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Autumn migration of Blue Tit *Parus caeruleus* at Falsterbo, Sweden 1980–94: population changes, migration patterns and recovery analysis

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Abstract

Extensive ringing data from Falsterbo, South Sweden, were used to analyse numbers, migration patterns and recoveries in the Blue Tit *Parus caeruleus* during 15 years (1980–94). The ringing totals as well as the totals from the migration counts at Falsterbo showed an overall increase of Blue Tits during this period. This corresponded with the trends from other monitoring projects in Sweden as well as the number of annually ringed nestlings. Analyses of the daily and seasonal migration patterns and the age and sex composition were carried out. The majority of the migrating Blue Tits were females, but with an increasing proportion of males with increasing numbers of migrating Blue Tits. The majority of the migrating Blue Tits were first-year birds and this proportion increased with the strength of migration. The results indicated that the same individuals may show repeated migration during several seasons, more like regular migrants than true irruptive species. The recovery analysis shows breeding area, migration routes and wintering areas for Blue Tits ringed or recaptured at Falsterbo. Obviously the major part of the birds originate from southern Sweden. They are short-distance migrants wintering in Denmark and northern Germany. Many Blue Tits also return inland when confronted with the sea at Falsterbo. The intensity of migration varied a lot from year to year. Strong migratory movements occurred more often towards the end of the study period and with increasing numbers of Blue Tits involved. It appeared that the key factors for the occurrence of strong migratory movements were a high population density, caused by high winter survival and good breeding results, in combination with a low amount of Beech mast or other food resources during the following autumn.

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Introduction

The Blue Tit *Parus caeruleus* is a widespread and abundant species in deciduous and mixed forests in southern Sweden. Since the 1960s the Blue Tit has increased its geographic range to the north as far as northern Sweden (Risberg 1990). Ulfstrand & Högstedt (1976) estimated the Swedish population at 200,000 pairs based on information from 1955, whereas the latest estimate (Koskimies 1993) is 400,000–1 million pairs. The same positive trend has been observed in the rest of Scandinavia. In Norway the population has increased since the 1970s (Gjershaug et al. 1994), and in Finland, it has increased considerably since the mid-1950s (Hyytiä et al. 1983, Hildén 1986). In Denmark the population is considered to have increased since the end of the 1970s (Asbirk & Braae 1988; Koskimies 1993). The population in Skåne (the southernmost province of Sweden), was estimated at 60,000 pairs at the beginning of the 1980s (Andell & Nilsson 1988, Risberg 1990).

The Blue Tits in Sweden are mainly sedentary, but parts of the population make migratory movements. In some years the migration is quite strong, reminding of an irruption. The direction of migration is mainly towards southwest (Rudebeck 1950, Risberg 1990). Being a typical forest bird and not a regular migrant, the open sea acts as a migration barrier to the Blue Tits. They will therefore rather follow coastlines than cross the sea. As a consequence, in autumn they will be concentrated on the Falsterbo peninsula (Rudebeck 1950, Ulfstrand 1962, Ulfstrand et al. 1974), which is the southwestern-most point of Sweden.

The high numbers of migrating Blue Tits at Falsterbo in some years have lead to several analyses (Ulfstrand 1962, Persson 1972a, 1972b, Lindskog & Roos 1979, 1980). Its migration in single years is also described in some of the annual reports on ringing and migration at Falsterbo, regularly published in the journal *Anser* (e.g. Karlsson et al. 1986, 1991, 1995, Roos 1993).

During the last 15 years the annual numbers of migrating Blue Tits have increased considerably. As a consequence of this, the number of Blue Tits ringed at Falsterbo, as well as the number of recoveries, have increased rapidly. Although ringing at Falsterbo started in 1947, there were only 53 recoveries of Blue Tits up to 1980 (Roos 1984), which should be compared to 322 at the end of 1994. The number of recaptures (controls) at Falsterbo of Blue Tits ringed elsewhere has increased from 6 to 154 during the same period. The recoveries at Falsterbo 1947–80 were analysed by Roos (1984). There are also two analyses of all Swedish recoveries of Blue Tits (Rendahl 1959, Källander 1983a).

This paper describes the migration of Blue Tits at Falsterbo during 1980–94, analysing numbers, seasonal and daily patterns of migration and variations in age and sex distribution. The numerous recoveries made it possible to map the breeding range, migration routes and wintering areas of Blue Tits passing at Falsterbo.

Material and methods

Observations of the bird migration in autumn at Falsterbo (55°23´N, 12°49´E) were done regularly during 1942–44 (Rudebeck 1950) and 1949–60 (Ulfstrand et al. 1974). Since 1973, strictly standardized migration counts are carried out every autumn from 11 August to 20 November (Roos 1974).

Ringing activities started already in 1947. Since the middle of the 1960s, regular ringing, mainly of passerines, has taken place in the garden surrounding the Falsterbo lighthouse (Roos 1984). Since 1980, the ringing scheme has been standardized (Roos & Karlsson 1981). The autumn ringing period at Falsterbo starts on 21 July and continues until 10 November. The daily trapping time is a minimum of six hours from dawn (though always starting at a full or half hour) and thereafter as long as at least 10 birds irrespective of species are caught per hour.

Depending on the weather, up to 21 mistnets are used at permanent sites in the lighthouse garden and at some shrubs just outside it. The lighthouse garden is about 100 x 100 m and situated in the middle of an open area (golf course). The vegetation of the lighthouse garden consists of 6–10 m tall trees, mainly Birch *Betula* sp. and Pines *Pinus* sp. with a dense undergrowth of different shrubs. Just outside the garden, there are some low plantations of Mountain Pine *Pinus mugo,* Common Alder *Alnus glutinosa* and Elder *Sambucus nigra.*

The nets are checked every 30 minutes. At ringing, the birds are always aged and, when possible, sexed. Biometric data (wing-length, fat score, weight and moult status) are collected from as many birds as time allows.

All Blue Tits included in this material were aged, primarily as first year birds (1K, Euring code 3) or older (2K+, Euring code 4) by moult characters (Svensson 1975). From 1984 and onwards iris colour was used to classify adult Blue Tits into two groups: birds from last year (2K, Euring code 5) or older (3K+, Euring code 6) (Karlsson et al. 1985). In 1985–94, 98.6% of the adult Blue Tits were aged according to this method. Sexing of the Blue Tits by colour differences in plumage (Drost 1951, own observations) started in 1981 and 99.7% of the Blue Tits were sexed in 1983–94 (Table 1).

The analysis of ringing numbers includes the autumns of 1980–94. During this period a total of 49,173 Blue Tits were ringed, all of which were caught at the lighthouse garden. A few Blue Tits ringed in July, August and up to 11 September, i.e. before the true migration started (Figure 1), were judged as local birds and therefore excluded from the analyses (n=152, 0.3% of the total). Thus, 49,021 Blue Tits were included in this study. Blue Tits ringed in spring were also excluded, since numbers were very small (range: 2–26 per season).

Spearman's Rank Correlation Coefficient (Fowler & Cohen 1994) was used to test the correlations between various variables, and circular statistics follow Batschelet (1981). The coefficient of variation (CV = standard deviation/mean value * 100) was used to express the distribution of observations around their mean value. The numbers of migrating Blue Tits were taken from the standardized migration counts at Falsterbo (Roos 1981–95).

The analysis of ringing recoveries includes all recoveries of Blue Tits ringed at Falsterbo and recoveries at Falsterbo of Blue Tits ringed elsewhere (controls) during 1947–94, but only when the distance between the ringing and the recovery sites was more than 10 km. In total, 322 recoveries and 154 controls were included.

Table 1. Number of ringed (RM) Blue Tits at Falsterbo during autumn 1980–94 (11 September–10 November) and the distribution of age and sex groups. For comparison, the number of migrating Blue Tits registered within the standardized migration counts at Falsterbo (Roos 1974–95) were added (MC). N.B. "All adults (2K+)" include 2K, 3K+ and some birds which were not aged as 2K or 3K+. M = male. F = female. M/F = not sexed.

Antal ringmærkede (RM, fordelt på alder og køn) respektivt udtrækkende (MC) blåmejser ved Falsterbo i perioden 11 september–10 november 1980–94. Bemærk, at "All adults (2K+)" inkluderer 2K, 3K+ samt nogle fugle, der ikke var bestemt til hverken 2K eller 3K+. M = han. F = hun. M/F= ikke kønsbestemt.

	First-year 1K				All adults (not first-year) 2K+				Second-year 2K				Older than second-year 3K+				Grand Total	
	M	F	M/F	Total	M	F	M/F	Total	M	F	M/F	Total	M	F	M/F	Total	RM	MC
80	-	-	2250	2250	-	-	31	31	-	-	-	-	-	-	-	-	2281	3868
81	6	169	1371	1546	6	74	101	181	-	-	-	-	-	-	-	-	1727	4208
82	21	63	11	95	2	29	5	36	-	-	-	-	-	-	-	-	131	35
83	36	162	4	202	1	7	-	8	-	-	-	-	-	-	-	-	210	180
84	1224	4271	23	5518	7	184	-	191	4	115	-	119	-	14	-	14	5709	22315
85	747	2974	1	3722	17	310	-	327	13	261	-	274	1	23	-	24	4049	11679
86	642	3081	-	3723	28	269	-	297	24	194	-	218	4	57	-	61	4020	15014
87	61	242	-	303	8	228	-	236	6	156	-	162	2	70	-	72	539	386
88	1475	4213	7	5695	8	157	-	165	5	87	-	92	3	68	-	71	5860	20258
89	133	658	10	801	22	316	1	339	19	260	1	280	3	56	-	59	1140	2301
90	1550	5124	9	6683	30	283	-	313	17	122	-	139	13	159	-	172	6996	49606
91	711	2400	9	3120	79	853	-	932	61	682	-	743	18	171	-	189	4052	10918
92	35	182	4	221	9	185	.	194	3	107	-	110	6	78	-	84	415	304
93	942	3922	25	4889	17	242	-	259	11	139	-	150	6	103	-	109	5148	43121
94	1262	4796	33	6091	49	603	1	653	41	428	1	470	8	175	-	183	6744	52483

Results

Number of ringed and migrating Blue Tits

During the autumns of 1980–94, a total number of 49,021 Blue Tits were ringed at Falsterbo with a large variation in seasonal numbers (mean: 3268, range: 131–6996, CV=74, Table 1). The corresponding numbers of Blue Tits recorded during migration counts varied to an even higher extent (mean: 15,778, range: 35–52,483, CV=113, Table 1). The totals of both ringed and migrating Blue Tits tended to increase over the years, but not statistically significantly (n=15; ringing: r_s=0.454, p>0.10; migration counts: r_s=0.481, p<0.10), due to the great variation in numbers from one year to the next.

