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Distribution and population changes of two subspecies of Chiffchaff *Phylloscopus collybita* in Sweden

Utbredning och populationsutveckling hos två raser av gransångare Phylloscopus collybita *i Sverige*

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Abstract

We describe the breeding distribution and population trends of the two subspecies of Chiffchaff *Phylloscopus collybita* that occur in Sweden. Our data come from the Swedish Bird Survey: free choice point counts (1975–2006) and fixed (and habitat-representative) line transects (1996–2006). *Ph. c. abietinus* occurs north of about 60ºN with a stronghold in central Sweden and along the coast of the Bothnian Bay. This population declined with about 75% between 1983 and 1997, but has increased again during the last decade, matching closely the changes in Finland. *Ph. c. collybita*, a recent immigrant, breeds mainly in southwesternmost Sweden. The population in 2006 was estimated to be 15 times larger than in 1975 but with little range expansion. The breeding distribution of the two subspecies does not yet overlap. The distribution of the northern subspecies seems to be determined by the occurrence of spruce forest, and the northern range border may be set by early autumn frost. The recent positive trend in the north may possibly be due to an increase in area of old spruce forest.

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Introduction

The Chiffchaff *Phylloscopus collybita* occurs as a breeding bird in Sweden with two subspecies (Svensson et al. 1999).

In northern Sweden Chiffchaffs belong to the subspecies *Ph. c. abietinus* (Nilsson 1819, SOF 2002). This subspecies is distributed from Norway to the Pechora River and the Ural mountains. It prefers old and rich spruce forests with interspersed deciduous trees (Svensson et al. 1999, Lapshin 2000). *Ph. c. abietinus* grades into the western and southern subspecies *Ph. c. collybita* through Poland and Ukraine (Tiainen & Wesolowski 1997). Berggren (1999) and Olsson & Wiklund (1999) reported strong declines between 1975 and 1998 in Västerbotten and Norrbotten (the northeasternmost provinces of Sweden) based on census work, ringing statistics and general observations. A similar decline took place over the same period in Finland (also *abietinus*), but there numbers started to increase again from 1998 onwards (Väisänen 2006). There is ambiguous evidence about the population trends further east, but there seems to be a common pattern of a rather strong decline between the early 1980s and the late 1990s (Lapshin 2000, Sokolov et al. 2000).

In southern Sweden the species is represented by the nominate subspecies *Ph. c. collybita* (SOF 2002), whose range includes western and southern Europe apart from the range of the Iberian Chiffchaff. The latter is now considered a separate species *Phylloscopus ibericus* (Svensson 2001). *Ph. c. collybita* occurs in a broader variety of habitats than *abietinus* and is often found in pure deciduous forests (Svensson et al. 1999). Although Ekman (1922, p. 133, 167) talks about "the Skåne population" and "a southern range in Skåne", and although breeding records exist from that southernmost province in 1898–1899 (Hedeby 1918), the Chiffchaff is a late newcomer. The first recent breeding was reported as late as the early 1970s from southernmost Sweden (Dahlman 1974, Svenaeus 1978, Ellegren & Pettersson 1985). During the Swedish atlas work in 1974–1984 (Svensson et al. 1999) there were many records of Chiffchaffs in various parts south of 60°N. However, records belonging to the category "confirmed breeding" were

restricted to the very south and very west of southern Sweden. The atlas work was carried out from early spring, so many of the records in central south Sweden may have referred to *abietinus* males that were singing during migration. According to the latest national evaluation, the area between the two subspecies is still not colonised to any substantial degree (SOF 2002). However, the number of southern Chiffchaffs in southern Sweden has increased substantially as expressed in ringing figures at bird observatories in southern Sweden like Ottenby (Håkansson & Rhönnstad 1993, Lindström et al. 2006) and Falsterbo (Karlsson et al. 2002).

The aim of this paper is to describe in detail the recent population trends of the two subspecies in Sweden and for the first time provide a quantitative distribution map based on one geographically representative census method. To do this we use Swedish breeding bird monitoring data from 1975–2006. We also discuss some potential causes of the population changes found.

Methods

The data presented here are based on two programmes included in the Swedish Bird Survey (Lindström & Svensson 2007), a monitoring scheme within the Environmental Monitoring Programme of the Swedish Environmental Protection Agency. Chiffchaffs are not determined to subspecies in the field and it is not known exactly where the present border between the two subspecies' breeding distributions is. However, based on the geographical distribution of breeding Chiffchaffs in the Breeding Bird Atlas (data from 1974–1984; Svensson et al. 1999) and from SOF (2002), we considered all birds recorded south of 60ºN as *collybita* and all records north of 60ºN as *abietinus* (see also Hansson et al. 2000). The exact choice of border will have no or very little effect on the overall conclusions.

Free choice routes

This programme started in 1975 and consists of several hundred routes, each with 20 point counts (Svensson 1975, Naturvårdsverket 1978). At each point all birds heard or seen were counted during five minutes. We used the sum of all birds observed at each route for our analyses. The geographical location of the routes and the exact position of the points were chosen by the observer. Observer-chosen routes are likely to be biased, on a regional scale to populated areas and on a local scale to areas close to roads and paths. How and if this sampling bias affects trends we do not know. A given route was censused once a year by the same observer at a route-specific date (± 5 days) and starting hour (±30 minutes). Routes abandoned by one observer were not taken over by a new observer and therefore the number of years a route was counted varied between 1 and 32. Point count data were used for trend analyses only.

