

THE EUROPEAN AUTUMN MIGRATION PATTERN
OF THE BLACKCAP, *SYLVIA ATRICAPILLA* –
FROM FAUNISTIC OBSERVATIONS TO A BASIC
ANALYSIS OF ORIENTATION CAGE FIELD DATA

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ABSTRACT

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Presentation of a general pattern of migration is very difficult in the case of small passerines, especially nocturnal migrants, as the few accepted methods are inefficient here. It is difficult to follow migration visually (by visual field observations or moon watching). Classic ringing must be extremely intensive due to low or very low recovery rates, especially in Africa, Eastern Europe and Asia, which additionally rule out any reasonable estimation of the intensity of migration towards different destinations. Radar studies tell us nothing about the migration of individual species. Even the most modern methods, such as geolocation and radio tracking, are of very limited use for population studies. For these reasons, in most cases our knowledge in this area is fragmentary and insufficient for a satisfactory description of migration. In many cases only the breeding areas have been faunistically described in detail, while the winter-quarters and areas where the species is observed during migration are frequently described with less precision. The introduction of an effective method for studying local headings of migrants, using 'orientation cages', has made it possible to study the migration patterns of small passerine nocturnal migrants. The presented work is a case study on the migration pattern of the Blackcap, using data from orientation tests collected in autumn as part of the work of SEEN (SE European Bird Migration Network), consisting of 5,392 tests performed at 28 ringing sites in Central/Eastern Europe and the Middle East. The paper continues the discussion of the problem of applying the method to presentation of migration patterns in a geographically wide territory (Busse 2018, 2019, 2020).

The hypothesis put forth by Busse (2019) that the arrival/departure heading axes are generally linear is accurate to within about one 10° sector was confirmed earlier. Here it was confirmed at the level of local patterns for the study sites. In general, the average deviation from the straight line is below 1°. However, there is some geographical variation, and this problem could be discussed when many more results of this kind become available for a few more species. Eight headings/streams of migrants are defined for the Blackcap within the area. Southward and south-eastern streams dominate in most of the study area. However, a very special, nearly longitudinal heading was found in southern Europe and the Middle East, which requires further study. Comparison of the patterns obtained from three different procedures strongly suggests that the general picture

of Blackcap migration in Central/Eastern Europe and the Middle East is clear and coherent. Some variation in migration stream parameters (linearity and reversed heading share) suggests that further research in this direction should be conducted using data from other species.

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INTRODUCTION

Information about the migration pattern of the Blackcap, *Sylvia atricapilla*, has been collected step-by-step over several decades, at least since the 1970s. The first general graphic presentations based on faunistic observations were collected in the 19th and the first half of the 20th century. These were species distribution maps presenting the breeding and wintering grounds of several species (Moreau 1972), and a bit later transit areas were added (Harrison 1982). For the Blackcap, these maps are presented in Figure 1. In parallel to the faunistic observations, since the beginning of the 20th century ringing data have been collected and summarized in ringing recovery atlases (Schüz and Weigold 1931, Zink 1971). Zink's atlas contains several detailed maps presenting the results of Blackcap ringing in Europe. This atlas showed that the roughly estimated migration patterns of various passerines are highly varied. One of the strangest of these was the distribution of ringing recoveries of the Blackcap; recoveries of Blackcaps ringed in a wide area in Central Europe were distributed from Portugal in the West to the Middle East. This was later described as 'fan-like'

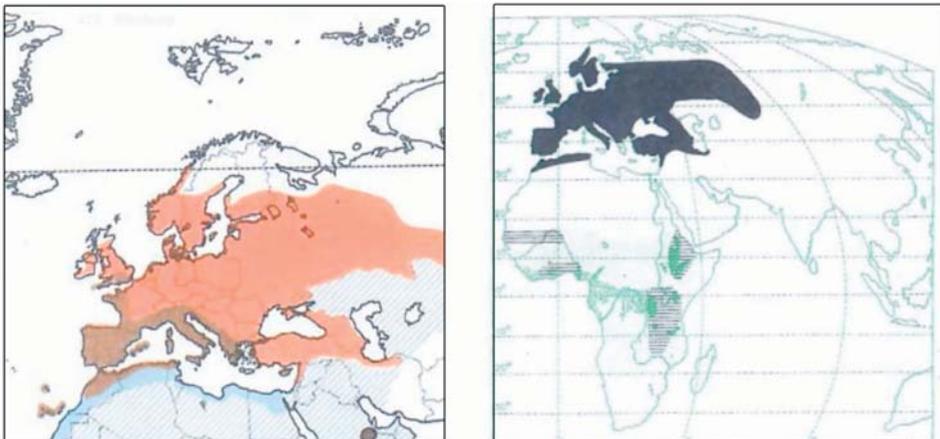


Fig. 1. Older presentations of the geographical distribution of the Blackcap. Left panel after Harrison (1982) – breeding area, northern wintering grounds and area of passage; right panel – after Moreau (1972) - breeding area and distant winter quarters.

