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EVOLUTION OF THE WESTERN PALAEARCTIC PASSERINE MIGRATION PATTERN PRESENTATION STYLE

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ABSTRACT

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The scientific knowledge available in many detailed studies needs, from time to time, some generalization that allows to provide a synthesis or at least presentation of certain problem to both, scientific community and wide public interested in the topic. This article presents evolution of the presentation style of spatial course of the passerine migration in the Western Palaearcic. According to developing knowledge in the topic the style of presentation of general migration pattern evolved from a "line – arrow" style suggesting that the birds use narrow "corridors" to more adequate to the phenomenon "carpet" style with called as "bottle-necks" concentrations being local and temporal effects of existing migratory barriers and guiding lines as maritime coasts, mountains and deserts. These details of migratory flyways are less visible in nocturnal passerine migrants than diurnal movements of both of passerines and gliding big birds. Generally, according to spatial relations between breeding and wintering areas of the bird populations living in Western Palaearctic four main flyways are defined and presented on maps: Western (Atlantic), Central (Apennine), South-Eastern (Balkan) and Eastern (Indian). Their background lies in the post-ice age history of distribution changes of the bird species, but details still evolve.

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INTRODUCTION

The scientific knowledge available in many detailed studies needs, from time to time, some generalization that allows to provide a synthesis of certain problem to both, scientific community and wide public interested in the topic. A good example is bird migration. This phenomenon has a very broad geographical coverage including local and intercontinental scale. Despite that most data collected at the bird ringing

stations have very limited spatial coverage. A pronounced step forward was made since national and then international networks of bird stations were launched – at the end of the fifties of the XXth century "Operation Recovery" was organized in America, while in 1961 the first long-term network in Europe started to work at the Polish Baltic coast (called later "Operation Baltic"). Later the stations from Latvia and Estonia, former German Democratic Republik, former Czechoslovakia and Hungary. This substantially enlarged the area covered by the activity of this network, but the political constrains made these attempts very difficult. In the meantime (1971) three German/Austrian bird stations launched the Mettnau-Ilmitz-Reit network. However this programme ran for a limited time (1972-1996). Then, in 1988, the programm "Piccole Isole" including the studies on the islands of the Mediterranean Sea started to work. In 1994-1996 the European Science Foundation Network covered the northwestern Europe and a few western African sites (Gargallo *et al*. 2011). Despite the discussions during the initial meeting of the ESF Network whether more central and eastern European areas and the Middle East should be included in this work, this idea was not supported. Thus, from the very beginning, the picture of bird migration in Europe was biased very much. In 1996 the network called "SEEN" – SE European Bird Migration Network was launched, that covered the southeastern flyway of European passerines. A few years later, in 2004, there was an attempt to organize similar network covering some Spanish, French and NW African sites. This was, unfortunately, not successful, but now the Atlantic Flyway Network started to work (http://www.atlanticflyway.org/). The idea of the broad/comprehensive network working on passerine migration returned in 2008, when it was discussed as the "European-African Network". The basic project assumed, the coverage of the western Europe and the western part of Africa. Once more the eastern part of the migration system was not included. The project has not started yet. So, any complex, coordinated/research network following the whole European passerine migration system is not working at the moment. However, even partial coverage of the area in question brings interesting results that can be the basis for some general synthesis.

Independently of the activity of bird ringing stations collecting the data on bird migration, since more than one hundred years bird ringing by individual ringers continues (Preuss 2001). As the result a huge number of ringing recoveries was collected. Despite well-known biases in the distribution of the recoveries in breeding, passage and wintering sites, these data are a very important source of information on the bird migration pattern (Kania and Busse 1987, Clark *et al*. 2009, Korner-Nievergelt *et al*. 2010a). Unfortunately, only a small part of collected recoveries were evaluated and presented in the generalized form, covering complete European analyses (Ashmole 1962, Rydzewski 1966, Busse 1969, Spencer 1975, Imboden and Imboden 1972, Remisiewicz 2002, Mokwa 2004).

Apart from bird ringing that provides information about bird movements, including migration patterns, the direct observations - very popular among both professional and amateur ornithologists – bring a lot of data about species distribution at the breeding and wintering grounds as well as along the migration routes.

All the information on the migration patterns need to be presented to the public and used in the general analyses and modelling of ecological processes, in planning

of conservation activities or even in epidemiological expectations. Thus, the knowledge about the bird migration patterns, flyways and the methods of their presentation should be accessible and well understood.

THE SPECIES LEVEL

The first general pictures presenting migration patterns were based on visual observations and ringing recoveries of birds that were easily observed (large species, huge flocks). They did not represent Passerines that we focused on. The most classic example is migration of storks (Fig. 1), as presented by Rüppell (1942), cited then many times (e.g. Verheyen 1950 and Dorst 1962). This picture fixed the style of thinking about presentation of the migration patterns – broad front and narrow, corridor migration. Many ornithologists and layman were "imprinted" with this picture and they easily forget that the Stork is the representative of only some migratory species – those migrating during a day, moreover being extremely dependent on air vertical currents in their gliding flight. The line presenting migration corridor was accepted and then used for presentation of assumed flight direction of passerines, even those migrating by night that are able to not depend on topographical guiding lines. The example is given in Dorst (1962) – Figure 2 – where arrows were drawn based on the author assumptions who deducted their location and pattern from relative distribution of breeding and wintering areas (they were mainly wrong in that case). This style of presentation can be frequently found in popular books for non-specialists, as published even contemporarily e.g. in Elphick (2011), where maps for passerines are drawn rather according to a fantasy of the drawer than the real knowledge of the species migration pattern.

Fig. 1. Flight directions of migrating White Stork (*Ciconia ciconia*). From Dorst (1962), after Rüppell (1942), modified by Verheyen (1950).

It is far better to resign from drawing certain migration lines based on the assumptions on the distribution of breeding and wintering grounds when only general information about the bird species passage is needed. This is the case in general atlases, as e.g. Moreau (1972), Harrison (1982) (Fig. 3) or field guides as Collins Bird Guide (Svensson *et al.* 2009).

