

LEAF WARBLERS (*Phylloscopus* spp.)
AS A MODEL GROUP IN MIGRATION ECOLOGY STUDIES

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ABSTRACT

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The aim of this paper is to review information on systematic position, distribution ranges, habitat requirements, morphology, and ecology of the leaf warblers (*Phylloscopus* spp.). Closely related species of this group present different migration strategies. Exhibiting many inter-specific similarities in morphology and ecological requirements, leaf warblers reveal high intra-specific variability. The morphological differentiation of individual species, subspecies, populations, and age-sex groups, affords considerable possibilities for migration studies, especially those concerning the basis of migration strategy. Leaf warblers make a group of model species, being a good subject for ecological studies. The knowledge of their migration strategies may be a good reference point for understanding a general pattern of the migration of European passerines.

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Leaf warblers (from the genus *Phylloscopus* Boie, 1826) belong to a large family of the Old World warblers (*Sylviidae*), sub-order songbirds (*Oscines*), order passerines (*Passeriformes*). It is a group of small birds. Length of their body varies from 9 to 13 cm, and mean body weight does not exceed 15 g. The genus *Phylloscopus* comprises 56 species (Dickinson 2003). Most of them are polytypical species forming several subspecies. They occur in Eurasia and Africa, and one species – the Arctic Warbler (*P. borealis*) – extends its range to the western part of Alaska. South-eastern Asia is the centre of the leaf warblers' occurrence, with the highest species diversity. In Western Palearctic 18-20 species have been reported and among them the most widely distributed are: the Chiffchaff (*P. collybita*), Willow Warbler (*P. trochilus*) and Wood Warbler (*P. sibilatrix*) (Glutz von Boltzheim and Bauer 1991, Cramp 1992, Snow and Perrins 1998).

SUBSPECIES DIFFERENTIATION

Individual species of the leaf warblers occurring in Palearctic are characterized by a different degree of intra-specific variation. The Wood Warbler is a monotypic species (Svensson 1992, Dickinson 2003), while the Willow Warbler is a polytypic species, including three distinct subspecies: the nominative subspecies *P. t. trochilus*, and also *P. t. acredula* and *P. t. yakutensis* (Svensson 1992, Dickinson 2003).

In the case of the Chiffchaff, the intra-specific differentiation is far more complex. Recently, the application of molecular techniques allowed to distinguish several forms within the 'Chiffchaff' *P. collybita sensu lato* species complex, and to consider them as separate valid species (Helbig *et al.* 1996, Salomon *et al.* 1997, Clement *et al.* 1998). This mainly applies to forms occurring in relatively small and isolated areas, distant from the main range, such as oceanic islands and mountain ranges. Therefore, the following species have been distinguished: the Canary Islands Chiffchaff (*P. canariensis*), with the nominative subspecies *P. c. canariensis* and the probably already extinct subspecies *P. c. exsul* – both occurring in the Canary Islands; the Mountain Chiffchaff (*P. sindianus*), with the nominative subspecies *P. s. sindianus* and the subspecies *P. s. lorenzii* – Caucasus Chiffchaff – occurring in the Caucasus and mountains of Central Asia. Also the Iberian Chiffchaff (*P. brehmii*) – occurring in the north-western part of Africa, the Iberian Peninsula, and south-western France – is considered as a separate species.

While within the 'Chiffchaff' *P. collybita sensu stricto* species the following subspecies have been distinguished: *P. c. collybita*, *P. c. abietinus*, *P. c. tristis*, *P. c. brevirostris*, *P. c. caucasicus*, and *P. c. menzbierii*. The latter three, occurring in the Middle East (Turkey, Iran, and the Caucasus), have limited natural ranges and are relatively well distinguished and geographically isolated. The taxonomic status of the *tristis* form – Siberian Chiffchaff – is unclear. Presently it is accepted as a subspecies, but probably future investigations will raise its rank to a valid species (Clement *et al.* 1998, Dean and Svensson 2005). Therefore, within a group of the three closely related leaf warblers there exists a gradient of the intra-specific differentiation.

