The ability of forest reserves to maintain original fauna – why has the Chiffchaff (*Phylloscopus collybita abietinus*) disappeared from eastern central Finland?

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We studied the occurrence of Chiffchaff Phylloscopus collybita at the Finnish and Russian border at ca. 65° N. This species shows an interesting distribution in the region, being virtually absent from the Finnish side (Kainuu) but being a common breeder on the Russian side (Viena). However, the species has been equally numerous on both sides of the border. In our study area, the landscape is structurally different on opposite sides of the border: in Russia, there is a continuous "green belt" of old-growth forests, whereas in Finland old-growth forests are embedded in a matrix of managed forests. However, fragmentation may not solely explain the difference in Chiffchaff abundance, because bird species even more strictly dependent on old-growth forests are either nearly equally or were even more abundant in Finland than in Russia. We suggest that the decline of the Finnish Chiffchaff population is due to multiple reasons, including the northern location. Fragmentation has probably provided the final push resulting in a crash in the Kainuu Chiffchaff population. This study underlines the need for detailed species-specific autecological knowledge in predicting fragmentation effects. Furthermore, a change in subspecific composition of Finnish and Swedish Chiffchaffs is apparently taking place. The ecologically different yet morphologically similar Ph. c. collybita may replace the native Ph. c. abietinus.

1. Introduction

Habitat loss, degradation and fragmentation are considered to impact 86% of the world's threatened birds (Baillie *et al.* 2004), forest destruction being the main culprit (Saunders *et al.* 1991, Fahrig & Merriam 1994). It is important to distinguish between the habitat-loss and fragmentation effects, because management actions to diminish their negative effects may differ (Fahrig 1997). Fragmentation can enhance the effects of habitat loss and cause population declines at the landscape scale greater than expected on the basis of the area remaining (Andrén 1994, Bender *et al.* 1998). This cumulative impact may result in population extinctions even if suitable habitat still remains. The



effect of habitat loss is easy to confirm, but to demonstrate fragmentation impacts appears more complicated (Fahrig 2004). Natural processes are often slow and the effects may not take place immediately after the fragmentation event. The socalled extinction debt (Hanski & Ovaskainen 2002) may lead to an underestimation of the need for protected areas. Our understanding of fragmentation effects is clearly limited (e.g., Lampila *et al.* 2005).

Global climate change is another process threatening populations. Long-distance migratory birds may be particularly vulnerable to climate change because they may not be able to adjust their migration and breeding phenology to the changing environmental optimums as effectively as residents and short-distance migrants (Both & Visser 2001, Strode 2003, Newton 2004). Habitat loss and climate may also interact (Warren *et al.* 2001, Root *et al.* 2003, Thomas *et al.* 2004). Further, effects of anthropogenic changes on populations are often non-linear, which makes them difficult to predict (Andrén 1994, Mönkkönen & Reunanen 1999).

The border between Finland and Russia provides an excellent opportunity to study the effects of forest fragmentation (Fig. 1, and an electronic Appendix on the journal web page; see also Rajasärkkä 2004). Topography and edaphic conditions of the forested landscape are similar on both sides of the border. On the Finnish side, however, bogs and mires cover a larger proportion of the land area, producing higher levels of natural subdivision. Forests and well-wooded bogs (suitable for forests birds) cover ca. 75% of the land area on the Finnish and ca. 80% on the Russian side. In Finland, industrial forest management has strongly affected the landscape structure over most of the 20th century. At present, over onethird of the old-growth forests are restricted to the nature reserves, which form ca. 3.6% of forest land in Kainuu and northernmost Karelia (Heikkinen *et al.* 2000, Virkkala *et al.* 2000). On the Russian side of the border, a tens-of-km wide "green belt" of nearly intact forests dominates the landscape.

The Chiffchaff *Phylloscopus collybita* is one of the most common forest birds in Europe. Two subspecies of Chiffchaff occur in northern Europe: the western, nominate *Ph. c. collybita*, and the northern and north-eastern *Ph. c. abietinus* (Svensson 1992). The latter has longer and more pointed-wings compared with *collybita*, which is probably an adaptation to longer migration distance (Mönkkönen 1995, Hansson *et al.* 2000). *Ph. c. collybita* inhabits broad-leaf forests and even shrublands, whereas *abietinus* mainly occurs in Norway spruce *Picea abies* dominated, coniferous forests (Glutz von Blotzheim 1991, Cramp 1992). However, there are no direct observations of the habitat use of *collybita* and *abietinus* from

their contact zone, and the image is blurred by the difficulty of subspecies identification.