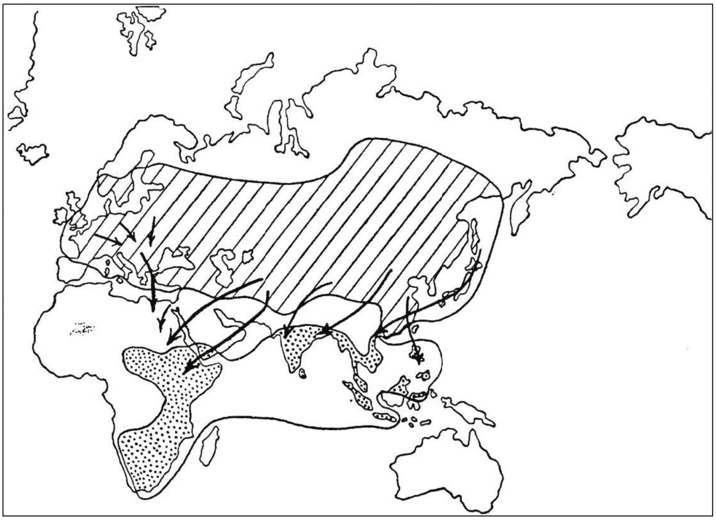

Fig. 2. Migration of shrikes of the *Lanius cristatus-collurio* group as presented by Dorst (1962) after earlier authors. *"Arrows indicate the chief migratory currents*." as imagined by the drawer.

THE POPULATION LEVEL

Ringing results as a source information of migration patterns

In professional ornithological analyses, modelling, conservation actions planning or studies on possible parasite/disease transfer, the general picture of the species migration is not sufficient. Pronounced differentiation in the migration patterns of populations living in various parts of the breeding area is typical for many species. It is necessary to study these phenomenon and to learn how to present results for general users applying this knowledge to their needs.

Spatial distribution of different migratory populations was proposed in the late 60-ties of XXth century based on the analyses of European corvids, especially the Rook *Corvus frugilegus* (Busse 1969). That population pattern (Fig. 4) showed areas inhabited by rook populations migrating to five winter-quarters: Northern (British), Western, Apennine, Balkan and Caucasus. Some areas where mixed population occurred were presented as well. In the case of the Rook it was not necessary to draw any arrows pointing at migration direction as this species is a short distance migrant and directions of the passage are clear.

The breaking point for the studies of population differentiation based on the analyses of recovery distributions was publication of the Zink's atlas of recoveries of passerines ringed in Europe (Zink 1973-1985). Despite it does not give a valuation of presented recoveries, it offers possibility to analyse them as a source data and to study population differentiation. Some of European passerines are clearly unipopulational (e.g. Lesser Whitethroat *Sylvia curruca*) while others show clear migratory di-

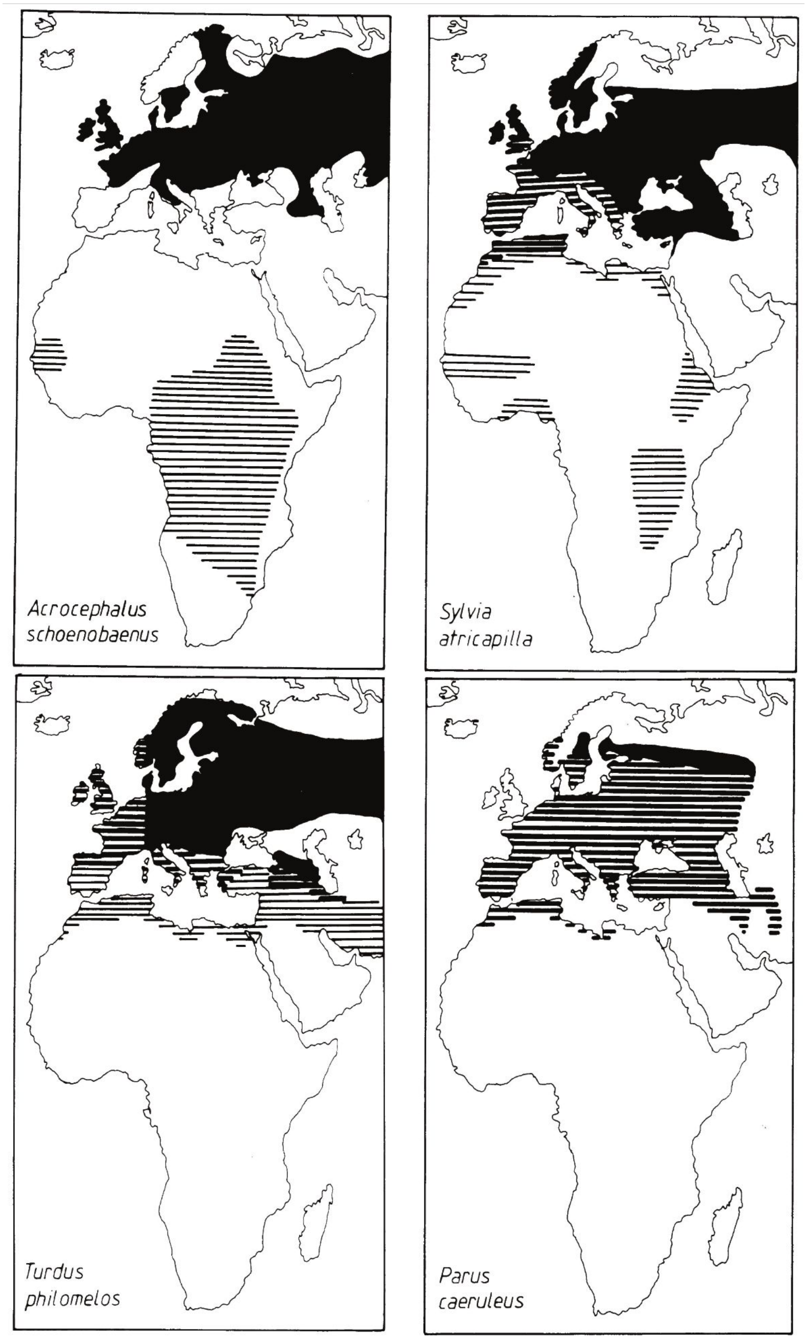

Fig. 3. Distribution patterns of the Sedge Warbler *Acrocephalus schoenobaenus*, Blackcap *Sylvia atricapilla*, Song Thrush *Turdus philomelos* and the Blue Tit *Parus caeruleus* as examples of different migration patterns: long distance, short distance and partial migration. Black – breeding grounds, thin striping – winter quarters, thick striping – wintering within the breeding range. From Busse (1987), after Moreau (1972) and Harrison (1982) combined.