RANGES OF SPECIES AND SUBSPECIES

The Wood Warbler is a species widely distributed in Western Palearctic (Cramp 1992, Wesolowski and Tiainen 1997). Its breeding grounds spread from the Pyrenees and British Isles to the Ural Mountains and the White Sea coasts, while its winter quarters are located in Africa, in the belt of forests and savannah south of the Sahara.

The Willow Warbler is one of the most numerous breeding species, widely distributed in Western Palearctic (Hustings and Foppen 1997). Breeding grounds of the subspecies *P. t. trochilus* spread from the British Isles and Western Europe to the southern part of Scandinavia and Central Europe. Winter quarters of this subspecies are located in West Africa. The subspecies *P. t. acredula* nests in the area spreading from the northern part of Scandinavia, through Central and Eastern Europe, to Western

Siberia. Its wintering grounds are located in eastern, central, and southern parts of Africa. The subspecies *P. t. yakutensis* nests in northern and north-eastern parts of Siberia, and winters in eastern and southern parts of Africa. In Europe, this form occurs exceptionally (Cramp 1992).

Range limits of *P. t. trochilus* and *P. t. acredula* run through Poland. Most of the country is inhabited by *P. t. trochilus*, gradually passing to the northeast into the subspecies *P. t. acredula*, which in pure form occurs in the Masurian Lakeland and most likely in Podlasie (Tomiałojć and Stawarczyk 2003).

Also the Chiffchaff is a widely distributed species in Palearctic. Breeding grounds of the subspecies *P. c. collybita* spread from the Iberian Peninsula to Central Europe reaching Poland and Ukraine in the east, and southern Sweden in the north (Tiainen and Wesolowski 1997). Winter quarters of this subspecies are located in Western Europe, from the British Isles, France, and the Iberian Peninsula to the western part of the Mediterranean Sea basin, and also in West Africa. The subspecies *P. c. abietinus* nests in Northern and Eastern Europe, from the northern part of Fennoscandia and Central Europe to the Ural Mountains (Tiainen and Wesolowski 1997, Hansson *et al.* 2000). Wintering grounds of this subspecies are situated in the eastern part of the Mediterranean Sea basin as well as in the Middle East and north-eastern and eastern parts of Africa (Isenmann 1984). The subspecies *P. c. tristis* – Siberian Chiffchaff – occurs in Asia, east of the Yenisei, bordering through the questioned form *fulvescens*, with the East European subspecies *P. c. abietinus* in the Ural Mountains (Cramp 1992, Dean and Svensson 2005). Wintering grounds of the Siberian Chiffchaff are situated in south-western and central parts of Asia (Dickinson 2003), and its migratory routes run outside Europe. Birds with characteristics of the *tristis* form reach Europe in a low number, however regularly, in late autumn.

Range limits of *P. c. collybita* and *P. c. abietinus* run through Poland. *P. c. abietinus* occurs in the eastern part of the country, gradually passing to the west into the form *P. c. collybita* (Tomiałojć and Stawarczyk 2003). Birds with characteristics of the form *P. c. tristis* were recorded in Poland only 25 times (Avifaunistic Commission 2006). Most of them were captured close to the Baltic Sea coast, while in the interior of the country this subspecies occurs exceptionally (Ciach 2006).

Western Palearctic is the main area of the occurrence of *P. c. collybita* and *P. c. abietinus* as well as *P. t. trochilus* and *P. t. acredula*. The pattern of range boundaries for the individual subspecies makes zoogeographic or population studies in this region, especially in Central Europe, very challenging. Due to the intra-specific variation and different ranges of individual taxonomic units, different subspecies combinations occur in different areas. Thus, there are situations that a given subspecies of one species occurs in some areas sympatrically with different subspecies of another species.

