

Diffuse, short and slow migration among Blue Tits

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Abstract The knowledge of migration systems in long-distance regular migrants is in many cases extensive. Our understanding of the migratory characteristics of partial migrants, on the other hand, is far more rudimentary. We investigated migratory characteristics of partially migratory Blue Tits *Cyanistes caeruleus* using ringing recoveries of Swedish birds, to answer questions about geographic migration patterns, age-specific migrations, migration speeds and synchrony of movements. Median migration distance of Swedish Blue Tits was 82 km, with a main autumn direction in the sector between S and W (large directional scatter). Northerly and southerly populations did not differ in migration directions or distances, suggesting chain migration to be the general pattern. A larger proportion of adult Blue Tits remained near the breeding grounds during winter than was the case for juveniles. Some of the migrating birds (17%) seemed not to return in spring but stayed to breed closer to the winter area. Swedish Blue Tits show an exceptionally slow migration speed (median 13 km/day), among the slowest speeds recorded for any migrant bird. The Blue Tit represents an extreme case of diffuse, short and slow bird migration.

Keywords Short-distance migration ·
Timing of migration · Adaptations to migration ·
Partial migration

Introduction

Populations from different geographical breeding areas may either share or use different wintering grounds, and migration systems of diverse patterns have evolved (Salomonsen 1955). One such system is leapfrog migration where the most northerly breeding populations winter furthest to the south, passing more southerly breeding populations on their route to the wintering grounds (Alerstam and Högstedt 1980; Lundberg and Alerstam 1986). Another migration system is called chain migration, where the breeding and wintering areas of different populations are situated in the same latitudinal order. This may have the consequence that a mid-latitude breeding population may be replaced by another population arriving from the north during the winter (Kelly et al. 2002; Smith et al. 2003).

Also, variation in migration within populations can be found. The most obvious variation within a population is the occurrence of both migratory and non-migratory individuals, i.e. partial migration (Terrill and Able 1988). Another common phenomenon is differential migration, i.e. variations in the length of migration between individuals. Usually, this pattern results in segregations between age and sex groups in their wintering grounds (Cristol et al. 1999).

The knowledge of the migratory system of regular migrants is in many cases extensive (Alerstam 1990; Berthold 2001). However, the knowledge of migratory patterns of partial migrants is much more limited and, therefore, we investigated some migratory characteristics of partially migratory Blue Tits *Cyanistes caeruleus* using ringing recoveries. The Blue Tit is a common woodland species in Europe. In the northernmost part of its breeding range it is a partial migrant, occurring regularly at migratory passage sites in autumn. A large proportion of the

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migrants are young females (Winkler 1974; Heldbjerg and Karlsson 1997). Generally, bird migration implies a return to the natal breeding grounds. Irruptive movements are less regular and the return of migrating individuals less certain (Ulfstrand 1963). In contrast to irruptive movements and migration, dispersal is the movement from an individual's natal site to the location of its first breeding attempt. Dispersal usually takes place in summer before autumn migration and, in Blue Tits, dispersal distances are very short, with almost 90% within 20 km according to ringing recoveries reflecting natal dispersal of British Blue Tits (Gosler 2002). The late timing of extensive Blue Tit movements in Scandinavia taking place in autumn well after the summer dispersal period, the regularity of occurrence at migratory sites and the impressive number of individuals at these sites (Winkler 1974; Heldbjerg and Karlsson 1997; Nilsson et al. 2006) indicate that individuals from these Scandinavian populations should be regarded as migrants. Our aim was to study different aspects of the migration performance of Blue Tits and find out to what degree these aspects differ from those of regular migrants.

We addressed the following questions. (1) Which geographic migratory system (leapfrog or chain migration) is prevailing among Blue Tit populations? (2) Do Blue Tits exhibit age-related differences in their migration patterns? (3) Do Blue Tits perform migrations involving a return trip to the breeding areas? (4) At what speed do Blue Tits migrate? (5) Do Blue Tit migrations occur during the same time period over a larger geographical area?

Methods

From the Bird-Ringing Centre at the Swedish Museum of Natural History, we obtained all ringing recoveries of Blue Tits ringed in Sweden. We restricted ourselves to movements ≥ 10 km resulting in a dataset that included 1,250 recoveries obtained from 1936 to 2005. The dataset included date of ringing and recovery, the time period between ringing and recovery (in days), direction of recovery and distance moved (defined as the shortest distance between the two locations on the great circle). Mean directions were calculated as mean vectors (Batschelet 1981). When appropriate, an axial distribution was used to describe the distribution of recovery directions of migrants. When discussing migratory movements, unless otherwise stated, we refer only to autumn migration.