These subspecies exhibit different migration patterns. Ph. c. collybita is mainly a short- and medium-distance migrant that overwinters mainly in the Mediterranean region, where it outnumbers abietinus all the way to Egypt (Cramp 1992). Part of the collybita population migrates to sub-Saharan areas north of the tropical rainforest biome. Ph. c. abietinus is a long-distance migrant that occurs over a wide area from Africa to northern India. Population trends of these subspecies have been different in Fennoscandia during the past few decades: abietinus has declined fairly rapidly and steeply in Finland and Northern Sweden, whereas collybita has strongly increased in numbers e.g. in Southern Sweden (Lindström et al. 2007). On the basis of the pan-European monitoring scheme, the overall population status of the Chiffchaff is considered "secure" (BirdLife International 2004: 237). No major population changes have been reported in abietinus outside Finland and Northern Sweden

The Chiffchaff is considered vulnerable in Finland (Rassi et al. 2001) due to a recent steep, longterm population decline which, however, seems to have stabilized since the late 1990s (Väisänen 2006). There are many possible explanations for this decline. For example, the species might have been out-competed by the Willow Warbler Phylloscopus trochilus and by the Goldcrest Regulus regulus (Tiainen et al. 1983). However, experimental evidence for such competition is difficult to obtain, and these species also have different lifehistory characteristics. The Willow Warbler is a generalist species and has benefited from intensive forestry. The Goldcrest, on the other hand, has not shown long-term population changes during the past few decades. Another suggested cause for the decline is forestry that must have been detrimental to the Chiffchaff (Väisänen et al. 1998). During the last 50 years, the area of mature and old-growth spruce forests has indeed greatly decreased and the remaining forests fragmented. Yet another plausible explanation is that the main threat for the Chiffchaff might be habitat change in the wintering areas or along migration routes (Rassi et al. 2001).

The purpose of the present study was to gain understanding on factors that have caused the decline of the boreal Chiffchaff populations. Comprehensive censuses of breeding birds have been conducted in old-growth forests in eastern Finland (Kainuu) and in adjacent Russia (Viena) during 1943-2002. With these data we assessed the population status of the Chiffchaff in two adjacent vet contrastingly-fragmented landscapes. We also compared the Chiffchaff abundance with the abundances of two putative competitors - Willow Warbler and Goldcrest - and other birds considered susceptible to negative effects of forest fragmentation, i.e., resident species associated with mature forests (Niemi et al. 1998). If competition is involved, a negative association between Chiffchaff density and the densities of competitors should be detected.

Censuses were conducted in habitats favoured by Chiffchaffs; as a result, we did not expect any effect of habitat loss or degradation. If there is a habitat fragmentation effect, however, Chiffchaffs should be less numerous in the heavily-fragmented Kainuu than in the continuous forests of Viena. A comparison with other old-forest associated species provides further information on fragmentation effects. Consistently higher densities in Viena than in Kainuu would support the role of fragmentation. By contrast, if long-term Chiffchaff population decline is a consequence of factors operating during migration and overwintering, the Chiffchaff abundance should be relatively similar in Kainuu and in Viena, and the longterm population trends should be parallel.

We also analyzed ringing-recovery data of Finnish and Swedish Chiffchaffs in order to examine whether autumn migration directions have remained constant. If an increasingly larger proportion of Chiffchaffs are of south-western origin (nominate subspecies), a change towards the south-west in autumn migration directions should be found. Such a finding would suggest expansion of the nominate subspecies, which in turn could explain the "apparent" stabilization of the Chiffchaff populations since the early 1990s.

2. Material and methods

We conducted line-transect counts in spruce-dominated old-growth or mature forests on both sides of the border between Finland and Russia at ca. 64–65° N during June 2002, for a total transect length of ca. 700 km. This effort involved censuses in 44 separate old-growth forest reserves in Kainuu, Finland, and 37 transects of a total length of ca. 200 km in Viena, Russia (Fig. 1). The transects were placed in forest reserves on the Finnish side and in similar (both protected and non-protected) forest areas on the Russian side. Censuses in 2002 were first conducted in the southernmost Finnish areas. The Russian transects were censused next, followed by the northernmost sites in Finland.