There was a strong correlation (n=15, r_s=0.964, p<0.01) between seasonal numbers of Blue Tits counted on migration and Blue Tits ringed. This indicates that these methods reflect the variation in

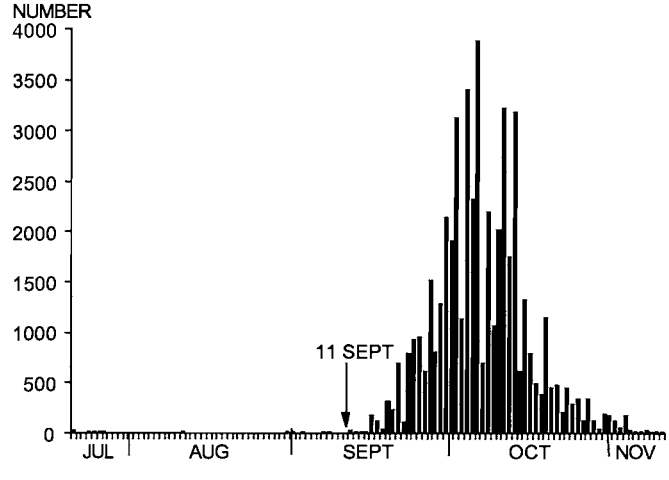


Figure 1. Seasonal distribution of Blue Tit captures at Falsterbo in autumn (21 July–10 November). Pooled data for 1980–94. Birds trapped before 11 September (152 individuals, left of arrow) were considered as local birds and were excluded from all analyses.

Dagsfordelingen af totalfangsten af blåmejse i Falsterbo i efterårene (21 juli–10 november) 1980–94. Blåmejser fanget før den 11 september (152 fugle, til venstre for pilen) betragtes som værende lokale fugle og er derfor ikke inkluderet i denne analyse.

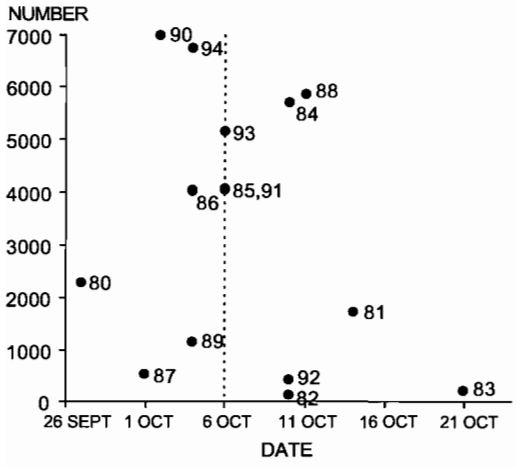


Figure 2. Median dates of captures of Blue Tits at Falsterbo. The dotted line indicates the median date for all seasons (1980–94).

Mediandatoer for fangst af blåmejse i Falsterbo. Den stiplede linie indikerer mediandatoen for alle årene 1980–94.

the true number of migrating Blue Tits in a similar way.

The ratio of counted to ringed Blue Tits (Table 1: MC/RM) increased significantly with increasing numbers (n=15, r_s=0.900, p<0.01). These changes may express the urge to migrate, especially since the number of counted Blue Tits was even lower than the number of ringed ones in some years with weak migratory movements (1982, 1983, 1987, 1992; see Table 1).

Seasonal timing of migration

The timing of migration was very similar in almost every autumn. The middle 90% (5–95%) of the Blue Tits were ringed during the period 23 September to 23 October (Figure 1) and the median date for all birds ringed in 1980–94 was 6 October (Figure 2). However, there were some differences between years, depending on the intensity of migration. The middle 90% were reached within a shorter period when the migratory movements were strong, though the correlation was not significant (n=15, r_s=-0.518, 0.05<p<0.10). The median dates occurred within eight days at the beginning of October in the eight years with the highest numbers of ringed Blue Tits. In the seven remaining years (with lower numbers), median dates varied much more (27 September–21 October, Figure 2). These differences were mainly an effect of single days with relatively high numbers of birds ringed. In years with only little migration, weather conditions are relatively more important for whether Blue Tits will occur at the trapping site at all and this may influence the median date.

In 1980–94 Blue Tits were trapped on 529 (57.8%) of all days 11 September–10 November. On 112 days (12.2%) the daily ringing total was higher than 100, on 25 days (2.7%) higher than 500 and on six days (0.7%) higher than 1000. The highest daily total, 1716, occurred on 6 October 1993.

The three highest daily totals together accounted for 44% (range: 36–53%) of the autumn total. This is a typical pattern in irruptive species and short distance migrants at Falsterbo (Lindskog & Roos 1979, Karlsson et al. 1995), while corresponding figures for nocturnal long distance migrants are distinctly lower (Table 2).

Table 2. The three highest daily ringing totals for Blue Tits expressed as percentages of the seasonal totals in the autumns of 1980-94 compared to those of some of the most numerously ringed species belonging to different migratory categories. CV = coefficient of variation. D/N = Diurnal or Nocturnal migrant.

De tre største dagstotalers procentuelle andel af sæsonstotalerne for efterårene 1980-94, samt variationskoefficient, CV, for blåmejse sammenlignet med andre talrigt ringmærkede arter, der tilhører forskellige trækkategorier. D/N = dagtrækkende henholdsvis nattrækkende arter.

	D/N	%	CV
Blue Tit *Parus caeruleus*	D	44	12
Partial migrants/Irruptive species:			
Coal Tit *Parus ater*	D	46	24
Great Tit *Parus major*	D	42	19
Siskin *Carduelis spinus*	D	65	25
Bullfinch *Pyrrhula pyrrhula*	D	55	30
Medium distance migrants:			
Wren *Troglodytes troglodytes*	N	43	25
Robin *Erithacus rubecula*	N	41	22
Goldcrest *Regulus regulus*	N	43	32
Chaffinch *Fringilla coelebs*	D	37	25
Long distance migrants:			
Redstart *Phoenicurus phoenicurus*	N	33	21
Garden Warbler *Sylvia borin*	N	33	24
Willow Warbler *Phylloscopus trochilus*	N	32	27

Table 3. Summary of age and sex distribution (%) in Blue Tits ringed at Falsterbo. Different periods were chosen according to accuracy of ageing and sexing (cf. Table 1): (1) 1980–94: All Blue Tits were aged as either first-year (1K) or adults (2K+). (2) 1983–94: As (1) but most of the Blue Tits (99.7%) were also sexed. (3) 1985–94: As (1)+(2) but most of the adult (2K+) Blue Tits (98.6%) were aged as either second-year (2K) or older (3K+). Read row/column, i.e. 2K were 71.0% of all adults and 6.8% of the total in 1985–94.

Oversigt over alders- og kønsfordeling (læs: række/kolonne) for blåmejser ringmærket ved Falsterbo. Der er angivet forskellige tidsperioder, da de forskellige metoder til alders- og kønsbestemmelse er taget i anvendelse til forskellige tidspunkter (jvf. Tabel 1).

	% of 1K	% of 2K+	% of 2K	% of 3K+	% of Total
(1) 1980–94:					
1K					91.5
2+					8.5
(2) 1983–94:					
1K M	21.5				19.6
1K F	78.2				71.4
2K+M		7.0			0.6
2K+F		93.0			8.1
Not sexed	0.3				0.3
(3) 1985–94:					
2K		71.0			6.8
2K M			7.6		0.5
2K F			92.4		6.3
3K+		27.6			2.6
3K+M				6,.3	0.1
3K+F				93.,7	2.6
Not aged		1.4			1.4

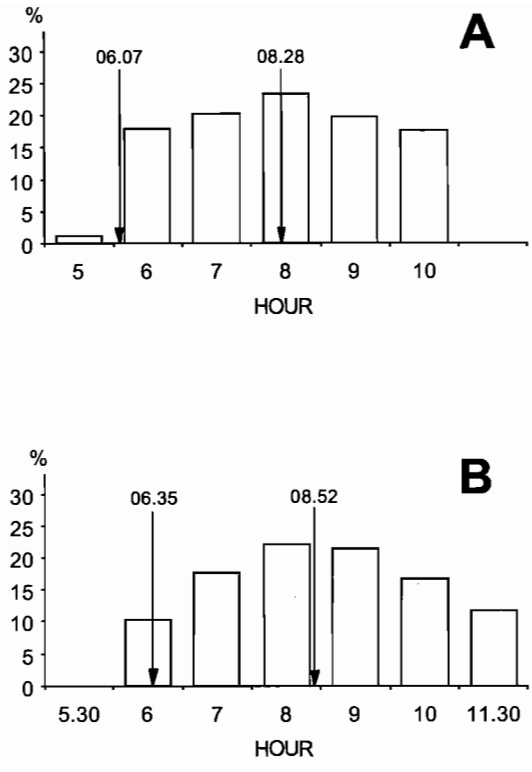


Figure 3. Daily distribution of captures of Blue Tits at Falsterbo as percentages per hour. Only the six first hours (minimum standard trapping time) included. A: 21 September–5 October. Ringing starts at 05.00 hrs. Average sunrise: 06.07 hrs. B: 6–20 October. Ringing starts at 05.30 hrs. Average sunrise: 06.35 hrs. The left arrow shows average sunrise and the right one shows the "theoretical median time" (TMT) during period A and B respectively. Hours according to Swedish Normal Time (UTC + 1 hour).

Fangstfordelingen af blåmejser i Falsterbo i procent per time. Kun de seks første timer er inkluderet i "minimum fangst tid". A: 21 september–5 oktober; ringmærkningen starter kl 05.00; B: 6–20 oktober; ringmærkningen starter kl. 05.30. Pilene til venstre viser tidspunktet for solopgang og pilene til højre viser det "teoretiske median tidspunkt" (TMT) for henholdsvis periode A og B. Tidsangivelsen relaterer til svensk normaltid (UTC + 1 time).

Diurnal timing of migration

The daily pattern of migration was difficult to analyse because the starting time of the ringing activities change stepwise during autumn, and neither clock hour nor elapsed time since sunrise were adequate ways to express this pattern. However, even though Blue Tits were mostly caught in flocks and the mistnets were emptied every 30 min, it was possible, by use of interpolation, to calculate a theoretical median time (TMT), i.e. the time of the day when 50% of the daily total were captured (Figure 3). Only the first six hours were included, since this is the minimum trapping effort per day. Blue Tits were sometimes also caught later, but the number of days with prolonged ringing differed much from year to year, making relevant comparisons impossible. However, the majority of the birds were caught during the first six hours in all years (see below).

The period around the median date (21 September –20 October) was selected for comparison. In this period, the ringing started at 05.00 hrs. (Swedish

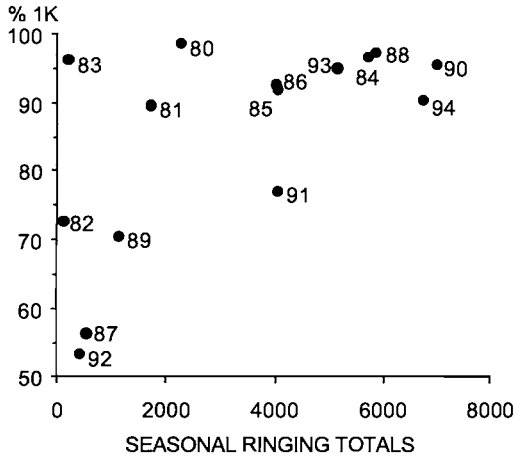


Figure 4. Percentage first-year (1K) of all ringed Blue Tits in relation to the seasonal totals in the autumns 1980–94 (n=15, r_s=0.500, p<0.10).