HABITATS, FORAGING AND STATUS WITHIN BIRDS COMMUNITY

The leaf warblers are characterized by a great plasticity regarding the choice of nesting places, and therefore they inhabit various kinds of forests and wooded areas. However, despite a wide habitat spectrum of all the species, each one of them has dis-

tinct preferences with regard to the habitat. The Wood Warbler is a species inhabiting the interior of mature broad-leaved and mixed forests, and sporadically coniferous forests (Wesołowski and Tiainen 1997). The Chiffchaff prefers mixed and coniferous forests, occurring most numerous in open riparian and alder swamp forests as well as coniferous stands (Tiainen and Wesołowski 1997, Tomiałojć and Stawarczyk 2003). The Willow Warbler prefers tree plantations and early succession forest stages, occurring most numerous in shrubby areas of moor meadows, osierbeds, and young forest stands (Hustings and Foppen 1997, Tomiałojć and Stawarczyk 2003). The wide environmental spectrum of the leaf warblers makes this group of birds interesting from the point of view of investigations concerning selection and use of habitats.

On breeding grounds, the Willow Warbler and Chiffchaff inhabit similar types of habitats using the same feeding niches, but the former species is more plastic in selection of feeding places (Sæther 1983a, Korner-Nievergelt and Leisler 2004). Both species use the same foraging techniques, although the Willow Warbler is again more plastic in this respect (Forstmeier and Kessler 2001). Each of these two species has its own preferences in selection of habitats in which they achieve the highest population density (Tiainen *et al.* 1983). However, research carried out in Scandinavia showed that breeding territories of both species situated in homogenous environment spatially exchange with each other (Sæther 1983b).

In Poland, and in almost entire Europe, the leaf warblers belong to common breeding species (Glutz von Boltzheim and Bauer 1991, Tomiałojć and Stawarczyk 2003). Their breeding biology and ecology are relatively well known (Tiainen 1983, Wesołowski 1985, Piotrowska and Wesołowski 1989, Rodrigues and Crick 1997, Lapshin 2000, Payevsky 2000, Wesołowski *et al.* 2009). Within the communities of birds breeding in forests and wooded areas, leaf warblers, depending on the type of habitat and its succession stage, most often are dominant or subdominant species, and among medium- and long-distance migrants they frequently form the most numerous group (Głowaciński 1975, 1981; Tomiałojć *et al.* 1984; Wesołowski *et al.* 2002). In Central Europe, during the migration period, the Chiffchaff and Willow Warbler are among the species abundantly occurring in all kinds of forest communities as well as in wooded and shrubby areas (Busse and Marova 1993, Tomiałojć and Stawarczyk 2003). Despite this, their habitat preferences during the non-breeding period are not well known.

MIGRATION AND WINTERING OF EUROPEAN POPULATIONS OF LEAF WARBLERS

In spite of the fact that leaf warblers are common and numerous breeding birds in Western Palearctic, their migration strategies are relatively little known. Leaf warblers belong to birds migrating mainly at night and supplementing their energetic reserves in the daytime. Despite considerable morphological and ecological similarity these birds show a surprisingly strong differentiation of migration strategies.

The Willow Warbler and Wood Warbler are regular long-distance migrants. The entire populations of both species undertake migration towards their wintering

grounds in the tropical and sub-tropical zones. The migration of the Willow Warbler through Europe takes place mainly in April and September, and in most cases the migrating birds form a broad front. The Wood Warbler mainly migrates along the West-European flyway (Zink 1973), but its migration strategy is surprisingly little known.

On the other hand, the diversified migration strategy of the Chiffchaff is an example of a mixed migration system (Cramp 1992). Populations from Northern and Eastern Europe and Siberia are regular migrants, and all individuals undertake migration. The distances between breeding and wintering grounds of the North- and East-European and Siberian populations indicate that this species is a typical long-distance migrant. The West-European populations are partial migrants. Probably a part of the population is sedentary, and a part undertakes a short- or medium-distance migration. In the case of the Chiffchaff the pre- and post-breeding migration in Central Europe are more distant in time than in the case of the Willow Warbler. The spring migration takes place in March while that in autumn – during September and October. The wintering area of the Chiffchaff includes sub-tropical as well as temperate zones, depending on a subspecies (Snow and Perrins 1998).