Fixed routes

A new monitoring programme was started in 1996 (Svensson 2000, Svensson & Lindström 2002). A total of 716 routes are systematically distributed over the whole of Sweden, with 25 km between the centres of near-by routes in both north–south and east–west directions. Each route is 8 km long and shaped like a square with 2 km sides so that the census person returns to the starting point at the end of the census. All birds seen or heard along the 8 km transect were counted and we used the sum of all birds per route for our analysis. Many routes have been shorter than 8 km because some parts are over water bodies. Five minute point counts were also made each one km, but these data are not used in this analysis. The aim is to census each route once a year at a date adapted to its latitude and elevation. The southernmost routes were carried out from mid May to early June with average dates gradually changing towards the north. The northernmost routes were counted between mid June and early July.

In contrast to the free choice routes the observer of a fixed route may change between years. Data from the fixed routes were used for analyses of both trends and breeding distribution. Since the number of routes censused in 1996–1997 was comparatively low, we only used data from 1998 onwards for the trend analyses. For the breeding distribution analysis we used the data from all eleven years.

Trend analyses

Population trends were calculated using TRIM (TRends and Indices for Monitoring data; Pannekoek & van Strien 2001), a statistical package developed especially for monitoring data of the kind we have. TRIM analyses time series of counts with missing observations using Poisson regression taking serial correlation and overdispersion into account. We used the "time-effect model" to estimate overall trends as well as yearly indices. For more information, see Pannekoek & van Strien (2001).

We did not look for observer or site effects. For the fixed routes the sampling scheme as such will take site effects into account. To allow for direct comparison between the two monitoring programmes we used 1998 as baseline year (index set to 1) for the nine years with parallel data.

Breeding distribution and densities

As an index of breeding density we used the yearly average number of Chiffchaffs observed on a given route. This means that for each route the density estimate is based on censuses from between one and eleven years. Since the fixed routes are systematically distributed over Sweden, the number of birds reported is proportional to the breeding densities in different regions and habitat types. The number of birds observed will vary not only due to variations in bird numbers, but also depend on weather and observer differences. Therefore routes censused many years, and averages from many nearby routes, will give more precise estimates of abundance than values based on single routes and years. How accurate these estimates are (in relation to true breeding density) we do not know, but we assume that the accuracy level does not vary systematically over Sweden.

Route coverage

In 1975–2006 the number of free choice routes censused in the two regions varied between 13 and 71 in the north and between 61 and 241 in the south. The overwhelming majority of counts were made in early mornings between 10 May and 20 June, but the total span of dates ranges from early April to early August.

The yearly number of fixed routes that were censused increased steadily over the period, from 48 in 1996, via 86 in 1997, 166 in 1998 to 411 in 2006. A total of 2855 censuses were carried out. With few exceptions the censuses south of 60°N were carried out between 15 May and 15 June, and those north of that latitude between 25 May and 25 June. Some routes in the Scandinavian mountain ridge were censused later in summer, but no Chiffchaffs breed in those areas. From about 2002 and onwards the southern half of Sweden was almost completely covered each year with proportionally fewer routes being censused in the north (Lindström & Svensson 2007). In 1996–2006 the fixed routes in northern and southern Sweden were censused on average 3.1 and 5.8 times, respectively. All routes within the regular breeding distribution of Chiffchaffs were censused at least once. The variation in number of routes censused in different years in a given scheme is taken into account in the TRIM analyses.

Results

The following data form the basis for our analyses. A total of 2656 northern and 1536 southern Chiffchaffs were recorded along the free choice routes. For the fixed routes, a total of 1459 northern and 393 southern Chiffchaffs were counted in 1996–2006, forming the basis for the distribution data. The trend estimates for the fixed routes in 1998–2006 were based on 1404 northern and 387 southern birds.

Breeding distribution

The data from the fixed routes show two distinct breeding areas for Chiffchaffs in Sweden, one in the very south and one in central Sweden (Figure 1).

North of 60°N, the yearly averages per route varied between 0 and 15 birds. The main distribution is in east central Sweden, that is, the provinces of Hälsingland, Medelpad, Jämtland and Ångermanland, with a marked presence of Chiffchaffs also in adjacent parts of Dalarna, Västerbotten and Norrbotten.

South of 60°N, the average number of Chiffchaffs per route varied between 0 and 6.2. The stronghold is in Skåne (the southernmost province), but there is also a continuous distribution along the western and southern coasts. The rest of the area south of 60°N had a more scattered and irregular occurrence of Chiffchaffs.

The design of the fixed route scheme assures that at a national level habitats and region are censused in proportion to their size. Assuming that birds of different subspecies, and birds in different habitats, are detected in equal proportion to their actual abundance, we have estimated the proportion of the two subspecies in Sweden. Should all 716 routes have been censused in a year and we found the same average abundance of Chiffchaffs per route as recorded in 1996–2006, we would have found 423 (standard deviation 27.4) birds in northern Sweden and 56 birds (s.d. 9.9) in southern Sweden. This means that in the period 1996–2006 about 88% of the Swedish Chiffchaffs were *abietinus* and 12% were *collybita*.