Andelen 1K i procent af alle ringmærkede blåmejser i forhold til sæsonstotalerne for efterårene 1980–94 (n=15, r_s=0,500, p<0,10).

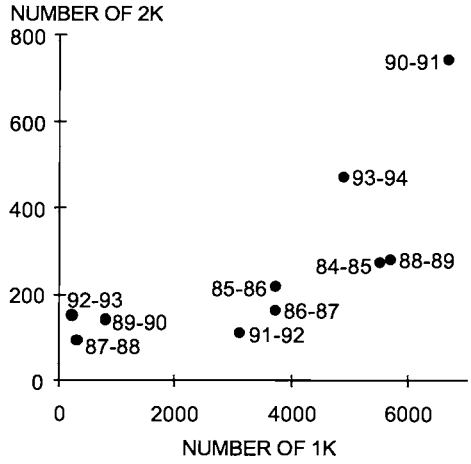


Figure 5. Number of ringed first-year (1K) Blue Tits 1984–93 in relation to the number of second-year birds (2K) during succeeding autumns 1985–94 (n=10, r_s=0.867, p<0.01).

Antallet af ringmærkede 1K blåmejser efterårene 1984–93 i relation til antallet af 2K blåmejser i det efterfølgende efterår 1985–94 (n=10, r_s=0,867, p<0,01).

Normal Time) from 21 September to 5 October (period A, Figure 3) and at 05.30 hrs. from 6 October to 20 October (period B, Figure 3). Compared to the total daily captures, 75% of the Blue Tits were caught within the first six hours in period A and 81% in period B, respectively.

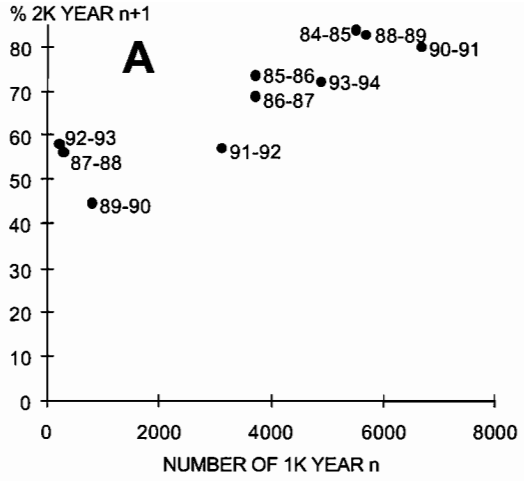
The distribution resembles a normal distribution in both periods (Figure 3). The difference of 24 minutes between the median for period A and the median for B indicates that the TMT depends on the sunrise, which is on average 28 minutes later in period B than in period A. The peak hour was between 08.00 and 09.00 in both periods, i.e. 2–3 hours after sunrise, which is similar to the pattern in some other regular or partial diurnal migrants like Dunnock *Prunella modularis*, Chaffinch *Fringilla coelebs*, Yellowhammer *Emberiza citrinella* and Great Tit *Parus major* trapped at Falsterbo (Roos et al 1983, own observations).

Age and sex distribution

A very high percentage of the Blue Tits (91.5%), were first-year birds (1K, Table 3), which corresponds well with the age distribution in many other species trapped at Falsterbo in autumn. There was a strong significant correlation (1980–94: n=15, r_s=0.986, p<0.01) between the number of first-year Blue Tits and the total number, whereas the correlation between the number of adults (2K+) and the total number was weak (1980–94: n=15, r_s=0.461, 0.05<p<0.10). The proportion of 1K birds was larger (90% or more) in years with many Blue Tits trapped. Thus, the four years with the lowest totals were also the years with the lowest proportions of 1K birds (Figure 4). The correlation was not quite statistically significant (n=15, r_s=0.500, 0.05<p<0.10), mainly due to two years, 1983 and 1991, which fell outside the general pattern.

In 1985–94, 98.6% of the adult (2K+) Blue Tits were aged as either second-year birds (2K) or older (3K+). On average 71% of all adults were aged as 2K birds (range: 44.4–82.6%; CV=18). Only in one year (1990) was the number of 3K+ birds higher than the number of 2K birds. There was an increasing trend in the number of 3K+ birds (1985–94: n=10, r_s=0.782, p<0.02). This may be a consequence of a general increase of the population, but it may also indicate that an increasing number of Blue Tits make regular (annual) movements, especially since the number of 2K birds was not significantly increasing over the years (n=10, r_s=0.067, p>0.10). However, ten years may be too short a timescale for any far-reaching conclusions.

There was a significant correlation between the number of 1K birds in one year and the number of 2K



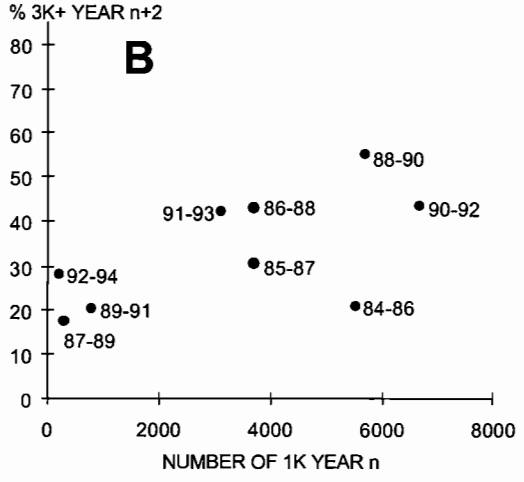


Figure 6. Percentages of second-year (2K) birds during year n+1 (A), and older (3K+) during year n+2 (B) of the total number of adults (2K+) during year n+1 and year n+2 respectively, related to the number of first-year (1K) Blue Tits ringed during year n ($n(2K)=10, r_s=0.830, p<0.01$; $n(3K+)=9, r_s=0.683, p<0.05$).

Andelen i procent af 2K blåmejser i år n+1 (A) og 3K+ i år n+2 (B) af det totale antal 2K+ i år n+1 henholdsvis n+2 relateret til antallet af 1K blåmejser ringmærket i år n ($n(2K)=10, r_s=0,830, p<0,01$; $n(3K+)=9, r_s=0,683, p<0,05$).

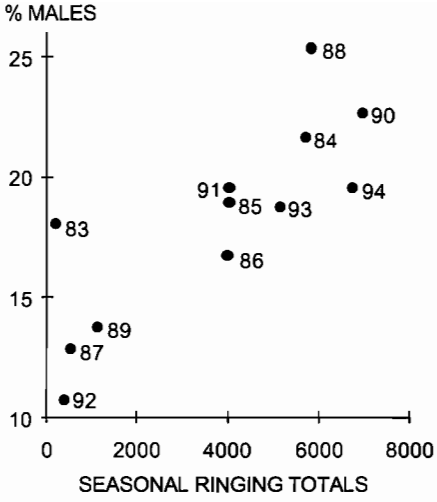


Figure 7. Percentage of males in relation to seasonal totals of Blue Tits ringed 1983–94 (n=12, $r_s=0.862$, $p<0.01$).

Andelen i procent af hanner i relation til antallet blåmejser ringmærket per efterårssæson 1983–94 (n=12, $r_s=0,862$, $p<0,01$).

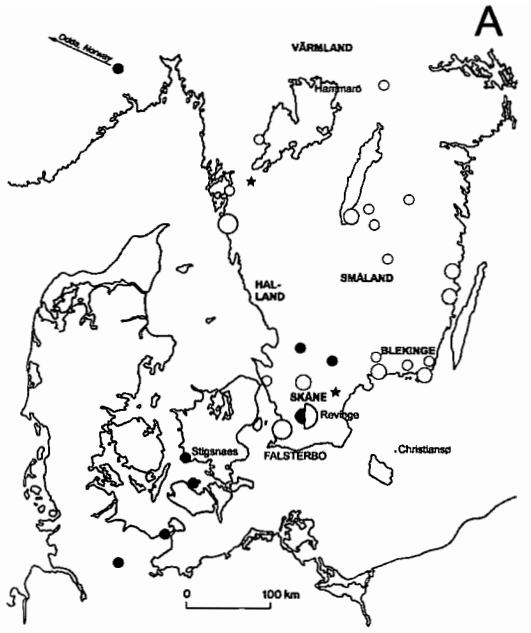
birds in the following year (1984/85–93/94: n=10, $r_s=0.867$, $p<0.01$, Figure 5). The proportion was on average 14:1. However, the proportions differed so much from year to year (range 1.5:1–28:1), that it was not possible to calculate survival rates from these data as it rather expressed the size of the annual cohort.

The correlations between the number of 1K birds and the proportions of 2K and 3K+ birds among adults (2K+), one and two years later respectively, were both significant (Figure 6). This suggests that birds which have migrated successfully as 1K also tend to migrate as adults. Further evidence for this is the increasing number of 3K+ birds and some recoveries (see below).

In all age classes, females were significantly more numerous than males (Table 3). The proportion of males was 21.5% (1983–94) of the 1K birds, but only 7.0 % of the adults. The proportion of males in one autumn, which ranged from 10.7% to 25.3% over the years, correlated significantly (n=12, $r_s=0.862$, $p<0.01$, Figure 7) with total numbers during the same season. This was because the proportion of males among first-year birds was significantly correlated with total numbers (n=12, $r_s=0.790$, $p<0.01$), whereas that for adults was not (n=12, $r_s=0.259$, $p>0.10$).

Recoveries

Until the end of 1994, there were 322 recoveries of Blue Tits ringed at Falsterbo (Table 4A), (0.5% recovery rate), and 154 controls of Blue Tits ringed elsewhere (Table 4B). Among the 322 recoveries, 232 (72%) were from abroad, mainly from Denmark (213).



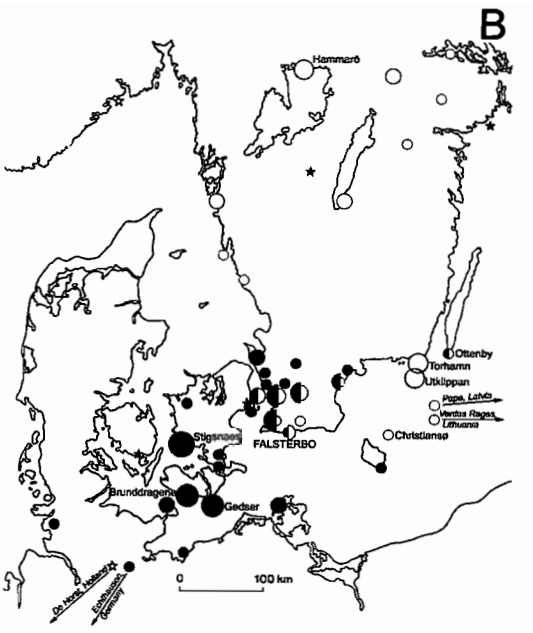
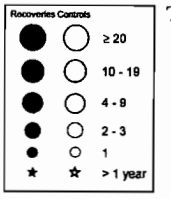


Figure 8. Recoveries of Blue Tits ringed at Falsterbo (filled symbols) and ringing sites for Blue Tits controlled at Falsterbo (open symbols). Circles = less than 1 year between ringing and recovery (no breeding season in between). Stars = 1 year or more between ringing and recovery (at least one breeding season in between). (A) Breeding season (May–July). (B) Autumn (August–November). (C) Winter (December–15 March). (D) Spring (16 March–April).