(Fig. 2 after Berhold and Terrill 1988). This generalization was based on the dominant style of presentation of ringing data at that time: they were presented on maps as lines connecting the ringing site and the location where the ringed bird was later found. Because most ringing at that time was performed in northern Europe, and the data were presented by the ringers or ringing centres, the typical patterns looked more or less like open fans with their top in the ringing areas. This was from the point of view of the ringing (mainly breeding) area, looking southwards in the direction of autumn migration. The shape and location of these fans depended on how broad the source/breeding area was. In the case of the Blackcap, division of the entire area covered by Zink's atlas resulted in the picture presented by Busse during the conference in Aula, Italy (Busse 1986, 1987; Fig. 3, made from the Zink's atlas data). The 'fan' shown by Berthold and Terrill (1988) was one of the possible distributions of the data available in Zink's atlas. At the Aula meeting, Busse proposed reversing the 'point of view' from that of the ringers (breeding grounds in the north) to that of the finders – looking from the south, where the population spends the winter, northwards in the direction of the population's breeding ground. This not only changed the 'optics' and presentation of the migration pattern, but introduced a method of defining the structure of the territorial breeding area of a population of the species studied. Thus, migratory population breeding areas and mixed zones/areas where interpopulation hybrids can occur are defined (Fig. 4). The existence of interpopulation hybrids in mixed zones had already been suggested for rooks by Busse (1969). In the late 1980s, the migration pattern of the Blackcap was commonly interpreted as the result of the 'migratory divide' for birds migrating SW and SE, with the division line set as the 12–15° meridian

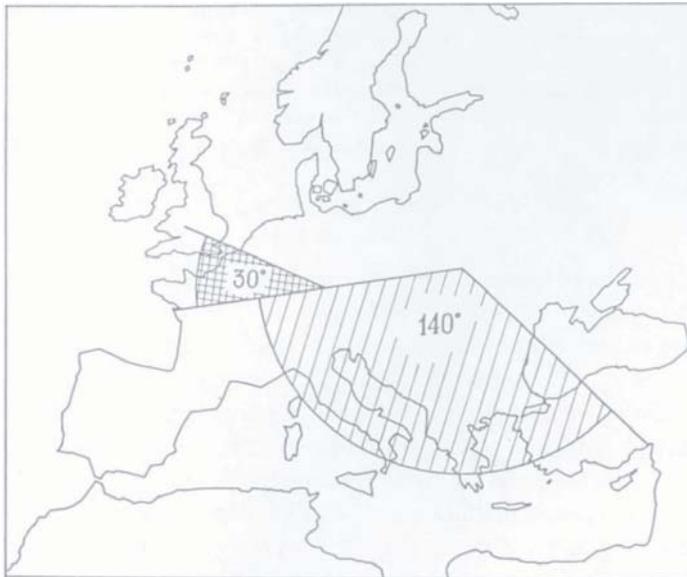


Fig. 2. "Fan-shaped" pattern of all migratory directions taken by Blackcaps breeding in Europe (after Zink 1973). Note that the angle of "normal" migration need only be increased by about 30 degrees for these birds to reach Britain and Ireland. (After Berthold and Terrill 1988). – After Busse (1992).

