Ann. Zool. Fennici 22:137-156. 1985

Establishment of breeding territory by the chaffinch, *Fringilla coelebs*, and the brambling, *F. montifringilla*, in northern Finland

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Mikkonen, A. V. 1985: Establishment of breeding territory by the chaffinch, *Fringilla coelebs*, and the brambling, *F. montifringilla*, in northern Finland. — Ann. Zool. Fennici 22:137-156.

The establishment of breeding territory by the chaffinch and the brambling was studied at Utajärvi (65°57'N, 26°58'E) in Finland in the springs of 1967-1972. Chaffinch males began establishing territories almost three weeks earlier than bramblings, but egg-laying took place at about the same time, viz. after mid-May. Chaffinch males dispersed singly to their territories, usually in familiar areas. The territory serves as a food source and attracts the female. Brambling males move within loose displaying groups in a new area each spring. They disperse to the decisive breeding territory only after pairing. The female selects the nest site. This means that chaffinch males control access to females by defending territory and brambling males more directly by defending the females.

The territorial system of the chaffinch develops earlier and less synchronously than that of the brambling. *Fringilla* males settling early clearly have a certain superiority in the competition for territories. The asynchronous settling of chaffinches may be advantageous in the early spring when the food supply is scarce and variable. Simultaneous settling leads to a rapid and more synchronized development of the reproductive activities. The time-saving mechanism at the onset of breeding in bramblings is a response to northern conditions. Sociality and time-saving are favourable when the available time for nesting is short and the abundant resources are unpredictable in space and time. Early settling may also extend time to accommodate renesting attempts following nest losses.

In the study area, chaffinches and bramblings nested in the same woods and their territories overlapped markedly. The establishment of breeding territories by them takes place in different ways. The species differ from each other in respect of breeding dispersal, social tendency, mate and resource defences in relation to territory. This suggests that their reproductive tactics diverge.

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1. Introduction

The chaffinch, *Fringilla coelebs*, and the brambling, *F. montifringilla*, are closely related species which live more or less in flocks in the non-breeding period and in territories in the breeding season. In Finland both the species are migrants. Although they are very similar in structure, feeding behaviour, and diets, there are some slight differences in these respects (e.g. Newton 1967, 1972). They partly differ in their geographic distribution (e.g. Palmgren 1938, O. Järvinen & Väisänen 1979), wintering behaviour (Newton 1972, Jenni 1984), spring migration time, selection of breeding grounds, and sociability (Mikkonen 1981a, b, 1983a, b, 1984).

The biological significance of territories has often been linked to reproduction, food, predation, and the limitation of numbers (e.g. Nice 1941, Lack 1954, Wynne-Edwards 1962, Klomp 1972, Davies 1978, Hixon 1980). The breeding dispersion results to a large extent from agonistic or territorial behaviour (e.g. Hinde 1956a, Tinbergen 1957, Wilson 1975). Brown & Orians (1970) have emphasized that the actual dispersal patterns bear an imprint of both ultimate and proximate factors. Since economic defence of the breeding territory and the mating system involve both costs and benefits, the development of an adapted social organization is important for successful nesting (e.g. Brown 1964, Crook 1965, Pitelka et al. 1974, Emlen & Oring 1977, Lott 1984).

Myers (1981) drew attention to the importance of social systems as a selective factor. Since territory establishment and mate selection usually occur early in spring, such behavioural adaptations as the defence of food and the mate also strongly affect the differentiation of both the dispersal and the mating systems between the bird species, especially in annually variable environments (e.g. Tinbergen 1959, Crook 1965, Best 1977, Emlen & Oring 1977, Greenwood 1980). In order to gain insights into the selective pressures influencing the dispersion mechanisms of breeding passerines, I studied and compared the territorial conditions of the chaffinch and the brambling on a sympatric nesting ground in Finland. The territorial behaviour of the chaffinch has been studied more in S. Finland (Palmgren 1933, von Haartman 1947, Bergman 1953, 1956) and in England (Marler 1956a, b, Newton 1972). On the other hand, earlier investigations of the territorial behaviour of the brambling are very sparse (Bergman 1952, Udvardy 1956, von Haartman et al. 1972). This paper is a report on the habits related to the establishment of breeding territories in the above species. Further, the significance of their breeding territories is discussed.

2. Methods

The present study was carried out at Juorkuna, Utajärvi (64°57'N, 26°58'E), in the southern part of N. Finland during the period 1967 to 1972. The study area (68 ha) and its habitats have been described in earlier papers (Mikkonen 1981a, 1984).

Each year, the field work commenced in early April and continued throughout the breeding season. It included direct observations, mist-netting, mapping of territories, and searching for nests. Annually, there were 22 to 30 pairs of chaffinches breeding, while 12 to 16 pairs of bramblings started to nest in the study area (Mikkonen 1983a). Observations were made on a total of 155 chaffinch territories and 80 brambling territories.

Observations were made on the territorial behaviour of local adult chaffinches and bramblings with the aid of colour-ringing. In 1967-1971, a total of 110 nesting chaffinches and 68 nesting bramblings were marked with both aluminium rings and individual combinations of 1-3 plastic colour-rings. Unringed nesting males were identified by behaviour, site specificity, and territorial song.

Territorial activities were used to delineate territories. During vigorous activities, the territories were plotted by mapping sites at which individually recognizable males sang, displayed, fought or responded to playback. The nesting *Fringilla* males were attracted to the site by playing species-specific song from a tape recorder. Sites where two or more males were observed displaying equally were included in the border zone between territories or in the neutral zone.

Temperature, cloudiness, and wind were recorded. The daily temperatures and rainfalls shown in the figures and the tables were recorded at the Pelso Meteorological Station, Vaala. 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 using an arbitrary scale from 0 to 5, were taken from the annual reports of the Forest Research Institute in Metsälehti (for details, see Mikkonen 1984).

The statistical analyses used have been described previously (Mikkonen 1981a, 1983a, 1984). In the regression equations the dates were calculated from 1 April = 1.

Definition of concepts

The *spring migratory period* and its stages were defined by Mikkonen (1981a). The *territorial behaviour* of birds may be easily observed by song, visual displays and

Table 1. Average lengths (in days) of the selected nesting phases for the chaffinch and the brambling at Juorkuna in the springs 1967-1972. The duration of the events were calculated from the data given in Appendix 2, where the phases are also definited. N = number of study years.

	Fringilla coelebs					*F. montifringilla*				
	Mean	*SD*	Range	*CV*%	*N*	Mean	*SD*	Range	*CV*%	*N*
Before territorial time										
Migration - First terr.	3	2.2	1-6	73	6	6	3.9	2-12	65	6
Migration - Median terr.	12	6.5	4-20	54	5	8	3.8	4-15	48	6
First females - Pairing	4	3.5	1-9	87	5	4	3.3	0-8	82	6
Establishment time of territories										
First terr. - Median terr.	8	5.3	3-14	66	5	2	1.0	1-4	50	6
First terr. - First females	7	5.7	0-14	81	6	−1	3.1	−4-+4	310	6
First terr. - Pairing	10	4.8	5-16	48	5	2	1.6	0-4	80	6
Before egg-laying time										
First terr. - Egg-laying	31	11.3	19-45	36	6	18	5.3	11-25	29	6
Pairing - Egg-laying	18	9.1	5-29	51	5	16	6.3	7-23	39	6
Migration - Egg-laying	34	10.8	23-49	32	6	24	6.4	14-32	27	6
First females - Egg-laying	23	11.4	6-38	50	6	19	7.3	7-29	38	6

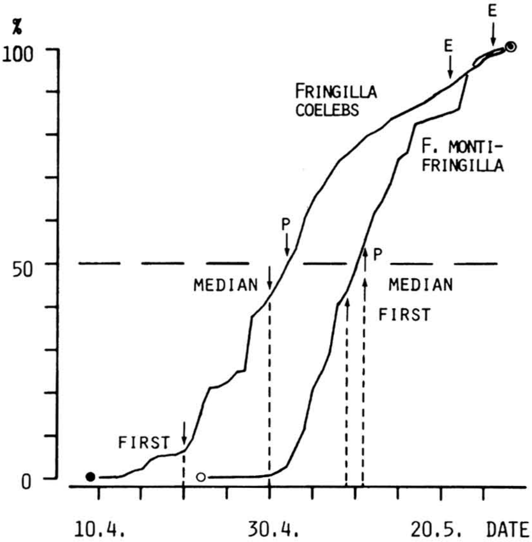

Fig. 1. The timing of territory establishment by the chaffinches (●) and the bramblings (○) in relation to the migrants at Juorkuna in the springs 1967-1972. The summed percentage curve of the species indicates the number of individuals which had passed the area by that time out of the total numbers in the study years. First = the mean of the settlement date of the first local male in his breeding territory. Median = the mean of the median dates of establishment of all the breeding territories. P = the mean of the pairing time of the first pair in the spring. E = the mean of the first date of egg-laying for the first clutch in the spring.