Migration of the Chiffchaff, in spite of its large occurrence area and high population density on breeding grounds, has not been studied in detail so far. In Central Europe only the paper of Lövei (1983) presents the analysis of the biometric variation of migrating individuals with reference to migration dynamics. The spring migration of the Chiffchaff was investigated only in southern Sweden (Ellegren and Pettersson 1985). Also the information on dynamics and biometry of birds in the western part of Europe is very general (Reynolds 1978). Only recently a little more attention has been paid to migration and wintering of the Chiffchaff along the western migratory route (Catry *et al.* 2003, Catry *et al.* 2005, Catry *et al.* 2007), *e.g.* pointing out differences in migration strategy depending on sex. The migration directions of European populations of the Chiffchaff are described in the atlas of recoveries (Zink 1973), indicating a migratory divide running through Central Europe. Due to this division, populations inhabiting the western part of the continent migrate along the West-European migratory flyway, while birds from the eastern part of Europe migrate in the south-eastern direction.

The knowledge of the migration of the Willow Warbler is markedly better, thanks to numerous studies carried out in the British Isles (Norman 1983, 1994; Lawn 1994; Norman and Norman 1985) and Scandinavia. Migratory routes of the Willow Warbler and its distribution in wintering areas seem to be relatively well known (Bensch *et al.* 1999). The atlas of recoveries indicates its general migration directions in Europe to be quite similar to those of the Chiffchaff (Zink 1973). Birds of the subspecies *P. t. trochilus* migrate along the western migration flyway, while *P. t. acredula* from Eastern and Central Europe migrates along the eastern migration flyway. Numerous authors pointed to differences in migration phenology of different age groups in southern Sweden, and to later migration of the northern subspecies *P. t. acredula* (Högstedt and Persson 1982, Hedenström and Pettersson 1984, Pettersson and Hedenström 1986, Lindström *et al.* 1996). Similar results on differences in migration phenology were obtained with regard to spring migration. An earlier arrival of mature as well as polygamous individuals was found (Lawn 1998). Also differences in spring migration phenology were found between individual sex groups (Tynjälä *et al.*

1994). Some authors concentrated on selected aspects of spring migration, especially the survival and condition as well as phenology of the returning individuals (Bentz 1983, Cuadrado and Hasselquist 1994, Fransson and Jakobsson 1998). The biometric analysis of migrating individuals (Hedenström and Pettersson 1986, Lundgren *et al.* 1995, Hedenström 1998) and the problem of moulting (Norman 1981, 1990; Hedenström *et al.* 1995) were presented in several papers.

In Fennoscandia, Hedenström and Pettersson (1984, 1987) found a migratory divide in the Willow Warbler population at 62°N. Recently, thanks to the use of molecular techniques in bird migration studies, the migratory divide in the population of the Willow Warbler as well as the diversification of its migratory routes and wintering grounds have been confirmed (Bensch *et al.* 1999, Chamberlain *et al.* 2000, Bensch *et al.* 2002, Bensch *et al.* 2006). In Scandinavia the migratory divide for the Willow Warbler is a 350-km-wide zone, in which the breeding grounds of two populations overlap. The populations are different not only in respect of their migration phenology and directions, but also regarding their morphology and genetic characteristics (Bensch *et al.* 1999, Chamberlain *et al.* 2000). Probably a similar migratory divide exists in the case of the Chiffchaff populations.

Relatively little studied problem is the changes in population numbers of individual species (Peach *et al.* 1995). This concerns breeding as well as non-breeding periods. Long-term trends in numbers of leaf warblers captured at bird ringing stations in Central Europe were analysed by Busse and Marova (1993), and Tynjälä *et al.* (1995). These authors found a significant decrease in populations of all the leaf warbler species during recent decades.

Also, a moulting strategy, different for each species, is associated with diversity of migration strategies. The Wood Warbler undergoes a complete moult in its winter quarters, while the Chiffchaff – on its breeding grounds. On the other hand, the Willow Warbler presents a unique for Palearctic passerines strategy of two complete moults annually, taking place in both wintering and breeding areas (Jenni and Winkler 1994).