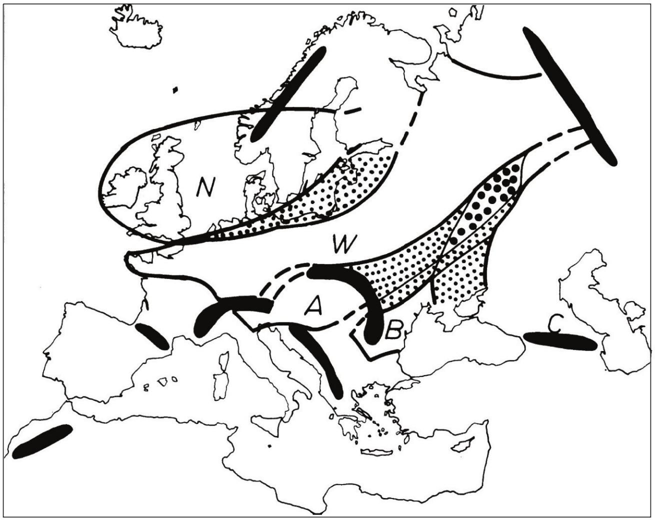

Fig. 4. Population pattern of European Rook *Corvus frugilegus*. Letters – symbols of different populations; heavy lines are limits of "pure" population areas; small dots – zones of mixing of two neighbouring populations; larger dots – multipopulation mixing zone; black stripes – main mountain ridges. From Busse (1987), after Busse (1969), modified.

vide (e.g. Reed Warbler *Acrocephalus scirpaceus* or Sedge Warbler *A. schoenobaenus*) – as it is shown in Figure 5. Single and clear cut migratory population divide is the simplest case in the population differentiation patterns. There are more complex and interesting patterns, however.

One of the most complex, but also quite well-studied is the migration pattern of the Blackap *Sylvia atricapilla*. According to the Zink's data there are areas in Europe from which Blackcaps migrate following the narrow angle pattern (Great Britain and Finland – Fig. 6 A), while Central European Blackcaps move in very wide angle – recoveries are located from Portugal to the Middle East (Fig. 6 B). This seems very strange as it would mean that these birds have no genetically fixed direction of migration, in contrary to the British and Finnish birds. Some researchers tried to define a migratory divide (Brickenstein-Stockhammer and Dorst 1956, Williamson 1964) and located it at 11°E (Williamson and Whitehead 1963), while Klein *et al*. (1973) shifted this divide to 15°E. He validated it as caused by the Alps acting as a migratory barrier (despite there was a number of recoveries just south of the Alps at the Apennine Peninsula). On the contrary, Helbig (1991) claimed that birds migrating to the south were hybrids of SE and SW migrating populations that mixed at the border zone in Germany. This pattern was explained differently by Busse (1987) who applied to the Blackcap recovery distribution a new concept of the recovery pattern interpretation – so called "looking from the south" method, that was first applied in the example of the Rook migration mentioned above (Busse 1969). The method was then developed based on the analysis of the Song Thrush *Turdus philomelos* migration (Busse and Maksalon 1986) and published in the paper discussing migration patterns of European passerines (Busse 1986, 1987). The basic assumption for this method was

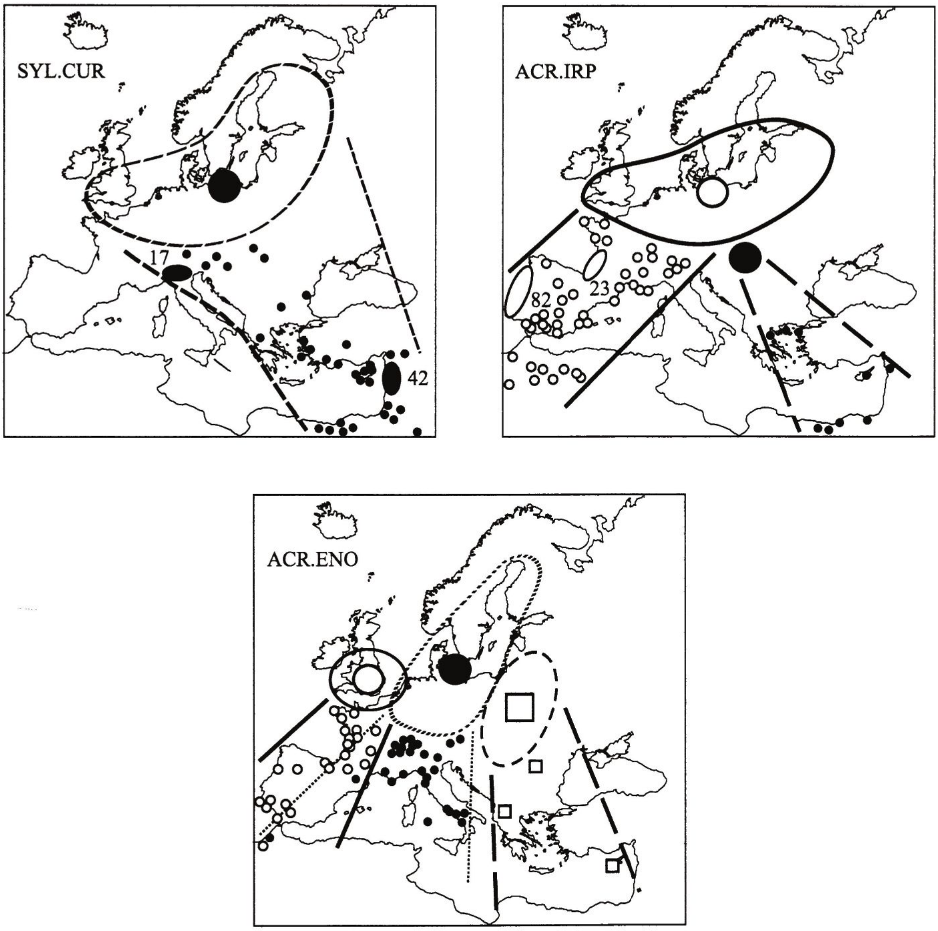

Fig. 5. Recovery patterns of the Lesser Whitethroat *Sylvia curruca* (SYL.CUR), Reed Warbler *Acrocephalus scirpaceus* (ACR.IRP) and the Sedge Warbler *A. schoenobaenus* (ACR.ENO). Each small symbol shows the recovery place of the bird ringed at the area defined by the larger symbol. The number at the Lesser Whitethroat panel shows the number of recoveries from the area. From Busse (2001), after Busse (1987), modified.

that the contemporary migration pattern reflected the expansion history of the bird populations after ice-age, consequently it was suggested that the migration pattern should be rather studied following expansion from the Pleistocene refuges. In the case of the Song Thrush the reconstructed dispersion pattern was proposed as shown in Figure 7 (Busse and Maksalon 1986) that finally resulted in contemporary distribution of the species populations (Fig. 8). The "migratory population" means in this concept that there are individuals bearing in their genotype one defined migratory programme. Thus, overlapping breeding population areas are inhabited by hybrids, which migration pattern results in the wide angle recovery patterns. Application of the method to the Zink's (op. cit.) data on the Blackcap resulted in the pattern given in Figure 9. Next steps of the studies on the basic migration pattern of the Blackcap