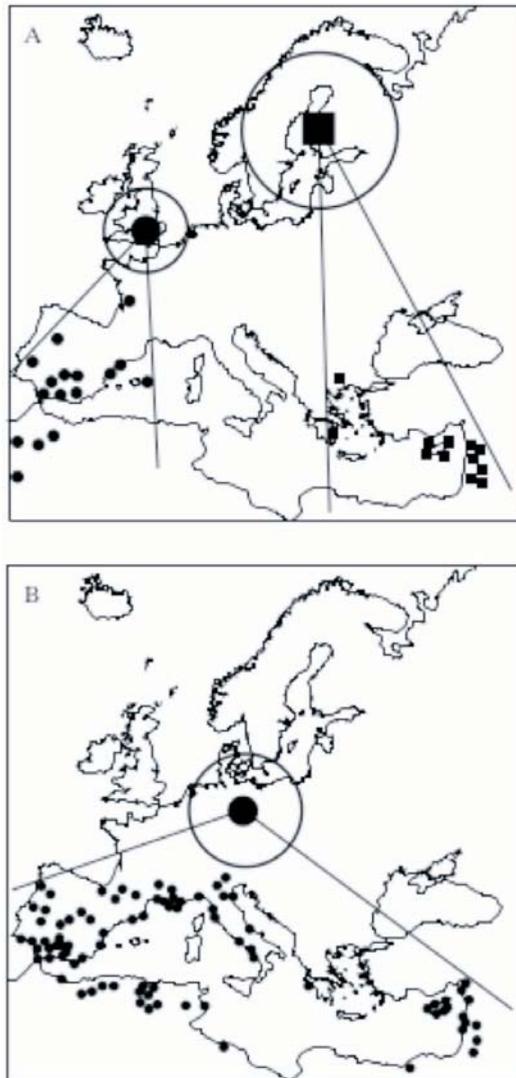


Fig. 3. 'A. Recoveries of Blackcaps ringed in Britain and Scandinavia as an example of narrow-angle migration patterns; B. Recoveries of Central European Blackcap as an example of wide-angle migration pattern... After Busse 1987, modified.' After Busse (2001).

(e.g. Klein *et al.* 1973, Helbig and Wiltchko 1987). At the same time, another strange property of the recovery distribution of Blackcaps was shown by Berthold and Terrill (1988). Unusual movements of migrating individuals were found in this species – north and north-west directions instead of the expected generally southward autumn migration. It was found for individuals ringed in the breeding season within Central Europe as well as individuals ringed during migration, even over the Polish Baltic coast and Scandinavia. Busse (1992), discussing this phenomenon, wrote the following: "Basing on Zink's (1973) and Polish data I calculated that as much as about 7.5%

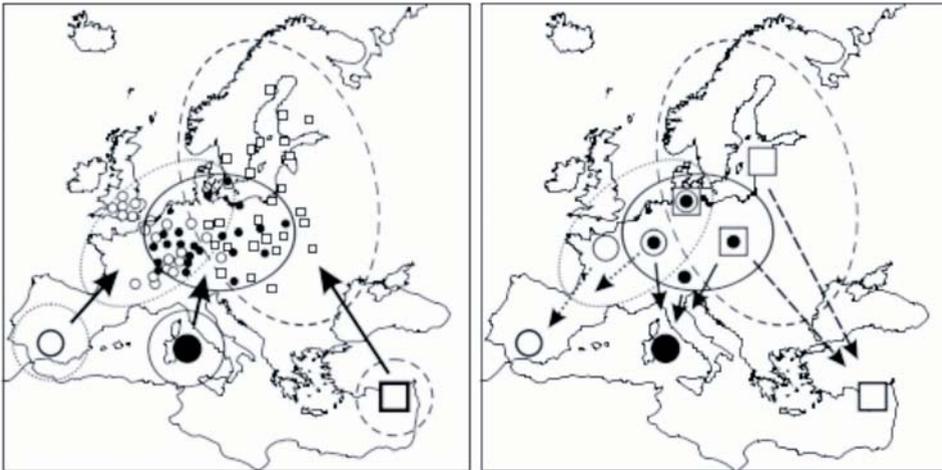


Fig. 4. 'A. Recovery pattern of the Blackcap drawn after 'looking from the south' method. Small symbols show the ringing places of birds found in the wintering quarters designated by the big symbols. B. Population areas of the Blackcap from that shown in A. The simple symbols at the breeding grounds show areas occupied by pure populations, combined symbols show zones where there is a mixture of two or three populations. After Busse 1987, modified.' After Busse (2001).

of Blackcaps ringed at autumn migration show then "strange" direction of further passage. This is an extraordinary high proportion and it seems to be unique, as to frequency phenomenon in European Passerines, e.g. out of few hundred recoveries of Robins (*Erithacus rubecula*) ringed by Operation Baltic only one or two show "wrong" direction of autumn migration." Berthold and Terrill (*op. cit.*) explained this phenomenon as the result of a shift in the western heading directions, which could be called the *direction shift model*. Busse (1992) discussed and rejected this model and proposed a *reversed migration model* based on the population distribution hypothesis presented above. As a very special phenomenon, the problem of the new breeding grounds recently created within the British Isles was not discussed in a PhD dissertation (Mokwa 2004) evaluating all available ringing results for Europe. The newly proposed population and migration pattern of the European Blackcap is given in Figure 5 with some corrections by Busse (2012). The correction in the Middle East was based on the field work of the SEEN network, especially data collected in Egypt, where very low intensity of Blackcap autumn migration was found in the easternmost part of the country (Ibrahim and Busse 2012).