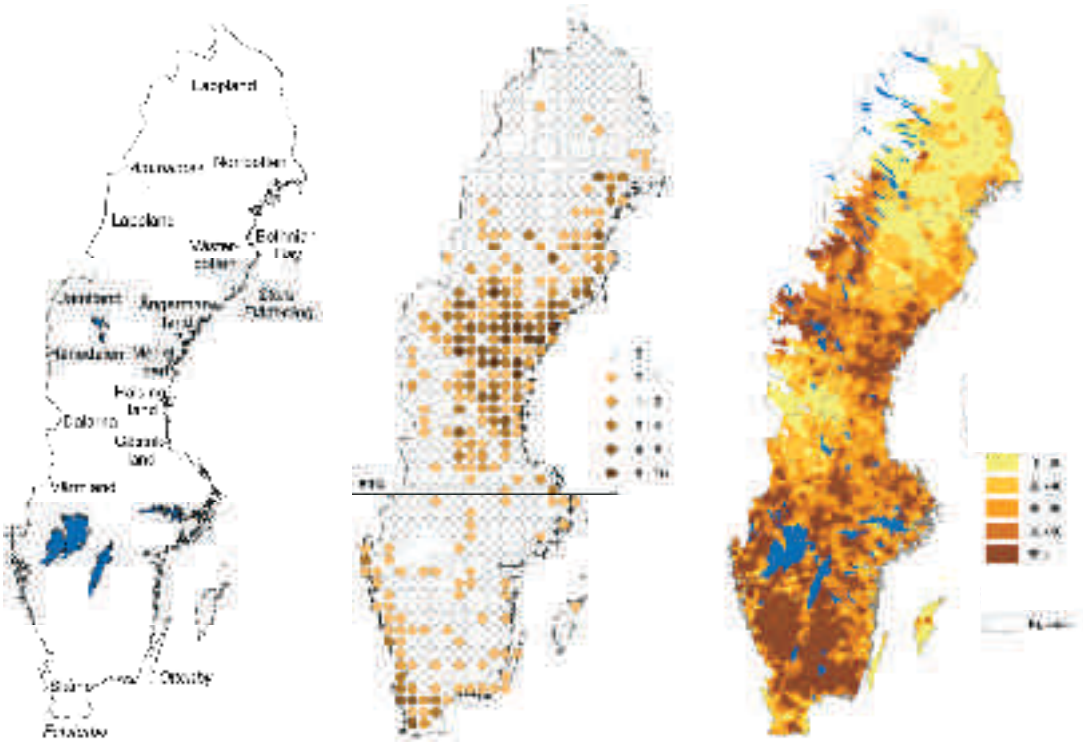

Figure 1. Left. Map of Sweden with regions and sites (circles, name in italics) mentioned in the text. Middle. The average number of Chiffchaffs recorded per fixed route in Sweden 1996–2006. Each route censused at least once is marked with a circle. The number of censuses per route varied between 1 and 11 and the number given is the yearly average number of Chiffchaffs recorded. The interval classes are set so that an average of 1.00 birds per route belongs to the class "0–1". An average of 1.01 belongs to "1–2", etc. Right. The volume (m^3/ha) of spruce in Sweden 1999–2003. Source: Swedish National Forest Inventory.

Vänster. Karta över Sverige med platser och områden nämnda i texten. Mitten. Antalet gransångare noterade på de svenska standardrutterna 1996–2006. Varje rutt som inventerats minst en gång är markerad med en cirkel. Antalet gånger en rutt inventerats varierar mellan 1 och 11. Det är medelantalet gransångare noterade för dessa inventeringar som anges. Intervallen är lagda så att medelvärdet 1,00 faller inom intervallet "0–1" och medelvärdet 1,01 faller inom "1–2", osv. Höger. Volymen levande gran (m^3/ha) i Sverige 1999–2003. Källa: Riksskogstaxeringen.

Trends

The northern Chiffchaff declined with on average 3.6% per year between 1975 and 2006 (TRIM, $p<0.001$, Figure 2), although there was a clear shift towards a positive trend from 1997 onwards. In the period 1975–1997 the decline was about 75%, with the most dramatic loss occurring between 1983 and 1997 (75% also for this period). The increase in 1997–2006 amounted to about 85%, but the numbers are still way below the values from around 1980. A similar recent increase was seen in the fixed routes 1998–2006, amounting to an average of 6.8% per year (TRIM, $p<0.001$, Figure 2) and a total increase of about 50%.

For the southern Chiffchaff the trends were overall positive in both programmes (Figure 2). Over the 32 years with point counts there was an average yearly increase of 9.7% (TRIM, $p<0.001$), amounting to a total increase of about 1400% (the indices increased from about 0.1 to about 1.3). It is noteworthy that the increase started first in 1985. For the shorter period 1998–2006 the fixed routes showed an increase of 11.9% per year (TRIM, $p<0.001$), leading to a total increase of 150% (indices increased from about 0.8 to 2). The corresponding increase based on point counts in the same period was 6.3 % per year (TRIM, $p<0.001$) and a total increase of about 60%.