Genfund af blåmejser ringmærket andetsteds og kontrolleret i Falsterbo (lukkede symboler) og ringmærkningslokaliteter for blåmejser kontrolleret i Falsterbo (åbne symboler). Cirkler = mindre end 1 år mellem ringmærkning og genfund (ingen ynglesæsoner imellem). Stjerner = 1 år eller mere mellem ringmærkning og genfund (1 eller flere ynglesæsoner imellem). (A) Ynglesæson (maj–juli). (B) Efterår (august–november). (C) Vinter (december–15 marts). (D) Forår (16 marts–april).



Teckenförklaring till Fig. 8 A–D.

Breeding area

There were 63 recoveries at Falsterbo of Blue Tits ringed elsewhere as nestlings, all in the southern third of Sweden, mainly Skåne and Blekinge, but a few as far north as Lake Vänern (Figure 8A). The average distance from the breeding grounds was 147 km, and the average direction was 223°, i.e. southwest.

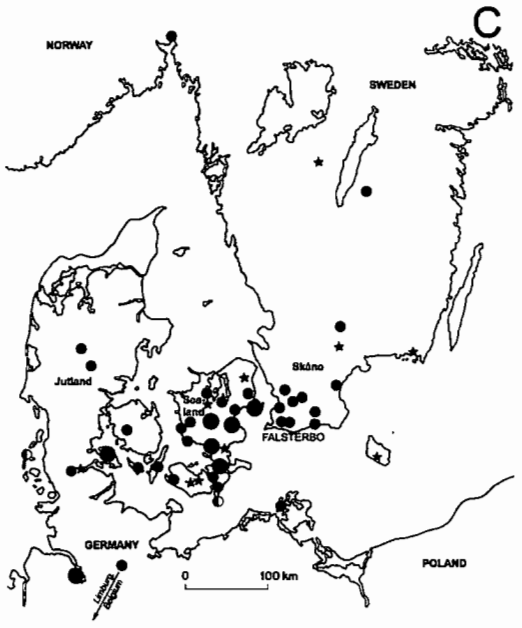
There were 11 recoveries during the breeding season (May – July) of Blue Tits ringed at Falsterbo. Six were from southern Sweden, one from Norway, two from eastern Denmark and two from northernmost Germany (Figure 8A). One Danish and one German bird were reported in early May, and they might still have been on migration.

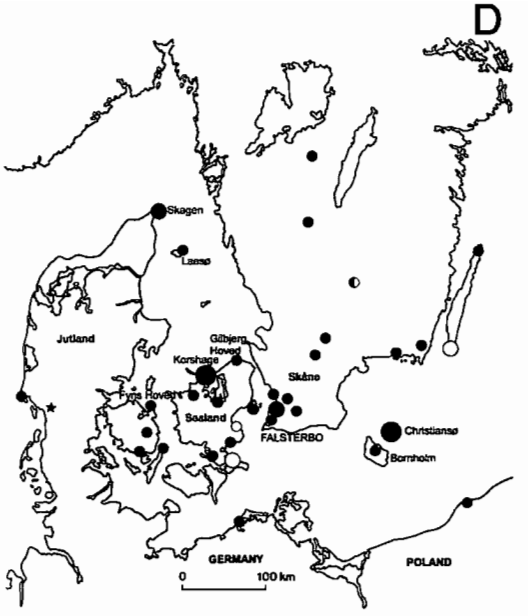
There was evidence that Blue Tits may breed considerably more to the south than they were hatched. A first-year female ringed at Falsterbo on 13 October 1985 was recaptured after six days at Stigsnæs, Denmark, and on 25 May the next year at the same place, breeding in a nestbox. Maybe the Blue Tit recovered in Kröss, Germany on 1 July 1989 was a breeding bird as well.

Autumn migration

For Blue Tits ringed elsewhere as 1K (n=63) and recovered at Falsterbo the same autumn (Figure 8B), the mean direction was 223° (SW), and the average distance from the ringing sites was 198 km (cf. nestlings above).

There were 100 recoveries at Stigsnæs Bird Observatory (100 km W of Falsterbo, Figure 8B) of





Blue Tits ringed at Falsterbo earlier during the same autumn (September–November). Of these, 91% were within 19 days. The average time between ringing and recovery was 12 days, corresponding well with the average time before recapture at two other ringing sites in southeastern Denmark, at nearly the same distance from Falsterbo; 14 days to Brunddragene on Lolland (122 km SW, n=13) and 16 days to Gedser on Falster (105 km SSW, n=13). The minimum time between ringing at Falsterbo and recapture at Stigsnæs was three days, indicating a migration speed of 36 km/day. Some Blue Tits migrated further, from the Danish islands to the northern parts of Germany. The minimum time between ringing at Falsterbo and recovery in northern Germany was six days (appr. 200 km SSW) also indicating a migration speed of c. 35 km/day. This is similar to results on Blue Tit migration in the Alps (29 km/day, Frelin 1979).

Of the recoveries (>10 km) during the first week after ringing, 32% were from southern Skåne, but during the second week this figure decreased to 8%. Concurrently, the proportion of recoveries in eastern Denmark increased from 66% during the first week to 87% during the second week.

The recoveries show that some of the Blue Tits ringed at Falsterbo obviously never cross the Strait of Öresund but return inland (Figure 8B). Most of these birds stay in the southernmost part of Sweden, but there were a few examples of Blue Tits moving longer distances, like the one recaptured at Ottenby, Öland, only 10 days after ringing at Falsterbo.

There was no significant difference in the age/sex distribution between the Blue Tits ringed at Falsterbo and those recovered during the first autumn and winter, neither in Sweden (>10 km) (χ^2=0.25, df=3, p>0.10) nor abroad (χ^2=3.68, df=3, p>0.10).

Evidently some adults migrate, since there were 17 controls at Falsterbo of Blue Tits ringed in Denmark in a previous autumn and three ringed in a previous spring. In addition there were four recoveries from eastern Denmark, one year or more after ringing, but like the Blue Tit at Stigsnæs mentioned above, these could be 1K migrants that never returned to the area where they were hatched.

Wintering areas and spring migration

There were 64 recoveries during winter (1 December–15 March, Figure 8C), of which 15 were from north of Falsterbo. Two recoveries from Oslo, Norway, and Tranås, east of Lake Vättern, respectively, indicate that Blue Tits ringed at Falsterbo in autumn sometimes winter considerably further north. However, three of the six northernmost recoveries were not from the first winter after ringing, indicating that

Table 4. Temporal and spatial distribution of (A) recoveries of Blue Tits ringed at Falsterbo and (B) recaptures at Falsterbo of Blue Tits ringed elsewhere 1947-94. The tables show month of recovery (A) and ringing (B) respectively. Only records with a distance of more than 10 km between ringing and recovery sites were included.

Tidsmæssig og geografisk oversigt over (A) genfund af blåmejser ringmærket ved Falsterbo respektivt (B) kontroller i Falsterbo af blåmejser ringmærket andetsteds 1947-94. Kun fund hvor afstanden mellem mærknings- og genfundslokalitet er større end 10 km er inkluderet.

A

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Skåne	5	-	6	4	2	2	-	-	6	27	15	3	70
Rest of Sweden	2	-	3	5	2	-	-	1	1	3	2	1	20
E. Denmark	12	7	13	6	2	-	-	-	2	124	10	9	185
W. Denmark	1	4	6	5	-	-	-	-	-	1	-	-	17
Bornholm	-	-	3	7	-	-	-	-	-	1	-	-	11
Germany	-	4	1	1	1	-	1	-	-	5	2	-	15
Belgium	-	-	-	-	-	-	-	-	-	-	-	1	1
Poland	-	-	-	1	-	-	-	-	-	-	-	-	1
Norway	-	-	-	-	1	-	-	-	-	-	-	1	2
Total	20	15	32	29	8	2	1	1	9	161	29	15	322

B

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Skåne	-	-	-	-	9	28	2	-	8	11	-	-	58
Rest of Sweden	-	-	2	1	10	18	1	4	19	8	-	-	63
Denmark	-	-	3	-	-	-	-	-	2	19	2	1	27
Germany	-	-	1	-	-	-	-	-	-	1	-	-	2
Latvia	-	-	-	-	-	-	-	-	-	1	-	-	1
Lithuania	-	-	-	-	-	-	-	-	1	-	-	-	1
Holland	-	-	-	-	-	-	-	-	-	1	-	-	1
Norway	-	-	-	-	-	-	-	-	1	-	-	-	1
Total	-	-	6	1	19	46	3	4	31	41	2	1	154

these birds probably did not migrate in the autumn preceding the winter they where recovered.

There were 52 recoveries from the first winter after ringing. The geographical distribution (Figure 8C) shows that Blue Tits passing Falsterbo are short-distance migrants. After November they move only a little, mainly to the west, and the recoveries from the western part of Denmark were all from late autumn or winter. The southernmost recovery was from Belgium in December 1965, but this seems to be an exception to the rule, since the rest of the recoveries showed that Scandinavian Blue Tits rarely move further south than northern Germany.

In spring, the Blue Tits head north again, but now the route is a little more to the west than during autumn, as indicated by recoveries mainly from northeasterly directed points such as Skagen, Læsø, Fyns Hoved, Korshage and Gilbjerghoved (Figure 8D).

One recovery from eastern Germany, one from Poland and five from the island of Christiansø in the middle of the Baltic Sea, shows that some of the Blue Tits choose a more easterly route during spring migration.

Discussion

Do the ringing numbers reflect long-term population changes?