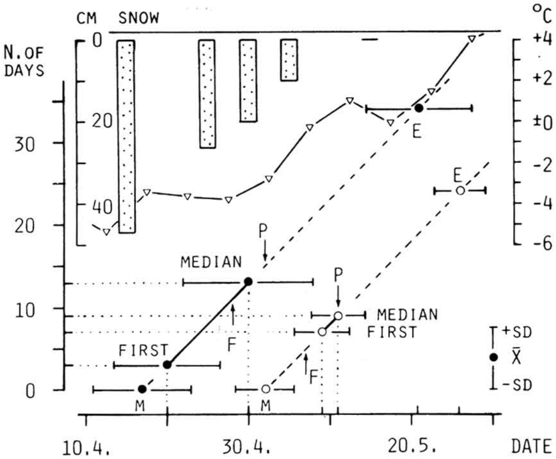

Fig. 2. The mean timing and duration of territory establishment by the chaffinches (●) and the bramblings (○) at Juorkuna in the springs 1967-1972. M = the mean date of the beginning of the spring migratory period. F = the mean date of arrival of the first females in the spring. For further explanations, see the text to Fig. 1. The minimum temperatures (—▽—) were the means of the temperatures of 5-day periods at Pelso, Vaala. The means of the snow cover (stippled column) values were measured at Särkijärvi, Utajärvi.

fighting (e.g. Hinde 1956b). According to Brown & Orians (1970), Noble's (1939) standard definition of *territory* as a defended area is adequate and useful. It excludes the individual distances of birds (see Conder 1949). The concept of *breeding territory* as defined by Brown & Orians (1970) as a fixed, exclusive area with the presence of defence that keeps out rivals is used in this study. The territorial area may change slightly during the breeding period (see Figs. 6 and 7). Here *pairing* means the formation of a pair-bond. For definitions of the other terms see also Appendix 2.

3. Results

3.1. Time of territory establishment

In the study area, the spring migratory period of the chaffinch began on average on 17 April and that of the brambling on average on 2 May (Appendix 2). For both of the species, males arrived earlier than females. Soon after arrival, local birds dispersed to their nesting sites, if the environmental conditions were suitable for territory settlement. The first chaffinch males seemed to occupy their breeding territories within a shorter time after the beginning of the spring migratory period than the first brambling males (Table 1). Only 7 % of all the chaffinches, but as much as 44 % of all the bramblings, had passed through the study area by the time the first males settled down in their territories (Fig. 1). The occupation of the first territories usually took place

Table 2. Interspecific differences (in days) in the timing of the selected nesting phases between the chaffinch and the brambling at Juorkuna in the springs 1967-1972. The duration of the events were calculated from the data given in Appendix 2. For further explanations, see the text to Table 1.

Phase	Mean	*SD*	Range	*CV%*	*N*
Migration	15	4.2	8-19	28	6
First terr.	18	5.6	9-26	31	6
Median terr.	10	5.6	6-20	56	5
First females	9	5.5	3-19	61	6
Pairing	10	4.8	6-18	48	5
Egg-laying	5	4.7	−1-12	94	6

Note: In the study years, the mean of the starting dates for egg-laying in the whole population was 28 May for both of the species.

Table 3. Simple correlation coefficients between the onset of the territory establishment by chaffinches and bramblings and external factors at Juorkuna in the six springs 1967-1972. The coefficients were calculated from the data shown in Appendices 1 and 2. First terr. = the establishment time of the first breeding territory in the spring. * denotes $P<0.05$, ** $P<0.01$, *** $P<0.001$, and ^{o} $P<0.10$.

Factors	Temperature	Snow cover	Cone crop	Rainfall	Migration
Fringilla coelebs					
Snow cover	−0.84*				
Cone crop	−0.16	−0.03			
Rainfall	+0.12	−0.32	−0.48		
Migration	−0.87*	+0.59	−0.04	+0.07	
First terr.	−0.89*	+0.75^{o}	+0.02	−0.23	+0.943**
F. montifringilla					
Snow cover	−0.82*				
Cone crop	−0.07	+0.13			
Rainfall	+0.15	−0.45	−0.68		
Migration	−0.53	+0.66	+0.55	−0.47	
First terr.	−0.89*	+0.89*	−0.19	−0.21	+0.35

Note: The temperature values used were those of 1-25 April for the chaffinch and 1-10 May for the brambling. The snow cover and rainfall values were recorded on 15 April and in April for the former and on 5 May and over the period 11 April - 10 May for the latter.

Table 4. Partial correlation coefficients between territory establishment by chaffinches and bramblings and external factors at Juorkuna in the springs 1967-1972. The coefficients were calculated from data shown in Appendices 1 and 2. The external factors in the correlations were: temperature (Temp), snow cover (Snow), size of the cone crop of the pine and the spruce (Cone), rainfall (Rain), the starting date of the spring migratory period in the first territory, and the arrival date of the first females in median territories (Migr), ind./obs. day (Ind). For further explanations, see the texts to Tables 3 and 5.

Factors		First territory		Median territories	
Corr.	Const.	*Fri coe*	*Fri mon*	*Fri coe*	*Fri mon*
Temp	Snow	−0.74	−0.61	−0.66	−0.45
	Cone	−0.903*	−0.924*	−0.79	−0.85^{o}
	Rain	−0.898*	−0.890*	+0.35	−0.896*
	Migr	−0.46	−0.890*	−0.59	−0.39
	Ind	—	—	−0.17	−0.901*
Snow	Temp	−0.02	+0.63	−0.63	+0.69
	Cone	+0.75	+0.946*	+0.70	+0.909*
	Rain	+0.73	+0.918*	−0.30	+0.883*
	Migr	+0.72	+0.941*	+0.32	+0.67
	Ind	—	—	−0.33	+0.74
Cone	Temp	−0.28	−0.56	−0.07	+0.00
	Snow	−0.06	−0.70	+0.13	−0.15
	Rain	−0.10	−0.46	−0.47	−0.40
	Migr	+0.18	−0.49	+0.49	−0.87^{o}
	Ind	—	—	+0.34	−0.15
Rain	Temp	−0.29	−0.16	−0.62	−0.66
	Snow	+0.01	+0.49	−0.71	−0.16
	Cone	−0.25	−0.47	−0.88	−0.59
	Migr	−0.910*	−0.05	−0.71	+0.11
	Ind	—	—	−0.54	+0.54
Migr	Temp	+0.75	−0.33	+0.01	+0.58
	Snow	+0.937*	−0.71	+0.08	+0.59
	Cone	+0.944*	+0.56	+0.75	+0.973**
	Rain	+0.990**	+0.29	+0.12	+0.85^{o}
	Ind	—	—	−0.69	+0.78
Ind	Temp	—	—	−0.30	−0.890*
	Snow	—	—	−0.59	−0.48
	Cone	—	—	−0.81	−0.84^{o}
	Rain	—	—	−0.24	−0.85^{o}
	Migr	—	—	−0.81	−0.66
No. of years		6	6	5	6

by 20 April for the chaffinch and by 9 May for the brambling (Fig. 2). The interspecific difference was most obvious at this phase of nesting, but decreased towards the egg-laying period (Table 2, Appendix 2).

The territory settlement took place more synchronously among the brambling males than among the chaffinch males in early spring. The median of the local territories had been inhabited by the time 43 % of all the chaffinches and 55 % of all the bramblings had passed through the area (Fig. 1). Annually, the average date was 30 April for the chaffinch and 11 May for the brambling (Fig. 2). The rest of the males usually rapidly settled down in their territories during May. The latest chaffinch male (before the second territorial song period of the same breeding season) was observed to occupy his territory on 12 June 1969 (Fig. 6). The last brambling pair arrived at their nesting site on 28 June 1970 (successful nesting).