Discussion

Distribution

Our data on the breeding distribution of Chiffchaffs in Sweden builds on a coarse net of routes (25 km between routes). Therefore, conclusions about local abundance from individual routes cannot be drawn with any certainty. However, at a larger scale the data are likely to be more representative. Generally, the distribution found accords well with earlier distribution maps, although these were basically presence/absence maps (e.g. Svensson et al. 1999, SOF 2002). However, this is the first time that relative densities are shown, emphasizing the drastic differences between different parts of the country and providing a new and better picture of the species' occurrence in Sweden.

Ph. c. abietinus. The distribution of the northern subspecies in the last decade is more restricted than earlier reported (SOF 2002), now forming an almost triangular (V) shaped area in central Sweden. The densities in Värmland, westernmost Härjedalen, Jämtland and southern Lappland were much lower than indicated in SOF (2002). Furthermore, the particularly high density described for southern Dalarna (SOF 2002) finds only weak support in our data. Rather, the highest densities in Sweden, according to our study, are found in Ångermanland. This partly new picture of the subspecies' distribution may be due to recent changes, but is more likely a result of more and better data being available due to our representative census methods.

The subspecies' distribution in northern Sweden closely coincides with the areas with the largest volumes of spruce (Figure 1). In much of the main breeding area of northern Chiffchaffs, spruce make up 50% of total tree volume (Source: Swedish National Forest Inventory). This gives further strong support to the general notion that the northern Chiffchaff is tightly connected to spruce (when translated, the Swedish name for the Chiffchaff is "Spruce Warbler"). It is not clear whether it is the spruce as such that is important for Chiffchaffs or the generally denser structure of spruce forest as compared to the more open pine *Pinus* forests (Lars Edenius, *pers. comm.*). It is noteworthy that in the spruce-dominated area northwest of the triangular Chiffchaff distribution area (northernmost Jämtland and southernmost Lappland), there are comparatively few Chiffchaffs. We do not know if this area differs in habitat quality for Chiffchaffs (the forest may be less dense), but there are climatic differences between the areas.

The main distribution area of northern Chiffchaffs coincides with a relatively mild belt across central Sweden and coastal northern Sweden, where the first autumn frost comes on average between 1 and 15 September (Source: Swedish Meteorological and Hydrological Institute). But only a short distance north and inland of this belt, where there is plenty of spruce but no Chiffchaffs (Figure 1), the first night frost comes already 14 days earlier. Possibly this early frost is the explanation of the *abietinus* range limitation towards the north and west. For comparison, young Bluethroats *Luscinia s. svecica* (a small insectivorous bird) near Ammarnäs, a climatically harsher area north of the *abietinus* range (Figure 1), start leaving their breeding grounds al-

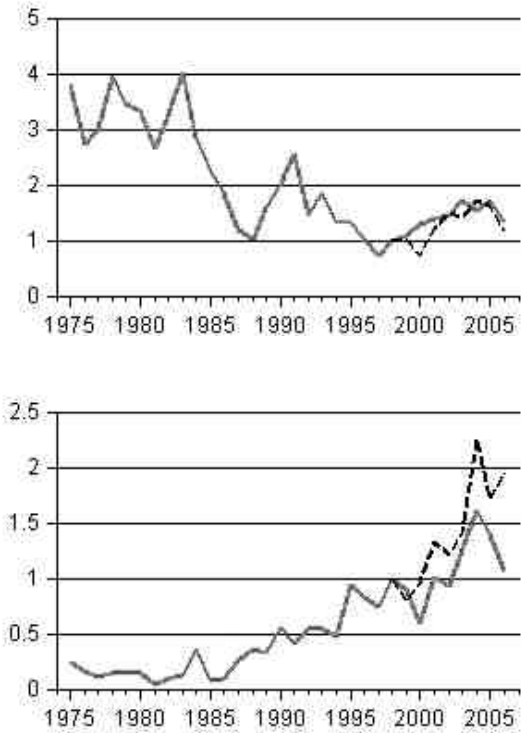

Figure 2. Population trends of Chiffchaffs in Sweden according to the free choice routes 1975–2006 (solid line) and the fixed routes 1998–2006 (stippled line). The graphs refer to Chiffchaffs north (upper) and south (lower) of 60°N, respectively. The population index is set to 1 for 1998.
Populationsutvecklingen hos gransångare i Sverige enligt punktrutterna 1975–2006 (heldragen linje) och standardrutterna 1998–2006 (streckad linje). De två figurerna visar gransångare norr (övre) respektive söder (undre) om 60°N. Populationsindex 1998 har satts till 1.

ready in early August. This coincides with the first frost in that area (1–15 August) and the birds leave with only small amounts of fuel (Lindström & Lind 2001). The same patterns hold for all the small insectivorous birds in the Ammarnäs area (Åke Lindström, pers. obs). When experimentally fed the Bluethroats are able to accumulate fat, suggesting that food shortage is a key factor surprisingly early in the season (Lindström et al. 1985, 1990, Hansson 1997). Whether northern Chiffchaffs, being smaller than Bluethroats, are so sensitive to a harsh climate that it explains their northern range limit remains to be investigated. The larger Bluethroat is a ground living bird feeding on invertebrates in the forest floor litter whereas the Chiffchaff is a leaf gleaner. Possibly, the effect of frost is stronger on insects and spiders in the trees than on invertebrates in the litter.

