a.m., cloudiness was 100 %, and there was an easterly wind of 3—4 m/s. Chaffinches and one Brambling aggregated into a large flock on the site which had remained snowless in the shelter of a pine-spruce forest after an overnight snowfall. Chaffinches were seen to gather in the following units: 22, 1, 6, 8, 8, 12, 5, 1, 3, 10, 25, 33, 5+1 Brambling, 16, 4, 4, and 6 in the order of arrival. The large flock (170 birds) did not disperse until the afternoon, when the newly fallen snow had melted almost completely. Early in the morning, other Chaffinch flocks were observed to migrate southwards.

In the study area, part of the migratory Chaffinches and Bramblings directly continued their journey, while part of them only continued after 1—3 days. In the spring 1968, large Brambling flocks were seen to stay in the area for as long as 6—10 days (see Mikkonen 1981a). The staying migratory flocks moved a lot around the open fields during the daytime (Fig. 11). Chaffinches and Bramblings arrived on good feeding sites in groups and single. They joined in large foraging flocks. The birds fed abundantly throughout the day. The flocks changed their feeding sites several times during the day. Members of the large flocks flew after the first leaving birds in a series of chains or groups to a new foraging place. They usually shifted by some tens of meters to hundreds of meters, but sometimes they flew outside the area. Simultaneously, the size of the large flock often varied according to the numbers of leaving or coming birds. In the study area, it was observed that *Turdus* and *Sturnus* flocks were often likely to be followed by especially Bramblings. Hard wind and adverse weather greatly diminished the daily movements of the Chaffinch and Brambling flocks.

On the feeding sites in open fields, especially migratory finches took part in numerous social movements of the flocks, depending on the degree of their sociability. Birds in well integrated flocks made highly synchronised movements. They made intensively social flights in which the whole flock took part, such as circle, difting, escape etc. (see Marler 1956a). Sometimes the flock circled several times above the feeding site, whereupon all the individuals joined in it. It either landed close by

Table 7. Relative distribution (%) of Chaffinches (Fc) and Bramblings (Fm) in the different habitats and their habitat breadth (B') at Utajärvi, Juorkuna, for the three periods in April-May 1968.

	Periods					
Habitat	Migratory (12 Apr—19 May)		Return-winter (20—24 May)		Beginning of breeding (25—31 May)	
	Fc	Fm	Fc	Fm	Fc	Fm
Young pine forest	9.4	16.0	10.9	3.4	19.6	19.4
Mature coniferous forest	10.4	4.2	22.6	18.8	26.1	29.2
Mixed forest	15.7	9.7	12.4	17.1	21.7	9.7
Deciduous forest	9.4	6.7	17.5	24.3	13.0	2.8
Fields and yards	55.1	63.3	36.5	36.3	19.6	38.9
N of individuals	1267	2926	137	292	46	72
B'	0.84	0.78	0.94	0.79	0.76	0.87

or moved farther to another feeding site. A Brambling flock of no more than 10 individuals was observed to make circle flights. After that the flock sometimes left to continue northwards. In difting flight, the flock as a whole tended to move gradually over the feeding place in the field which was being observed (see also Marler 1956a). The advance was made by finches left behind, which made a short flight over the group and landed in the van. Only a small number of birds were in flight at any one moment. During the migration time, the flock escaped quite frequently from its feeding site. The feeding stopped. Eventually one bird or a small group took off and the rest of the flock followed. At a high social stage, the flock escaped as a mass. Escape flights were seen to occur without visible cause and with disturbances.

When large migratory flocks flew to trees or bushes, members of the flocks dispersed into groups, where activities, such as preening, sitting, singing, and even chasing and fighting behaviours, were synchronised almost completely. At the staying sites during the migratory period, subsong and other calls by individuals were often heard as a confused chorus. Groups of singing males were very typical of the Brambling, but also of the Chaffinch.

Aggressive and chasing behaviour of the birds was very common in spring flocks. This also affected the individual distances. In social migratory Chaffinch flocks, the individual distances were shortest (15—20 cm) in forage on the ground, but became manifold immediately upon lifting to trees, especially between males. Bramblings often fed nearly side by side (individual distance was below 5 cm) in very social flocks. Their individual distance was 20—50 cm in trees and over 50 cm in the singing groups of large flocks.

Dispersal of flocks. In the present study area, breeding Chaffinches separated from migrating birds early in spring (see also Bergman 1953). Soon after their arrival, they dispersed singly to their own territories, if the weather was not too cold. In contrast, Bramblings dispersed in loose groups or single to suitable terrestial points. Later in spring, a group of singing males remained on a certain site and females also aggregated in "display flocks" or near them. No such behaviour was observed among Chaffinches.

During cold spells local individuals sometimes aggregated again in groups. Especially after heavy snowfalls, settled local Chaffinches and Bramblings flew to forage to other places (not near their territories). The shifting usually took place during the morning activity. They stayed in one place from a few minutes to even several days, especially in adverse conditions (for instance in 1968).