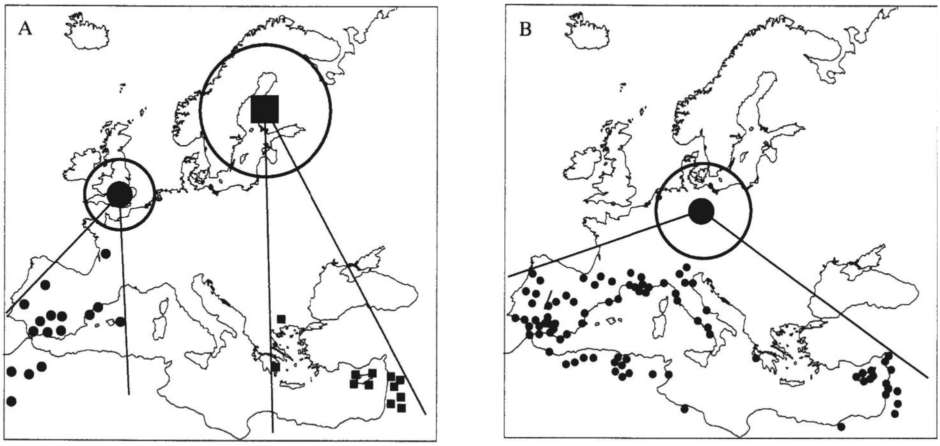

Fig. 6. Recoveries of the Blackcap *Sylvia atricapilla*. A. Individuals ringed in Britain and Scandinavia as an example of narrow-angle migration pattern; B. Individuals ringed in Central Europe as an example of wide-angle migration pattern. Explanations as in Fig. 5. From Busse (2001), after Busse (1987), modified.

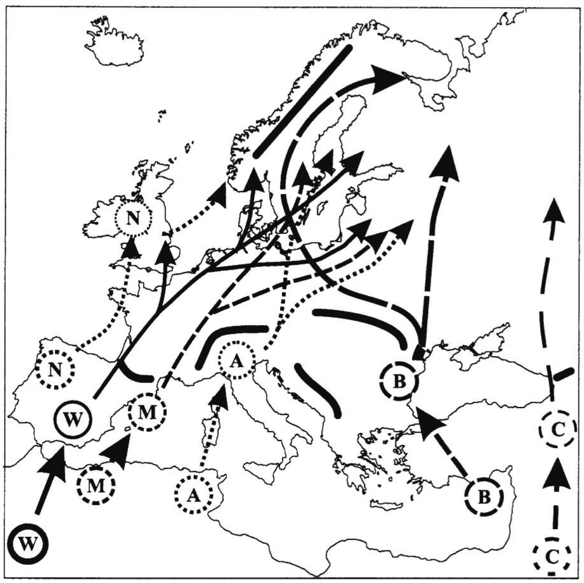

Fig. 7. Dispersion pattern of European populations of the Song Thrush *Turdus philomelos* reconstructed based on recent migration pattern. Letters in thin-line circles – actual winter-quarters, letters in bold line circles – primary winter-quarters during the last glaciation; arrows indicate assumed directions of expansion. From Busse (2001), after Busse and Maksalon (1986), modified.

showed that the picture of migration of this species was even more complicated. The resulting pattern of the analyses of nearly all European recoveries of the Blackcap is given in Figure 10 (Mokwa 2004, updated with data from the Egyptian studies – Ibra-

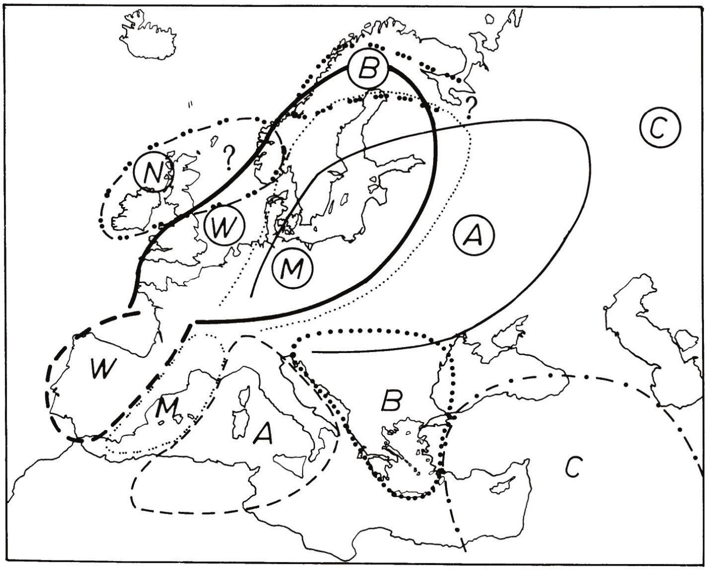

Fig. 8. Wintering and breeding grounds of the Song Thrush *Turdus philomelos* populations – five populations named by letters being shortened names of the winter-quarters: N – Northern, W – Western, M – Mediterranean, A – Apennine, B – Balkan and C - Caucasian. Breeding grounds – encircled letters. From Busse and Maksalon (1986).

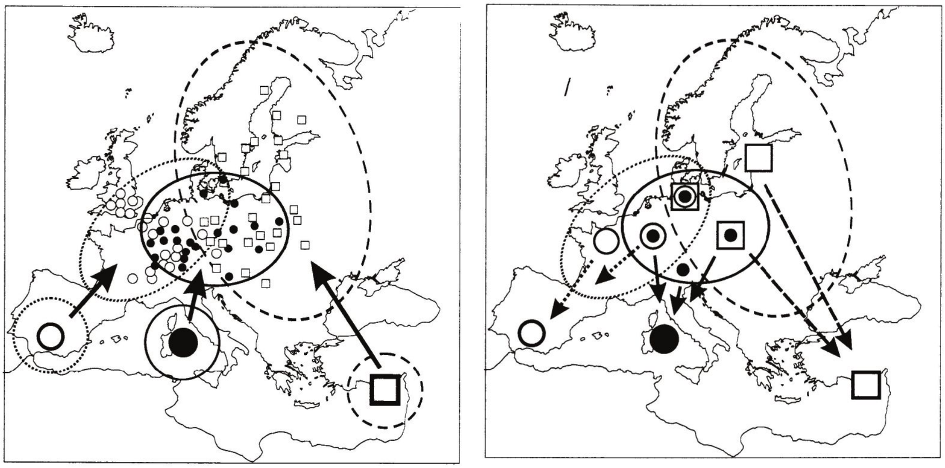

Fig. 9. Recovery pattern of the continental European Blackcap *Sylvia atricapilla* drawn according to "looking from the south" method. Left panel – location of the ringing places (small symbols) of individuals found later on different winter-quarters (large symbols); right panel – areas occupied by a single and a few populations (single and combined symbols). From Busse (2001), after Busse (1987), modified.