One of the most effective methods for studying the migratory patterns of nocturnal passerine migrants by checking their local headings is the use of orientation cages as a regular supplementary procedure at ringing sites, introduced in 1995 (Busse 1995). The new construction of the flat orientation cage called now *Busse's flat cage* and a novel standard procedure (only 10-minute testing during the daytime) enabled intensive data collection. Moreover, a new evaluation method was introduced (Busse 1995, Busse and Trocińska 1999). Since that time more than 43,000 tests have been

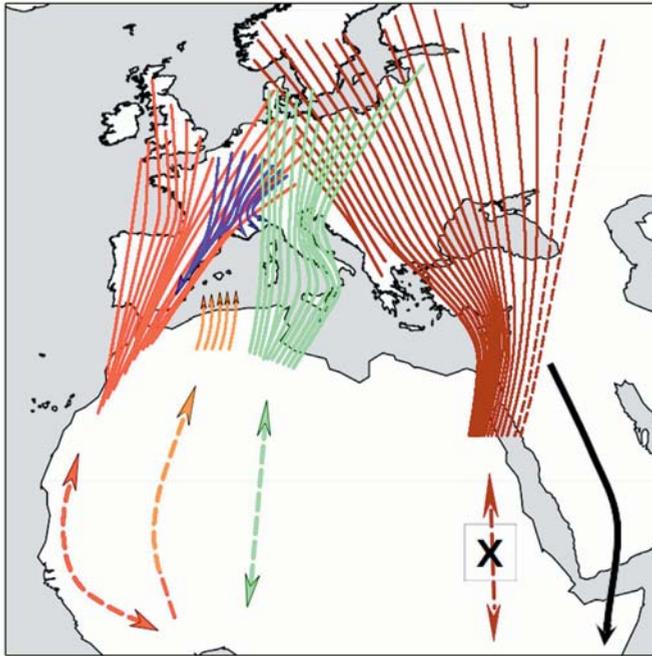


Fig. 5. Migration pattern of Blackcap migration according to Mokwa (2004), corrected by Busse (2012).

collected from nocturnal migrants at more than 40 European ringing sites in autumn, mainly by Operation Baltic and SEEN (SE European Bird Migration Network) (Busse 2019). The development of the evaluation of test data was discussed by Busse (2018), and the general pattern of nocturnal migration of passerines (all species included) based on collected data was presented in a subsequent paper by Busse (2019). It was found that at every location studied a few migration streams directed towards different destinations can be defined. They are usually highly coherent over wide territories and thus reflect different species/population migration patterns. Before analysing the migration patterns of individual species, a few basic properties of the data should be clarified.

This was done in a case study on the Blackcap at the Polish ringing station Bukowo/Kopań (Operation Baltic/SEEN), as the station whose orientation data set covered the longest period (1995-2010) and where the Blackcap was one of the most commonly tested species (Busse 2020). It is well known that most single individuals show multimodal headings in the cage (e.g. Busse 1995; Busse and Trocińska 1999; Muś 2005, 2008; Ożarowska and Muś 2008), and the same holds when we add up these headings into group/sample headings at the test site. In most cases, especially in the group heading patterns, the heading axes were found to be located more or less on opposite sides of the wind rose, and were interpreted as *input* (arrival) and *output* (departure) headings. Distributions in group headings are varied as to 'power', so we can roughly estimate the number shares of groups migrating in different directions.

This paper is an attempt to draw a large-scale autumn migration pattern for a sample species – the Blackcap, which has been mentioned several times in this type of study (e.g. Busse *et al.* 2001, Adamska and Rosińska 2006, Stępniewska *et al.* 2011) as a basis for subsequent specific evaluations and study of the migratory habits of several passerines living in Central and Eastern Europe.

MATERIAL

As in the general passerine migration pattern presentation (Busse 2019), the study area (Fig. 6) covers mainly the SE European Flyway, but also includes a few sites located on the Central European Flyway (Croatia and Italy) and a site in Medvedivka, Russia, which partly belongs to the Indian Flyway. The sites, years of work and numbers of individuals tested are given in the Appendix and characterized below, in alphabetical order of the station letter codes used in Figure 6 and elsewhere.

AA – Aras, Turkey (2006–2007, $N = 38$) – *general location*: river valley running from west to east at the southern foothills of the Caucasus; *habitat*: riverine vegetation, mainly tamarisks with some reeds, garden at the border of a village and meadows.

AC – Carpatica, Poland (2000–2002, 2004, $N = 247$) – *general location*: valley running from north to south on the northern side of the Carpathian Mountains; *habitat*: riverine willow shrubs, young pine forest, shrubs of over 20 species.