We also used older transect-count data from the same area, collected in 1940s and during 1983–2003, resulting in 16-years data from Finland and 5-years data from Russia (Fig. 2). These data were collected in a less systematic way than the 2002 data but were interpreted accordingly. All these censuses were done in spruce-dominated old-growth or mature forests and were situated in forest reserves on the Finnish side of the border and in similar, continuous old-growth forests on the Russian side.

All the above-listed data were obtained from censuses conducted using a standard line-transect method (Järvinen & Väisänen 1976). In these censuses, all bird observations (by sight or sound) are recorded on a 50-m wide main belt (25 m on either side of the observer) and on a supplementary belt (>25 m on either side of the observer). These together form the so-called survey belt, which records the total observed bird individuals during the census. Observations are transformed into densities by dividing the number of the survey-belt observations by the length of the census line and multiplying with a species-specific correction coefficient, in order to correct variation in detectability (Järvinen & Väisänen 1983).

These are calculated from large line-transect data from the ratio of main and supplementary belt observations: the higher the detectability of a species, the larger the proportion of observations that come from the supplementary belt. We used coefficients that were obtained from line-transect counts done in Finnish nature conservation areas [ca. 14,000 km in total; coefficients in Rajasärkkä (2004: 116–118)].

Data from the early 1940s were taken from Lehtonen (1946). Note that these data originate from both sides of the present Finnish–Russian



Fig. 2. Total length of transects in km on each census year. Star indicates the 1940s censuses.

border. Unfortunately, Lehtonen (1946) did not provide exact transect lengths for each country, although he stated that "the lengths of the census lines are almost similar on both sides of the border". The method used by Lehtonen (1946) differed slightly from Järvinen and Väisänen (1976): he applied a 60-m wide main belt and ignored birds >200 m away. For this reason, we used only the main belt data from Lehtonen's data. Furthermore, Järvinen and Väisänen (1978) concluded that the bird numbers reported by Lehtonen (1946) may have been low because his data-collection season extended into early July (when birds sing less actively), and the fact that during the census work he wrote detailed descriptions of forest structure.

We tested the similarity in the numbers of survey-belt observations between Kainuu and Viena for 2002; for other years, we were unable to control for the annual (random) variation in bird populations and testing was therefore not conducted. Differences in densities were tested using chisquare tests, with transect length to calculate expected values.

Recovery compass directions of Chiffchaffs ringed in Finland and in Sweden were explored using a general linear model (GLM), where the recovery year was contrasted against the autumn migration direction measured in degrees (0–360°, 0° = north, 90° = east, 180° = south, etc.). In order to be included in the analysis, a given recovery had to be made either during the autumn migration or on the wintering grounds and at least 50 km from the ringing location. This yielded n = 20 for Finnish and n = 54 for Swedish ringing data. The earliest



recoveries were from 1959 both in Finland and in Sweden, and the most recent ones were from 2004. Most of the birds were ringed as adults outside the breeding season; hence, data probably also includes individuals born in regions other than the ringing location.

4. Results

4.1. Line-transect censuses

In 2002, we found 51 Chiffchaff territories (i.e., singing males, equivalent of ca. 0.6 pairs/km²) in Viena, Russia, and none on the Finnish side (Kainuu; $\chi^2 = 136$, p < 0.001). Also the older census data (Fig. 3) from the same area showed a corroborating pattern: the species was virtually absent from Kainuu since the 1990s, whereas in Viena the

species remained fairly numerous throughout the years. Still, the present densities were fairly low even in Russia as compared with data from the 1940s, which may indicate a long-term decline over the whole study region, especially when considering the likely underestimation of densities by Lehtonen (1946; see Material and methods). The Chiffchaff, however, appeared to be the only species showing a consistent decline on the Finnish side, with much higher densities in Russia than in Finland. The Willow Tit Parus montanus also declined from the 1940s to the 1990s, but increased since then in both Kainuu and Viena. Even oldgrowth forest specialists did not show consistent patterns: the Siberian Jay Perisoreus infaustus increased and even had higher average densities on the Finnish side (for 2002, $\chi^2 = 8.09$, p = 0.004) and the densities of the Three-toed Woodpecker Picoides tridactylus fluctuated but showed little Densities of the putative competitors – the Willow Warbler and the Goldcrest – did not show consistent increases that would have corresponded with Chiffchaff decrease (Fig. 3). Both species fluctuated considerably from year to year, probably resulting from varying conditions during migration and overwintering (Väisänen *et al.* 1998). In 2002, the densities of Willow Warbler and Goldcrest were over two times higher in Kainuu than in Viena ($\chi^2 = 185.82$, p < 0.001 and $\chi^2 = 10.79$, p = 0.001, respectively), but decreased on both sides of the border between the 1990s and 2002.