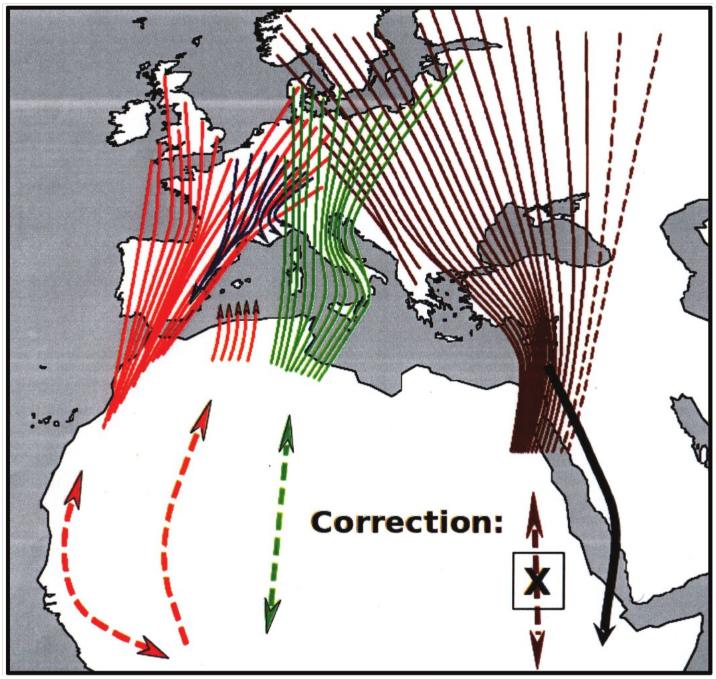

Fig. 10. Migration pattern of the European Blackcap *Sylvia atricapilla* based on the ringing recoveries analyses (birds wintering in Britain and Ireland were excluded). Note that any single line does not represent any concentrated stream of birds, but lines concentrations point at the density of migration. From Mokwa (2004), corrected by the data collected later within the SEEN network program.

him and Busse 2012). Note the new style of presentation of results that empasizes two important properties of the migration patterns: (1) at the species breeding grounds there could be wide overlap of populations migrating along different flyways, and (2) in passerines the basic type of migration is a wide front movement, concentrated, however, at certain areas being resulting from the optimization of the flight conditions and/or history of the post ice-age distribution changes. Evolution of the migration patterns is an on-going process as there is still possibility to adjust the details of the migration pattern to changing environment. These resulted in adaptations and, for example, loop migration – e.g. in the Red-backed Shrike *Lanius collurio* (Zink 1973-1985), Pied Flycatcher *Ficedula hypoleuca* (Winkel and Frantzen 1991), shortening of the migration distance – e.g. the Rook (Busse 1969), Blackcap (Mokwa 2004) and even establishment of a totally new winter-quarter (Blackcap wintering in Great Britain - Stafford 1956, Leach 1981, Berthold and Terrill 1988, Busse 1992, Bearhop *et al*. 2005, Kopiec and Ożarowska 2012). This last phenomenon was skipped in the discussion of the Blackcap migration pattern above, because of its controversy widely discussed elsewhere – see: Busse 1992.

The population aspects of the migration pattern are the deepest levels of discussion about different flyways, as the destination areas of individuals that are members of the breeding population could be, and frequently they are, situated on differentiated

winter-quarters. As a rule, different subspecies have own flyways and own winter-quarters (e.g. in Willow Warbler *Phylloscopus trochilu*s the *Ph. t. trochilu*s and *Ph. t. acredul*a living side by side in Scandinavia migrate to different winter-quarters using different flyways (see e.g. Fig. 11). They are similar in this aspect to the sibling species.

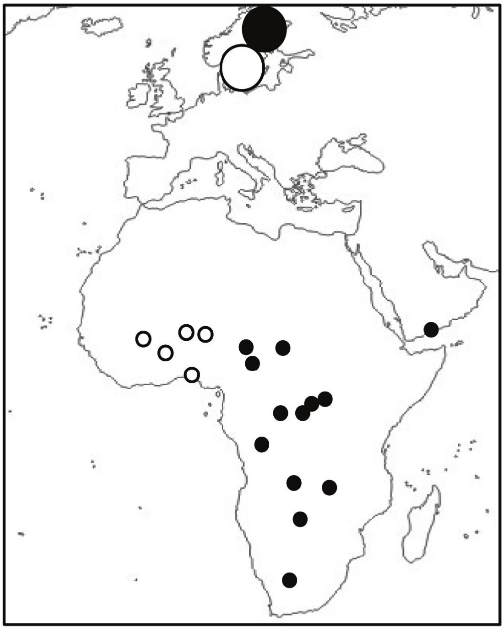

Fig. 11. Winter-quarter recovery pattern of the Willow Warbler *Phylloscopus trochilu*s of two neighbouring at the breeding area subspecies: *Ph. t. trochilu*s (open circles) and *Ph. t. acredula* (black circles). After Newton (2008), based on Chamberlain *et al*. (2000), modified.

Directional preferences of passerines – field tests

The examples given above showed that bird ringing brought a lot of information about the migration patterns of passerines. However, since many years different authors stressed that the recovery maps could be biased very much by differentiated detectability of ringed birds on different areas (Kania and Busse 1987, Busse 2000, Clark *et al*. 2009, Korner-Nievergelt *et al*. 2010a, b). This could dramatically change the picture of the species migration. A good example is the Robin *Erithacus rubecula*. During nearly 50 years of bird ringing at the Operation Baltic stations, located along the Polish Baltic coast, more than 350 000 individuals of this species were ringed that resulted in more than 1000 recoveries. The map of the recovery distribution is presented in Figure 12. Such distribution may suggest that huge majority of individuals migrated to the SW: to the western Europe and western Mediterranean. A few recoveries from the eastern European/Mediterranean areas seem to be accidental. So, the analyses of these recoveries stressed a role of the Atlantic and Apennine flyways (Remisiewicz 2002), but due to the constrains of the method and non-equal detectability of ringed birds in the West and East, it was proposed that also the SE (Balkan/Middle East) flyway is used (broken arrow in Fig. 12). After implementation of a new method of testing of directional preferences of passerine migrants (Busse 1995, Busse and Trocińska 1999) at several ringing stations, both in Poland and in the Middle East, the picture of the European robins migration was modified (Fig. 12) – the SE direction was confirmed and it changed the status from "*assumed*" into "*validated and important*". The value of the directional preference tests, especially in the eastern parts of the Western Palaearctic, is well- shown by the results collected at Eilat bird station and published by Ożarowska *et al.* (2004). The migration pattern of the Lesser Whitethroat (Fig. 13) based on the recovery distribution was confirmed by directional