AN – Antikythera (Greece, 2009, $N = 12$) – *general location*: small island north of Crete; *habitat*: dry open area.



Fig. 6. Geographical distribution of study sites in Europe. For legend see text (p. 9) and Appendix. After Busse (2019), modified.

AK – Akyatan, Turkey (2003, $N = 117$) – *general location*: south-eastern part of the Turkish Mediterranean, narrow spit between the sea and a huge coastal lagoon; *habitat*: strip of bushes along the coast of the lake, bordering with mixed forest opposite a narrow road.

AR – Arosio, Italy (2005–2009, $N = 342$) – *general location*: a *rocollo*, a traditional artificial garden prepared in the past as a site for hunting and catching migratory birds in the hills south of the Alps; *habitat*: diverse trees and bushes, especially attractive for migrants, attracting them with berries and water as well as with caged birds.

AS – Siemianówka (Poland, 2002–2004, $N = 148$) – *general location*: inland site in a farmland region near a lake, north of the vast Białowieża Forest National Park; *habitat*: wet bushy habitat surrounded by reeds and meadows.

AZ – Azraq (Jordan, 2002–2003, $N = 16$) – *general location*: large, inhabited oasis within a desert, previously a large swampy area with open water, about 60 km SE of permanent human settlements; *habitat*: several small open water bodies with reed beds and mainly tamarisk bushes.

BK – Bukowo/Kopań (Poland, 1995–2010, $N = 1554$) – *general location*: narrow strip of forest between the southern Baltic coast and open meadows; *habitat*: a coastal strip of pine forest as well as strips of shrubs, mainly willow, along ditches crossing a meadow and bordering on Lake Kopań, which is surrounded by reed beds.

CR – Cernek (Turkey, 2002–2004, 2009, $N = 858$) – *general location*: coastal site on a bay of the Black Sea; *habitat*: strips of shrubs with fragments of meadows.

DH – Dhleil (Jordan, 2002, $N = 539$) – *general location*: border between inhabited rural area and desert; *habitat*: vast orchard area (e.g. olive, apple, and almond trees).

DI – Dicle (Turkey, 2003–2005, $N = 76$) – *general location*: valley of the Tigris near Diyarbakir, on university property, but several hundred metres from the university buildings; *habitat*: bushes along the river bordering on open dry meadow habitat.

DR – Drużno (Poland, 1996–2007, $N = 107$) – *general location*: bordering on Lake Drużno, much overgrown with reed beds; *habitat*: mainly willow and alder bushes within reed beds and *Carex* wetlands.

EI – Eilat (Israel, 1999–2002, $N = 48$) – *general location*: an area close to the town of Eilat on the northern coast of the Gulf of Aqaba; *habitat*: artificially arranged, but planted with natural local vegetation; an area of many hectares with fresh and salt water bodies.

GU – Gumbaritsy (Russia, 2000–2001, $N = 6$) – *general location*: southern coast of Lake Ladoga; *habitat*: clearing partly covered with meadows within a wet forest, with buildings of the Biological Station.

HA – Haademeeste (Estonia, 1996, 2001, $N = 32$) – *general location*: –; *habitat*: –.

HY – Hashimyia (Jordan, 2001, $N = 340$) – *general location*: a garden of a few hectares within an inhabited rural area; *habitat*: – orchard (olive and others) orchard, vineyard.

KB – Karabogaz (Armenia, 2004, $N = 28$) – *general location*: western coastal area of the Caspian Sea; *habitat*: –.

KK – Kalimok (Bulgaria, 2001, $N = 14$) – *general location*: inland site bordering on a huge reed bed; *habitat*: bushy habitat within a wetland.

KN – Kinburn (Ukraine, 2001, $N = 32$) – *general location*: seaside locality; *habitat*: -.

MV – Makarovka (Russia, 1998–2001, $N = 34$) – *general location*: an island (about 2 km long, 1 km wide) at the confluence of the Volga, Kama and Myosha Rivers; *habitat*: meadows with some willow shrubs and trees, as well as small water bodies with rushes.

MW – Mierzeja Wiślana (Poland, 1996–2008, $N = 229$) – *general location*: Vistula Spit, narrow spit between the Vistula Lagoon and the Gulf of Gdańsk; *habitat*: forest bordering on reed beds.

OL – Olenivka (Ukraine, 2006, $N = 218$) – *general location*: western coast of the Crimean Peninsula on the northern Black Sea; *habitat*: open steppe with a small valley overgrown with sparse bushes.