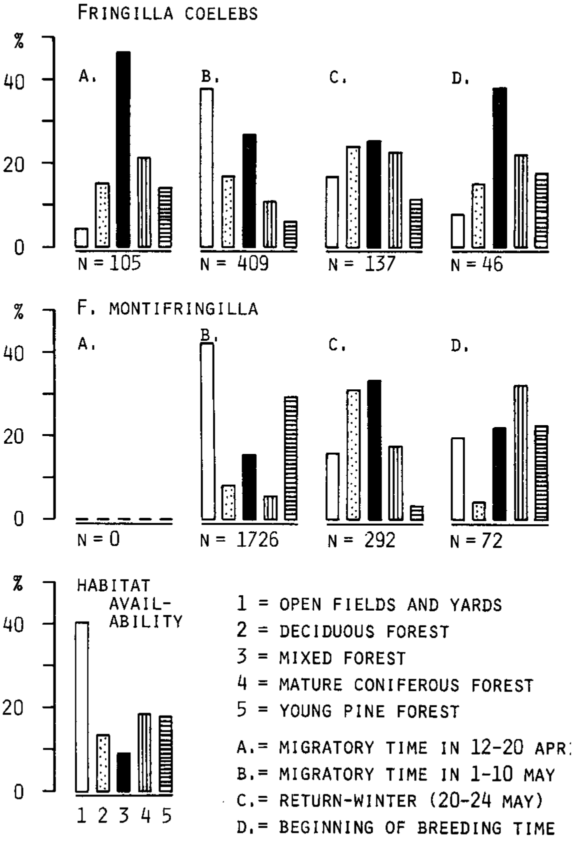

Fig. 10. Habitat selection by Chaffinches and Bramblings in relation to the habitat availability distribution along the census line in the study area in the spring 1968. The calculations were based on the data (individuals/obs.day/km) presented in Table 7.

The local Chaffinch males were definitely seen to shift over 2 kilometers at Juorkuna. Cold weather spells prolonged the dispersal phase of flocks for both of the species. After migratory flocks had left the area, local individuals concentrated on the

Table 8. Habitat overlaps C_{xy} between the Chaffinches and the Bramblings for different periods and habitats at Utajärvi, Juorkuna, in the spring 1968. Calculations based on the data shown in Table 7.

Period	C_{xy}
Migratory	0.85
Return-winter	0.89
Beginning of breeding time	0.78
Habitat during April—May	C_{xy}
Young pine forest	0.37
Mature coniferous forest	0.62
Mixed forest	0.50
Deciduous forest	0.49
Fields and yards	0.42

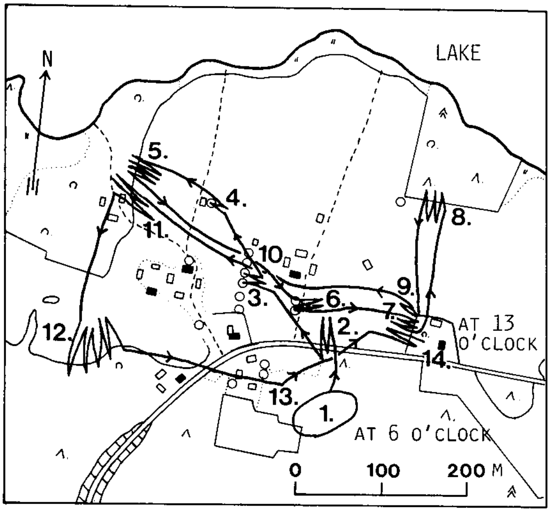

Fig. 11. Daily movements of a large migratory flock in the study area between 06 and 13 o'clock on 4 May 1968. The staying sites of the flock were numbered in the shifting order. The large flock consisted of about 500 individuals, of which 70 % were Bramblings and 30 % were Chaffinches. Weather at 06.20 o'clock: Temperature —0.5°C, cloudiness 100 %, wind 3—5 m/s NW. ——‹—— movement route of the flock; ww frequent to and fro flights between feeding and resting sites.

feeding sites only into small accidental groups, which broke up suddenly after the feeding. Aggression increased notably between the members of the flocks. This was indicated by increasing song, chase and fight in the flocks.

Discussion

There are three main tendencies which probably influence the flocking behaviour of birds, as shown by several field and laboratory studies (e.g. Miller 1922, Moyniham 1962, Thompson et al. 1974, Ulfstrand 1975, Lazarus 1979, Caraco 1979, Pulliam & Millikan 1982). They are (1) protection from predators (e.g. Vine 1971, Powell 1974, Goldman 1980, Stinson 1980), (2) more efficient foraging (e.g. Rand 1954, Turner 1965, Cody 1971, Krebs et al. 1972, Baker et al. 1981), and (3) a social component or a mutual attraction between individuals (e.g. Emlen 1952, Kalela 1953; see also Gannon 1934, Darling 1938). Several authors have pointed out that those tendencies may be interacting in flocks, and that the main function may undoubtedly be different among different species and in different situations (e.g. Werth 1960, Lazarus 1972, Moriarty 1976, Barnard 1980a, Kushlan 1981, Caraco & Bayham 1982). In addition, birds obtain relatively other advantages in single-species groups than in heterospecific groups (Morse 1977; see also Buskirk 1976, Jones 1977).

It is well known that the flocking behaviour is determined by innate instinctive activities of birds. It can be directed either towards conspecific individuals or towards other species (e.g. Morse 1977). Both Chaffinches and Bramblings clearly preferred individuals of their own species, although they also formed mixed flocks. Both of the species have special contact and alarm calls and conspicuous marks on their wings, tail or rump (e.g. Marler 1956a, c, von Haartman et al. 1972, Newton 1972) to help in social communication between the members of flocks (Moyniham 1960, Wynne-Edwards 1962, Balph 1977). In my study area, spring flocks of the Chaffinch and the Brambling are quite common at margins of fields and woods (see also Marler 1956a, Bergman 1979). They are typically migratory or foraging groups and sometimes displaying Brambling groups.