Migrations from northerly and southerly breeding areas

When investigating lengths and directions of the migratory movements undertaken by northerly and southerly

populations, the analysis was restricted to birds ringed during the breeding period (May–August) before any migratory movements have been initiated. Furthermore, only birds recovered during their first autumn and winter (September–February) were included. As a comparison, an analysis was also carried out on the much smaller dataset including only recoveries from the winter (November–February). Birds being recovered during these periods originated from a latitude range of $55^{\circ}35'–65^{\circ}39'N$ and a longitude range of $13^{\circ}00'–22^{\circ}04'E$. We arbitrarily defined recoveries of birds being ringed between 55 and $58^{\circ}N$ as originating from southerly populations and those ringed between 58 and $66^{\circ}N$ as originating from northerly populations. Recoveries at bird observatories, such as Falsterbo at the southwestern tip of the Swedish mainland ($55^{\circ}23'N$, $12^{\circ}49'E$) and Sundre at the southern tip of the island of Gotland ($56^{\circ}55'N$, $18^{\circ}08'E$), where birds have to cross large bodies of water, tend to truncate migration distances, and recoveries from these sites were therefore excluded from this analysis.

Change in wintering areas with increasing age

When comparing distances and directions of migrating Blue Tits recovered during their first winter with those recovered during later winters, we used all birds ringed during migration (September–October) and recovered during the winter period (November–February). Autumn migratory movements have subsided in November and spring migration does not start until mid-March (Heldbjerg and Karlsson 1997). To compare recoveries in the normal southwesterly direction with recoveries in the northeasterly return direction, recoveries were divided into two different sectors; $136–315^{\circ}$ and $316–135^{\circ}$, respectively.

Distance and direction of spring and autumn migration

To characterise the migration pattern of Blue Tits, distances and directions between the site of ringing and the site of recovery for two different parts of the migration were calculated: (1) birds ringed during the breeding period and recovered during autumn migration, and (2) those ringed on autumn migration and recovered on the breeding grounds. The breeding period was defined as May–August and the migratory period as September–October. Only recoveries within a year from ringing that were reported as alive or recently dead were included in the analysis.

Speed of migration

The speed of migration (km/day) was calculated based on birds ringed during migration (September–October) and recovered within 50 days of ringing. Normal southwesterly

migration (136–315°) was contrasted with reversed north-easterly migration (316–135°).

The degree of synchrony in Blue Tit migratory movements over large geographical areas

To investigate the timing of Blue Tit migration across a larger geographical area, data from four bird observatories was compared: Falsterbo, Ottenby at the southern tip of the island of Öland (56°12'N, 16°24'E), Hammarö at a peninsula in lake Vänern (59°15'N, 13°30'E) and Sundre. The analyses were divided into two parts. First, an analysis of timing based on birds ringed at each observatory during September–October and later recovered. Thus, only birds generating recovery data are included in this analysis. Second, an analysis of the yearly median date of migration, including all Blue Tits captured during September–October, at three of the bird observatories during 1980–2005: Falsterbo, Ottenby and Hammarö (Blue Tit migration outside this period is negligible at all sites). The standardised capture period at Sundre Bird Observatory did not include September–October and Sundre was therefore excluded from this analysis.

The timing of breeding at different geographical regions was measured as the dates when nestling Blue Tits were reported to be ringed to the Bird-Ringing Centre. Areas corresponding to latitude ranges 59–61°N were assigned to the middle region of Sweden and 55–56°50'N to the southern region, corresponding to probable areas of origin for birds captured at the northernmost Hammarö bird observatory and the southernmost Falsterbo bird observatory. The comparison of timing of migration in relation to breeding between the southern and the middle region were analysed as the annual difference between median breeding

and migration date of the closest bird observatory. Due to annual variation in numbers of migrating Blue Tits (years with number of captured birds falling below 25% of mean annual number of captures were excluded) and availability of breeding data, certain years had to be excluded from the analysis, resulting in 14 years for comparison.

Statistical analyses

Distances were ln-transformed before the computation of all statistical analyses to comply with normal distribution. Mean directions, axial directions, Rayleigh test and Watson's *U* test were calculated according to Batschelet (1981). Other statistical analyses were performed using SPSS 12.0.

Results

During autumn migration, Swedish Blue Tits move comparatively short distances with directions mainly towards southwest (Fig. 1a, b). The median distance was 82 km and the maximum distance recorded in our data set was 967 km, a recovery from the Netherlands in 1990. The majority of all recoveries were from within Sweden, although a substantial part (35%) of them came from neighbouring countries, such as Denmark (339 recoveries), Germany (28), Norway (22) and Finland (19).