The most enigmatic question is rather why the northern subspecies has not expanded southwards. There is clearly plenty of spruce forest in south Sweden that at least superficially seems suitable for northern Chiffchaffs. Several Swedish species consists of a southern and a northern subspecies, for example Yellow Wagtail *Motacilla flava*, Sedge Warbler *Acrocephalus schoenobaenus*, Willow Warbler and Common Redpoll *Carduelis flammea*, where the two subspecies are assumed to have colonized Sweden from two different directions following the last glaciation (SOF 2002). The Yellow Wagtail and the Willow Warbler have closed the gap between the two subspecies creating hybrid zones, and the Sedge Warbler is probably about to do it (cf. the maps in Ekman 1922, p. 92, and Svensson et al. 1999, p. 391). As far as northern Chiffchaffs are concerned, Ekman (1922) wrote that it was impossible to understand why a bird that thrived in Poland and southern Russia would not do so in southern Sweden unless the southern limit of the range in Sweden was a result of its immigration history. Today we know that the *collybita* subspecies was well adapted to the conditions of southern Sweden as soon as it got a foothold, albeit not in the southern spruce forests.

Ph. c. collybita. The southern subspecies has its stronghold in Skåne and to some degree the coastal areas of southern and western Sweden. In contrast to the habitat selection of its northern conspecifics it seems to avoid the dense spruce forests of southern Sweden (Figure 2). This fits well with the notion that the southern Chiffchaffs strongly prefer deciduous forests (Svensson et al. 1999).

There is some other information about how the distribution of southern Chiffchaffs has changed since the first occurrence in southernmost Sweden in the 1970s. An ongoing repeat of the breeding bird atlas in Skåne (the southernmost province of Sweden) has revealed that the subspecies now occurs in high numbers over much of the province, while 20–30 years ago it was found mainly along the very coast and in much lower numbers (Martin Green, unpublished data). Over the same period in nearby Denmark, the subspecies went from covering half of the country to occupying almost every corner (Grell 1998). The expansion is a part of a process that has been going on south of Scandinavia for a long period of time (invasion of Schleswig-Holstein c. 1850 and southern Denmark at the end of the 19th century; review in Bauer et al. 2005). From this respect the colonization was expected. It is quite possible that the invasion of southern Sweden could have come long ago if only the first immigrants had happened to form a viable population. Ekman's (1922) "Skåne population" may have been an attempt that failed not because it did not find suitable habitats but simply due to stochastic mortality.

It is difficult to judge what the few and scattered observations in central south Sweden, outside the main distribution areas, represent (Figure 1). Most likely the migration of northern birds has passed when the censuses are carried out in late May and early June. The median passage date of northern Chiffchaffs at Ottenby Bird Observatory in southeasternmost Sweden is already around 1 May (Håkansson & Rhönnstad 1993). Therefore the birds observed during the censuses are most likely southern birds. However, given that none of the routes had Chiffchaffs in all the years the route was censused (all yearly averages were below one), the population in general must be small and not very stable. In line with this view SOF (2002) describes central south Sweden as almost devoid of breeding Chiffchaffs. Thus, although we have possibly had a slow spread northward and eastward in Sweden the last decades and a strong population increase (Figure 2), it is clear that the two populations have not yet met to any substantial degree. It is possible that the large coniferous forests of southern Sweden to this date have formed an expansion barrier.

Hansson et al. (2000) compared birds from Skåne and Central Sweden and found them not only to be morphologically different but also that males (in playback experiments) reacted differently to population-specific song. This implies that if and when they meet they may behave as two separate species.

Population trends

Both populations of Chiffchaffs in Sweden clearly have undergone pronounced changes in population size the last decades (Figure 2).

Ph. c. abietinus. The strong long-term decline of the Chiffchaff population in northern Sweden, Finland and further east, amounting to the very same 75% in both Sweden and Finland (Väisänen 2006), has yet to be explained. Equally unexplained are the remarkable trend shifts that occurred almost simultaneously in Sweden and Finland (1997–1998), when the declines turned into strong increases. Further support for such a trend shift comes from ringing figures at Stora Fjäderägg ringing station, a coastal site just east of the main breeding areas, where the trend in trapping figures in autumn closely match the breeding bird survey data (Lars Edenius, pers. comm.).