The establishment of the first territories was strongly correlated with the spring migration time for the chaffinch, but not for the brambling (Fig. 3). Although there was still a lot of snow at that time, the males succeeded in obtaining enough conifer seeds on the snow or other seeds at snow-free spots. Low temperatures delayed the settlement of the first chaffinch territories (Tables 3 and 5). Later in the spring, the establishment time of the first brambling territories were more correlated with snowfall and temperature than with any other factors. Cold weather spells and newly fallen snow occasionally delayed the arrange-

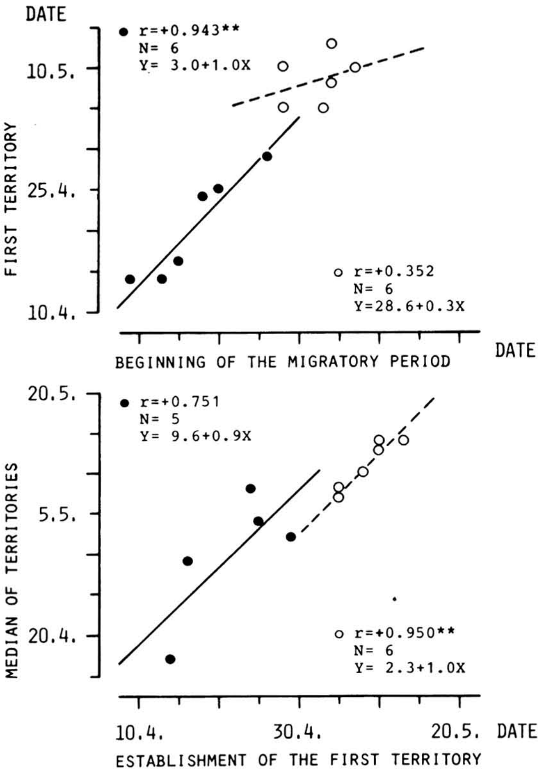

Fig. 3. Linear correlation and regression between the beginning of the spring migratory period and the two stages of establishment of a territory system for the local chaffinch (●) and brambling (○) males at Juorkuna in the springs 1967-1972.

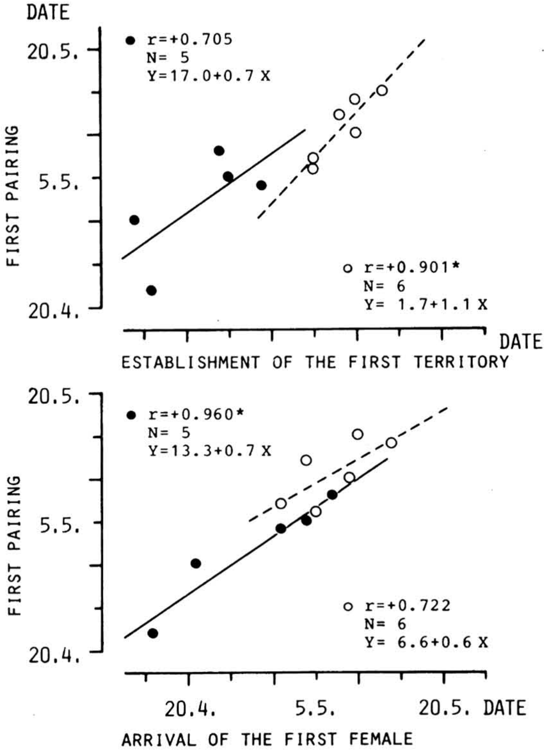

Fig. 4. Linear correlation and regression between the first pairing and the establishment of the first territory and the arrival of the first female among the local chaffinches (●) and bramblings (○) at Juorkuna in the springs 1967-1972.

Table 5. Simple correlation coefficients between the median of the territory establishment by chaffinches (5 years) and bramblings (6 years) and external factors at Juorkuna in the springs 1967-1972. Median terr. = the median date of establishment of all the breeding territories. For further explanations, see the text to Table 3.

Factors	Temperature	Snow cover	Cone crop	Rainfall	First females	Ind/ obs.day
Fringilla coelebs						
Snow cover	−0.987**					
Cone crop	−0.55	+0.44				
Rainfall	+0.974**	−0.926*	−0.67			
First females	−0.89 *	+0.934*	+0.10	−0.79		
Ind/obs.day	+0.947*	−0.968**	−0.27	+0.88*	−0.967**	
Median terr.	−0.81^o	+0.75	+0.41	−0.87^o	+0.72	−0.82^o
F. montifringilla						
Snow cover	−0.82*					
Cone crop	−0.07	+0.13				
Rainfall	+0.15	−0.45	−0.68			
First females	−0.86*	+0.82*	+0.47	−0.58		
Ind./obs.day	+0.51	−0.78^o	−0.17	+0.78^o	−0.69	
Median terr.	−0.85*	+0.908*	+0.06	−0.47	+0.89*	−0.84*

Note: The temperature and rainfall values used were those of 11 April - 10 May and the snow cover values those of 30 April for the chaffinch. All the values used were the same as in Table 3 for the brambling.

ment of breeding territories by both of the species for several days. The arrival of females appeared to advance the time by which the median of the breeding territories had been occupied by the brambling. In addition, if there were a lot of migrants, the establishment time of the breeding territories was also advanced in both of the species (see Tables 4 and 5).

After pairing, females also settled in the territories. The first chaffinch females arrived about a week after the time when the territorial behaviour of males had first been observed (Table 1). In contrast, the first brambling females appeared roughly a day before the territorial behaviour of males was seen on fixed terrain sites. The first pair formations were observed for both of the species about 4 days after the arrival of the first females. In early May, chaffinch females soon paired with territory owners, while brambling females paired with males in displaying sites before establishing the breeding territory. This conclusion was reinforced by the relationships shown in Fig. 4. The correlation coefficients between the pairing dates and the selected proximate factors are shown in Table 6.

As a whole, the brambling males arrived and occupied their nesting territories later (interspecific difference, $F=72.93$, $P<0.001$, $df=1$ and 29), but more simultaneously (interspecific difference, $F=13.09$, $P<0.001$, $df=2$ and 29) than the chaffinch males in the sympatric breeding ground. In the same way, the brambling females also arrived and settled down later (interspecific difference, $F=15.14$, $P<0.001$, $df=1$ and 29) and much faster (interspecific difference, $F=48.23$, $P<0.001$, $df=2$ and 29) than the chaffinch females.

3.2. Habits associated with establishing breeding territory

Chaffinch

After their arrival, the chaffinch males began their breeding period by singing and fighting around the selected display sites. The first males inhabited the edges of coniferous or mixed woods with large snow-free spots, and thereafter other woods. These woods were probably optimal at the time of arrival, but not necessarily later, after the snow had melted. The first 2-3 chaffinch territories occupied were usually close together, and later

Table 6. Simple and partial correlation coefficients between the time of the first pair formation and external factors for the chaffinch and the brambling at Juorkuna in the springs 1967-1972. The pairing time is an approximation of the territorial settling down of the females. For further explanations, see the text to Table 3. The external factors in the correlations were: temperature (Temp), snow cover (Snow), size of the cone crop of the pine and the spruce (Cone), rainfall (Rain), the settlement date of the first local male in his breeding territory (Terr), the arrival date of the first females in the spring (Fem).

Factors		First pairing	
Corr.	Const.	*Fri coe*	*Fri mon*
Temp	—	−0.82^{o}	−0.77^{o}
	Snow	+0.961*	+0.85^{o}
	Cone	−0.952*	+0.77
	Rain	−0.74	−0.75
	Terr	−0.67	+0.19
	Fem	+0.25	−0.41
Snow	—	+0.90*	+0.979***
	Temp	+0.977*	+0.956*
	Cone	+0.979*	+0.990**
	Rain	+0.89	+0.975**
	Terr	+0.80	+0.90*
	Fem	+0.01	+0.981**
Cone	—	+0.04	−0.01
	Temp	−0.85	−0.10
	Snow	−0.89	−0.71
	Rain	−0.71	−0.44
	Terr	+0.16	+0.38
	Fem	−0.19	−0.57
Rain	—	−0.59	−0.42
	Temp	+0.32	−0.48
	Snow	+0.58	+0.13
	Cone	−0.82	−0.58
	Terr	−0.40	−0.55
	Fem	−0.06	−0.005
Terr	—	+0.70	+0.901*
	Temp	+0.40	+0.75
	Snow	+0.27	+0.27
	Cone	+0.71	+0.916*
	Rain	+0.59	+0.916*
	Fem	−0.47	+0.72
Fem	—	+0.960**	+0.72
	Temp	+0.88	+0.20
	Snow	+0.77	-0.75
	Cone	+0.961*	+0.82^{o}
	Rain	+0.937^{o}	+0.65
	Terr	+0.937^{o}	+0.12
No. of years		5	6

Note: All the values were the same as in Table 5 for both of the species.