Migrations from northerly and southerly breeding areas

When comparing migration (recaptures from September to February) between individuals originating from northerly and southerly breeding areas, respectively, the distances of

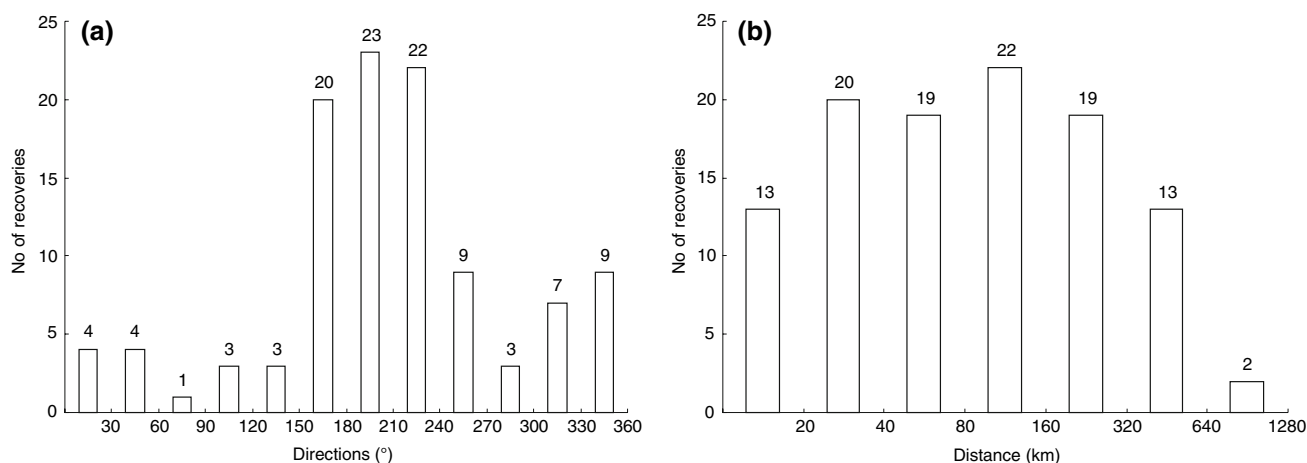


Fig. 1 **a** The direction and **b** distance of migrating Blue Tits *Cyanistes caeruleus* ringed during the breeding period (May–August) and recovered during autumn migration or on the wintering grounds (September–February) ($n = 117$). Displayed numbers above columns

are number of observations in each category. Data from Falsterbo and Sundre bird observatories are excluded from this analysis (see “Methods”)

migratory movements were very similar; individuals from northerly populations having a median of 83 km ($n = 27$) and individuals from southerly populations having a median of 81.5 km ($n = 90$). Thus, there was no difference between individuals from northerly and southerly populations in migration distances (t test: $t = 0.34$, $df = 106$, $P > 0.1$). Individuals from northerly populations had a non-significant mean direction of 211° ($r = 0.27$; Rayleigh test: $Z = 1.77$, $n = 25$, $P > 0.1$) and individuals from southerly populations a mean direction of 210° ($r = 0.51$; Rayleigh test: $Z = 21.84$, $n = 83$, $P < 0.001$), again showing no difference (Watson's U test: $U^2 = 0.12$, $n = 108$, $P > 0.1$). The same pattern was evident for the more restricted data set when only recoveries from November to February were included in the analyses (northerly populations ($n = 14$): median distance = 65 km, direction = 199° ; southerly populations ($n = 28$): median distance = 84 km, direction = 265°). Northerly and southerly populations did not differ significantly with respect to either distances (t test: $t = 0.96$, $df = 31$, $P > 0.1$) or directions (Watson's U test: $U^2 = 0.14$, $n = 33$, $P > 0.1$).

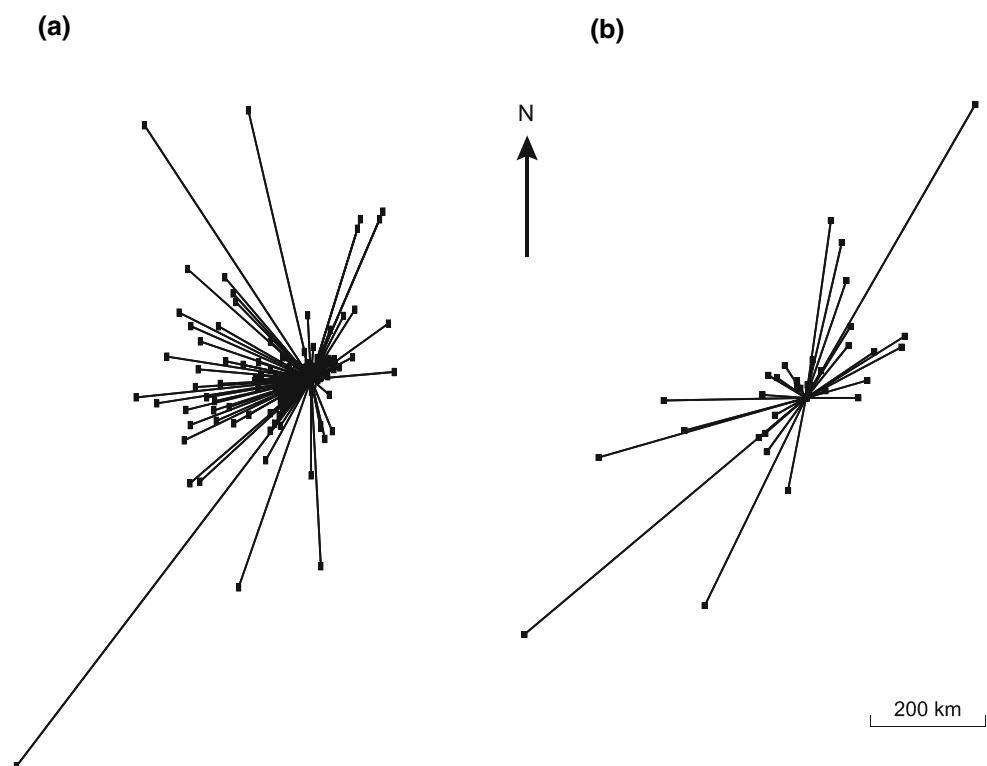
Change in wintering areas with increasing age