Several bird-monitoring projects in Sweden show that the Swedish Blue Tit population has increased considerably since the early 1980s (Svensson 1996, Report on Swedish Bird Ringing 1980–93). The number of Blue Tits ringed at Falsterbo (Figure 9), also shows a long-term increasing trend, although not significant due to some years with very weak migratory movements. The strong increase in num-

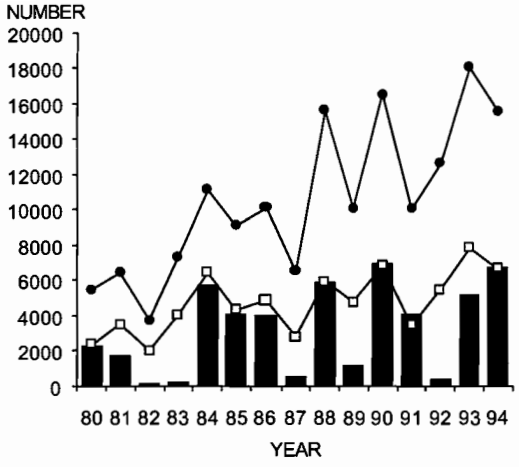


Figure 9. Seasonal totals of Blue Tits ringed at Falsterbo in the autumns of 1980–94 (columns), compared to annual totals of Blue Tit nestlings (squares) and all Blue Tits (dots) respectively, ringed in Sweden except Falsterbo, during the same period.

Sæsonstotaler af blåmejser ringmærket i Falsterbo efterårene 1980–94 (søjler) i relation til antallet af unger (firkanter) henholdsvis alle blåmejser (prikker) ringmærket i Sverige (exclusiv Falsterbo) i samme periode.

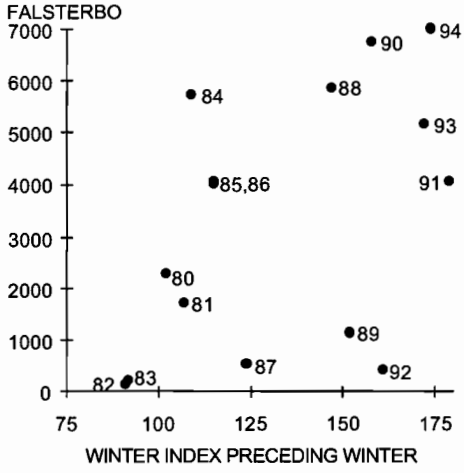


Figure 11. Seasonal totals of Blue Tits ringed at Falsterbo in the autumns of 1980–94 correlated to average winter indices 1979/80–1993/94 from the Swedish Winter Bird Census (Svensson 1996; n=15, r_s=0.546, p<0.05).

Sæsonstotaler af blåmejser ringmærket i Falsterbo efterårene 1980–94 korreleret til gennemsnitlige vinterindex 1979/80–1993/94 fra Vinterfågelräkningen (Svensson 1996; n=15, r_s=0,546, p<0,05).

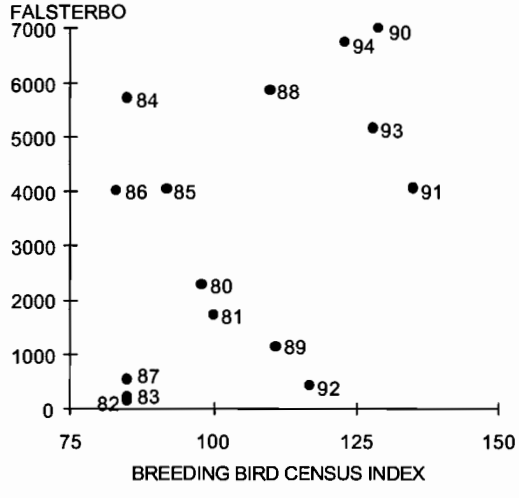


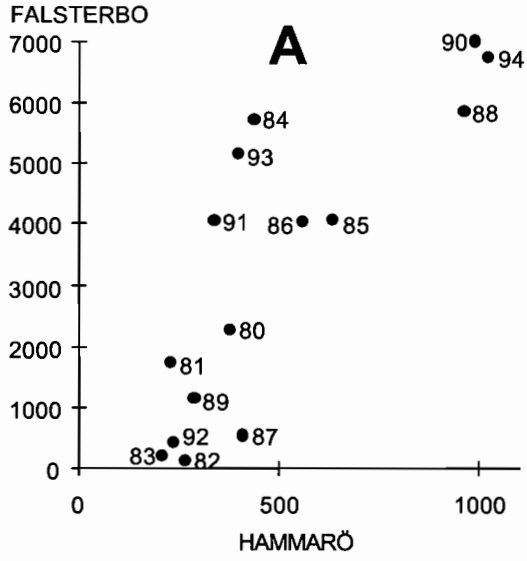
Figure 10. Seasonal totals of Blue Tits ringed at Falsterbo in the autumns of 1980–94 correlated to indices from the Swedish Breeding Bird Census (point counts) 1980–94 (Svensson 1996; n=15, r_s=0.464, p<0.10).

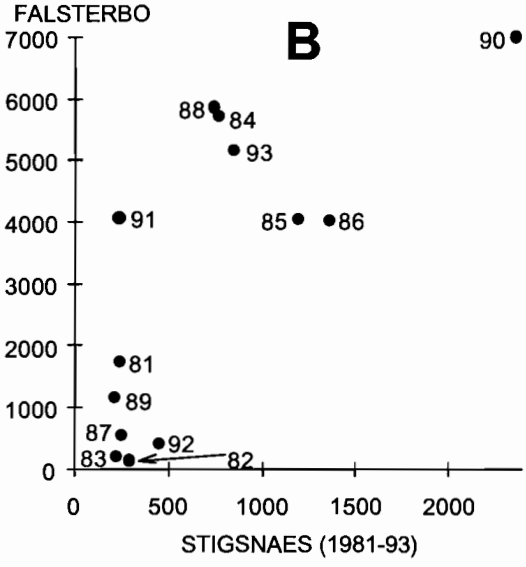
Sæsonstotaler af blåmejser ringmærket i Falsterbo efterårene 1980–94 korreleret til index fra Svenska Häckfågeltaxeringen (punkttaxering) 1980–94 (Svensson 1996; n=15, r_s=0,464, p<0,10).

bers most likely reflects an increase of the Blue Tit population, but maybe also that the triggering factor for migration has changed.

The number of nestling Blue Tits (1980–94: n=15, r_s= 0.743, p<0.01) ringed annually in Sweden, as well as the annual totals for all ringed Blue Tits (1980–94: n=15, r_s= 0.646, p<0.02), have increased significantly during the study period. Since the early 1980s, the annual total was doubled to its present level at about 20,000 birds ringed (Report on Swedish Bird Ringing 1980–93, Figure 9). The annual number of ringed nestlings probably reflects fledgeling production, provided that ringing efforts were fairly constant between years.

There was a significant positive correlation between the seasonal number of Blue Tits ringed at Falsterbo and the number of nestling Blue Tits ringed in Sweden in the same year (n=15, r_s=0.702, p<0.01, Figure 9). Thus, autumns with high numbers of Blue Tits at Falsterbo were preceded by a successful breeding season. Exceptions, such as 1983 and 1992, when relatively high numbers of nestlings were ringed, but only very weak migratory movements were registered at Falsterbo (Figure 9), show that other factors besides the abundance of Blue Tits





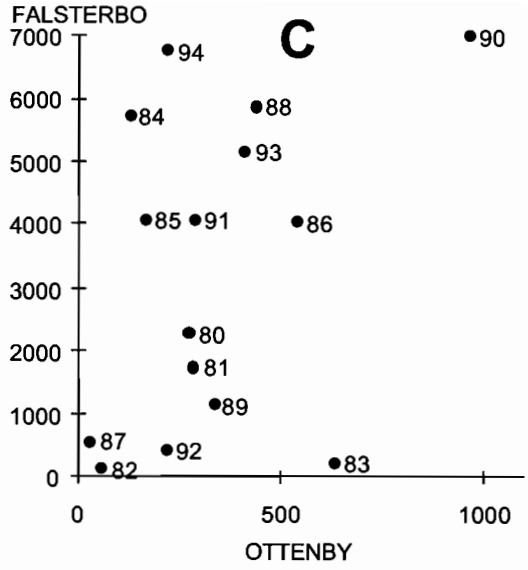


Figure 12. Seasonal totals of Blue Tits ringed at Falsterbo in the autumns of 1980–94 correlated to corresponding figures at (A) Hammarö Bird Observatory, Värmland (430 km N of Falsterbo): n=15, r_s=0.821, p<0.01, (B) Stigsnæs Bird Observatory, Sealand (100 km W): n=13, r_s=0.582, p<0.05 and (C) Ottenby Bird Observatory, Öland (240 km ENE): n=15, r_s=0.314, p>0.10.

Sæsonstotaler af blåmejser ringmærket i Falsterbo efterårene 1980–94 korreleret til ringmærkningscifrene fra (A) Hammarö, Värmland (430 km N for Falsterbo): n=15, r_s=0,821, p<0,01, (B) Stigsnæs, Sjælland (100 km W): n=13, r_s=0,582, p<0,05. and (C) Ottenby, Öland (240 km ENE): n=15, r_s=0,314, p>0,10.

in the breeding areas, influence the strength of migration (see below).

The correlation between the ringing totals at Falsterbo and the population indices for Blue Tits from the annual censuses of breeding birds in Sweden (Svensson 1996) was not significant (n=15, r_s=0.464, 0.05<p<0.10, Figure 10), although the indices from the breeding bird censuses themselves were significantly increasing over the years, indicating a population increase. In this context, it is interesting to note the stronger correlation between ringing totals at Falsterbo and the number of ringed nestlings (Figure 9). However, the indices from the breeding bird censuses are based on observations of singing males. Consequently, the correlation between these indices and the number of adults only, ringed at Falsterbo the following autumn, was somewhat stronger (n=15, r_s=0.530, p<0.05).

Another way of monitoring a breeding population is to record all breeding pairs in a limited area. A positive correlation was found between ringing totals at Falsterbo and the number of pairs recorded within a nestbox project at Revinge, c. 60 km northeast of Falsterbo (1984–94, n=11, r_s=0.670, p<0.05, J.Å. Nilsson pers. comm.).

Also, according to the indices from the Swedish Winter Bird Census (Svensson 1993, 1996), the Blue Tit population has increased since 1985 (Svens-

son 1996). These indices are averages of five counts during winter (October, November, New Year, February and March) for the whole of Sweden, although most of the routes are concentrated in the southern part (Svensson 1993). Mean winter indices (all five counts) for the Blue Tit were significantly positively correlated with the ringing total at Falsterbo in the succeeding autumn (n=15, r_s=0.546, p<0.05, Figure 11).

In conclusion, the ringing totals and migration counts of Blue Tits at Falsterbo are useful tools for monitoring population changes, provided that factors that triggers the seasonal migration strength are considered.

Comparisons with other ringing stations

The correlations between the annual number of Blue Tits ringed at Falsterbo and the corresponding figures from some other ringing stations with regular trapping differed depending on location and distance (Figure 12 A–C). A strong positive correlation (n=15, r_s=0.821, p<0.01) was found between totals from Falsterbo and Hammarö, Värmland, some 430 km north of Falsterbo (Figure 12A). This can be interpreted as if the same birds were involved at the two places. However, there were only four recaptures at Falsterbo of Blue Tits ringed at Hammarö in the same autumn, but such a low number could be an effect of the distance and direction between the sites. The Blue Tit populations a bit further north in Sweden (north of and around lake Vänern) make migratory movements not only to the south or southwest but also towards northwest to wintering grounds in Norway (Ehrenroth 1976, Källander 1983a), which is analogous to the migration pattern in the Great Tit *Parus major* (Alerstam 1982, Källander 1983a). Such movements to milder climatic conditions in coastal areas were also observed in Blue Tits in Belgium (Thielemans & Eyckerman 1975).