Occurrence of spring flocks. According to Laine & Hildén (1979), on the southern coast of S Finland the main spring migration of the Chaffinch and the Brambling does not clearly separate from each other, because these two species travel commonly in mixed flocks. However, in N Finland they differed significantly (Mikkonen 1981a, 1983b; see also Zetterberg 1921). Chaffinches arrive earlier in spring than Bramblings. The former's migratory period took place on an average during 17 April–19 May and the latter's during 2—26 May (Appendix 2). It has been verified by Mikkonen (1981a, 1981b) that such proximate factors as the temperature, the abundance of snow, the size of the available food supplies, and the social interactions have a marked effect, but in interspecific ways, on the progress of the spring migration of both of the *Fringilla* species. Simultaneously, the environmental factors modify the occurrence of spring flocks. Furthermore, their influence and importance change during the spring (see Nice 1937, Mikkonen 1981a).

The course and timing of migration can be considered as an adaptation (e.g. Alerstam 1981). The beginning of the migratory period of the Chaffinch (a southern migrant) vary annually more than its end, while, contrariwise, the beginning of the migratory period of the Brambling (a northern migrant) vary much less than its end (Mikkonen 1983b). The spring flocks are most numerous during the peak time of migration. However, the main flocks of both of the species occurred here at different times of the spring (cf. Laine & Hildén 1979). Soon after the peak numbers of migrants had passed the study area, breeding individuals only occasionally aggregated in flocks.

Exhibiting interspecific differences in the spring migration and in the dispersal of individuals to their nesting sites, Chaffinch flocks may also be seen for a longer time in the spring than Brambling flocks. Annual variations in the occurrence of spring flocks of both of the species may be caused by severe weather, variations in the food supplies or variations in the timing of the migration. Thus, several ultimate and proximate factors together influence the occurrence of Chaffinches and Bramblings in flocks. In the present study area, 73.5 % of all the Chaffinches and 94.9 % of all the Bramblings were in flocks during April–May in 1967—1972.

Size of spring flocks. The optimal group size is modified by different selective pressures within certain limits (e.g. Bertram 1978). For example, it has been experimentally established among House Sparrows *Passer domesticus* that when the group size is greater than 5, the members of the flock do not gain any further advantage in their predator surveillance effort (Elgar & Catterell 1981, Studd et al. 1983). Several authors have demonstrated that the size and density characteristics of flocks vary, depending on either internal or environmental factors (e.g. Emlen 1952, Koskimies 1957, Wilson 1975, Caraco & Bayham 1982). Caraco (1979) and Barnard (1980a) emphasize the importance of environmental factors in determining the flock size of Dark-eyed Juncos *Junco hyemalis* and House Sparrows. According to Wiens & Johnston (1977), one consequence of feeding behaviour is that flock size may be quite variable and responsive to local conditions (see also Cody 1971). However, these environmental factors may partly act through their influence on social behaviour (Emlen 1952, Caraco 1979, Pulliam & Millikan 1982).

It has been shown that the flocking patterns of territorial finches change through the year (Newton 1972). In England, small groups of Chaffinches are much more numerous than great ones during July—September (Marler 1956a). Afterwards the flock size increases during the winter months. In wintering grounds, Chaffinches usually feed in large flocks (Marler 1956a). Bramblings have been reported to concentrate even in millions around good beechmast supplies (e.g. Sutter 1948, Jenni 1982). Bergman (1949) noted that in S Finland, migrating Chaffinch flocks flew mostly in groups of 5—25 individuals and seldom in groups of more than 50 individuals (see also Gruys-Casimir 1965).

In the northern breeding grounds, Chaffinch and Brambling flocks contain from a few individuals to several hundreds, or rarely thousands. Flocking is most advantageous when the demand of food is high (e.g. Pulliam et al. 1974). It has been shown that the energy requirements of Chaffinches also increases with decreasing temperature and with migration travel (e.g. Dolnik 1982). In N Finland, the air temperature affected notably the spring flocking of Chaffinches and Bramblings. During the prenesting time, Chaffinches were here typically seen alone or in only small groups and less frequently in greater flocks. Contrariwise, Bramblings generally joined in flocks of several birds, being only seldom single in spring. Goldman (1980) suggests in Dark-eyed Juncos that small flock size may reflect non-linear increase of advantages with increasing flock size and disadvantages associated with large flocks.

In this work, Chaffinch flocks were usually small in size at the beginning of the spring migratory period, when only males were seen in flocks and the available food supplies were often limited by the snow. The abundance of snow and the point of spring migration modify the relative numbers of small Chaffinch flocks. On the other hand, the temperature and the seed crop of conifers mostly affect the relative numbers of small Brambling flocks. The mean flock sizes of both of the species were greatest at the peak of their spring migration. It is at that time that females and young males are most numerous in flocks (Shumakov & Sokolov 1982; see also Mikkonen 1981a). The higher sociability and the increased availability of food (after the melting of snow, especially in springs with poor tree seed yields) cause an increase of the mean flock size. At suitable feeding places, small groups of Chaffinches and Bramblings also aggregate in large flocks. The sizes of foraging groups often changed during the day. In spring, the single birds were numerous particularly among Chaffinches. They were individuals either on their migratory journey, searching for territory in an area or settled down in a territory. The interspecific difference in the numbers of single birds is mostly due to the different establishment strategies of the breeding territories (Mikkonen, unpubl.).