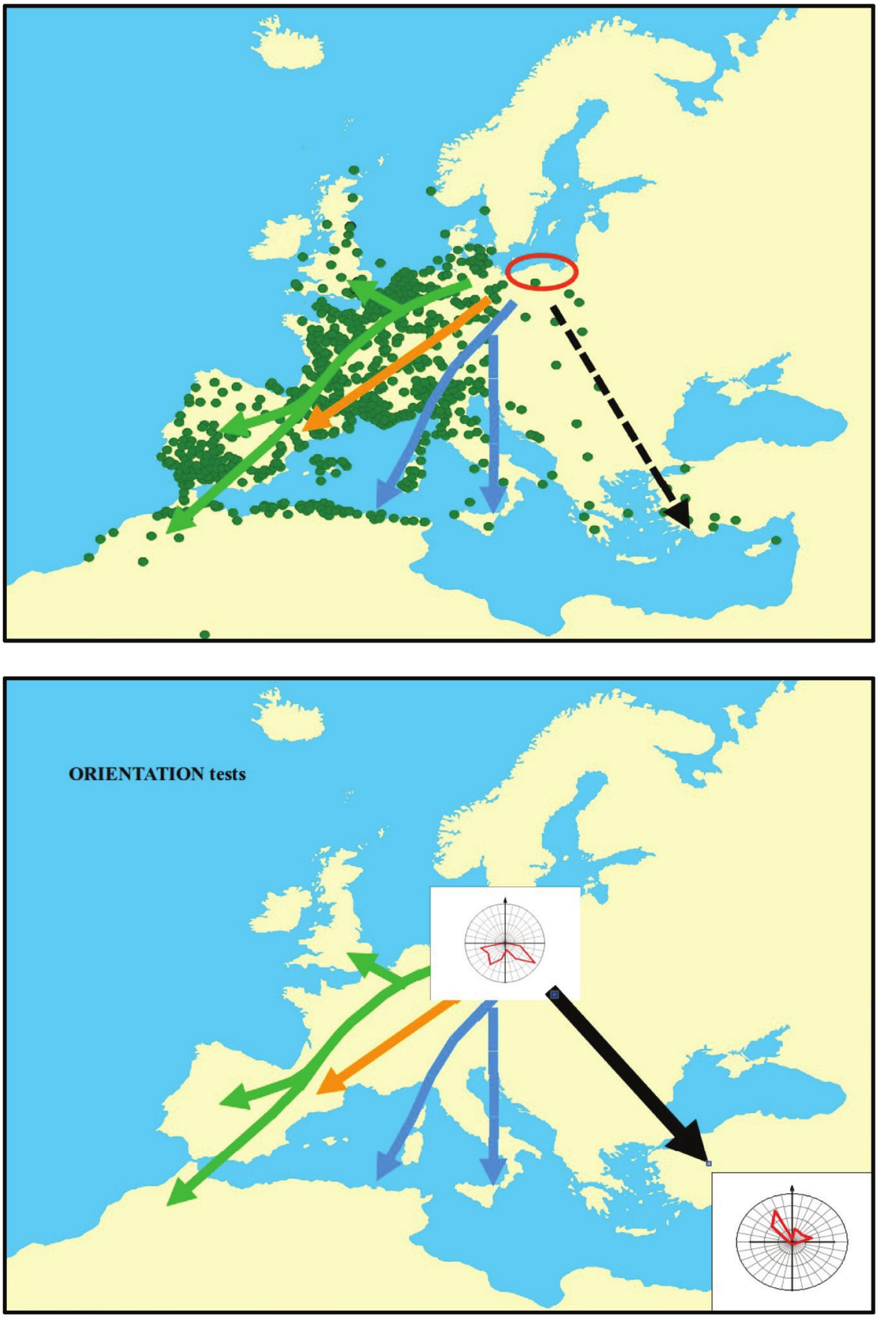

Fig. 12. Migration pattern of different populations of the Robin *Erithacus rubecula* passing the southern Baltic coast. Upper panel – after the analysis of 1082 recoveries, the SE direction of migration was still unsure (broken arrow); lower panel – after adding information from the field orientation tests (panels with observed heading distributions), this direction of the passage was confirmed. After Remisiewicz (2002) and Ożarowska (2005) modified.

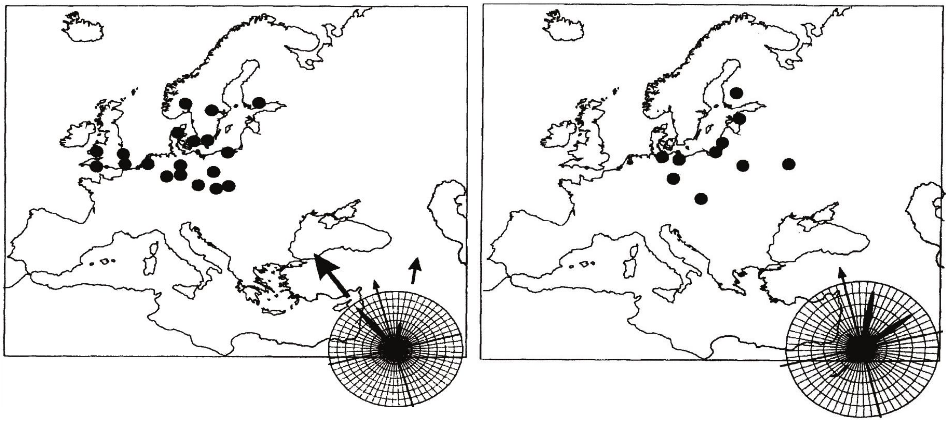

Fig. 13. Distribution of headings of the Lesser Whitethroat *Sylvia curruca* (left panel) and the Chiffchaff *Phylloscopus collybita* (right panel) tested in the orientation cages in Eilat, Israel, in spring 1999 (radar graphs at the bottom of panels) and recovery places of individuals ringed in Israel as well as ringing places of individuals recovered later in Israel (dots). Ringing recovery distribution shows rather ornithological activity in Europe than real breeding distribution of birds migrating through Eilat. From Ożarowska *et al.* (2004).

tests – most headings pointed at the recoveries in Central Europe and Great Britain (high detectability of ringed birds), while the smaller direction had no counterpart recoveries in NE direction (documented very low detectability of ringed small passerines). In the Chiffchaff *Phylloscopus collybita* (Fig. 13) birds were recovered exclusively in Central Europe, however this was supported by the secondary direction detected during the tests in the orientation cage, while the majority of cage headings pointed at the poor detection area of the easternmost part of Europe.