Birds recovered during the first winter after being ringed on migration had a mean direction of 293.0° ($r = 0.34$; Rayleigh test: $Z = 44.67$, $n = 133$, $P < 0.001$) (Fig. 2a). Birds

recovered during later winters were best described by an axial distribution of directions, i.e. towards 41.5° and 221.5° , respectively ($r = 0.36$; Rayleigh test: $Z = 4.28$, $n = 34$, $P < 0.019$) (Fig. 2b). There was no overall difference in the directions migrated between first- and later-year winter recoveries (Watson's U test: $U^2 = 0.14$, $n = 167$, $P > 0.1$). However, there was a significantly larger proportion of later-year birds (62%) recovered during winter in the northeastern sector ($136\text{--}315^\circ$), i.e. on reverse migration, than was the case for recoveries of first-year birds (41%) in that sector ($\chi^2 = 4.90$, $n = 167$, $df = 1$, $P = 0.027$). The major part of the first-year migrating Blue Tits consisted of females (72 and 69% in the northeastern and southwestern sectors, respectively), which were also true for later-year recoveries (70 and 88%, respectively). In the latter case, birds recovered in the northeastern sector may not only represent reversed migrants, but also individuals that have become sedentary close to their natal breeding areas during their second and later winters. There was no difference in the sex ratio between first- and later-year winter recoveries found in the northeastern and southwestern sectors ($\chi^2 = 0.30$, $n = 76$, $df = 1$, $P > 0.1$).

The median distance of birds ringed during migration and recovered during their first winter was 88 km ($n = 133$) (Fig. 2a), whereas birds recovered during later winters migrated a median distance of 115 km ($n = 34$) (Fig. 2b). Since recoveries of birds in their second or later winters were better described by a bimodal distribution of

Fig. 2 The distribution of recoveries of Blue Tits ringed during migration (September–October) and **a** recovered the first winter after the migratory period ($n = 133$) and **b** recovered second or later winters after migration ($n = 34$). Winter is defined as November–February. Each square represents one recovered individual and each line the distance and direction to recovery site



directions, the distances were calculated also separately for the two main directions giving a median distance of southwesterly recoveries (normal migration) of 122 km ($n = 13$) and a median distance of northeasterly recoveries (reverse migration or later-year residency) of 96 km ($n = 21$). When restricting the analysis to winter recoveries in the southwest sector, i.e. normal autumn migration, it turned out that first-year winter birds had moved similar distances as Blue Tits migrating during their second or later year (t test: $t = 1.69$, $df = 90$, $P = 0.094$).

Distance and direction of spring and autumn migration

Distance and direction of migrating Blue Tits during autumn migration (ringed during the breeding period and recaptured on autumn migration) and spring migration (ringed on autumn migration and recaptured during the next year's breeding season) were compared. Birds recovered during autumn migration had a mean direction of 216° ($r = 0.84$; Rayleigh test: $Z = 200.0$, $n = 281$, $P < 0.001$), while birds recovered during the breeding period had a mean direction of 25° ($r = 0.64$; Rayleigh test: $Z = 7.33$, $n = 18$, $P < 0.05$). The median distance for birds recovered during autumn migration was 53 km ($n = 281$) and birds recovered after spring migration had moved 57 km ($n = 18$) (Fig. 3). The length of spring and autumn migration did not differ (t test: $t = 0.1$, $df = 21.8$, $P > 0.1$).