As a whole, Chaffinches aggregated, on an average, in clearly smaller species flocks than Bramblings (5 vs. 13 individuals) in April–May. However, relative variation (CV%) of flock size was of the same order in both species. Lehtonen (1958) observed that the mixed-species flocks of tits were large as compared with the groups of conspecifics (see also Ulfstrand 1975, Ekman 1979). Similarly, for both of the *Fringilla* species the mean size of mixed flocks (37 birds, see also Fig. 9) was greater than that of species flocks. Thus my results suggest that there is an interspecific difference in the gregariousness of the Chaffinch and the Brambling in spring, and that several environmental factors modify greatly the sizes of their spring flocks. Simultaneously, the habitat utilization and the social tendency of the birds also change quickly during the phase of flock dispersal.

Habitat selection. Such factors as the availability of food, vegetation structure, shelter against predators or adverse weather, social attraction and competition contribute to habitat selection by the birds in the area (Hildén 1965, Alatalo 1981, Cody 1981). According to my field observations, food is an essential resource for migrating finches (see Cody 1971, Newton 1972, Hogstad 1982). They need a lot of energy for their passage (Dolnik & Blyumental 1967, Shumakov & Sokolov 1982). Seeds are rich in fat and their energy value is very high (e.g. Pulliainen 1973, 1974). The diets of Chaffinches and Bramblings are about the same (Newton 1972). In spring, both of the species also show diet changes at the breeding time (Marler 1956a, Hogstad 1977). Dolnik (1982) reports that the Chaffinch is 97 % granivorous during its spring migration and 90 % insectivorous through the summer period.

In N Finland, the dispersion of suitable food may often present a mosaic pattern early in spring. In years with good seed crops of conifers, the food sources are distributed fairly evenly over a wide area, allowing birds to spread out as they feed, as, for example, in 1971 (see also Cody 1971). The flocks are usually small in size when the ground is covered by snow. The other food sources, such as seeds of annual plants in snowless spots, are more or less concentrated in space, so that the flock members feed close to each other. Especially after overnight snowfalls or during return-winters in April–May, Chaffinch and Brambling flocks may move over large areas and settle when they find a suitable feeding and sheltering place. Barnard (1980b) noted for House Sparrows that the birds changed their feeding behaviour when they moved from one type of habitat to another, depending on selective pressures in winter.

It is well known that changes in the social tendency are consistent with changes in the habitat selection (e.g. Emlen 1952, Koskimies 1957, Lind 1963, Mikkonen 1974). There are differences in habitat use between migrating and breeding birds among both Chaffinches and Bramblings. The migrants are typically found to stay on edge habitats. Large migratory flocks or foraging groups were here often seen in open fields and most of the single birds were observed in forests (see also Werth 1960). The habitat use modes of the Chaffinch and the Brambling greatly resembled each other in spring (Table 8). There were, however, some very important differences. Individuals in the spring flocks of the two species use the same habitats at the different times of the spring period or they concentrate in mixed flocks around superabundant food supplies (see also Newton 1972). Interspecific competition between them therefore decreases strongly in a sympatric breeding area in N Finland (see also Cody 1974, Wiens & Johnston 1977). Fretwell (1972) accepted the idea that the food is competed for mainly by nonbreeding populations (see also Cody 1974).

In the study area, Chaffinches and Bramblings nest in the same woods (see Mikkonen 1979). However, they disperse to their territories at different times (Mikkonen 1983a), and the former favours slightly more mixed or deciduous woods and the latter pine woods in the study area. Saether (1982) observed that in a Grey alder forest in Central Norway, Chaffinches and Bramblings chiefly utilized the same habitat, but at different foraging heights, during the breeding time (see also Udvardy 1956).

Sociability in spring. The attractiveness of other individuals, i.e. the social tendency, is the stronger the more social the species is (e.g. Emlen 1952, Wynne-Edwards 1962, Wilson 1975). Moyniham (1960) thought that alternatively, most of interspecific differences in actual gregariousness may be explained by differences in hostility. Here the social tendency is clearly more obvious among Bramblings than among Chaffinches. This is indicated by significant differences in the mean sizes and social behaviour of the spring flocks. The above conclusion is supported by similar variations (CV%) in flock size in the same environmental conditions. Furthermore, both the fringillids aggregated in smaller species flocks than in mixed flocks.

Chaffinches and Bramblings often migrate in mixed flocks in S Finland and S Sweden (Laine & Hildén 1979, Alerstam 1981). In N Finland, social interaction between them was observed a subsidiary factor modifying the time of arrival of the first Bramblings (Mikkonen 1981b). During the spring migration and the prenesting time, social stimulation between members of flocks appears to be very important for e.g. feeding and reproductive activities (e.g. Marler 1956a, Lehrman 1959, Evans & Patterson 1971, Wiens & Johnston 1977). Species that feed in aggregations typically choose places where other birds are foraging (Kushlan 1981). On communal feeding grounds in open fields, Brambling flocks often follow e.g. *Turdus* and *Sturnus* groups.