Olsson & Wiklund (1999) suggested that the decline in the 1980s and 1990s may at least in part have been due to the loss of older spruce forests in their area (Västerbotten), but also recognized that seemingly optimal and untouched habitats had lost their Chiffchaffs in this period. We compiled information about the temporal trend in the amount of thicker (older) spruce trees within the main breeding areas of the northern Chiffchaff (Figure 3, Source: Swedish National Forest Inventory). When looking at the total volume of larger spruce trees, being either 20, 25 or 30 cm or more in diameter, there is no overall loss of large trees coinciding with the population decline of the Chiffchaff in the period 1983–1997. However, this is only one of many factors influencing the breeding habitat quality of the Chiffchaff and therefore cannot be taken as evidence that the availability of large spruce trees is not important. There was indeed an increase in the volume of larger trees between the last two periods, coinciding with the Chiffchaff population recovery, but if there is a biological connection remains to be investigated. Another data set gives the total area of old forest (all tree species, but mainly spruce and pine) in the boreal parts of Sweden, that is, the northern two thirds of Sweden (Figure 4, Source: Swedish National Forest Inventory). Although this data set is less specifically applicable to Chiffchaffs (it includes a larger geographical area and all forest types), it is nevertheless interesting to see that a decade's decline in the total area of old forest from mid 1985 onwards turns into a significant increase from about 1993. This is just a few years before the shift in population trend of the northern Chiffchaff.

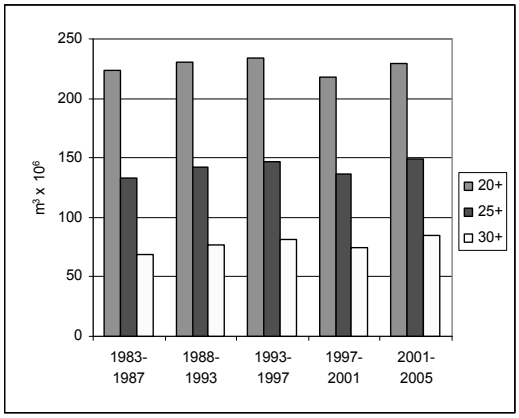

Figure 3. The volume of spruce trees (millions of m^3) in the area of Sweden where the northern Chiffchaff breeds (see Figure 1). The area includes Norrbotten and Västerbotten, Jämtland, Härjedalen, Ångermanland, Medelpad and Hälsingland. Values are five-year averages, for trees with 20, 25 and 30 cm diameter or more, respectively, starting at the time of the main population decline of Chiffchaffs (see Figure 1). Source: Swedish National Forest Inventory.
Volymen levande gran inom det område som är den nordliga gransångarens huvudområde, nämligen de kustnära delarna av Norrbotten och Västerbottens län, hela Jämtlands och Västernorrlands län, samt landskapet Hälsingland (Figur 1). Värdena är fem års medelvärden, för granar med 20, 25 respektive 30 cm diameter eller mer, från och med den tidpunkt när gransångarens minskning började. Källa: Riksskogstaxeringen.

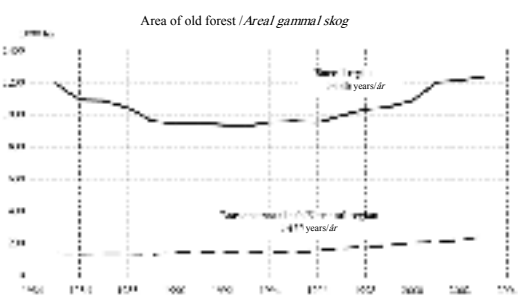

Figure 4. The area of old forest (more than 140 years, all tree species, millions of m^3) in boreal Sweden (approximately the northern half). Values are sliding five-year averages. It is noteworthy that there is a trend shift from decline to increase around 1993, a few years before the shift in population trend of the northern Chiffchaff. Source: Swedish National Forest Inventory.
Arealen gammal skog (>140 år, alla trädslag) i de boreala delarna av Sverige (Norrland, samt Dalarnas, Värmlands och Örebro län). Värdena är löpande fem års medelvärden. Notera att mängden gammal skog börjar öka i norra Sverige runt 1993, några år innan gransångarkurvan vänder uppåt. Källa:Riksskogstaxeringen.

Local habitat change, as expressed in the forest data above, cannot easily explain the population dynamics of *abietinus* Chiffchaffs and it is likely that also other factors are at play. The parallel trends in northern Sweden and Finland (cf. Väisänen 2006), and possibly in a still larger part of northeastern Europe (Lapshin 2000, Sokolov et al. 2000), hints at large scale factors being important. This could be a change in climate or of habitat quality along the migration routes or in the wintering grounds.

We know very little about the ecology of northern Chiffchaffs outside the breeding period. Actually, even the migration route and wintering grounds of northern Chiffchaffs have yet to be established. The ringing recovery maps of *abietinus* for Sweden (Fransson & Hall-Karlsson in press), Norway (Bakken et al. 2006), and Finland (Zink 1973) are suggestive but inconclusive. There are several recoveries hinting at an easterly component during autumn migration for *abietinus* in contrast to the more westerly component of migration in the southern *collybita* Chiffchaffs. Thus, there may be a migratory divide between the subspecies similar to the one found in the two Scandinavian subspecies of Willow Warblers *Phylloscopus trochilus* (Bensch et al. 1999). How far the birds migrate is also not really known. There are a few recoveries within and just south of the Sahara of birds that probably were *abietinus*. Since so little of the migration ecology is known we refrain from speculating in migration-related causes of population change in *abietinus* Chiffchaffs.