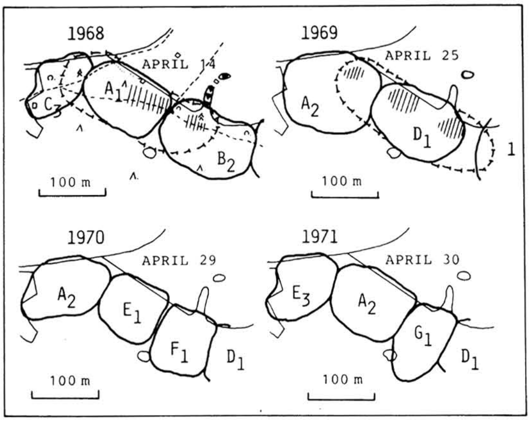

Fig. 5. Territory establishment by the chaffinch males (A–G) in one wood in the different springs 1968–1971. The Arabic numerals show the order of occupying the territories. (shaded) the main singing area of the first-arriving male; (⊣ ⊣ ⊣) territorial boundary before the definite size of the territory; (—) definite territorial boundary. The date is the arrival date of the first males. In the spring 1972, a cold weather spell occurred on April 23-27 and all of the breeding males were newcomers to the wood.

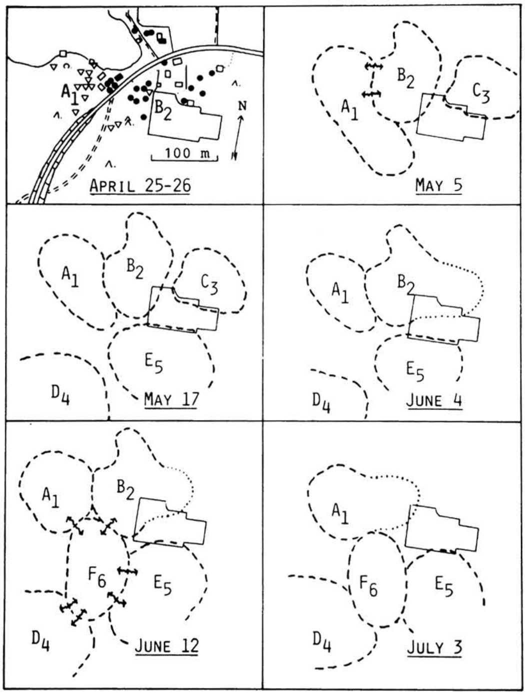

Fig. 6. The development of territorial conditions among chaffinch males (A–F) in a wood at Juorkuna during the breeding season, 1969. The Arabic numerals show the order of occupying the territories. (∇) song-post of the A-male; (●) song-post of the B-male; (arrow) intense fights; (– – –) territorial boundary; (····) boundary of a new defended area. C-male died at 7.30 p.m. on 3 June. F-male remained unpaired.

ones further away. A large area of the similar available habitat remained unoccupied.

An old marked chaffinch male uttered more than a hundred *fink*-calls within a few minutes immediately after alighting in his territory. Early in spring, when the population density was low and the snow-free spots were small, the chaffinch males defended much larger territories than later in the breeding season (Figs. 5 and 6). They tended to expand their territories until checked by other males. A male occasionally flew from his own territory over the field (300 m) and attacked a singing newcomer. Singing and fighting soon became intensive at particular points, concentrating on commanding song-posts, and if the territory was large, these points were sometimes a hundred metres or more apart. The male may, or is forced to, later relinquish part of his large territory. Further, old males often tended to return to a familiar territory the following year (Fig. 5). Sometimes they were lucky, but sometimes not, owing to late arrival. At this early phase, especially in adverse weather, some males also moved far away from their previous territories. Thus, chaffinch males arriving early might directly prevent settlement by other males arriving later. A late arrival establishing his territory behaved differently from the males arriving early or old males. Singing, he moved restlessly throughout the wood and searched for a suitable site to settle down (Fig. 6). One yearling ringed in the study area came back, settled in the marginal part of the area, and bred there.

Especially during the early spring or during cold weather spells, the birds tended to forage in open fields, even far from their own territories, although feeding in the territory increased rapidly following settlement. The home range was therefore much larger than the nesting territory. The boundaries of the territory became firmly established where natural boundaries, such as conspicuous trees, a forest margin, glades, or a fence occurred, but elsewhere the boundaries were usually a zone rather than a line.

The process of territory establishment by females began during pairing. The female wandered repeatedly across the boundaries of the territory of her mate. The male made efforts to bring her back by singing, courting, or leading flight. She defended the territory against other females. All the territorial boundaries seemed to be a zone, rather than a sharp line, for the females.

During the study years, all of the males settling early obtained mates, but one male arriving later was left without a mate (Fig. 6).

Brambling

In spring, bramblings were often observed to make courtship displays in flocks or in loose groups. Several males aggregated to sing intensively in one, or a few, neighbouring trees. They kept longer-than-usual individual distances and by singing and displaying attracted females. After the arrival of the females the males often began to court vigorously. The members of these groups were without topographically fixed territories. They frequently shifted their sites or broke up.

For example, on 5 May 1972, after staying for two days in the study area, a large brambling flock broke up into groups. At 5 p.m., eight brambling males were in a group where one of the males courted with a female on the upper branches of an old pine. He displayed his white rump, white wing flashes, and orange shoulders at a distance of 30-50 cm from her. The courting male was a slightly forward crouching posture, the drooping of the wings (see also Montell 1917) being very conspicuous, as was also the white rump with the fluffing of the feathers. The male did not directly face the female, but turned round first on one side and then on the other in front of her. (During the courtship display, males uttered *ksiip* and *grrr* calls.) At this phase, the female was passive and silent. After some minutes, the whole group together with the females moved elsewhere in the wood.

Soon some of the brambling males became attached to a certain terrestial point, where they began to sing regularly and defend a small display territory (see also Fig. 7). Around the local male/males, some newcomers also aggregated, singing and courting. Part (sometimes the whole) of the displaying group (the distances between the males were tens of metres) occasionally changed, especially after a cold weather spell and early in the spring. The courting territories often moved with the birds, probably appearing in the area that would become the nesting territory.

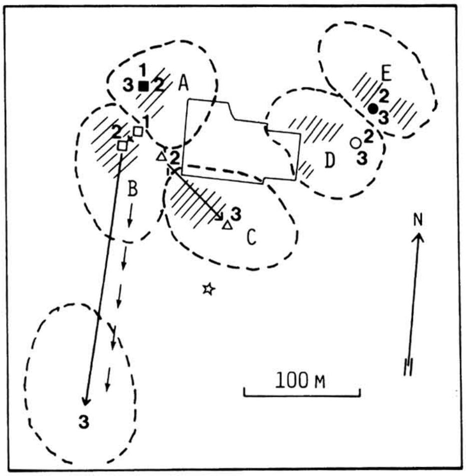

Fig. 7. Territory establishment and nest sites of the bramblings in relation to the singing centre of the displaying males (A-E) in a wood at Juorkuna in 1967. (shaded) singing centre of male; (–––) territorial boundary; (■,□,△,○,●) nest; the nest site on the different observation days: 1=17 May, 2=27 May, 3=7 June. Further, (☆) nest of the other pair after 7 June.

Pair formation in bramblings often took place rapidly in a courting territory. A male attracted a female by singing and by courting her. A male sometimes found a mate while they were both members of a displayig flock. In such a case the two birds arrived at the nesting site simultaneously.

After pairing, the female selected her nest site, usually in the courting territory of the male or near it, but occasionally also elsewhere (Fig. 7). During this phase the male defended a territory centring around the female and the nest (Fig. 8). Both of the mates defended the vicinity of the nest site against conspecifics. The male attacked from a longer distance than the female; the male only attacked other males, while the female attacked intruders of both sexes. In the study area, an aggregation of 3-5 brambling territories was most usual (max. eight territories). This was caused by a dispersal from the courting groups of the local birds after/during pairing according to the selection of the nest site by the females. At first, therefore, the territorial boundaries were diffuse, but after about three weeks they stabilised for some time. The feeding, drinking or bathing sites were often located outside the territory.