As expected, totals at Falsterbo and Stigsnæs, Denmark (100 km W of Falsterbo) were well correlated (n=13, r_s=0.582, p<0.05, Figure 12B). In this case the same populations are definitely registered at the two sites, a statement strongly supported by the 100 recaptures at Stigsnæs of Blue Tits ringed at Falsterbo in the same autumn.

By contrast, there was no correlation (n=15, r_s=0.314, p>0.10) between the totals from Falsterbo and Ottenby, Öland, 240 km ENE of Falsterbo (Figure 12C). Maybe Blue Tits ringed at Ottenby have a different origin e.g. local birds or more easterly breeding popoulations and therefore other factors may influence their migration. Only one Blue Tit ringed at Ottenby was recaptured at Falsterbo in the same autumn.

Table 5. Coefficient of variation (CV) in seasonal ringing totals for Blue Tits in the autumns of 1980-94 compared to those of some of the most numerously ringed species belonging to different migratory categories. Only seasonal totals higher than 30 were included, restricting the basic data in Coal Tit and Bullfinch to 7 years only. D/N = diurnal respective nocturnal migrant.

Variationskoefficienten (CV) for sæsonsstotalerne efterår 1980–94 for blåmejse sammenlignet med CV for udvalgte arter. D/N = dagtrækkende henholdsvis nattrækkende arter. Sæsonstotaler med færre end 30 er ikke inkluderet, hvilket indebærer at beregningsgrundlaget for sortmejse og dompap kun udgør 7 sæsoner.

	D/N	CV
Blue Tit *Parus caeruleus*	D	76
Partial migrants / Irruptive species:		
Coal Tit *Parus ater*	D	182
Great Tit *Parus major*	D	71
Siskin *Carduelis spinus*	D	139
Bullfinch *Pyrrhula pyrrhula*	D	125
Medium distance migrants:		
Wren *Troglodytes troglodytes*	N	83
Robin *Erithacus rubecula*	N	43
Goldcrest *Regulus regulus*	N	59
Chaffinch *Fringilla coelebs*	D	62
Long distance migrants:		
Tree Pipit *Anthus trivialis*	D	66
Redstart *Phoenicurus phoenicurus*	N	72
Garden Warbler *Sylvia borin*	N	65
Willow Warbler *Phylloscopus trochilus*	N	69

The comparisons show that the migratory movements of Blue Tits at Hammarö, Falsterbo and Stigsnæs seem to vary synchronously, while those at Ottenby do not.

Migration patterns

As shown in Figures 1 & 2, the timing of the migration was very similar in almost every autumn. The rather "fixed" migration period is more similar to that of regular migrants than to true irruptive species. Roos (1993) showed, on basis of migration counts at Falsterbo, that the coefficient of variation (CV) in the annual number of migrating Blue Tits

was higher than the CVs of true migrants and lower than true irruptive species. Ringing totals showed the same result (Table 5), and correspond well with Roos' (1993) characterization of the Blue Tit as "a partial migrant with irruptive tendencies". A study of migrating Blue Tits in the Alps showed that the birds were physiologically adapted to migration (Frelin 1979), which is another argument for classifying Blue Tits as partial migrants.

The daily migration intensity depends to a considerable extent on the weather conditions (Lindskog & Roos 1980). Sometimes, when weather conditions are not good enough for migration, the Blue Tits return when confronted with the sea and flocks of hundreds of birds land in the lighthouse garden. On such occasions, many Blue Tits are trapped for ringing while relatively few are migrating. A good example was 6 October 1993, when 1716 Blue Tits were ringed (highest number ever), but only around 1100 were actually seen migrating (Nils Kjellén, pers. comm.).

The hesitation to cross the sea may lead Blue Tits to stay a week or more around Falsterbo before continuing migration. Although retraps were not registered, the general experience was that relatively few birds were retrapped. More likely, the birds returned further inland, and once they did so, they did not come back. Return migration was well documented by Persson (1972a) on the basis of trapping figures from Ljunghusen, c. 10 km E of Falsterbo. Recently, a study on the same subject, based on ringing recoveries, showed that the mean direction of recoveries ten days or less after ringing was significantly different from the mean direction after more than ten days (Åkesson et al. 1996). This pattern was valid in a wide spectrum of passerine migrants, including Blue Tit, and the general conclusion was, that birds return inland in search of favourable resting sites before continuing migration. In Blue Tits, the body mass was also significantly lower in return migrants than in forward migrating individuals (Åkesson et al. 1996). The average time, 12 days, between ringing at Falsterbo and retrapping at Stigsnæs, Denmark, only 100 km away, also indicates that the birds obviously rested on some of these days, but they may very well have done so on either side of the Strait of Öresund.

Age and sex distribution

The significant correlation between the number of first-year (1K) Blue Tits in one autumn and the number of second-year (2K) Blue Tits the next year (Figure 5) indicates that if a bird has migrated once, there is a higher probability that it will migrate again. The number of 1K birds in one year will, of course, to a certain degree influence the number of 2K birds next year, but if expected lack of food is one of the main reasons for migration, then mortality among 1K birds should be relatively higher in years with strong migration.

The overrepresentation of 1K birds and females (Table 3) is known from other studies of Blue Tits (Ehrenroth 1976, Smith & Nilsson 1987) and irruptive species (Hildén 1974). The ratio between 1K birds and adults was 8.8:1 among females and 31.9:1 among males.

The biased age/sex distribution may be explained by the "hypothesis of dominance", which means that the strongest and dominant individuals (here: adult males) maintain their territories and the weakest (here: 1K females) migrate (Smith & Nilsson 1987). This was also supported by the increasing proportion of males with increasing numbers of migrating tits (Figure 7), caused by high population density in combination with low food accessability. The worse the conditions, the more males migrated, as they could no longer successfully compete for food.

Recoveries

Blue Tits ringed as nestlings or as 1K birds and retrapped at Falsterbo in autumn showed the same average migratory direction (SW), while the mean distance between ringing sites and Falsterbo was somewhat longer in 1Ks. As to direction, one must have in mind, that Swedish Blue Tits can only originate from areas to the north and east of Falsterbo, because of its geographical location, i.e. the direction from a Swedish ringing site to Falsterbo will always be between 180 (south) and 270 degrees (west).

The difference in distances probably only shows the different locations of ringing sites during breeding time and migration time, respectively. The nestlings were ringed in forest areas, mainly in the southernmost part of Sweden, whereas the 1K birds were ringed at ringing sites mainly along the coasts.

Not only the abundance of birds, but also of ringers, may influence the recovery patterns. The number of Blue Tit nestlings ringed in each Swedish county (län) were checked and the recovery rates from recaptures at Falsterbo were calculated. As expected, the chance of recapture at Falsterbo decreased with the distance to the breeding area. However, there were no recaptures at all from two of the

southern counties (Hallands and Kronobergs län). In these counties very few Blue Tit nestlings were ringed, rather a consequence of low ringing activity than of sparse occurrence of Blue Tits. However, there should be little doubt that most Blue Tits migrating at Falsterbo originate from the southern third of Sweden (Figure 8A).

There were no recaptures at Falsterbo of Blue Tits ringed in northern Sweden. It is not yet fully known if and where Blue Tits from northern Sweden migrate. Since they are distributed over a vast area and are relatively few in number, not many have been ringed and, of course, even fewer have been recovered so far.

There were very few recoveries during breeding season of Blue Tits ringed at Falsterbo. Again, this is partly depending on ringing efforts, but also on the statistical probability of catching a bird that is already ringed. Naturally, this will happen more often where many birds are caught, i.e. at migration sites, and not when the birds are spread out on the breeding grounds. Another reason is the annual mortality in Blue Tits of 70–75%, (Thielemans & Eyckerman 1975, Perrins 1979), which strongly reduces the number of birds "available for retrapping" from autumn to the following summer.

The recovery patterns through the year show that Blue Tits from southern Sweden migrate to Denmark and northern Germany in autumn. In winter they move a little further to the west and spring migration is following either a more westerly route than in autumn or, though less frequented, a route along the southern coast of the Baltic Sea - Bornholm. Thus the recovery patterns form two loops, but these may very well be the consequences of the location of points where the birds concentrate on autumn and spring migration respectively and where ringing activities are carried out.

What triggers the migration and what makes the birds stop?

As shown in Figure 9, the numbers of migrating and ringed Blue Tits depend on the fledgeling production during the previous breeding season. This is in turn dependent on the population size during the previous winter (Figure 11). There was an even stronger correlation between the winter indices for March and the ringing total in the succeeding autumn (n=15, r_s=0.678, p<0.02, Figure 13A). Consequently, the number of migrating Blue Tits especially depends on the population size at the end of the previous winter (see also Källander 1983b). A high number of breeding pairs with a moderate number of fledged nestlings will probably influence the total fledgeling production to a higher degree than a lower number of breeding pairs with a large number of fledged nestlings.

This is well illustrated by the two aberrant autumns of 1983 and 1991 (cf. Figure 4). In 1983 only 210 Blue Tits were ringed with an unexpectedly high proportion of 1K birds (96%). Very likely, this was a consequence of a low number of adults, especially second-year birds (2K), caused by bad breeding results in 1982 (Figures 9, 10). In 1991, 4252 Blue Tits were ringed with an unexpectedly low proportion of 1Ks (77%). Accordingly, this was probably a consequense of a high number of 2Ks, caused by very good breeding results in 1990 (Figures 9, 10), but also, since there were quite many 3K+s, an effect of the very mild winters around 1990. In addition, 1991 was a bad breeding season for many passerine birds, reflected by the exceptionally low autumn ringing totals (Karlsson et al. 1992). Even if the Blue Tits also had a bad breeding season, there were so many pairs making breeding attempts (cf. Figure 10) that a relatively high total number of fledged nestlings was produced.

The winter indices for October were also significantly positively correlated with the ringing total for the same autumn (n=15, r_s=0.629, p<0.02, Figure 13B), showing that simultaneously, there were many Blue Tits all over southern Sweden. However, the correlation with the mean winter indices for the succeeding winter was not significant (n=15, r_s=0.363, p>0.10). Since only a relatively small proportion of the population migrates, there will be a high mortality among the sedentary specimens, if the food accessability is low, even in years with strong migration.

Ulfstrand (1962) pointed out, that irruptive-like migration of Blue Tits in certain years was related to poor Beech *Fagus sylvatica* mast crops. In this study indices on beech mast crops from Grib Skov, Denmark, 1980–94 were used. They express only the beech mast crop in the Danish National Forestry's particularly selected stands and not in hedges, edges of forests etc., where the crops often are better (Flemming Knudsen, pers. comm.). However, they should be useful as an index also for beech mast crops in South Sweden, as crops are of similar size in large areas (Flemming Knudsen, pers. comm.).