The sociability of territorial birds changes in spring. There are conflicting tendencies between gregariousness and solitary life. Several authors have suggested that the birds (especially males) become increasingly aggressive as the spring season progresses and the time for flock break-up and establishment of territories approaches. This also includes fight, flight pursuits, escape and song between members of finch flocks (e.g. Marler 1955, 1956a, d, 1957, Hinde 1956, 1959, Wilkinson 1982). Further, it has been verified that an increasing secretion of sex hormones stimulates birds into aggressive behaviour (e.g. Collins 1952, Hinde 1959, Davies 1963, Vanderberg 1964). Marler (1956a, b) noted that the individual distances between Chaffinches increased from winter to early spring, and the flocks were consequently more dispersed in spring than they were in winter. This was supported well by my field observations on an increase of agonistic behaviour and enlarged individual distances in Chaffinch and Brambling groups. The individual distances of the Chaffinch are clearly longer than those of the Brambling in spring. However, the latter species is dominant against the former one (see also Bergman 1952, Udvardy 1956). The body size (weight and wing length) is smaller in Chaffinches than in Bramblings (von Haartman et al. 1972, Eck 1975).

Marler (1956a, b) reported that Chaffinches may change from the territorial to the flocking model over a period of minutes. This study confirms the finding of Zahavi (1971) demonstrating that changes in social behaviour may rapidly follow changes in food dispersion. This is very true in the far north during the prenesting time. Cold weather spells may hence cause a re-formation of flocks, more strongly among Bramblings than among Chaffinches (see Marler 1956a, Pulliainen 1978). So in spring, the social behaviour of territorial birds may change suddenly depending on proximate factors.

Further, the decreasing trend of sociability is also shown by the fact that the relative proportions of flocking Chaffinches and Bramblings are here significantly greater in early springs than in late ones. The same tendency appears in the mean sizes of their spring flocks. In the same way, the changing of sociability could be suggested by partial correlation coefficients for the relative proportions of the small species flocks.

Chaffinch males spread out solitary to their breeding territories, but usually remain in the familiar breeding area (Mikkonen 1983a). However, singing by other local males seems to attract them to occupy a neighbouring territory (see Bergman 1953, Kalela 1953, Lack 1968). Brenowitz (1981) showed that among Red-winged Blackbirds *Agelaius phoeniceus* territorial song outside the breeding time serves as an important signal in the establishment and maintenance of groups (see also Kalela 1953). On the other hand, Brambling males were here likely to sing and display in groups. They settled down to their territories in loose groups or single, but in different areas each year (Mikkonen 1983a; see also Udvardy 1956). It has been suggested that the clustering of males is favourable for females, leading to a rapid and synchronised development of reproductive activities (Crook 1965, Emlen & Oring 1977). Brambling males may begin to pair, by courting a female, while they are still in flocks. This is often observed in N Finland (for *Carduelis* finches, see Newton 1972). Chaffinch males hence acquire a fixed territorial site for pair formation (Newton 1972), but Brambling males do not. My results suggest that the interspecific difference in sociability reflects the flocking behaviour and the development of social organization for the nesting time among Chaffinches and Bramblings.

Some aspects of the significance of spring flocking. Birds derive some advantages from forming flocks at migration times (see Alerstam 1981). During the migratory passage, the flocking of individuals may facilitate orientation (e.g. Balph 1977). It also appears to aid in the location of rich food resources (e.g. Rand 1954, Zahavi 1971, Krebs 1974, Thompson et al. 1974). Newton (1972) reported that gregariousness itself is a help for the birds in finding the abundant food supplies. Social stimulations enhance the feeding efficiency in flocks (e.g. Turner 1965, Murton 1971, Murton et al. 1972, Baker et al. 1981). However, the distribution of flocks cannot be explained by sociability alone, for the amounts of food supplies and the detection of predators also have obvious influences on the flocking of birds (e.g. Miller 1922, Lazarus 1972, Powell 1974). Newton (1972) suggested that increased protection from predators and ease of food-finding are the two major reasons why finches aggregate to feed in flocks (see also Barnard 1980b). Cody (1971) emphasized the significance of food supplies for flocking finches. My results agree well with this for Chaffinches and Bramblings in the northern conditions in spring.

The formations and dispersions of spring flocks sometimes took place here rapidly, depending on the variable environmental factors in the north. During the prenesting time, this plasticity is a very important ability and it seems to be more sensitive among Bramblings than among Chaffinches. This notion was supported by field observations on the behavioural habits of Chaffinch and Brambling spring flocks. Social stimulation also plays an important role in the synchronizations of birds (e.g. Darling 1938, Lehrman 1959, Crook 1965; see egg-laying in Appendix 2). Mutual interactions between the members of a flock or individuals may help in the selection of suitable nesting places and in the formation of breeding pairs (see also Cody 1974, Moriarty 1976), as it was observed in Brambling groups in springs. In N Finland, this allows the rapid beginning of breeding activities as soon as suitable nesting sites become available. According to Crook (1965), there are special reasons in the shift from flocking to territorial behaviour for feeding, e.g. the protection of the nesting sites against predators and the diet changes in spring (see also Lack 1968).