Of the Blue Tits recaptured during the breeding period, 83% were found in the northeastern sector and, thus, they had probably migrated back during spring. However, three birds (17%) recaptured in the southwestern sector during the breeding period indicate that some birds may also stay and breed on the winter areas. Indeed, at least one of them was captured in a nest box.

Speed of migration

Distances travelled by Blue Tits ringed on early migration (September), increase almost linearly during the first 20–25 days (even slightly accelerated during the first 10 days), which seem to be the duration of the main migration period (Fig. 4a). This corresponds to an average speed of about 11 km/day. Analysing the recoveries of Blue Tits ringed later during autumn migration (October) in the same way (Fig. 4b), shows a rather high initial instantaneous speed of migration (21 km/day), which is rapidly declining (average speed 16 km/day during the first 5 days) and the duration of the migration period seems to end after about 10 days. For reverse migration (recoveries in the northeastern sector 316 – 135°), the average speed drops from about 10 km/day initially to zero after about 20 days, marking the end of the reverse migration period (Fig. 4c).

If the analyses of migration speed are restricted to the first 10 days after ringing in both September and October (Fig. 5), the maximum speed recorded was 69 km/day (206 km in 3 days) and the median was 13 km/day. For reversed migration, the maximum speed was 49 km/day and the median was 8 km/day.

The degree of synchrony in Blue Tit migratory movements over geographically different areas

Based on the ringing dates of recovered birds, the median date of Blue Tit migration passing Falsterbo was 4 October ($n = 411$), Ottenby 4 October ($n = 52$), Hammarö 29 September ($n = 33$) and Sundre 3 October ($n = 36$). There was no significant difference in date of migratory passage between the bird observatories (Kruskal–Wallis test; $\chi^2 = 3.56$, $df = 3$, $P > 0.1$).

Based on the total number of ringed Blue Tits at Falsterbo, Ottenby and Hammarö, the median date for Blue Tit passage was 6 October at Falsterbo, 7 October at Ottenby and 5 October at Hammarö. There was no difference in the median date of migratory passage at the different bird observatories (Kruskal–Wallis test: $\chi^2 = 4.26$, $df = 2$, $P > 0.1$).

In contrast to the synchronous migration, the median date of breeding (indexed as the median date of nestling ringing) in southern Sweden was 6 June and in the middle region of Sweden 11 June. Blue Tits in southern Sweden had on average 7 more days between breeding and migration than had Blue Tits from more northerly populations in the

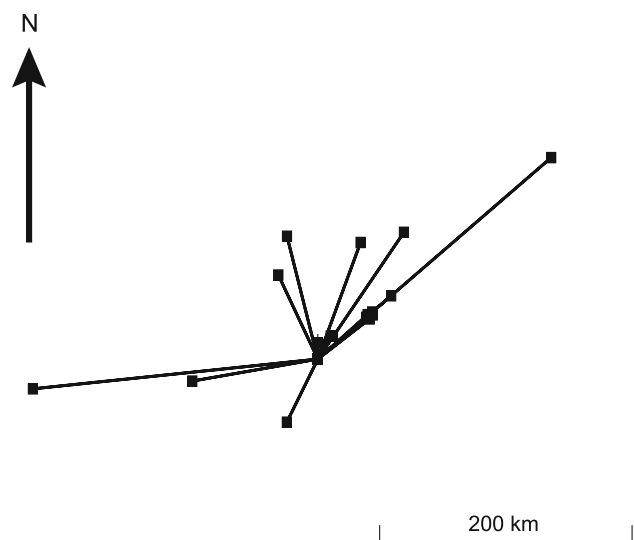


Fig. 3 Distribution of recoveries by birds ringed on migration (September–October) and recovered during the breeding season (May–August). Each square represents one recovered individual ($n = 18$) and each line the distance and direction from ringing to recovery site