4.2. Ringing recoveries

Winter recoveries of Chiffchaffs, ringed in Finland, spread over a wide area. Many old recoveries were from the southeast, e.g., Uganda, Saudi-Arabia, Iraq and Iran. However, many of the more recent recoveries were from different areas: Finnish Chiffchaffs were captured, for example, in January in France and in November in the Netherlands. GLM for the Finnish and Swedish ringing data indicated a consistent shift in migration directions of Finnish and Swedish Chiffchaffs from southeast towards southwest (year: F = 7.988, p = 0.006; country: F = 1.121, p = 0.293; country*year: F =1.112, p = 0.295; Fig. 4).

5. Discussion

5.1. Chiffchaff and forest fragmentation

We found that the Chiffchaff were much more numerous on the Russian side of the border and had disappeared from Kainuu. This result suggests Chiffchaffs may have disappeared from the Finnish side of the border because of forest fragmentation, which may have led to increased (nest) predation, disturbed dispersal and/or decreased food resources. The Chiffchaff favours old-growth spruce-dominated forests and avoids edges (Tiainen *et al.* 1983). If fragmentation was the main factor, however, other species with large area requirements should also have been declining, but



Fig. 4. Changes in the recovery compass directions of Chiffchaffs ringed in Finland (open circles) and in Sweden (solid dots). Migration compass directions on the vertical axis are given in degrees (0–360); the horizontal axis shows years.

we found no evidence for this. On the contrary, area-sensitive species, such as the Three-toed Woodpecker or Siberian Jay, were either more abundant in Finland than in Russia or showed increasing temporal trends (Fig 3). We suggest that fragmentation effects are involved in the Chiffchaff population decline, but the difference in abundance between Kainuu (Finland) and Viena (Russia) is simply too large for habitat fragmentation to solely explain it.

5.2. Natural habitat subdivision

We use the term natural subdivision to describe habitat patches that are naturally small and isolated, i.e., they form a minority of landscape elements in a landscape dominated by other habitat types. Although natural subdivision alone may not be able to cause Chiffchaff declines, it may play a significant role in determining Chiffchaff distribution at and adjacent to the Finnish–Russian border. On the Finnish side, open peatlands cover a larger proportion of the land area than on the Russian side (see electronic Appendix), apparently making forests on the Finnish side less favourable for Chiffchaffs, as the *abietinus* subspecies avoids edges during the breeding season (Tiainen *et al.* 1983). This structural difference may be significant because anthropogenic fragmentation may have stronger effect on species if the favoured habitat is already naturally subdivided.

5.3. The role of interspecific competition

In our 2002 censuses, we discovered nearly twice as high densities of the putative competitors, the Willow Warbler and Goldcrest, in Kainuu as compared to Viena. Long-term national trends suggest that the Willow Warbler has benefited from modern forestry (e.g., Helle 1985, Virkkala 1987) which has increased early-successional habitats. Consequently, Willow Warbler has increased in Finland between the 1950s and the 1990s (Väisänen et al. 1998). Individuals of the increased Willow Warbler populations might have penetrated into the fragmented coniferous habitats, thus potentially increasing competition pressure on Chiffchaff. Finnish Goldcrest populations, on the other hand, have shown marked annual fluctuations with no consistent increase or decrease. In our study region, long-term temporal changes in the abundance of these two species have not been opposite to the temporal trends in Chiffchaff numbers. For example, Chiffchaff densities had not increased between the 1990s and 2002, even though Willow Warbler and Goldcrest had dramatically decreased on both sides of the border at the same period. Hence competition or its avoidance may not be the main cause for the lack of *abietinus* in eastern Finland, nor a good explanation for its declining population size.