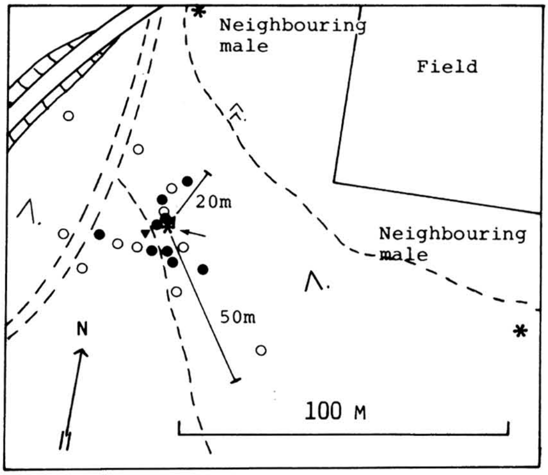

Fig. 8. Song-posts of a brambling male in relation to the nest (*) in the study area at 10.15–11.15 a.m. on 29 May 1967. The female was in her nest with 3 eggs at that time. Use of the song-posts: (○) used once (50 %), (●) used 2–5 times (40 %), and (△) used 10–12 times (10 %).

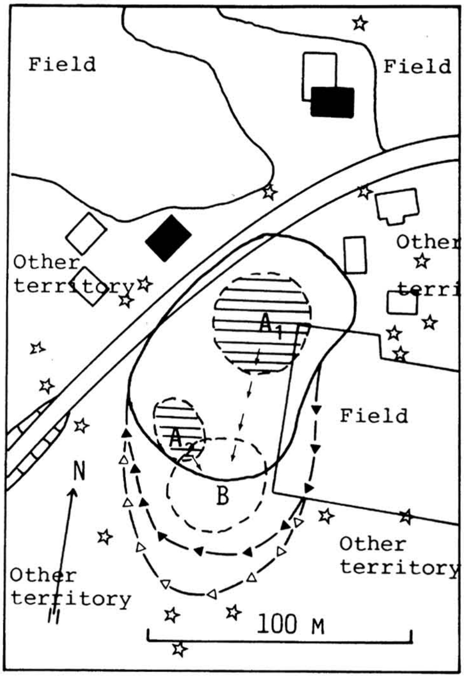

Fig. 9. Expansion of the territory of an unpaired brambling male (arrived on 5 May) before leaving the study area in 1968. — territory boundary on 25 May, —▼— on 30 May, and —▽— on 1 June. A is the main area of singing before 30 May, and B after that date. ☆ is a song-post outside the territory on 3 June. The male disappeared from his territory after 5 June.

Annually in early June, about 10–30 % of the territorial brambling males were unmated in the study area. A male settling early occasionally also remained without a mate. He expanded his territory before shifting elsewhere (Fig. 9). Furthermore, several (annually 20–40 %) territorial males left the area throughout the breeding season (see Mikkonen 1983a). Similarly, some brambling pairs also arrived in the study area later in summer and nested successfully. They settled down either at vacant sites or in a weakly defended part of the territory of another pair.

3.3. Song sites

In the study area, the average density of chaffinches and bramblings nesting annually was 53.5 and 27.7 pairs/km^2, respectively (Mikkonen 1983a). They commonly settled down in the same woods and their breeding territories overlapped. Both of the *Fringilla* species voiced their territorial song on tree-tops or other conspicuous posts and their courtship display song lower down (see Bergman 1953). They used the same height-scale of song sites in the study area (Fig. 10). Furthermore, most of the song sites were at the boundaries of individual territories and in the nuclear area near the nest site. Although chaffinches

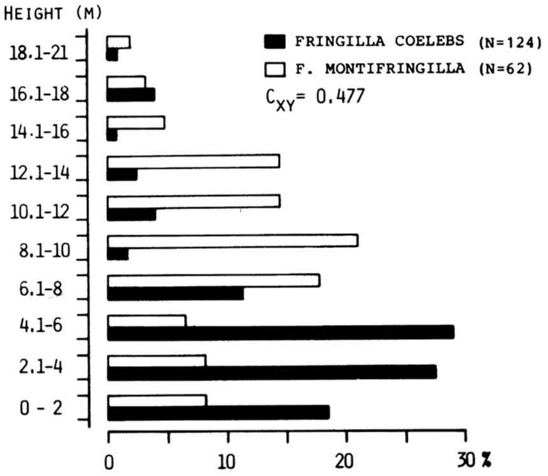

Fig. 10. Heights of the song-posts recorded for a chaffinch male and a brambling male on the same site, where their territories overlapped by about 90 %, at 7–9 a.m. during the period 20–31 May 1970.

arrived earlier than bramblings, their egg-laying took place at almost the same time in late May (see Mikkonen 1981a). At this nesting stage, the brambling male sang on markedly higher posts ($C_{xy}=0.48$) than the chaffinch male on a topographically similar site (Fig. 10). In conflicting situations the brambling males usually dominated over the chaffinch males.

According to play-back experiments, the meaning of the song differed in some respects between the two species. Especially before the egg-laying period, species-specific song stimulated the chaffinch males to sing or attack, while the brambling males only sang more vociferously. The chaffinch song increases aggressiveness among the males (but does not repel interlopers too far) and attracts the females near (see also Marler 1956a). (In the mating phase, chaffinch females were successfully attracted to a mist-net by playing back the song.) The brambling song seems to be sexual, but not aggressive, because the males only concentrated and/or began to sing more intensively when they heard a species-specific song.

4. Discussion

The main problem facing migratory birds occupying their breeding grounds are the availability of food, competition, predation, and the time available for successful nesting (e.g. Thomson 1950, Lack 1954, Myers 1981, Slagsvold 1982). It has been suggested that in the northern bird populations the significance of competition and predation would be less intense than in the southern ones (e.g. Salomonsen 1972, O. Järvinen 1979). Furthermore, it is generally agreed that, at high latitudes, breeding birds are faced by food availability and timing problems under short-summer and annually changeable conditions (Miller 1960, Morton 1976, Slagsvold 1976, Väisänen 1977). There will be an optimal time for territory establishment in each species, locality, sex, and age class (Hinde 1956a). The defensibility of mates within an ecological framework has been considered a main component in the evolution of reproductive tactics (e.g. Emlen & Oring 1977, Greenwood 1980). Information on arrival schedules and territory establishment is therefore necessary for predicting the adaptation of birds to nesting in N. Finland. For example, Myers (1981) and Ketterson & Nolan (1983) tested and explained the differential migration patterns by means of such information.

4.1. Arrival and territory establishment times

In the far north, a certain flexibility in the migration times is important for such migratory passerines as the chaffinch and the brambling (e.g. Mikkonen 1981a, b, 1983b). In N. Finland, the former species (a southern migrant) arrives discernibly earlier in April – May than the latter one (a northern migrant). The interspecific difference may also ultimately be due to their different responses to the same environmental factors (Mikkonen 1981a, see also Slagsvold 1976). Dolnik (1963) demonstrated that chaffinches respond to shorter daylength than bramblings. The daily photoperiod seems to be initially responsible for migratory restlessness and gonadal development, which other modifying factors terminate in the breeding area (see Lofts & Marshall 1960, Haase 1973, Murton & Westwood 1977, Dolnik & Gavrilov 1980). Additionally, the time of occupying the first territories correlated significantly with migration time for the chaffinch, but not for the brambling. This is due to the different behaviour in the establishment of breeding territory. The local chaffinch males disperse to their nesting sites soon after returning from their migratory passage, while the brambling males settle down after a slightly longer time.

The proximate factors influencing the distribution and establishment of breeding territories for both the chaffinch and the brambling appear to include food, habitat, weather conditions, and social competition. According to Brown (1969), it is important to note that complex interactions exist between the environmental conditions, the number of birds competing for territories, and territorial behaviour. Bergman (1953, 1966) observed in S. Finland that the snow considerably delayed territory establishment by chaffinches. In N. Finland, if there are some snow-free spots in the woods, the snow cover is no direct hindrance for the settling of the chaffinch males arriving early. However, a freshly fallen snow layer and cold weather (or a return-winter) quite distinctly delay territory establishment in the whole population, when territorial males may also cease displaying and re-join foraging flocks (see Mikkonen 1984). In early spring, the air temperature is strongly correlated with the speed of development of the territorial system (see also Marler 1956a). Bramblings, however, do not become establish in fixed territories before the snow has melted almost entirely in the forests in May.