Buskirk (1976) suggested that interspecific flocking can be considered a complementary or alternative strategy to intraspecific flocking. Further, the different selective pressures operate in different ways within them (e.g. Moyniham 1962, Jones 1977, Morse 1977, Greig-Smith 1978, Ekman 1979). Birds in mixed flocks obtain more protection from predators, experience less food competition, and have at least the same or greater foraging efficiency than birds in species flocks. Chaffinches and Bramblings formed here mixed flocks particularly on good feeding sites and during the peak of their spring migration, when the sociability of the birds was also high. Thus, when the group size increases beyond a certain limit, individuals of other species are obviously more fit as company than those of the same species. For the above reasons, the size of mixed flocks was greater than that of species flocks.

In addition to the above advantages, there are some disadvantages involved in flocking, such as attraction of predators and promotion of intraspecific competition for the essential resources amongst flock members (e.g. Moyniham 1962, Balph et al. 1979). The spring flocking of the Chaffinch and the Brambling may therefore be viewed as a compromise between the benefits and the costs (see also Emlen 1952, Ekman 1979, Goldman 1980, Baker et al. 1981). All in all, my results support well the three main tendencies which affect the flocking of birds.

Final remarks. The spring migration of the Chaffinch and the Brambling differed greatly in N Finland (Mikkonen 1981a, 1981b). The main flocks of both the species used the same habitats in the area, but chiefly at different times of the spring. According to the size and the behaviour of the spring flocks, the social tendency was more conspicuous among Bramblings than among Chaffinches. Thus the flocking habits of the species diverged in some important aspects, although they also resembled each other.

The strategies of selecting of the breeding grounds among Chaffinches and Bramblings are quite opposite (Mikkonen 1983a). The social organization of the Chaffinches for the breeding time is ready by the time the Bramblings come. When both of the *Fringilla* species nest in the same woods, they use habitats at different heights (Saether 1982, Mikkonen, unpubl.). Especially in late springs, interspecific conflicts may sometimes be obvious near the nest or at the time when the courtship display by Brambling males is most intensive (see also Bergman 1952, Kumari 1962, Mikkonen 1979, cf. Udvardy 1956).

In N Finland, the above mentioned differences diminish markedly the interspecific competition between the Chaffinch and the Brambling during the critical period before true nesting. In the northern unpredictable circumstances, Bramblings are able to start nesting rapidly, since their spring flocking also facilitates the use of sporadic food supplies and leads to a brief duration of the mating system (courtship display in groups). In N Finland, this is consistent with the rapid amelioration of the environmental conditions in spring. By contrast, the spring flocking habits of Chaffinches are adapted to increasing the chances of males to secure a breeding site for coming season, but not directly to help in mating (or to get a mate).

As a whole, coexistence of the Chaffinch and the Brambling on a sympatric breeding ground in N Finland is achieved by several mechanisms operating simultaneously (see Udvardy 1956). During the prenesting time, when the competition is hardest (see Wynne-Edwards 1962, Crook 1965, Lack 1971), there was here a clear separation between the species in social ecology.

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Selostus: **Peipon ja järripeipon kevätparvista Pohjois-Suomessa**

Peipon ja järripeipon kevätparvia tutkittiin Pohjois-Suomessa, Utajärven Juorkunankylässä (64°57'N, 26°58'E) 6 perättäisenä keväänä 1967—1972. Tutkimuksessa analysoitiin yhteensä 968 parvea, 1233 yksinäistä peippoa ja 405 yksinäistä järripeippoa (Liite 3 ja 4). Kaikista peippoyksilöistä (N = 4653) 73.5 % ja kaikista järripeippoyksilöistä (N = 7995) 94.9 % oli parvissa huhti-toukokuun aikana. Kokonaisyksilömäärä oli yhteensä 12 684.

Keväällä peipot saapuivat Pohjois-Suomeen huomattavasti aikaisemmin kuin järripeipot (liite 2, kuva 1). Havaintovuosina peipon keskimääräinen kevätmuuttokausi oli huhtikuun 17 pv:stä toukokuun 19 pv:ään ja vastaavasti järripeipon toukokuun 2 pv:stä 26 pv:ään. Runsaimmin parvia tavattiin tutkimusalueella kevätmuuton huippukausina (kuvat 2 ja 3). Silloin parvien keskikoko oli myös korkeimmillaan (taulukko 2). Huhti-toukokuussa peipot esiintyivät tavallisesti yksin tai pienissä ryhmissä ja vain harvoin isompina parvina (kuvat 1, 6 ja 7). Sitävastoin järripeipot olivat tavallisesti muutaman kymmenen yksilön parvina ja harvemmin yksin. Peipon ja järripeipon lajiparvien keskikoot erosivat merkitsevästi (t = 5.844, $P<0.001$, df = 889) toisistaan. Edellisen lajiparvien keskikoko oli 5.0 (SE = 0.4, N = 479) ja jälkimmäisen 12.9 (SE = 1.2, N = 412) yksilöä (taulukko 3). Jos yksinäiset yksilöt otettiin huomioon ryhmäkokoa laskettaessa, niin ryhmän keskimääräinen koko oli peipolla 2.1 ja järripeipolla 7.0 yksilöä. Lajien sekaparvien keskikoko, 36.6 (SE = 7.0, N = 95), oli huomattavasti suurempi kuin niiden puhtaiden lajiparvien keskikoot (kuva 9).