Ph. c. collybita. The numerical increase in *collybita* Chiffchaffs in southern Sweden has amounted to several hundred percent in just two to three decades. A recent local breeding bird census at Kullaberg in northwestern Skåne, the area where the first Chiffchaffs were found to breed (Dahlman 1974), showed that the numbers of Chiffchaffs had increased from 10 to 107 between 1974 and 2004 (Peterz & Rellmar 2007). In Denmark, also inhabited by *collybita* Chiffchaffs, the population increased with 6% per year from 1976 to 2004, a total increase of about 500% (Heldbjerg 2005). We know that this follows a long-term expansion from the southwest (Bauer et al. 2005), but the reasons behind this dramatic range expansion and increase in numbers of *collybita* Chiffchaffs are not known.

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Sammanfattning

Gransångaren *Phylloscopus collybita* företräds i Sverige som häckfågel av två raser. I norra Sverige finns *Ph. c. abietinus* som föredrar gammal och rik granskog med visst lövinslag. För denna ras rapporterades kraftiga minskningar mellan 1975 och 1998 i Västerbotten, Norrbotten och Finland. Möjligen var trenden liknande i Ryssland. I Finland ökade dock antalet igen efter 1998. I södra Sverige finns nominatrasen *Ph. c. collybita*, som främst förekommer i ren lövskog. Den sydliga gransångaren är en sentida invandrare i Sverige, med de första häckningarna rapporterade i början av 1970-talet. Rasen har ökat kraftigt i antal de senaste decennierna, enligt fångststatistik från våra sydligaste fågelstationer. Enligt den senaste nationella kartläggningen är det dock fortfarande en stor utbredningslucka mellan raserna (Sveriges Fåglar, 3:e uppl.).

Vi använder i denna uppsats data från det nationella miljöövervakningsprogrammet Svensk Fågeltaxering för att presentera de båda rasernas nuvarande utbredning i Sverige samt deras populationsutveckling 1975–2006. Vi har i analyserna ansett fåglar påträffade söder om 60°N vara *collybita* och de norr om 60°N vara *abietinus*. Data kommer från de ”fria punktrutterna” som pågått sedan 1975 samt från ”standardrutterna” som startade 1996.

En fri punktrutt består av 20 punkter som inventeraren valt själv. Vid varje punkt räknas alla fåglar som ses eller hörs under fem minuter. Rutten upprepas sedan en gång per år vid ungefär samma datum (i huvudsak mellan 10 maj och 20 juni) och tid på dygnet. Vid analysen användes för varje rutt summan av fåglarna observerade på de 20 punkterna. Antalet rutter utförda per år varierade mellan 13 och 71 i norr och mellan 61 och 241 i söder. Antalet år en rutt räknats varierade mellan 1 och 32. Totalt räknades 2656 nordliga och 1536 sydliga gransångare på punktrutterna. Dessa data användes enbart för att analysera trender.

Totalt finns 716 standardrutter i Sverige, utlagda systematiskt med 25 km lucka över landet (Figur 1). Varje rutt är 8 km lång, formad som en kvadrat. Alla fåglar som ses och hörs längs dessa 8 km räknas. För en del rutter utgår en del av sträckan på grund av vattenhinder mm. Målet är att en rutt skall inventeras en gång per år, från mitten av maj i södra Sverige till början av juli längst upp i nordligaste Sverige, men alla rutter har dock inte kunnat räknas varje år. Vem som inventerar en given rutt kan variera mellan åren. Standardruttsdata har använts både för trendanalys (data för åren 1998–2006) och

för att beskriva rasernas utbredning i Sverige (data för åren 1996–2006). Antalet utförda standardrutter ökade från 48 under 1996 till 411 under 2006.

Populationstrender analyserades med statistikprogrammet TRIM, där antalet fåglar år 1998 gavs index 1 både för punkt- och standardrutterna. Eftersom standardrutterna är systematiskt utlagda över Sverige och därmed kan anses vara representativa för de olika habitatens utbredning i landet använde vi det genomsnittliga antalet gransångare registrerade på en rutt som ett mått på tätheten i detta område (medelvärdet baserat på 1–11 år, beroende på hur ofta rutten gjorts). Värdet för enskilda rutter har i många fall ganska stor osäkerhet, men för större områden bör värdena vara representativa. På standardrutterna räknades totalt 1459 nordliga och 393 sydliga gransångare perioden 1996–2006, på vilka utbredningsdata beräknats. Trendanalysen grundades på 1404 nordliga och 387 sydliga fåglar för den något kortare perioden 1998–2006.

Gransångarens häckningsutbredning i Sverige är tydligt tvådelad (Figur 1). Norr om 60°N finns en tydlig koncentration av gransångare i Hälsingland, Medelpad, Jämtland och Ångermanland, med god förekomst även i närliggande delar av Dalarna, Västerbotten och Norrbotten. Upp till 15 gransångare registrerades i genomsnitt på rutter i området. Söder om 60°N sågs upp till 6 fåglar per rutt, med en markant tyngdpunkt på utbredningen i Skåne och till viss del Västkusten och i Blekinge. Resten av området söder om 60°N kännetecknas av ströfynd och genomsnittliga värden på färre än 1 fågel per rutt. Om vi antar att gransångare upptäcks i samma utsträckning på olika rutter runt om i landet bör under perioden 1996–2006 ungefär 88% av Sveriges gransångare ha varit nordliga *abietinus* och 12% sydliga *collybita*.