The comprehensive migration pattern could be obtained when the orientation tests are performed at several sites over the migration area. The example is given in Figure 14, where the migration pattern is reconstructed based on the analysis of the test data collected at 12 ringing sites. Note that the arrows show directions of movements as estimated from the headings' distributions in the test cages and they do not represent any streams or concentrations of migrants. In the real world passerines rather form "migrating carpets" heading to different goals (stop-over sites, wintering quarters) along some general flyways.

Summing up, it should be remembered that the migration patterns are very complex and cannot be exact enough when presented as the generalization used for the summary or large scale modelling. As there is an obvious need to present some general patterns/synthesis, one should bear in mind that these are simplifications frequently adjusted to special needs and problems, as it can be found, for example, on the internet bird flue tracking site (www.flutrakers.com) where the presented flyways included only birds that were the most common avian flue vectors, namely ducks and waders. Thus, these patterns are not applicable to most migrants, despite they are given as "... *major flyways of migratory birds*".

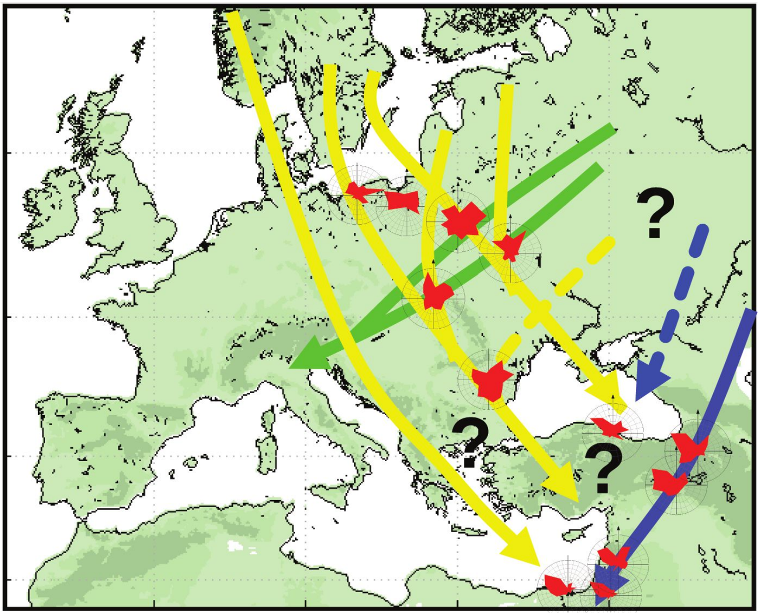

Fig. 14. Estimated migration pattern of the Chiffchaff *Phylloscopus collybita* in the eastern part of Europe and the Middle East according to the analysis of orientation tests at twelve SEEN stations (local direction distributions in red). Arrows point at migration directions rather than defined streams. After M. Filar (pers. comm.), modified.

THE FLYWAYS PRESENTATION

Since many years, despite of increasing knowledge on the real migration patterns of passerines the style the flyways were presented, was dominated by the "lines and/or/arrows" suggesting that migration follows the "corridors" or "streams" along the sea coasts or around migratory barriers. A very popular poster of the bird migration system issued by the BirdLife International which was used in education and during the bird conservation campaigns, was very simplyfied. It was impressive but showed rather fiction than facts to both ornithologists and laymen brains. The number of clear mistakes in this poster urged to present the more accurate image (however, still with a number of incorrect details) as the map on the home page of the SEEN (Fig. 15, www.seen-net.eu). This map exposed the importance of the SE migration flyway compared to other European flyways. Despite of these weaknesses the map attracted number of users, asking for rights to reproduce it in education or as a basis to build general models. All these urged us to present the general Western Palaearctic flyways pattern in generalized, not too detailed, but clear enough form. The source data were published as bird ringing national atlases (Dorst 1962, Kania 1981, Hedenström and Pettersson 1987, Bruderer and Jenni 1990, Zehnder *et al*. 2001, Re-

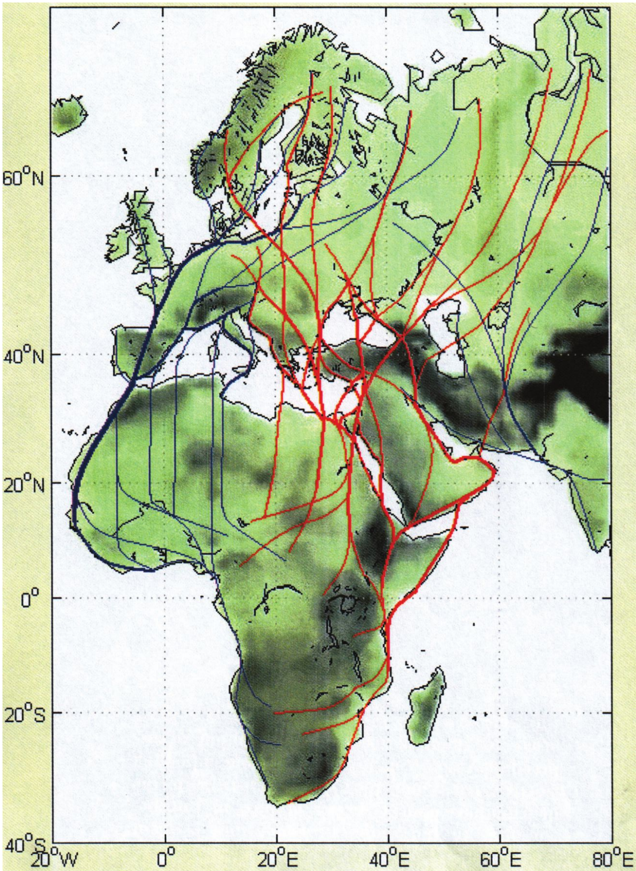

Fig. 15. The South-Eastern migration flyway as shown in 2006 at the main screen of SEEN web page www.seen-net.eu.

misiewicz 2001, 2002, Procházka and Reif 2002, Wernham *et al*. 2002, Mokwa 2004, Bakken *et al*. 2006, Břnlřkke *et al*. 2006, Cepák *et al*. 2008, Fransson and Hall-Karlsson 2008, Spina and Volponi 2008, Csörgo *et al*. 2009, Schmidt 2009) as well as several papers and still unpublished data of the SEEN stations .