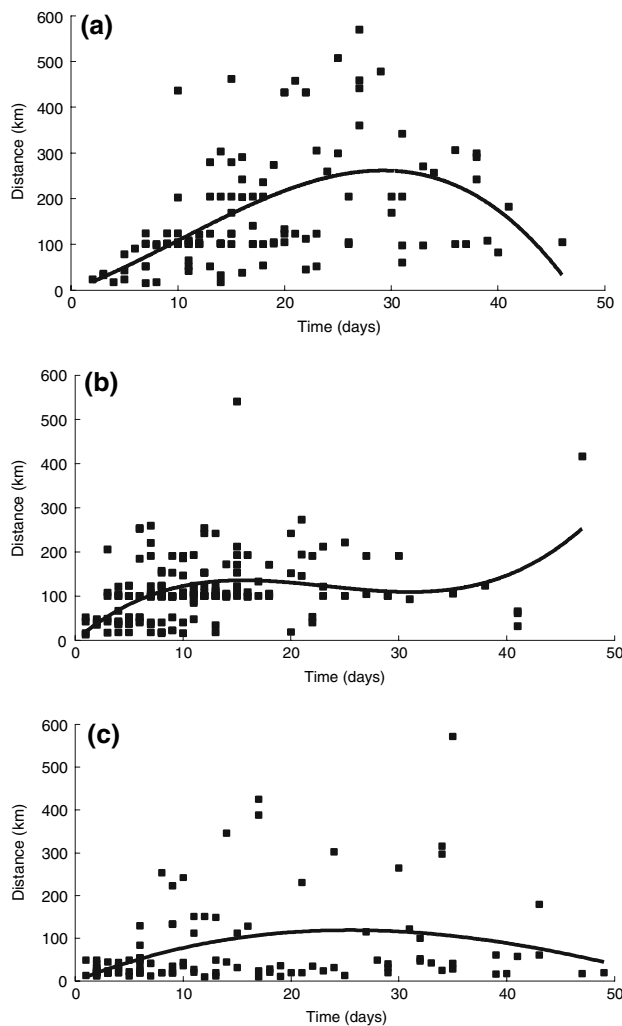
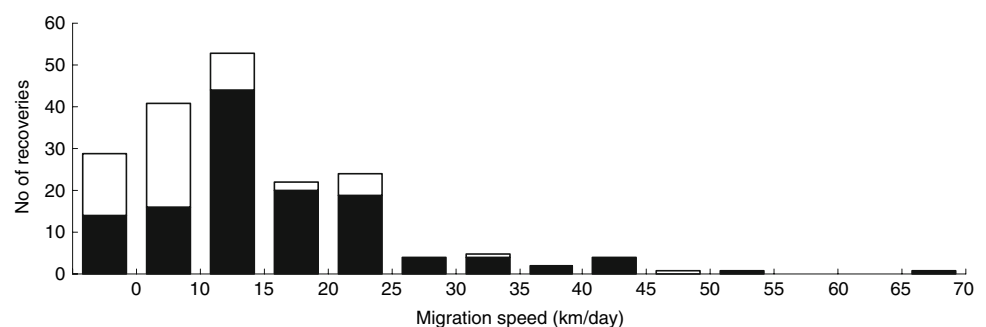


Fig. 4 The distance (km) and time (days) between ringing and recapture of Blue Tits ringed in **a** September or **b** October with a southwesterly direction (136–315) and recaptured within 50 days of the ringing event (September: $n = 124$; distance = $8.6 t + 0.33 t^2 - 0.01 t^3$; $R^2 = 0.28$, October: $n = 186$; distance = $20.9 t - 1.01 t^2 + 0.01 t^3$, $R^2 = 0.16$, where t is number of days between ringing and recovery). **c** The distance (km) and time (days) between ringing and recapture of Blue Tits ringed in September–October and recovered in northeasterly directions (i.e. reversed migration) within 50 days of the ringing event ($n = 114$; distance = $10.0 t - 0.23 t^2 + 0.001 t^3$, $R^2 = 0.12$)

Fig. 5 Distribution of migration speeds (km/day) for Blue Tits ringed in September–October and recaptured within 10 days of the ringing event. Normal migration in a southwesterly direction is shown as *black fillings* ($n = 129$) and reversed migration in a northeasterly direction as *white fillings* ($n = 58$)



middle region (Paired samples t test: mean difference = 7.21 days, 95% confidence interval: lower = 4.0, upper = 10.5, $t = 4.78$, $df = 13$, $P < 0.001$).

Discussion

Migrations from northerly and southerly breeding areas

We found very similar migratory patterns in Blue Tits from northerly and southerly breeding populations. Distances migrated by these two arbitrarily divided populations were the same, as were general directions of migration. Therefore, both leap-frog migration and migration to the same wintering areas can be excluded as explanations for the migratory pattern of Blue Tits, as both these hypotheses predict northerly populations to migrate farther than southerly populations. Since the Blue Tit has a wide distribution, leapfrog-migrating Blue Tits would have to make long migrations to avoid competition with conspecifics. Thus, Scandinavian Blue Tits would have to leap-frog the central European and Mediterranean populations (Perez-Tris and Tellería 2002). Instead, the chain migration hypothesis is supported by the similarity of distances migrated and directions headed by the Blue Tits. In comparison with leap-frog migration, chain migration seems to be a fairly unusual strategy, although Sharp-shinned Hawks *Accipiter striatus* in North America and Icelandic populations of Redshanks *Tringa totanus robusta* are known to be chain migrants (Salomonsen 1954; Smith et al. 2003).