PP – Pape (Latvia, 2000–2003, $N = 21$) – *general location*: eastern coast of the Baltic Sea; *habitat*: strip of forest along the coast, bordering on meadows and a lake.

RA – Lake Rakutowskie (Poland, 2010, $N = 44$) – *general location*: inland lake in a rural area; *habitat*: bushes on the shore of the lake, partly within a reed bed and a meadow.

TK – Talitha Kumi (Palestine, 2000, $N = 170$) – *general location*: small park with fruit trees within a densely inhabited area; *habitat*: a small fruit garden with a group of coniferous trees.

TM – Tulkarem (Palestine, 2015, $N = 21$) – *general location*: several hectares of the Agricultural University, bordering on the town; *habitat*: diverse fruit demonstration/experimental garden.

TU – Turov (Belarus, 2000, $N = 18$) – *general location*: inland site; *habitat*: -.

UC – Ucka (Croatia, 2014, $N = 83$) – *general location*: western coast of the Istria Peninsula; *habitat*: forest on coastal hills.

There are a few sites where data from several years on a vast number of birds have been collected: the longest time spans are 14 years at Bukowo/Kopań (1554 birds tested) and 10 years at Mierzeja Wiślana (229 individuals). Yearly samples at individual sites frequently numbered dozens or even hundreds of tests (e.g. 858 at Cernek or 539 at Dhleil sites). At some SEEN sites, however, only a few autumn data are available, and in some cases only single or no Blackcaps were caught or tested. Therefore there is pronounced variation in the actual value of local directional patterns. Nevertheless, the sample sizes, in terms of number of sites (28) and number of tests performed (5,392), are large enough to provide a general pattern of the movements of this passerine species on a wide geographic scale. Generally, the analysis contains data from 26 ringing sites at which more than 15 tests were performed. On a few maps, two additional sites were presented where fewer tests were carried out (6 at Gumbaritsy and 12 at Antikythira).

METHODS

The general data evaluation methods in this work are exactly as described in previous papers by Busse (2017, 2019, 2020). Because it is essential to understand the reasoning used in this work, some parts of this section are exact quotations from the previously published papers. If any doubts remain regarding the methods presented here, it is recommended to consult the papers mentioned above for details omitted from this abbreviated description.

“Birds were caught using mist-nets, sexed/aged, measured (wing-length, tail-length, wing-formula), scored for the fattness and weighted according to the Operation Baltic/SEEN standards (Busse 2000). Instantly (within 2 hours) individuals were tested in Busse’s Flat Orientation Cage (Busse 1995) ... Test lasted 10 minutes. Total number of Blackcaps caught at ringing sites was usually much higher than tested, thus numbers of these tested do not reflect intensity of blackcaps migration at these sites. Individuals for testing were taken randomly, mainly according to availability of man-power for running tests.

Basic field data processing was presented and discussed in detail in the paper by Busse (2017), using the procedure accepting multimodality of distributions at both levels of evaluation: individual bird and group distribution of headings. Individual bird level based on real numbers of scratches in eight sectors of the cage that were made by an individual tested. The individual distributions of scratches passed through the ORIENT 4.6 software program, which gave individual heading pattern (none significant heading according to chi-square test, or one to a maximum four vectors, that were classified to one of 16 sectors of the wind-rose). Every vector had own “power” - a percent share in a total number of scratches. Individual heading pattern can be presented as vectors (direction and length illustrating the “power”) on a wind-rose panel. These presentation is used rarely, as the main goal of testing is to reach the group distribution of headings. At the group level vectors of all individuals included into defined sample were summarized in sectors. Group headings distribution was the distribution of percent shares (indices of the number of headings) of above sector sums in the total sum of powers. Group distributions are usually presented as polygons at a radar graphs on the wind-rose panel...

According to the procedure of estimation of the main headings described in detail in the paper by Busse (2018) the distribution was interpreted as several estimated headings presenting “input” (arrival) and “output” (departure) heading directions” (Busse 2020).

A problem that was solved earlier (Busse 2020) for the Blackcap on the basis of data from one ringing site – Bukowo/Kopań – is confirmation of the suspected axially of arrival and departure headings. Thus the axially of headings is assumed here, and the opposite or quasi-opposite headings found at the various ringing sites are presented in the figures using fixed colours representing axes of migration at a given location. Thus, the *RED* stream is heading very much westward (traditionally called the Atlantic Flyway), the *BLUE* stream heads towards the western Mediterranean, *GREEN* heads SW towards the Chad Lake area (?), *ORANGE* heads directly to the eastern

part of Africa, and *YELLOW* is directed towards the Middle East/Arabian Peninsula (the last two together are usually called the SE European Flyway), while *WHITE* heads towards a winter quarters very far eastward. The *BLACK* heading is surprisingly longitudinal and has never before been described, but mentioned only by Busse (2019).