There was a significantly negative correlation between the annual numbers of Blue Tits ringed at Falsterbo and the size of Beech mast crops (n=15, r_s=-0.635, p<0.02, Figure 14). However, many Blue

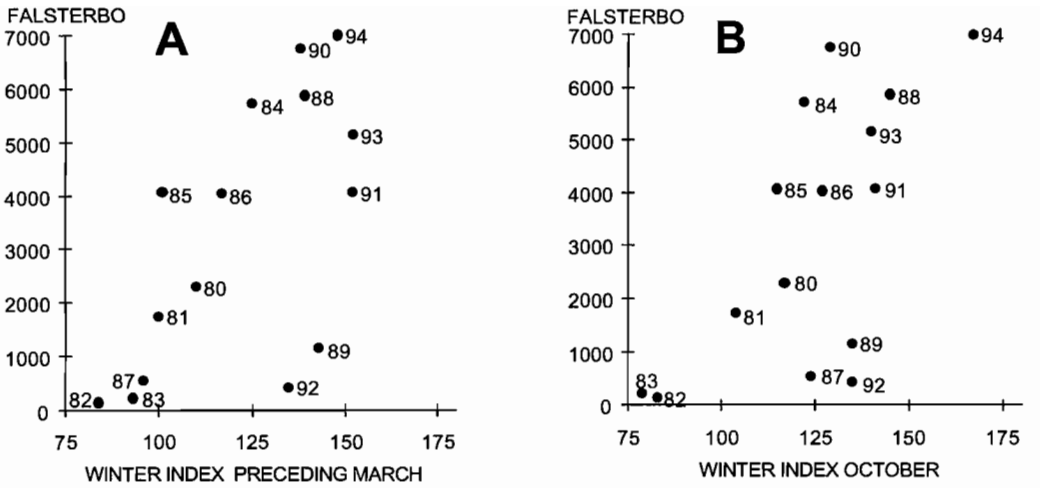


Figure 13. Seasonal totals of Blue Tits ringed at Falsterbo in the autumns of 1980–94 correlated to indices from the Swedish Winter Bird Census (Svensson 1996). (A) indices from March 1980–94, n=15, r_s=0.678, p<0.02, (B) indices from October 1980–94, n=15, r_s=0.629, p<0.02.

Sæsonstotaler af blåmejser ringmærket i Falsterbo efterårene 1980–94 korreleret til index fra Vinterfågelräkningen (Svensson 1996). (A) indeks fra marts 1980–94, n=15, r_s=0,678, p<0,02, (B) index fra oktober 1980–94, n=15, r_s=0,629, p<0,02.

Tits originate from areas where the Beech is sparse. Unfortunately, we have no data on other crops like for example in the Birch. Nevertheless, low food accessability seems to be an important factor for the onset of strong migratory movements in the Blue Tit. In large parts of Europe, migration of Blue Tits depend on the size of beech mast crops. When the Beech mast crops differed between areas, corresponding differences were noticed in the strength of migration (Perrins 1979).

Figures 11 and 13A–B show, that high winter indices mainly occurred in the late 1980s and in the 1990s, which was a period with extremely mild winters. However, a high winter index was not necessarily followed by an autumn with a high ringing total. In some years, like 1989 and 1992, there were extremely rich Beech mast crops (Figure 14), so even though there were many Blue Tits, they did not migrate.

Another interesting year was 1987, with a very low index for March and the previous winter, but a considerably higher index for October and the succeeding winter. The amount of Beech mast was almost the same in 1986 and 1987 (Figure 14), but there was a considerable difference in the numbers of Blue Tits ringed: more than 4000 in 1986 and only a little more than 500 in 1987 (Table 1). A reasonable explanation could be that breeding success was far better in 1986 than 1987 (Figure 9), which was very rainy during the breeding season (H. Källander, pers. comm.). Another reason could be, that there was a higher mortality in the winter of 1986/87 which was very cold, in contrast to the winter of 1987/88 which was very mild.

Blue Tits may estimate the Beech mast crop, or some other food resource, already in autumn and the amount of food in autumn may covary with the amount of food in winter (Perrins 1979). The Blue Tits may also know from population density the anticipated degree of competition for food in winter.

However, since Beech mast crops often are synchronous over large areas, there is an obvious risk that migration does not bring the Blue Tits to an area where there is more food (Perrins 1979). This must be true, at least for the Blue Tits passing Falsterbo on migration, since they stop in Denmark, where for instance the Beech mast crop should be similar to the one in southern Sweden and where they must compete with the local Danish populations. The most probable explanation, why the migration stops already on the Danish islands, is that the somewhat milder winters in Denmark make the food more easily accessible to the Blue Tits and there might of course be other food sources, of which we know

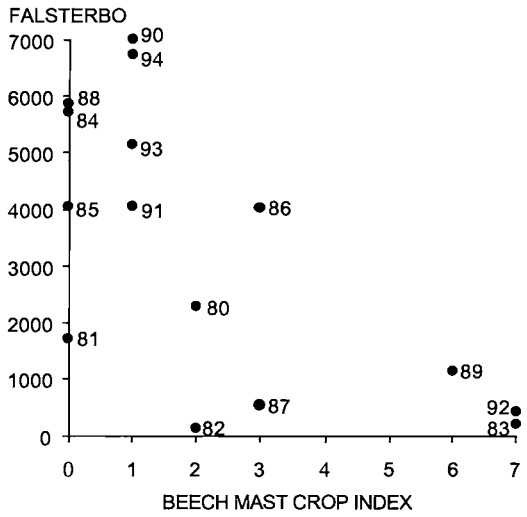


Figure 14. Seasonal totals of Blue Tits ringed at Falsterbo in the autumns of 1980–94 correlated to Beech mast crop (index 0–7; n=15, r_s=-0.635, p<0.02).

Sæsonstotaler af blåmejser ringmærket i Falsterbo efterårene 1980–94 korreleret til frøsætningen hos bøg (index 0–7; n=15, r_s=-0,635, p<0,02).

nothing. Finally, it will also be a bit less energy-demanding to spend the winter in a milder climate, but since the average differences in temperature between western Denmark and southern Sweden are quite small, the energy saved should be of little importance.

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References

Alerstam, T. 1982. *Fågelflyttning.* Signum. Lund.

Andell, P. & Nilsson, L. 1988. Svensk fågelatlas i Skåne. Slutrapport. Del 7. *Anser* 27: 165–180.

Asbirk, S. & Braae, L. 1988. Status og udviklingstendenser for fugle. Pp. 64–70 in *Naturen i Danmark – status og udviklingstendenser* (Asbirk, S. ed). Skov- og Naturstyrelsen, Miljøministeriet. Arnold Thomsen A/S, Esbjerg.

Batschelet, E. 1981. *Circular Statistics in Biology.* Academic Press. New York.

Drost, R. 1951. *Kennzeichen für Alter und Geschlecht bei Sperlingsvögeln. Ornithologische Merkblätter Nr 1.* Vogelwarte Helgoland, Wilhelmshaven.

Ehrenroth, B. 1976. Vandringsrörelser hos mesar *Paridae* vid Hammarön, norra Vänern. *Vår Fågelvärld* 35: 261–278.

Frelin, C. 1979. Physiological Adaptation of Blue Tits (*Parus caeruleus*) to Migration. *Die Vogelwarte* 30: 33–41.

Fowler, J. & Cohen, L. 1994. *Practical statistics for field biology.* Redwood Books, Trowbridge.

Gjershaug, J.O., Thingstad, P.G., Eldøy, S. & Byrkjeland, S. (eds.) 1994. *Norsk fugleatlas.* Norsk Ornitologisk Forening, Klæbu.

Hildén, O. 1974. Finnish bird stations, their activities and aims. *Ornis Fennica* 51: 10–35.

Hildén, O. 1986. Long-term trends in the Finnish bird fauna: methods of monitoring and some results. In: Baltic Birds IV (Hjort, C., Karlsson, J. & Svensson, S. eds.). *Vår Fågelvärld*, Suppl. 11: 61–70. SOF, Stockholm.

Hyytiä, K., Koistinen, J. & Kellomäki, E. (eds.) 1983. *Suomen Lintuatlas.* SLY:n Lintutieto Oy. Helsinki.

Karlsson, L., Persson, K. & Walinder, G. 1985. Fotografisk dokumentation av ålders- och könsskillnader hos fåglar – målsättning, arbetssätt och exempel på resultat. *Vår Fågelvärld* 44: 405-478.

Karlsson, L., Persson, K. & Walinder, G. 1986. Ringmärkningen vid Falsterbo fågelstation 1985. *Anser* 25: 93–112.

Karlsson, L., Ehnbom, S. & Walinder, G. 1991. Ringmärkningen vid Falsterbo fågelstation 1990. *Anser* 30: 141–166.

Karlsson, L., Ehnbom, S. & Walinder, G. 1992. Ringmärkningen vid Falsterbo fågelstation 1991. *Anser* 31: 109–120.

Karlsson, L., Ehnbom, S. & Walinder, G. 1995. Ringmärkningen vid Falsterbo fågelstation 1994. *Anser* 34: 173–194.

Koskimies, P. 1993. *Population sizes and recent trends of breeding birds in the nordic countries.* Publications of Water and Environment Administration – series A 144. Helsinki.

Källander, H. 1983a. Återfynd av talgoxar och blåmesar ringmärkta i Sverige. *Vår Fågelvärld* 42: 413–424.

Källander, H. 1983b. Density dependent migration of Great and Blue Tits. In: Aspects of the breeding biology, migratory movements, winter survival and population fluctuations in the Great Tit *Parus major* and the Blue Tit *P. caeruleus.* Lund.

Lindskog, H. & Roos, G. 1979. Höststräckets förlopp hos blåmes *Parus caeruleus* och talgoxe *Parus major* vid Falsterbo 1973–1978. *Anser* 18: 171–188.

Lindskog, H. & Roos, G. 1980. Vädrets inflytande på mesarnas, särskilt blåmesens *Parus caeruleus*, uppträdande vid Falsterbo under höststräcket. *Anser* 19: 1–10.

Perrins, C.M. 1979. *British tits.* William Collins Sons & Co Ltd., Glasgow.

Persson, C. 1972a. Mesarnas årsrytm och vandringsrörelser på Falsterbohalvön. *Vår Fågelvärld* 31:167–177.

Persson, C. 1972b. Återfynd av talgoxe *Parus major* och blåmes *Parus caeruleus* från märkningarna på Falsterbohalvön. *Vår Fågelvärld* 31:178–182.