Useat ympäristötekijät muovaavat peipon ja järripeipon parveutumista keväällä. Osittaiskorrelaatiokertoimen perusteella ilman lämpötila oli niistä tärkein (taulukot 4 ja 5). Tämän lisäksi siemenravinnon määrä ja lumisuus vaikuttivat huomattavasti järripeipon parveutumisasteeseen. Pohjois-Suomessa lämpötila, lumisuus ja siemenravinnon määrä selittivät yhdessä (käyttäen R^2) 98.4 % peipon ja 99.5 % järripeipon parveutumisprosentin vuosivaihteluista. Leutona keväänä kummankin lajin parveutumisprosentti oli korkeampi kuin kylmänä keväänä (kuva 5). Samalla lajiparvien keskikoko korreloi negatiivisesti kevätmuuton alkamisajankohdan kanssa (kuva 8). Se oli sitä suurempi mitä aikaisemmin muuttokausi alkoi. Reviirilajilla yksilöiden sosiaalisuusaste laski nopeasti varsinaisen pesimisajan lähestyessä.

Kirjallisuudessa on todettu, että ravinto, kasvillisuuden rakenne, suoja petoja ja säätä vastaan, sosiaalisuus sekä kilpailu vaikuttavat lintujen elinympäristön valintaan. Tutkimusalueella peipon ja järripeipon ympäristönvalinta ja -hyväksikäyttö muistuttivat suuresti toisiaan, etenkin takatalven aikana (kuva 10, taulukot 7 ja 8). Merkittävin lajien välinen ero ympäristöjen hyödyntämisessä alueella oli se, että kummankin lajin muuttoparvet käyttivät samoja ympäristöjä eri aikaan keväästä. Lisäksi paikalliset peipot suosivat pesimäympäristönään hivenen enemmän lehti- ja sekametsiä ja paikalliset järripeipot taas mänty- ja sekametsiä (kuva 10).

Lajin sosiaalisuus heijastuu parvikäyttäytymisessä ja sosiaalisen organisaation kehittymisessä pesinnän ajaksi. Reviirilajeilla (etenkin koirailla) aggressiivisuus lajikumppania kohtaan lisääntyy voimakkaasti, kun parvien hajaantuminen ja pesinnän aloitus lähestyvät. Tämä näkyi parvien oleskelupaikoilla laulun, takaa-ajon ja taistelun lisääntymisenä. Parvien keskikoon ja käyttäytymisen perusteella samoissa ympäristöoloissa järripeipon sosiaalisuusaste oli keväällä selvästi korkeampi kuin peipon. Olosuhteiden salliessa paikalliset yksilöt hajaantuivat parvista pesimäpaikoilleen lajille ominaisella tavalla. Yksinäisten peippojen suuri osuus johtui siitä, että lajin koiraat pyrkivät turvaamaan pesintäpaikan saannin tulevaksi pesintäkaudeksi nopeasti ja yleensä tutulta alueelta. Toisaalta järripeippoparvien käyttäytyminen auttoi runsaiden ruokavarojen paikallistamisessa ja pesintäaktiivisuuden nopeassa käynnistämisessä ja synkronoitumisessa. Järripeipolla todettiin sellaisia soidinparvia, joissa esiintyi pariutumiskäyttäytymistä koiraiden ja naaraiden välillä.

Tutkimusalueella peipon ja järripeipon kevätparvet olivat tyypillisesti joko muuttavia tai ruokailupaikoilla olevia parvia sekä joskus järripeipon soidinparvia. Saadut tulokset tukevat voimakkaasti sitä, että useat ultimaattiset ja proksimaattiset tekijät yhdessä vaikuttavat molempien *Fringilla*-lajien kevätparveutumiseen, mutta lajille tyypillisellä tavalla (kuvat 1, 2, 5, 8; taulukot 4, 5, 6). Yleisesti kevätparveutuminen auttaa yksilöitä suojautumaan petoja vastaan, löytämään ravintoa kriittisenä ajankohtana, kohottamaan ruokailun tehokkuutta ja sosiaalista stimulointia yksilöiden kesken. Vaikka peippo ja järripeippo ovat molemmat ns. reviirilajeja, niin keväällä niiden pesintää edeltävässä sosiaalis-ekologisessa käyttäytymisessä on selviä lajien välisiä eroja. Erot viittaavat erilaiseen sopeutumaan pesinnän aloituksessa Pohjois-Suomessa.

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Appendix 1. The temperatures (°C) were the means of the daily minimum temperatures during 11 April — 20 May and average temperatures in May. The snow cover values (cm) were measured on 30 April and 5 May and the rainfall values (mm) during 11 April — 20 May. The cone crops of conifers were recorded at Utajärvi.

Spring	Temperature		Snow cover		Rainfall	Cone crop		
	Min. 11 Apr —20 May	Mean in May	30 Apr	5 May	11 Apr —20 May	Pine	Spruce	Total
1967	—1.2	+6.9	15	8	70	4	0	4
1968	—1.5	+5.4	10	1	84	1	3	4
1969	—2.3	+5.5	25	20	55	2	1	3
1970	—3.0	+6.4	25	10	33	3	1	4
1971	—4.0	+6.2	45	20	28	3	5	8
1972	—1.8	+6.7	0	0	52	4	2	6
$\bar{x}$	—2.3	+6.2	20	10	54	2.8	2.0	4.8
SD	1.0	0.6	15.5	8.8	21.3	1.2	1.8	1.8
CV%	43	10	78	88	39	43	90	38

Appendix 2. Time of migration and egg-laying by Chaffinches and Bramblings at Utajärvi, Juorkuna, in the springs 1967—1972. The dates of the different stages of the spring migratory and egg-laying periods for both the finches are according to Mikkonen (1981a).