*“The properties of the field method – orientation cage wind-rose divided onto eight sectors only – caused that heading vectors cannot be too precise, both as to direction and their length. Till now, estimations of the precision suggest that directions set using estimation procedures can be precise at the level of plus/minus 6–11°, that means one of 32 rose-wind sectors. Estimation procedure, as after Busse (2019), takes under consideration mainly the local maxima of the polygon of headings distribution ... If we want to set more quantitatively the heading direction (and its “power” - the number index of the heading vector) we can use in the result vector calculation not only the local maximum value, but those closely bordering (minus one and plus one sectors values) and summarize these three values. The result vector will be **more** precise than previously and we will have **some information** about its power (index share in the total distribution). The power values will be still estimated, but they will be called later as “**calculated**”. ... In any general bird migration study the level of precision reached here is enough high to discuss migration patterns in the continental scale.”* (Busse 2020).

In the present work, the axially of the arrival and departure headings is checked at the inter-site level. For every study site, headings assigned to a specific stream were compared with respect to the wind-rose sectors they belong to, and deviations from the straight line were determined (‘0’ = opposite sector, ‘+’ – departure heading shifted clockwise, ‘-’ – shift anti-clockwise). Comparisons were made separately for *raw* and *calculated* headings.

Apart from axially, another parameter characterizing the departure/arrival number indices was studied: the *Departure/Arrival* number relations vary at different sites and for different streams of migrants. Two aspects of this parameter were studied – the geographic location of the site and the stream of migration.

The geographical description of the Blackcap migration pattern is presented using three different procedures – a rough graphical estimation, a more precise graphical procedure, and a calculation procedure. (1) In the first, local heading patterns have traditionally (Busse 2019) been situated on the map (as in Fig. 8). Following that tradition, areas where specific streams of Blackcap migration were observed and the approximate directions of these streams were drawn (as in Fig. 9). (2) Another variant of graphical estimation of the pattern used a basic map with the distribution of local headings in a geographical space (see Fig. 10A). Then the local headings were extended using straight lines in both directions: arrival headings to the north and departure headings to the south (see Fig. 10B). Next, the average crossing points of the migration heading lines with the edge of the map were determined (see Fig. 11). A summarizing figure (Fig. 12) presents a general estimation of the axes of the Blackcap populations' migration. (3) In the calculation procedure, the data from stations where the defined heading stream was observed were studied, i.e. the centre of the station's location (average geographic co-ordinates) and average arrival and departure tracks (see Fig. 13).

Table 1

Basic heading parameters for streams of migrants. Track – average heading sector of 32-sector wind-rose; Deviation – deviation of departure heading from straight extension of arrival heading (as number of sectors); Index – average number index of stream heading; Axis – sum of arrival and departure indices; % – percentage share of Axis within total distribution of stream; Dep./Arr. – average ratio of departure to arrival index within the stream distribution.

Stream	N sites	Track				Index			
		Arrival	Departure	Deviation	Arrival	Departure	Axis	%	Dep./Arr.
<i>RED</i>	Avg	7.71	23.59	-0.03	10.49	8.67	19.15	25.34	1.00
	<i>SD</i>	0.43	0.76	0.34	2.85	4.12	3.31	3.69	0.79
<i>BLUE</i>	Avg	4.27	20.19	-0.01	11.29	9.02	20.31	27.70	0.95
	<i>SD</i>	0.39	1.14	0.79	4.21	3.22	3.26	5.20	0.46
<i>GREEN</i>	Avg	4.19	20.65	0.14	8.87	8.25	17.12	23.97	1.12
	<i>SD</i>	1.30	1.47	0.47	4.76	3.16	6.21	10.49	0.61
<i>VIOLET</i>	Avg	3.78	20.06	-0.03	9.00	7.74	16.74	23.35	0.80
	<i>SD</i>	1.46	1.55	0.69	3.29	4.44	6.07	8.15	0.46
<i>ORANGE</i>	Avg	30.84	15.48	0.14	8.71	9.96	18.68	23.87	1.51
	<i>SD</i>	1.42	0.83	0.68	5.45	4.64	7.80	9.34	1.10
<i>YELLOW</i>	Avg	27.56	11.76	0.20	14.94	12.24	27.18	37.56	0.95
	<i>SD</i>	1.08	1.16	1.30	5.95	5.28	7.47	12.54	0.47
<i>WHITE</i>	Avg	26.58	9.53						
	<i>SD</i>	0.41	0.54						
<i>BLACK</i>	Avg	7.26	21.82	0.16	9.88	14.68	24.56	32.08	1.61
	<i>SD</i>	2.20	6.59	0.36	1.75	6.92	6.13	7.84	0.99
Total	Avg	0.07	0.07	9.15	8.82	17.97	24.23	0.99	
	<i>SD</i>	0.09	0.09	3.94	3.98	7.59	10.25	0.46	

Some additional parameters, i.e. the number indices of different streams, relations between the departure and arrival number indices, and their relations with the location (geographic co-ordinates), were studied by means of Pearson's correlation.