In the maps shown in Fig. 16 the lines connect the centres of breeding range of different species or populations of passerines with their wintering areas. For technical reasons and the clarity of the picture, most of similar lines were omitted. So, the area between the certain colour lines is the source area of the flyway. The source areas of the flyways overlap much at different parts of Europe and they varied between the species. One should remember that the lines show overall migration directions – not the concentrations of flying individuals following any defined, narrow routes. Passerines along most of their migration route fly in the "carpet style" broad front, and their flight tracks are more or less parallel. However, at the bottle-neck areas the density of individuals grows, but it does not mean that there must be a corridor of birds flying in the same direction, even the migrants move within the same flyway

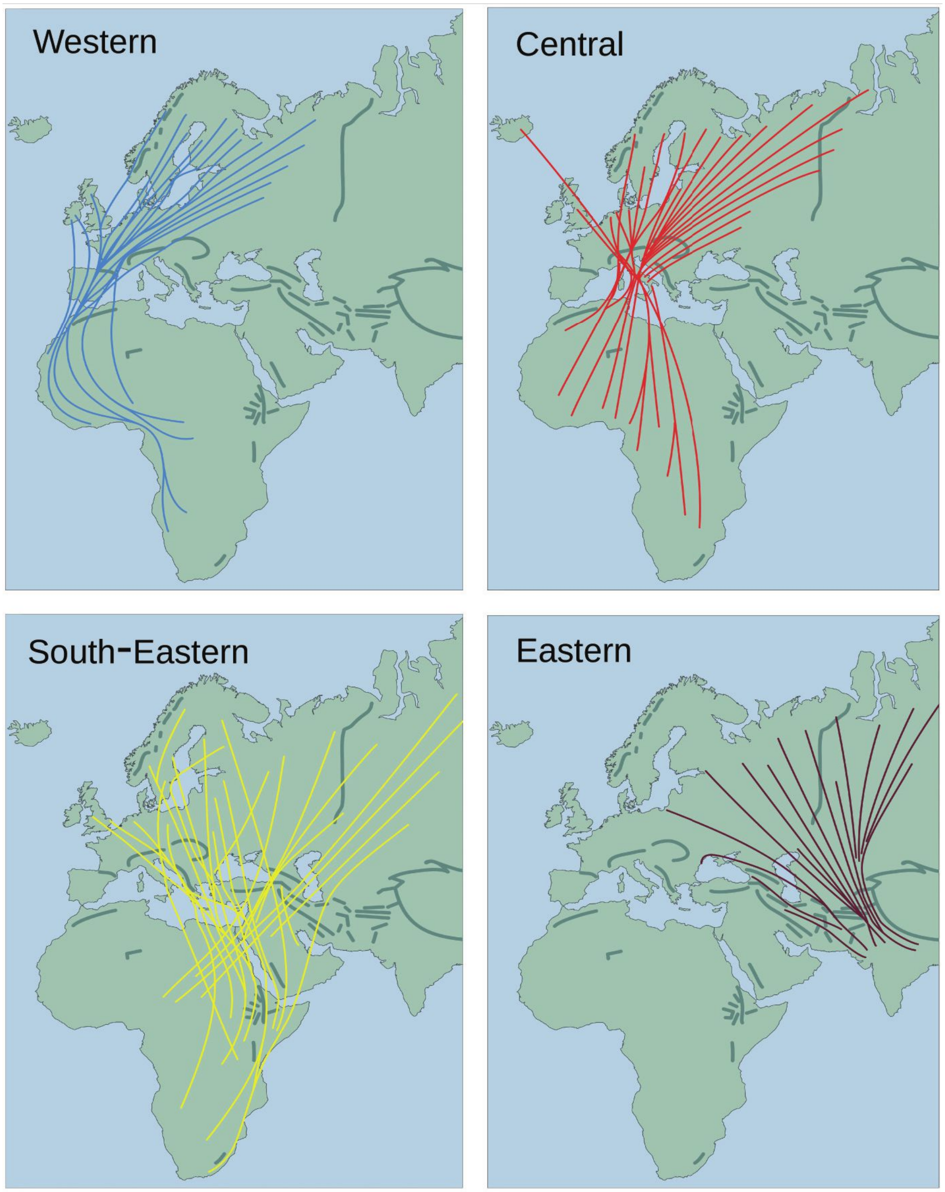

Fig. 16. Source, transient and destination areas of Western Palaearctic passerines migrating along the main flyways: Western (Atlantic), Central (Apennine), South-Eastern (Balkan) and Eastern (Indian).

can have different goals of movement. After passing the bottle-neck area birds can disperse again and continue passage in a broad front.

In the Western Palaearctic there are four main passerine flyways: (1) the Western/Atlantic flyway, which in some species, according to more detailed studies (Remisiewicz 2001, 2002, Mokwa 2004) consists of two branches – western and eastern

Iberia, (2) Central (Apennine flyway), (3) South-Eastern (Balkan/SE flyway) and (4) Eastern (Indian) flyway. These flyways are defined here by the areas where the birds cross the southern border of the Palaearctic and they lead the birds to different parts of tropical and subtropical wintering areas – respectively: western, central and eastern/southern Africa and India.

The picture shown in Figure 17 can be used as the contemporary general pattern of the flyways of passerines originating from the western Palaearctic.

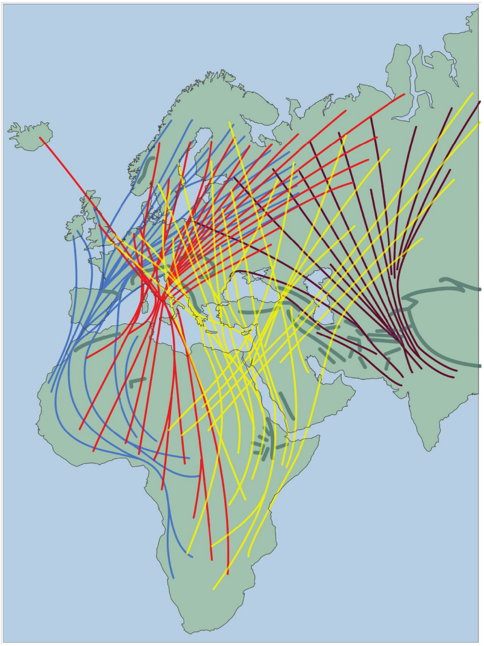

Fig. 17. General migration pattern of Western Palaearctic passerines

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