Although the overall territorial system of the local chaffinches is formed more slowly than that of the bramblings, it is, however, approximately ready before the settlement of the local bramblings. The interspecific difference in the timing of the breeding events is hence largest during the phase of occupancy of the first territories (on average, 20 April for the chaffinch and 9 May for the brambling). Dolnik (1963) explained that the adaptive differences in thresholds to photostimulation may ensure the earlier onset of sexual activity in chaffinches compared to bramblings. He found the latter species associated with a more rapid growth of the gonad. In the study area, bramblings use less (42 % for males, and 11 % for females) time for the defence of their breeding territories prior to egg-laying than chaffinches (average 18 cf. 31 days for males, and 16 cf. 18 days for females, respectively). This is partly due to the interspecific differences in spring migration and territory establishment and the external factors influencing them, or the different breeding start strategy.

4.2. Habits associated with breeding territory establishment

Conder (1949) has suggested that the breeding territory develops from the increased individual distance. The first signs of territorial behaviour can already be seen in the spring flocks (e.g. Marler 1956a, Hinde 1959). This is supported by my field observations on an increase of aggressive encounters and enlarged individual distances in chaffinch and brambling groups. Kalela (1953, 1958), however, has pointed out that even the males singing in their territories form a closely-knit social group — a stationary flock with unusually long "individual" distances. The social stage reflects the development of the species-specific territorial system at the beginning of the breeding period (Tinbergen 1957, Wynne-Edwards 1962). According to the size and behaviour of spring flocks, the sociability of chaffinches is discernibly weaker than that of bramblings (Mikkonen 1984). In N. Finland, the former (especially males) migrate and occur much more often singly or in small groups than the latter.

Chaffinch males spread out singly to their own territories. Early in spring, however, they usually settle down, initially as aggregations of 2–3 territories, in the biotope most favourable at the time of arrival. A chaffinch male soon sets up an enlarged (or full-sized) territory. Thereafter the defended area shrinks steadily, until it is of a "definite" size, when competitor density and the amount of food increase. Several studies have revealed that males settling early tend to have large territories which gradually decrease in size when more males settle in the area (e.g. Huxley 1934, Bergman 1953, Marler 1956a, b, Verner 1977, Hixon 1980). In contrast, brambling males disperse to nest in loose groups or aggregations and less often singly. The grouping of brambling territories has also been reported by Udvardy (1956). Montell (1917) noted in Lapland that several males defend the same nest site. My results show that the display sites of males are firstly fixed at certain topographical points, being occupied by groups of 2–8 males in the study area. After pairing, the territory centres around the female and shifts sensitively according to her choice of nest site. In fact, paired bramblings establish their definite territories after the nest site has been chosen and maintain it only while the nest is in use. At the same time the size of the breeding territory expands. This agrees well with Conder's (1949) suggestion that some migratory species have a phase, a small mobile territory centred on the female, interposed between the individual distance and the fixed breeding territory.

In the social communication of birds audible and visible signals are alternative or complementary (e.g. Wynne-Edwards 1962). Singing and display play an important role in the advertisement and defence of the territory for both the *Fringilla* species (e.g. Bergman 1952, 1953, Hinde 1953, 1956b, Marler 1956a, b, c, Mairy 1969). My data support the observations by Marler (1956a, c) that chaffinch song increases the aggressiveness of the other males and attracts females in spring. On the contrary, brambling song only stimulates the males to aggregate and/or to sing more and more. It is therefore not aggressive, but stimulative, as Udvardy (1956) has also observed, for both males and females. In addition, territorial boundaries may change, especially after long adverse spells, if some of the territory owners have perished or gone elsewhere (see Figs. 6 and 7).

As a whole, the settlement of local birds in their territories takes place more synchronously among bramblings than among chaffinches. On the other hand, asynchronous settling, as among chaffinches, ensures the acquisition of suitable territory for the individuals arriving earlier or which are otherwise dominant. It has also been found that simultaneous settlement, as among bramblings, stimulates and synchronizes the reproductive activities (e.g. Crook 1965, Morton 1976, Emlen & Oring 1977, Oring 1982), and increases the population density on a local scale (e.g. Tompa 1962, Knapton & Krebs 1974).

A certain degree of spacing out may also be a defence against predators (e.g. Lack 1954, 1968, Crook 1965). The breeding territories of a species also serve a dispersive function in early summer (e.g. Holmes 1970). However, the aggregation of territories, found especially among bramblings, increases the awareness of approaching enemies (they join forces to mob a predator), the pooling of information on local food sources, and social stimulation. According to Emlen & Oring (1977), a clumping of territories may arise in situations where the resources are superabundant, unpredictable in time and space, or very costly to defend.

4.3. Food versus initial territory establishment

In spring, the first settlers usually occupy the best habitats in the area (e.g. Hildén 1965, Brown 1969, von Haartman 1972). Palmgren (1938) and Bergman (1953, 1956) emphasized that the arrival of spring is important in inducing chaffinches to occupy territories. Glas (1960) noted in the Netherlands that non-migratory chaffinches inhabited mixed woods about two weeks earlier than pine woods, whereas in the interior of S. Finland chaffinches first settled in pine stands and only afterwards in spruce stands, apparently because the snow melts earlier in the former than in the latter (Haapanen 1966). According to Lundberg et al. (1981), Brown (1975) has pointed out that the sequence of territory occupation can also be due to the order in which food becomes abundant. My present results agree well with the above findings; in N. Finland the first settlers of the two *Fringilla* species established their territories in the most attractive parts of the breeding area at their time of arrival, but in a species-specific fashion. The first chaffinch males defended enlarged territories in mixed and coniferous woods, where the snow-free spots were larger than in the others or conifer seeds were plentiful. Later on, the territories shrank in size. In the same woods, the corresponding bramblings were likely to aggregate and nest around good food supplies (or even in *Turdus pilaris* colonies, as mentioned by e.g. Slagsvold 1980), but after the snow had melted. Their small initial territory expands into a larger breeding territory. This also suggests interspecific differences in the function of the breeding territory in relation to food.

The foraging habits affect the dispersion pattern of breeding birds (e.g. Lack 1954, 1968, Crook 1965). Seastedt & MacLean (1979) believed that it is the food density in productive habitats rather than the total quantity of food that is important for the birds. Brown (1964) suggested that large territories occur among species which utilize them for feeding, which would indicate that this type of territoriality has evolved in response to competition for food. In early spring, chaffinches often fed on seeds on the snow in their territories or netural places and, after the snow melted, even on open fields. On the other hand, bramblings frequently fed outside their territory throughout the nesting season. At that time, the former species seems to prefer spruce seeds and the latter pine seeds (Engström 1955, Slagsvold 1977, Angell-Jacobsen 1980, Mikkonen 1981a). For both species, open fields serve as important reserves of food supplies during the breeding season. My results are thus consistent with Marler's (1956a, b) postulation that for chaffinches the food supply of the territory may be important during critical phases, although normally some feeding occurs outside the territory and the boundaries tend to disappear at the time of the greatest need. In the study area, territory owners may leave their territories and join with nearby flocks to feed, when the feeding conditions are inadequate. On days when feeding conditions in their territories or near them have improved, they immediately spend a lot of time there. This flexibility in the use of the available resources is important in the far north. During late cold spells, the territorial behaviour of both the chaffinch and the brambling may change suddenly according to the location of food (see Mikkonen 1984).

There are species, e.g. the crossbill, *Loxia curvirostra,* and the redpoll, *Carduelis flammea,* which may change their breeding areas according to food supply (e.g. Newton 1967, 1972, Pulliainen & Peiponen 1981). In N. Finland, the abundance of food may clearly operate as a modifying factor, but in a species-specific manner, for both of the *Fringilla* species at the time of their territory establishment. This conclusion is also supported by the observation that bramblings nested in a new area every year and that the return of the younger adult (as over 3 years old) chaffinches, not the older ones, was significantly less in springs with superabundant food supplies and exceptional weather conditions than it was in "normal" springs (Mikkonen 1983a, see also Appendix 1). At that time chaffinch males defend the available food more than brambling males. The asynchronous settling of chaffinches may be advantageous when food supplies are variable and scarce. The more simultaneous settling of bramblings is favourable when the resources are abundant and unpredictable in time and space (see Emlen & Oring 1977).