Rendahl, H. 1959. Die Wanderungen der schwedischen Mei-

sen. Mit berücksichtigung des gesamten fennoskandischen Gebiets. *Bonner Zoologische Beiträge* 10:351–386.
Report on Swedish Bird Ringing 1980–93. Naturhistoriska Riksmuseet, Stockholm.
Risberg, L. 1990. *Sveriges Fåglar.* Vår Fågelvärld, supplement nr 14.
Roos, G. 1974. Sträckräkningar vid Falsterbo hösten 1973. *Vår Fågelvärld* 33: 270–285.
Roos, G. 1981–95. *Fågelsträckräkning vid Falsterbo.* Årsrapporter i Anser 1981–94 samt från Statens Naturvårdsverk 1986–95.
Roos, G. 1984. *Flyttning, övervintring och livslängd hos fåglar ringmärkta vid Falsterbo (1947–1980).* Anser, supplement 13, Lund.
Roos, G. 1993. Sträckräkningar vid Falsterbo hösten 1990, särskilt förekomsten av fyra invasionsarter: mindre korsnäbb, svartmes, blåmes och sidensvans. *Anser* 32:1–28.
Roos, G. & Karlsson, L. 1981. Ringmärkningsverksamheten vid Falsterbo fågelstation 1980. *Anser* 20: 99–108.
Roos, G., Karlsson, L., Persson, K. & Walinder, G. 1983. Ringmärkningsverksamheten vid Falsterbo fågelstation 1982. *Anser* 22: 77–88.
Rudebeck, G. 1950. *Studies on Bird Migration.* Vår Fågelvärld, Suppl. 1.
Smith, H.G. & Nilsson, J-Å. 1987. Intraspecific variation in migratory pattern of a partial migrant, the blue tit (*Parus caeruleus*): An evaluation of different hypotheses. *The Auk* 104: 109–115.
Svensson, L. 1975. *Identification Guide to European Passerines.* 2nd revised edition. Stockholm.
Svensson, S. 1993. Vinterfågelräkningen. In: *Fågelåret 1992.* SOF, Stockholm.
Svensson, S. 1996. *Övervakning av fåglarnas populationsutveckling. Årsrapport för 1995.* Ekologiska institutionen, Lunds universitet, Lund.
Thielemans, L. & Eyckerman, R. 1975. Migration and mortality in the blue tit (*Parus c. caeruleus* L.). *Biologisch Jaarboek Dodonaea* 43:252–265.
Ulfstrand, S. 1962. *On the nonbreeding ecology and migratory movements of the Great Tit* (Parus major) *and the Blue Tit* (Parus caeruleus) *in southern Sweden.* Vår Fågelvärld, Suppl. 3.
Ulfstrand, S. & Högstedt, G. 1976. Hur många fåglar häckar i Sverige? *Anser* 15: 1–32.
Ulfstrand, S., Roos, G., Alerstam, T. & Österdahl, L. 1974. *Visible bird migration at Falsterbo, Sweden.* Vår Fågelvärld. Suppl. 8.
Åkesson, S., Karlsson, L., Walinder, G. & Alerstam, T. 1996. Bimodal orientation and the occurence of temporary reverse bird migration during autumn in south Scandinavia. *Behav. Ecol. Sociobiol.* 38: 293–302.

Resumé

Efterårstrækket af blåmejse Parus caeruleus *ved Falsterbo, Sverige 1980–94: populationsforandringer, trækmønstre og genfundsanalyse.*

Blåmejsen er en art, der har øget betydeligt i Skandinavien i løbet af de seneste årtier. Om efteråret trækker et stort, omend stærkt varierende, antal blåmejser ud ved Falsterbo og arten optræder formentligt mere talrigt ved Falsterbo end noget andetsteds inden for udbredelsesområdet. I årene 1980–1994 er der i forbindelse med den standardiserede ringmærkning i Falsterbo (55.23N, 12.49E), blevet ringmærket 49.021 blåmejser om efteråret (11. september–10. november; Tabel 1).

Både antallet per år og frekvensen af år med mange trækkende blåmejser i Falsterbo er øget i løbet af perioden (Figur 9). Dette har bevirket, at det totale antal blåmejser ringmærket i Falsterbo er seksdoblet, samt at antallet af genfund og fremmede kontroller er forøget betydeligt. Dette har muliggjort denne analyse, der omfatter antal, sæson- og døgnmønstre og -variationer samt alders- og kønsfordeling foruden en genfundsanalyse, der beskriver rekruteringsområde, trækruter og overvintringskvarter for de blåmejser, der passerer Falsterbo om efteråret.

Både ringmærkningscifrene og cifrene fra træktællingerne i Falsterbo er stigende (Tabel 1) og afspejler utvivlsomt, at arten øger i antal i den del af populationen, der passerer Falsterbo på efterårstrækket. Dette bekræftes også af, at antallet af ungemærkninger er stigende i Sverige (Figur 9). Ud fra sammenligninger af materialet med indeks fra de svenske tællinger af ynglefugle (Figur 10) og vinterfugle (Figur 11, 13) ses det, at antallet af trækkende og ringmærkede blåmejser afhænger af antallet udfløjne unger, der igen er afhængig af populationsstørrelsen i den forudgående vinter. Antallet af trækkende blåmejser om efteråret er således afhængigt af antallet af fugle, der overlever vinteren og danner ynglepar.

Antallet af trækkende blåmejser er stærkt varierende fra år til år, men signifikant korreleret til efterårets ringmærkningscifre i Hammarö, Sverige og Stigsnæs, Danmark (Figur 12). Antallet af trækkende blåmejser er signifikant korreleret med antallet af ungemærkninger i Sverige og signifikant negativt korreleret med størrelsen af frøsætningen hos bøg *Fagus sylvatica* (Figur 14). Forudsætningen for et stort antal trækkende blåmejser i Falsterbo er således en god ynglesæson i et år, hvor der er ringe frøsætning hos bøg.

Trækket af blåmejse følger stort set samme tidsmæssige mønster hver sæson. De midterste 90% (5%–95%) af fuglene ringmærkes i perioden 23 september–23 oktober (Figur 1) og mediandatoen for alle blåmejser ringmærket i årene 1980–94 er 6. oktober (Figur 2).

Trækkets forløb over døgnet er kendetegnet ved,

at arten kan trække langt op ad dagen og det gennemsnitlige træktidspunkt afhænger af tidspunktet for solopgang (Figur 3).

Summen af de tre største dages total udgør 44% af årstotalen. Dette procenttal er højere end hos langdistancetrækkere, men lavere end hos typiske invasionsarter (Tabel 2). Variationskoefficienten (CV) på de årlige ringmærkningscifre for blåmejse er ligeledes intermediært langdistancetrækkere (lave) og de typiske invasionsarter (høje) (Tabel 5).

Samtlige blåmejser, der indgår i dette materiale, er aldersbestemt til årsunger (1K) eller ældre (2K+) ud fra fældningskarakterer. I 1984 påbegyndtes aldersbestemmelse af de adulte blåmejser til toårige (2K) eller endnu ældre (3K+), ud fra irisfarve, og i perioden 1985–94 er 98,6% af de adulte blåmejser aldersbestemt på denne måde (Tabel 3).

Af det totale antal blåmejser er 91,5% juvenile. Andelen af juvenile er stigende med antallet af ringmærkede (Figur 4). Af de adulte fugle er 71,0% toårige (2K), mens 27.6% er treårige eller ældre (3K+) (Tabel 3). Antallet af 3K+ fugle per år viser desuden en signifikant stigende tendens. Der er ligeledes en signifikant korrelation mellem antallet af 1K fugle et år og antallet af 2K-fugle det efterfølgende år (Figur 5).

Korrelationerne mellem antallet af 1K-fugle og andelen af 2K henholdsvis 3K+ af de adulte (2K+) henholdsvis et år og to år efter, er begge signifikante (Figur 6), hvilket indikerer, at ungfugle med succesfuldt træk også senere foretager trækbevægelser. Dette indikerer, at arten er en partiel trækfugl snarere end en typisk invasionsart.

Allerede i 1981 påbegyndtes kønsbestemmelse ved hjælp af dragtkarakterer og i perioden 1983–94 er 99,7% af de ringmærkede blåmejser blevet kønsbestemt. Hunnerne udgør majoriteten af fuglene i alle alderskategorier. Andelen af hanner af de juvenile fugle udgør 21,6% (1983–94), mens det hos de adulte fugle blot er 7,0% (Tabel 3).

Der ses en signifikant positiv korrelation mellem andelen af hanner, der udgør 10,7–25,3% af fuglene fra år til år, og efterårets totalfangst (Figur 7). Den delvise migration kan forklares af "dominanshypotesen", hvilket vil sige, at det er de stærkeste individer, der kan opretholde territorie og følgelig de svageste der trækker; der skal således være ringere forhold til stede før hannerne, der er dominerende i konkurrencen om føde, tager del i trækket.

Frem til og med 1994 er der genmeldt 322 blåmejser mærket i Falsterbo, hvilket svarer til en genmeldingsprocent på 0,5% og der er kontrolleret 154 blåmejser mærket på andre lokaliteter (Tabel 4).

Genfundene har vist, at de fugle der er ringmærket som redeunger og kontrolleret i Falsterbo er opvokset i den sydligste trediedel af Sverige (Figur 8A), hovedsageligt i Skåne og Blekinge. Fra Falsterbo trækker blåmejserne mod sydvest hovedsageligt til Danmark og sjældent længere end til Nordtyskland (Figur 8B). Genfund fra tre ringmærkningslokaliteter i det sydøstligste Danmark har vist, at den gennemsnitlige træktid fra Falsterbo til de tre lokaliteter, der alle er beliggende godt 100 km mod sydvest, er henholdsvis 12, 14 og 16 dage, men kan foregå på tre dage, hvilket svarer til en gennemsnitlig trækhastighed på cirka 36 km/dag.

I løbet af vinteren trækker blåmejserne mod vest til Jylland (Figur 8C), hvilket muligvis kan tilskrives de dér mildere klimatiske forhold. I løbet af forårsmånederne viser en række genmeldinger fra nord- og østvendte spidser i Danmark (Figur 8D), at det nordgående forårstræk sker ad en vestligere rute end efterårstrækket, hvorfor hele trækforløbet får en sløjfeform. Der ses desuden en spejlvendt sløjfe, idet genfund fra Østersøområdet viser, at et fåtal af blåmejserne vælger en østligere rute om foråret end om efteråret.

Det er givet, at størrelsen af frøsætningen hos bøg er en væsentlig faktor for antallet af trækkende blåmejser. Med tanke på, at frøsætningen som oftest er synkron over store områder kan det undre, at blåmejserne ikke trækker videre mod syd, idet så relativt korte trækbevægelser som de sydsvenske blåmejser foretager, ikke fører dem til områder med mere føde og ydermere overvintrer de i et område, hvor de lokale ynglefugle er standfugle, hvilket må bevirke yderligere konkurrence. Da blåmejserne ikke fortsætter længere mod syd, må det dog formodes, at fødegrundlaget er tilstrækkeligt stort til begge delpopulationer og en plausibel forklaring kan være, at vintrene er mildere og den givne fødemængde lettere tilgængelig i disse egne.