Den nordliga gransångaren minskade med i genomsnitt 3,6% per år perioden 1983–1997, med en total minskning på 75% (Figur 2). Den därpå följande ökningen 1997–2006 uppgick till 85%, men antalen 2006 är fortfarande långt under värdena runt 1980. En liknande sentida ökning noterades även på standardrutterna, med i genomsnitt 6,8% per år och sammanlagt 50% (Figur 2).

Den sydliga gransångaren ökade med ungefär 1400% över punktrutternas 32 år, en genomsnittlig årlig ökning med 9,7% (Figur 2). Ökningen startade dock inte markant förrän 1985, så ökningen har egentligen skett på bara drygt 20 år. De senaste 9 åren var ökningen ungefär 60%, fördelat på 6,3% per år. Över motsvarande period var ökningen ungefär 150% på standardrutterna, med i genomsnitt 11,9% per år.

Eftersom standardrutterna bildar ett ganska grovmaskigt nät över landet kan man från dessa inte dra slutsatser om lokala detaljer i rasernas förekomst, men över större områden bör de ge en rättvisande bild. I det stora hela bekräftas den utbredning som presenteras i Svensk Fågelatlas och Sveriges Fåglar. Dock kan spännande detaljskillnader urskiljas, främst kanske beroende på att det för första gången är möjligt att beskriva variationen i täthet över Sverige med en enhetlig metod.

Den nordliga gransångarens tätheter är i Värmland, södra Dalarna, västra Härjedalen, västra Jämtland, samt södra Lappland, lägre än vad som anges i Sveriges Fåglar. Huruvida denna nya bild är en effekt av ett krympande utbredningsområde eller på att mer jämförbara data finns tillgängliga är okänt. Rasens utbredning i främst Norrland sammanfaller till stor del med områden där granen är dominerande trädslag (Figur 1). Kanske är det något med granen som sådan som är viktigt. Det kan också vara att granen bildar tätare skogar än tallen och att det är denna skogsstruktur, oavsett trädslag, som gransångaren föredrar. Vidare återstår att förklara varför de grandominerande skogarna i norra Jämtland och västligaste Västerbotten håller så få gransångare. En möjlig förklaring är klimatet. I detta område kommer frosten på hösten 14 dagar tidigare än i rasens klimatmässigt mildare huvudutbredningsområde något längre söderut. Tättingar studerade i Ammarnäs, lite längre norrut i Lappland, har visat sig vara väderkänsliga och de har svårt att finna mat redan i början av augusti. Kanske missgynnas gransångaren speciellt mycket i områden där sensommaren blir kall tidigt. Varför den nordliga gransångaren inte koloniserat de stora granområdena längre söderut i Sverige är än mer svårbegripligt!

Den sydliga gransångaren har sitt huvudfäste i Skåne och sydligaste Sveriges kusttrakter. Det pågående atlasarbetet i Skåne visar att rasen nu förekommer i höga antal över hela landskapet, till skillnad från artens fåtaliga och kustnära fördelning för 30 år sedan. Under samma period i Danmark har arten expanderat på ett motsvarande sätt. De fåtaliga och till synes tillfälliga observationerna i övriga Sydsverige (Figur 1) rör visserligen med stor sannolikhet den sydliga rasen (de nordliga har då flyttat förbi), men arten verkar inte ha fått något riktigt fotfäste där ännu. För denna lövälskande fågel har möjligen Smålands granskogsområden varit en rejäl spridningsbarriär. De två raserna har med andra ord ännu inte överlappande utbredning i Sverige. Studier av morfologi och sångigenkänning hos de två raserna indikerar

att de kan komma att bete sig som två skilda arter om de en gång möts.

Både de nordliga och sydliga gransångarnas populationssvängningar återstår att förklara. Enligt skogsstatistiken verkar ingen dramatisk förändring i volymen kraftigare (äldre) gran ha inträffat inom den nordliga rasens utbredningsområde i Sverige de senaste decennierna (Figur 3), men skogens kvalitet som häckningsbiotop speglas inte nödvändigtvis så väl av denna variabel. Däremot sammanfaller förändringen av ytan gammal skog (alla trädslag, skog äldre än 140 år) i norra Sverige relativt väl med gransångarens populationsutveckling, med först en minskning och sedan en ökning från mitten av 1990-talet (Figur 4). Om detta samband bara är en tillfällighet återstår att undersöka. De parallella populationssvängningarna i norra Sverige och Finland indikerar att även mer storskaliga faktorer kan ha betydelse, såsom förändring i klimat eller förändringar i habitatkvalitet längs flyttningsvägar och i övervintringsområden. Ringåterfynd indikerar att de nordliga gransångarna flyttar mer östligt och längre (strax söder om Sahara?) än de sydliga. Dock är flyttningsvägar, övervintringsområden och vinterekologi överlag så dåligt kända att en noggrannare analys inte låter sig göras. Någon bra förklaring till den sydliga gransångarens enorma framgång finns inte heller, men ökningen har föregåtts av en långvarig och kraftig spridning norrut i Europa över de senaste 150 åren.