The ultimate link between food supply and territory size could be forged by more birds attempting to settle where food is most abundant (e.g. Lack 1954). It has been reported for many territorial birds that there is an inverse relationship between the food supply and the size of the breeding territory, which, in a given area, may be significantly influenced by local conditions (e.g. Tompa 1962, Brown 1969, Holmes 1970, Watson & Moss 1970, Newton 1980). It is well known that the chaffinch densities are remarkedly higher and the territory size smaller in luxuriant habitats than in barren ones (e.g. Palmgren 1933, von Haartman 1947, Bergman 1953, Glas 1960, Haapanen 1966). Similarly, brambling densities are very high where the suitable food supplies are temporarily superabundant (e.g. Silvola 1967, Ytreberg 1972, Mikkonen 1983c).

4.4. Pairing in relation to breeding territory

In spring, males arrive before females in both the *Fringilla* species (Mikkonen 1981a). This difference is usually linked to male and female roles in nesting behaviour (e.g. Hildén 1979, Myers 1981). At the onset of breeding, mutual stimulation (by audible and visible signals) appears to be important for the reproductive activities of males and females (e.g. Hinde 1953, Marler 1956a, Lehrman 1959, Moore 1983). The pair formation involves a gradual increase of mutual tolerance as well as sexual behaviour, as described in chaffinches by Hinde (1953, 1956a, b).

There are several aspects of territorial behaviour which may have a role in pairing (e.g. Hinde 1956a). My observations suggest that in both of the *Fringilla* species the time required to form a pair bond may be more or less similar (see Table 1), but the relationship to breeding territory is different. In N. Finland, the topographical fixation of the breeding territory of chaffinch males takes place mostly long before pairing and that of brambling males usually just before or after pairing (Appendix 2). The chaffinch male must acquire a territory, where he sings and otherwise displays, before he can acquire a mate (Newton 1972, see Marler 1956a, b). In contrast, the pair formation of bramblings seems to be independent of the breeding territory. A male may already begin to court with a female in moving display groups. The location of the definite breeding territory depends on nest site selection by the female. This implies an interspecific difference in the pairing system, because chaffinch males control access to females indirectly by means of a fixed territory and brambling males more directly without a fixed territory.

The pairing dates for the chaffinch and the brambling are strongly correlated with proximate factors, which affect either directly or indirectly the availability of food. Adequate food supplies are of fundamental importance to females before egg-laying (e.g. Siivonen 1957, Perrins 1970, Ojanen 1983). Thus, the territory size and/or the amount of food within the territory may constitute the basis for the female choice (e.g. Best 1977, Hixon 1980, Oring 1982). Females generally tend to choose the best available territory or mate, whereas a male usually accepts the first female arriving in his territory or coming near him (review Oring 1982). This would also seem to be supported by the smaller return rates (marked birds) of the females compared to the males (e.g. Best 1977, Greenwood 1980), as seen among chaffinches (Mikkonen 1983a). The clustering of singing males may make the area more attractive for unmated females and lead to a rapid and synchronized development of the reproductive activities (e.g. Crook 1965).

In N. Finland, where bird densities are low (O. Järvinen & Väisänen 1980), a male who is in one of a group of adjacent territories should find a mate more easily than one in an isolated territory (see Seastedt & MacLean 1979). In the study area all the early-settling chaffinch males paired, but late settlers occasionally remained without a mate (see Palmgren 1933, Bergman 1953). Brambling males, on the other hand, are likely to occur in displaying aggregations, where they sing intensively before pairing. Annually, several (10–30% of all) territorial males remained unpaired in the study area.

After pairing, chaffinch and brambling females begin to display territorial behaviour. The female's learning of the boundaries is slow and imprecise (Marler 1956a). She most likely defends only the nest site, especially in the case of the brambling female. This may be important in ensuring a certain spacing out of nests (Lack 1968), because a loose grouping of nests/territories among bramblings is obvious (e.g. Montell 1917, Udvardy 1956, Slagsvold 1980). The concentration of their nests may be partly explained by the habit of territory establishment.

4.5. Competition

Intraspecific competition

Social competition (for a mate, a site and food) among territorial birds is naturally strong before the onset of breeding (see Kalela 1958). Local familiarity is advantageous, because it increases, for example, the fighting potentiality and the information on food sources and shelters (against adverse weather and predators). Thus, the owner of the territory is usually the winner. It is a generally accepted hypothesis that an animal will defend a territory of a size that is just sufficient to satisfy its own requirements (e.g. Davies 1978, Rothstein 1979). However, Verner (1977) has suggested that individuals may defend territories much larger than is necessary for their own survival and reproduction (cf. Rothstein 1979).

Nice (1937) concluded that the chronology of territory occupancy was insignificant for the song sparrow, *Melospiza melodia*, because old males returning late were usually successful in reclaiming the former territories from first-year males. However, the order of establishing breeding territories seems to be important for both chaffinches and bramblings. Glas (1960) and Haapanen (1966) suggested that chaffinches inhabit the suboptimal woods later in spring than they do the optimal woods by the repellent effect of territory-holding birds (the "buffer effect"). This is verified by my present results. The earlier arrivals may quickly obtain sufficient experience of the area (see also Marler 1956a). It appears to be true that chaffinches, and especially bramblings, accumulate experience of the locality by short visits. Therefore, the territory settlement may be made difficult by the territoriality of the males arriving earlier (see Gauthreaux 1982), although older chaffinch males often try to return to the same breeding area and to their former territories (see also Bergman 1953, Anvén & Enemar 1957), and returning brambling males always nest in a new area the following year (Mikkonen 1983a).

On the average, adult chaffinches arrive earlier than juveniles (e.g. Sumakov & Sokolov 1982) and they are larger in size than the latter (e.g. Busse 1976). Lundberg et al. (1981) found in the pied flycatcher, *Ficedula hypoleuca*, and Tiainen (1982) in the willow warbler, *Phyllopscopus trochilus*, that larger (wing length) males occupy territory in better habitats and at an earlier date than small ones. A confusing factor is that both size and experience often increase with age (e.g. Searcy 1979, see also Gauthreaux 1982). Thus also age correlates positively with dominance. Ketterson & Nolan (1983) proposed that the priority of arrival is not sufficient for contesting over a claim with a former owner of territory (cf. Myers 1981). My observations, however, suggest that early-settling *Fringilla* males (body size and age unknown) have an obvious superiority in the competition over territories in N. Finland. This conclusion is also supported by the marked breeding birds, the turnover rates of which varied much more than the numbers of breeding pairs (Mikkonen 1983a). The changes of territory owners were notable in springs with superabundant food supplies, exceptional weather conditions, and slow occupying rate of territories, as was the case in 1971 and 1972 (see also Appendices 1 and 2), though the marked males did not return unusually late. Simultaneously, habitat changes in respect of territories (which were already more frequent in the cold spring of 1970) were also most numerous.

In the study area, marginal habitats were always available for birds excluded from the better ones, and breeders which died/left were replaced by the later arrivals in May, but usually no longer in June. Saether & Fonstad (1981) showed that a surplus of chaffinch males existed in a high density population in Central Norway in early May. Cederholm et al. (1974) pointed out that several brambling males and females belonged to the floating population at Ammarnäs, Swedish Lapland. According to my results, this may be partly due to the mode of territory establishment, unsuccessful breeding (destroyed nests), and unpaired birds.

Intraspecific competition and environmental factors influence the spacing of the local chaffinches and bramblings species-specifically. Males of both of the species disperse to nest in different habitats in ways which may be based on either the ideal free model or the ideal despotic model of Fretwell & Lucas (1969) and Fretwell (1972). Owing to the mating system, the situation among bramblings is more complicated than among chaffinches. They disperse to their breeding territories definitely only after pairing and not, as the chaffinches do, before pairing. At the same time, my results agree well with Brown's (1969) idea of an optimal mix between habitats and also optimal changes in the time scale. Depending on the species, the spacing behaviour will probably always be a compromise between conflicting selective factors, such as food, competition, mate, predation, and weather (e.g. Brown 1969, Watson & Moss 1970, Fretwell 1972, Davies 1978, Mikkonen 1983a). This can be seen in the development of the territorial system.