In spite of many years of research and relatively numerous publications in the case of the Willow Warbler, the present knowledge of the leaf warblers' migration is still incomplete. Their numbers as well as densities and habitat preferences in particular parts of their wintering grounds and migration routes are little known (Rabøl 1987, Salewski *et al.* 2002). Many possibilities for studies on migration routes exist thanks to bird ringing. However, there are many interpretation problems connected with this practice. A scarce number of recoveries in the case of so small birds is faced. In order to learn about the migration strategies of these birds it is necessary to widen our knowledge of components and processes of the environment in which the migration takes place as well as to use new research methods, *e.g.* physiological, behavioural, and molecular techniques.

MORPHO-ECOLOGICAL DIFFERENTIATION

The Willow Warbler and Chiffchaff show a sexual dimorphism expressed by a greater wing length in males (Tiainen 1982, Tiainen and Hanski 1985). Differences in the wing length also occur in age groups, *i.e.* mature birds (except for the Chiffchaff

females), being after complete moult, have longer wings (Tiainen and Hanski 1985). Moreover, in the Willow Warbler there are differences in wing shape parameters between sexes. Such differences, however, were not observed between *P. t. trochilus* and *P. t. acredula*. In the case of the Chiffchaff no differences in wing shape parameters were found between sexes, but they occur between *P. c. collybita* and *P. c. abietinus* (Tiainen and Hanski 1985). The differences in wing shape parameters were also observed between age groups. Detailed morphological studies showed a small geographical differences between the Willow Warbler populations (subspecies), and a distinct differentiation in the case of the Chiffchaff (Hanski and Tiainen 1991). Despite this, the existence of local morphological differences, depending on habitat, was found for the Willow Warbler males (Tiainen 1982, Michalak 1995). In the Willow Warbler, research on variation depending on the migration phenology showed that a greater differentiation, expressed by the body asymmetry, occurs in individuals migrating earlier (Rintamäki *et al.* 1995). The authors suggested that this variation occurred due to intra-specific competition, which forced the low quality individuals to migrate earlier.

INTER-SPECIFIC SIMILARITY *VERSUS* INTRA-SPECIFIC DIFFERENTIATION

Leaf warblers, as a group of species closely related and similar with regard to morphology and ecology, were frequently of interest to investigators. Many comparative reviews of the genus *Phylloscopus* were made yielding conclusions of a general biological character. Gaston (1974) found that migratory subspecies of some species from the genus *Phylloscopus* have longer and more strongly pointed wings than sedentary subspecies. Marchetti *et al.* (1995) reported a similar relationship at the species level. They found that species having longer and more pointed wings migrate for longer distances and show different foraging behavior, *i.e.* they feed in higher parts of tree crowns and use less frequently the hovering as a foraging method (proper for species with rounded wings).

Moreover, the relationship between the body size of individuals of a given species and the location of their wintering grounds was also found for the leaf warblers – larger species winter further south (Katti and Price 2003). Leaf warblers confirm Rapoport's rule, which states that species occurring at northern latitudes have larger ranges (Price *et al.* 1997). Morphological differences between the Chiffchaff and the Willow Warbler confirm this relationship. The Willow Warbler is a larger species with a broader niche. It is more plastic with regard to breeding and feeding habitats choice and use of different foraging techniques. It is nesting further north, and wintering further south, thus undertaking a longer migration in comparison with the Chiffchaff.

Considering large ranges of occurrence, a wide spectrum of habitats, contrasting spectra of migration behaviour, and a high morphological and ecological diversification, the leaf warblers are particularly interesting for the research concerning migration ecology. However, despite a frequent interest in the genus *Phylloscopus*, the present state of knowledge about their migration is highly incomplete, and does not permit to make any substantial generalizations. Despite numerous papers on various problems connected with migration and wintering of these species, no synthetic elaboration concerning their migration has been made so far.

The leaf warblers make a specific group of model species being a good subject of ecological research. The morphological differentiation of individual species, subspecies, populations, and also sex and age groups of the leaf warblers, creates great possibilities for the migration research, especially for studies aiming at finding the basis of the differences in migration strategies and patterns (comp. James 1982). Besides the internal genetic and physiological conditions, the bird migration is determined by external environmental factors – atmospheric, habitats, or intra- and inter-specific behavioural relationships. The knowledge of the migration strategy and ecology of the leaf warblers may be a good reference point for understanding a general migration pattern of European passerines.

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