5.4. Interactions of different factors

No single factor seems to be strong enough to alone explain the recent disappearance of Chiffchaffs from central eastern Finland. Apparently several independent factors simultaneously and negatively affect the Chiffchaff population. Suboptimal Chiffchaff habitats have been more prevalent in Kainuu than in Viena already in mid-1900s, although the difference in densities has not always been considerable. Since then, the population of *abietinus* Chiffchaffs started to decline, and changes in the wintering and migration areas may have been involved. Chiffchaff suffers from dry years in the Sahel zone, as do many other Eurasian-Afrotropical migrant passerines (Peach et al. 1998, Newton 2004). The longer-distance migrant abietinus may also have suffered more from climate change than the nominate *collybita*, partly explaining the different population trends of the two subspecies (although different habitat requirements probably are the main cause). These negative impacts, together with fragmentation and possibly fragmentation-induced competition, may have led to the dramatic differences in Chiffchaff abundance between Kainuu and Viena. The fact that chiffchaff is more abundant in the southern parts of Kainuu (see Introduction) supports our hypotheses, although we cannot exclude other explanations.

It is also important to note that Chiffchaff populations in our study region are at the northern edge of the species distribution. Populations at the extremes of a species' range are more sensitive to environmental changes and more extinction-prone than are populations closer to the distribution core (Channell & Lomolino 2000). Human-induced habitat fragmentation may have provided the final push resulting in a crash in the Kainuu Chiffchaff population.

If the list of the possible causes behind the Chiffchaff disappearance in central eastern Finland appears correct, this may have important implications for conservation biology. Predicting fragmentation effects can be difficult in circumstances when animal populations are under considerable environmental stress, and this would require detailed autecological information. Gathering such information often appears problematic and in many cases impossible. However, insufficient species-specific autecological knowledge may lead to serious underestimations of conservation efforts needed for species protection.

The analysis of ringing recoveries indicated that the migration direction of Finnish and Swedish Chiffchaffs has shifted from south and southeast in the 1960s and the 1970s to more southwesterly direction in 1980–2000. This finding suggests that the subspecific composition of Chiffchaff populations may have changed during the past decades. The southeast-migrating *abietinus* may be partly being replaced by the southwest-migrating populations, possibly with *collybita* influence. For Chiffchaffs, therefore, it might be reasonable to include only *abietinus* into the Finnish red list. The probable future increase in the invading nominate subspecies may result in a removal of Chiffchaff from the red list unless the subspecific status is not acknowledged. Due to the difficulties in subspecific recognition, we might lose an original subspecies from the Finnish fauna without even noticing it.

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Suojelualueiden kyky säilyttää alkuperäislajistoa – miksi tiltaltti (*Phylloscopus collybita abietinus*) on kadonnut itäisestä Keski-Suomesta?

Tutkimme tiltaltin (*Phylloscopus collybita*) esiintymistä Suomen ja Venäjän rajalla Kainuun korkeudella (n. 65° N). Lajin esiintymiskuva alueella on mielenkiintoinen: Suomen puolelta tiltaltit puuttuvat lähes täysin, Venäjän puolella laji on melko yleinen. Ilmeisesti se on kuitenkin lähimenneisyydessä ollut melko yleinen molemmin puolin rajaa. Tutkimusalueen Venäjän puolella maisema on lähes koskematon vanhojen metsien "vihreä vyö", Suomen puolella puolestaan vanhat metsät rajoittuvat suojelualueisiin, muun osan metsistä ollessa lähinnä metsätalouskäytössä.

Kuitenkaan metsän pirstoutuminen ei yksinään riitä selittämään havaittua ilmiötä, sillä yhdelläkään muulla vanhan metsän lajilla ei havaittu vastaavaa säännönmukaisuutta. Ilmeisesti syitä tiltaltin taantumiseen on monia, ja pirstoutuminen Suomen puolella on ollut eräänlainen "viimeinen pisara". Myös tutkimusalueen pohjoisella sijainnilla saattaa olla merkitystä. Tämä on yksi osoitus siitä, kuinka pirstoutumisen vaikutuksia voi olla vaikea ennustaa. Lisäksi havaittiin, että Suomen ja Ruotsin tiltalttikantojen alalajikoostumus saattaa olla vaihtumassa. Kenties ekologisesti erilainen mutta morfologisesti lähes identtinen *Ph. c. collybita* korvaa *Ph. c. abietinuksen* lähitulevaisuudessa.

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Electronic Appendix. LANDSAT satellite image of the study area. Dark green areas are spruce-dominated old-growth forests and paler green areas are younger forests. Blue-green areas are peatlands; black areas are lakes and ponds, and reddish areas are clear-cuts or other open habitats. Note the contrast in land-scape structure between the Finnish (Kainuu, left) and Russian (Viena, right) sides of the border (marked with a red line).