Chain migration and partial migration both imply that individuals leave areas that can be used by others for wintering. Among partial migrants, part of the population remains at the breeding grounds and time constraints may therefore prevent long return migrations in spring, as competition for breeding territories and nest holes are fierce during this time (von Haartman 1968; Alerstam and Högstedt 1980). A late return to the breeding grounds in spring might imply lost opportunities for breeding. In a short-lived species, like the Blue Tit, missed breeding opportunities will seriously reduce individual fitness

(McCleery and Perrins 1988). Thus, we suggest that partial migration in a widely distributed species, like the Blue Tit, involving a mixing of resident and migratory birds in most populations during winter, is associated with general selection for short migration distances.

Change in wintering areas with increasing age

In the past, there has been much debate whether the migratory strategy of partial migrants is fixed or can change during the life of the individual (Berthold 1984; Lundberg 1988). Schwabl (1983) found a change in the migratory strategy of Blackbirds *Turdus merula* as individuals starting out as migrants later in life changed strategy and became residents. Two factors indicate that Blue Tits also change migratory strategy with increasing age. First, adult Blue Tit recoveries (birds ringed during autumn migration and recovered as adults during second or later winters) have an axial distribution, suggesting that only part of this age group continue to migrate in successive years, while the other part stops migrating after their first year and remain resident during the following years. Second, a significantly higher proportion of adult winter recoveries are found in the northeastern sector, indicating that a major proportion of adults shift strategy from migration to residency with increasing age.

Distance and direction of spring and autumn migration

In general, the definition of bird migration involves a return migration to the breeding grounds. However, a few of the Blue Tits participating in the autumn movements were recovered as potential breeders and had apparently not made a return journey in spring. Although the major part of the potentially breeding migrants was recovered on breeding grounds in a northeasterly direction (83%), implying that they had made a return spring journey, these results still indicate that almost every fifth surviving migrant (17%) may not return in spring. However, long-distance migrants have also been recorded to occasionally breed at their tropical winter quarters, such as the Common Sandpiper *Actitis hypoleucos* and White Stork *Ciconia ciconia* (Moreau 1972). Also British and German Stonechats *Saxicola torquata* have been found to interrupt their migration and occasionally breed away from their original breeding grounds (Helm et al. 2006). An alternative explanation would be that the migratory movements of Blue Tits are mixed with movements made by dispersing individuals that would become residents when offered an opportunity. However, this is unlikely as the three individuals that bred on the wintering grounds had moved distances of between 56 and 227 km. Such distances stand in sharp contrast to known dispersal distances by sedentary

Blue Tits in Britain, where dispersal distances are very short and almost 90% of all recoveries are within 20 km (Gosler 2002). We are not aware of any similar indications for other partial or short-distance migrants and it would be very interesting to see if the pattern of an imperfect return migration with a proportion of birds breeding on the wintering grounds may occur also among other species. This would be crucial information when analysing the genetic structure of populations in different parts of their distribution range.

Speed of migration

The speed of Blue Tit migration late in the migratory period was slightly higher than the speed of migration during the early part of the migration period. Ellegren (1993) also found the same pattern of increasing migration speeds during the migratory period in other species and he suggested that the migratory strategy might vary among individuals. Alternatively, if there is competition for winter resources, late migrants would be more in a hurry to reach their wintering grounds (Ellegren 1993). For Blue Tits spending the winter in areas where resident Blue Tits also occur, the probability of being lowest in rank in wintering flocks would be high (Nilsson 1990; Perez-Tris and Tellería 2002). However, we do not know to what extent wintering and resident individuals use the same resources or habitats. Migratory Blackcaps *Sylvia atricapilla* wintering in Spain have to compete with resident Blackcaps during winter, and a large proportion of the migrants are confined to low-quality habitats (Perez-Tris and Tellería 2002).

Blue Tits proceed very slowly on migration, with a median speed of 13 km/day, compared to tropical migrants (median speed = 75 km/day) and regular migrants wintering in southern Europe (median speed = 53 km/day) (Hildén and Saurola 1982; Alerstam and Lindström 1990). Comparatively slow migration speeds seem to occur mainly among irruptive and partial migrants, such as the Great Tit *Parus major* (11 km/day) and the Willow Tit *Parus montanus* (10 km/day) (Hildén and Saurola 1982). Frelin (1979) theoretically estimated Blue Tit migration in the French Alps to proceed with a speed of 29 km/day, which he compared to ringing records showing speeds of 20–50 km/day. Van Balen and Speek (1976) estimated Baltic Blue Tits recovered in the Netherlands to have proceeded with a speed of 40 km/day during autumn migration. Our estimates of migration speed in Blue Tits are considerably lower with few movements faster than 25 km/day, in line with estimates from ringing recoveries in Finland yielding speeds of 8–12 km/day (Hildén and Saurola 1982) and estimates from another Swedish study giving an overall speed of 17 km/day (Ellegren 1993).