Interspecific competition

The complementary distribution pattern of the *Fringilla* species provides strong evidence for interspecific competition (e.g. Udvardy 1951, O. Järvinen & Väisänen 1979). Congeneric species which co-occur in the same habitats may reduce competition in several ways (Lack 1971, review in Cody 1974). Merikallio (1951) suggested that there is interspecific territoriality between the chaffinch and the brambling (see also Bergman 1952). In the study area they nest in the same woods and their territories may completely overlap horizontally. The territorial system of chaffinches is mostly complete at a time when local bramblings are still in flocks. Bramblings usually dominate over chaffinches (as stated by Udvardy 1956). I sometimes noted in the area that bramblings behaved very aggressively towards chaffinches, especially males at the intensive courtship phase and females near the nest (see also Bergman 1952; cf. Udvardy 1956).

The modes of habitat use by the two *Fringilla* species greatly resemble each other. In spring, however, there are some important differences in their habitat utilization with regard to the time scale (Mikkonen 1984). Saether (1982) demonstrated in Central Norway that during the breeding time chaffinches and bramblings chiefly use the same habitat, but partly at different foraging heights. A similar difference was revealed by my own data on the utilization of singing sites by chaffinch and brambling males.

It has earlier been reported that in Norway the brambling and the willow warbler exhibit partial interspecific competition in heath birch forests during the breeding period (Hogstad 1975, Angell-Jacobsen 1980). However, Fonstad (1984) demonstrated that the most likely explanation for this phenomenon is the difference in habitat preferences and not interspecific territoriality. In the study area I, too, noted no such competition between those species.

5. Concluding remarks

In N. Finland, where the favourable season for reproduction is short, the arrival and breeding start of the chaffinch and brambling are affected by two opposing selective pressures. On the one hand, an excessively early arrival involves risks, such as low temperature, heavy snowfalls, and scarcity of food (e.g. Hussell 1972, Mikkonen 1981a). Sometimes breeding may fail completely due to adverse weather (e.g. Pulliainen 1978, Ojanen 1979, Hildén et al. 1982, A. Järvinen 1983). On the other hand, early arrival increases the chance of establishing an optimal breeding territory and of finding a nest site and a mate (e.g. von Haartman 1968, Hildén 1979). Nest-losses by both the *Fringilla* species are very high, especially in early spring (Bergman 1956, Hildén 1967, Svensson 1978). They also need sufficient time to allow re-nesting attempts.

The reproductive tactics of the chaffinch and the brambling differ. Chaffinch males usually arrive early and tend to secure a territory in the familiar area. They immediately occupy a territory, partly for ensuring adequate food and partly for attracting a female. Bramblings arrive later on. They settle down to nest around good food supplies, depending on the proximate conditions in the new area each year. Pair formation in bramblings takes place before the breeding territory is set up (differenting from the habit of chaffinches). It is, therefore, independent of the topographically fixed territory. This means that chaffinch males have acquired a resource defence mating system and brambling males have acquired a female defence mating system (see also Greenwood 1980).

The territorial system of the brambling develops more synchronously than that of the chaffinch. Several breeding events before egg-laying occur for a shorter time among the former species than among the latter one. This may be partly due to a different development rate of the gonads (see Dolnik 1963), but also to differences in social behaviour (see Irving 1960). Indeed, the high degree of synchronism seems to be important for reproductive success (e.g. Wiens & Johnston 1977). Irving (1960) described this phenomenon as being a key to the adaptation of arctic breeders. The time-saving mechanism of bramblings, in response to environmental stress, may be important, especially in late springs. Chaffinches may secure enough time for nesting by their early arrival (see Slagsvold 1976). However, birds arriving and settling down too early may waste a lot of energy waiting in breeding readiness for the arrival of a late spring (e.g. Miller 1960).

Coexistence of the two *Fringilla* species in a sympatric breeding area in Finland is achieved by several mechanisms operating simultaneously (Mikkonen 1984). Cox (1968) suggested that problems of interspecific competition must be solved primarily through behavioural mechanisms or through isolation in space or time (see also Cody 1974). They are all used during the critical period before true nesting. The territorial systems of the chaffinch and the brambling are arranged in different ways and at different times in spring. This may be a consequence of interspecific differences in spring migration, selection of the breeding area, sociability, territory establishment, and the pairing system (see Mikkonen 1981a, b, 1983a, 1984). My results suggest that the two *Fringilla* species have different breeding strategies in N. Finland (Table 7).

Table 7. Comparison of the development of the territorial systems by the two *Fringilla* species in a sympatric breeding ground at Juorkuna in N. Finland.

Event	*Fringilla coelebs*	*F. montifringilla*
Arrival	earlier on	later on
Territory (males)		
spacing	singly; asynchronously	aggregations; more synchronously
size (at first)	large territory with secure food reserves in early spring	smaller territory feed more elsewhere
establishment time	rapidly after arrival; before pairing	more slowly after arrival; more or less after pairing
Breeding site tenacity	strong	no

Note: Breeding site tenacity is according to Mikkonen 1983a.

Acknowledgements. I wish to thank E. Mikkonen for his assistence in the field work, and E. Pulliainen, S. Sulkava, J. Tiainen, S. Panelius, and an anonymous referee, for their useful comments on the manuscript. I also wish to express my sincere thanks to Sirkka-Liisa Leinonen and Leigh Plester for their revision of the English. My work was supported by grants from the Emil Aaltonen Foundation.

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Appendix 1. Data for the period 1967-72 at Utajärvi. Temperature (°C, mean daily minimum) and rainfall (mm) at Pelso Meteorological Station, Vaala. Snow depth (cm) at Särkijärvi Observation Point, Utajärvi. Cone crops in arbitrary scale from 0 to 5.

	1967	68	69	70	71	72	Mean	*SD*	*CV*%
Temperature									
1-25.IV	−2.7	−4.8	−6.1	−7.1	−6.9	−3.6	−5.2	1.8	35
11.IV-10.V	−2.4	−1.9	−3.6	−3.5	−5.9	−2.0	−3.2	1.5	47
1-10.V	−1.9	+0.5	−3.6	−0.8	−2.5	−1.2	−1.6	1.4	87
Snow cover									
15.IV	21	40	85	58	78	0	47	33.0	70
30.IV	15	10	25	25	45	5[a]	20	15.5	78
5.V	8	1	20	10	20	0	10	8.8	88
Rainfall									
1-30.IV	23	51	36	38	17	43	35	12.6	36
11.IV-10.V	34	48	51	31	15	47	38	13.7	36
Cone crop									
Pine	4	1	2	3	3	4	2.8	1.2	43
Spruce	0	3	1	1	5	2	2.0	1.8	90
Total	4	4	3	4	8	6	4.8	1.8	38

Note: [a] = locally corrected value.

Appendix 2. Times (A = April, M = May) of migration, territory establishment, pairing, and egg-laying by chaffinches and bramblings at Juorkuna in the springs 1967-1972. Migration = the starting date of the spring migratory period. First females = the arrival date of the first females in the spring. First territory = the settlement date of the first local male in his breeding territory. Median territory = the median date of the settlement of all the breeding territories. Pairing = the pairing time of the first pair in the spring. Egg-laying = the starting date of egg-laying for the first clutch in the spring. Individuals/observation day were recorded during the migratory period (see Mikkonen 1981a). P = significance of interspcific difference (F-test). In the years 1968 and 1972 there were cold spells 20-24 May and 23-27 April, respectively.

	Fringilla coelebs								*Fringilla montifringilla*								
	1967	68	69	70	71	72	Mean	*SD*	1967	68	69	70	71	72	Mean	*SD*	*P*
Migration	9 A	13 A	20 A	26 A	18 A	15 A	17 A	5.9	28 A	28 A	4 M	4 M	7 M	3 M	2 M	3.6	<0.001
First females	28 A	21 A	4 M	1 M	7 M	16 A	28 A	8.0	9 M	1 M	10 M	4 M	14 M	5 M	7 M	4.7	0.033
First territory	14 A	14 A	25 A	29 A	24 A	16 A	20 A	6.5	10 M	5 M	13 M	8 M	10 M	5 M	9 M	3.1	<0.001
Median "	—	17 A	4 M	2 M	8 M	29 A	30 A	8.0	13 M	7 M	14 M	10 M	14 M	7 M	11 M	3.3	0.014
Pairing	—	30 A	5 M	4 M	8 M	22 A	2 M	6.2	10 M	7 M	15 M	12 M	14 M	6 M	11 M	3.7	0.016
Egg-laying	28 M	29 M	23 M	19 M	13 M	16 M	21 M	6.5	27 M	30 M	27 M	24 M	21 M	28 M	26 M	3.2	0.132
Ind/obs.day	19	59	29	30	14	61			57	187	93	49	14	210			

Received 30.VIII.1984
Printed 11.VII.1985