Spring	*Fringilla coelebs*				*F. montifringilla*			
	Migratory period			Egg-laying$^{1)}$	Migratory period			Egg-laying$^{1)}$
	Beginning	Median	End		Beginning	Median	End	
1967	9 Apr	30 Apr	10 May	28 May	28 Apr	10 May	22 May	27 May
1968	13 Apr	30 Apr	23 May	29 May	28 Apr	8 May	9 Jun	30 May
1969	20 Apr	3 May	18 May	23 May	4 May	13 May	24 May	27 May
1970	26 Apr	6 May	24 May	19 May	4 May	22 May	28 May	24 May
1971	18 Apr	8 May	25 May	13 May	7 May	14 May	26 May	21 May
1972	15 Apr	23 Apr	14 May	16 May	3 May	5 May	14 May	28 May
$\bar{x}$	17 Apr	2 May	19 May	21 May	2 May	12 May	26 May	26 May
SD	5.9	5.2	6.1	6.5	3.6	5.9	8.5	3.2
N	6	6	6	6	6	6	6	6

Note: $^{1)}$ = the starting date of egg-laying of the first clutch in the spring.

Appendix 3. Number of Chaffinces and Bramblings occurring single, in species flocks or in mixed flocks at Utajärvi, Juorkuna, in the springs 1967—1972.

Spring	Single		In species flocks		In mixed flocks		Together	
	N	%	N	%	N	%	N	N/obs.day$^{1)}$
			Fringilla coelebs					
1967	44	14.2	219	70.4	48	15.4	311	17.3
1968	315	16.4	846	43.9	765	39.7	1926	58.4
1969	135	34.3	209	53.0	50	12.7	394	26.3
1970	344	38.5	456	51.0	94	10.5	894	28.8
1971	196	61.2	120	37.5	4	1.3	320	13.9
1972	199	24.6	536	66.3	73	9.0	808	47.5
1967—1972	1233	26.5	2386	51.3	1034	22.2	4653	34.0
SE		0.6		0.7		0.6		
			F. montifringilla					
1967	21	3.1	478	69.4	190	27.6	689	53.0
1968	84	2.1	2568	65.5	1269	32.4	3921	178.2
1969	44	5.5	598	74.8	157	19.7	799	72.6
1970	135	12.1	724	64.7	260	23.2	1119	48.6
1971	62	29.2	136	64.2	14	6.6	212	14.1
1972	59	4.7	803	64.0	393	31.3	1255	89.6
1967—1972	405	5.1	5307	66.4	2283	28.6	7995	81.6
SE		0.3		0.5		0.5		

Note: $^{1)}$ = number of observation days was calculated after the arrival date of the first individuals.

Appendix 4. Numbers of Chaffinch and Brambling flocks of different sizes at Utajärvi, Juorkuna, in the springs 1967—1972.

Spring	Flock size (number of individuals in flocks)												Total	
	2—3		4—5		6—10		11—20		21—99		>100		Total	
	N	%	N	%	N	%	N	%	N	%	N	%	N	N/obs.day
	Species flocks of *Fringilla coelebs*													
1967	18	44	15	37	4	10	3	7	1	2	0	—	41	2.3
1968	95	61	20	13	20	13	18	11	4	3	0	—	157	4.8
1969	44	75	7	12	5	8	2	3	1	2	0	—	59	3.9
1970	91	77	9	8	12	10	4	3	2	2	0	—	118	3.8
1971	35	90	2	5	1	3	0	—	1	3	0	—	39	1.7
1972	35	54	6	9	13	20	7	11	3	5	1	2	65	3.8
1967—1972	318		59		55		34		12		1		479	3.5
	Species flocks of *F. montifringilla*													
1967	9	39	0	—	2	9	7	30	3	13	2	9	23	1.8
1968	48	27	31	17	38	21	34	19	25	14	3	2	179	8.1
1969	19	45	1	2	12	29	4	10	4	10	2	5	42	3.8
1970	38	50	9	12	13	17	10	13	5	7	1	1	76	3.3
1971	12	46	9	35	3	12	1	4	1	4	0	—	26	1.7
1972	25	38	11	17	13	20	7	11	9	14	1	2	66	6.0
1967—1972	151		61		81		63		47		9		412	4.3
	Mixed flocks of *F. coelebs* and *F. montifringilla*													
1967	0	—	0	—	0	—	1	25	2	50	1	25	4	0.3
1968	2	3	7	11	13	21	16	25	21	33	4	6	63	2.9
1969	0	—	2	40	1	20	0	—	1	20	1	20	5	0.5
1970	1	9	1	9	2	18	1	9	5	45	1	9	11	0.5
1971	0	—	1	50	0	—	1	50	0	—	0	—	2	0.1
1972	0	—	2	20	4	40	2	20	1	10	1	10	10	0.9
1967—1972	3		13		20		21		30		8		95	1.0