Why do Blue Tits migrate so slowly? In general, diurnal migrants travel slower than nocturnal migrants (Ellegren 1993), as they also have to forage during daytime. However, Blue Tits migrate much slower than most other diurnal migrants (Ellegren 1993). First of all, reverse movements in migrating Blue Tits are frequent and could potentially bias our estimates of migration speed. However, Blue Tits could also explore the possibilities for suitable wintering grounds during the progress of migration, which would explain a very slow speed of migration. Possibly, as Blue Tits only migrate very short distances, they can afford to travel slowly, minimising energy expenditure and risks, as suggested by Alerstam and Lindström (1990). In line with this, Blue Tits also seem to select the safest occasions possible for their migratory flights with respect to weather (Nilsson et al. 2006).

The degree of synchrony in Blue Tit migratory movements over geographically different areas

Migratory movements of Blue Tits appear to occur synchronously over a large part of the species' distribution range in Sweden. Median dates at the different migratory passage sites, located between 55 and 61°N, were very similar.

The mean difference between the southern and the middle region of Sweden in the time between breeding and migration was 7 days. In some years, the contribution of adult migrants is significant (Winkler 1974; Heldbjerg and Karlsson 1997) and their moult is completed in about 120 days (Ginn and Melville 1983), but the number of days available for moult between the independence of young and the timing of migration in southern Sweden is only on average 106 days compared to 99 days in the middle region. However, the majority of migrants are juveniles with only moult of body feathers after independence. Thus, the Blue Tit populations in the northern distribution range have less time to finish breeding and moult before they potentially can leave on migration. As a result, the annual routines of northern Blue Tits are likely to be somewhat more time constrained than their southern conspecifics. Whether the geographically constant timing of migration is the result of adaptations to the different latitudinal conditions or a plastic response to environmental cues, such as day length, cannot be determined with the present study.

Conclusions

Our results demonstrate that the Blue Tit is at the lower extreme end of a spectrum of migratory performance among birds, ranging from partial, diffuse (with a wide directional scatter), short and very slow migration in the Blue Tit to fast

and precise long-distance migration among global migrants. Compared to other migratory patterns, chain migration is a rather unusual strategy. Chain migration, just like partial migration, implies that individuals leave where others can spend the winter. One of the driving forces behind chain migration and short migratory distances in a partial migrant could very well be time constraints on the return journey. As prior occupancy is an important aspect of dominance in tits (Nilsson 1990), competition with residents is probably asymmetric (Krebs 1982), leaving only few openings in the territorial system for migrants. These vacancies will be taken by those individuals returning to the breeding grounds first preventing long migratory journeys. The slow speed of migration in a wide directional sector with frequent return movements may also be adaptive by allowing exploration for wintering opportunities and promoting risk minimisation on migration.

Migration usually implies a return journey, at least in higher vertebrates. One-way journeys are labelled dispersing movements. In the Blue Tit, dispersal takes place soon after fledglings become independent of their parents and is, thus, separated in time from the long-distance movements reported here. Still, some migratory Blue Tits breed on the wintering grounds, suggesting a somewhat opportunistic strategy of migrating Blue Tits. With its migratory characteristics at the lower end of the performance scale among birds, the Blue Tit represents a highly interesting case for further investigations of the evolutionary transition between residency with dispersal movements and true (albeit partial) migration.

Zusammenfassung

Diffuse, kurze und langsame Migration bei Blaumeisen

Das Wissen über Migrationssysteme bei regulären Langstreckenziehern ist in vielen Fällen umfassend. Unsere Kenntnisse über die Zugcharakteristika von Teilziehern sind dagegen weit beschränkter. Wir haben die Zugcharakteristika teilziehender Blaumeisen *Cyanistes caeruleus* anhand von Ringwiederfunden schwedischer Vögel untersucht, um Fragen nach geographischen Zugmustern, altersspezifischen Migrationen, Zuggeschwindigkeiten und Synchronität der Zugbewegungen zu beantworten. Die mediane Zugentfernung schwedischer Blaumeisen betrug 82 km mit einer hauptsächlich Herbstzugrichtung im Sektor zwischen S und W (starke Richtungsstreuung). Nördliche und südliche Populationen unterschieden sich nicht in Zugrichtungen und -entfernungen, was auf Kettenmigration als generelles Muster schließen lässt. Bei Altvögeln verblieb im Winter ein größerer Anteil in der Nähe des Brutgebiets, als es bei Jungvögeln der Fall war.

Einige der ziehenden Vögel (17%) schienen im Frühjahr nicht zurückzukehren, sondern brüteten in größerer Nähe zum Überwinterungsgebiet. Schwedische Blaumeisen haben eine außergewöhnlich langsame Zuggeschwindigkeit (Median 13 km/Tag), eine der langsamsten bei Zugvögeln erfassten Geschwindigkeiten überhaupt. Die Blaumeise stellt einen Extremfall des diffusen, kurzen und langsamen Vogelzugs dar.

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