RESULTS AND DISCUSSION

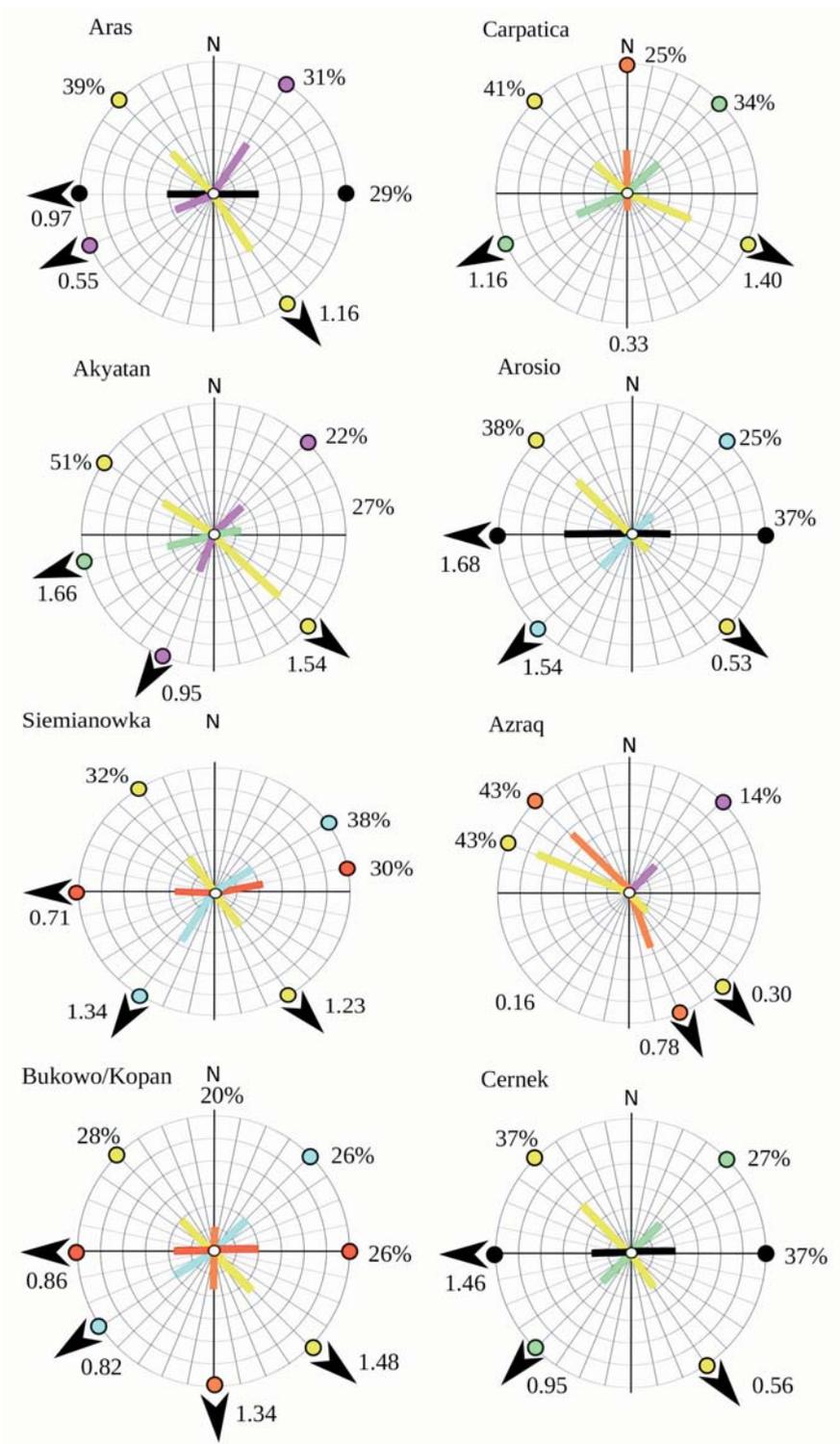
Local heading patterns

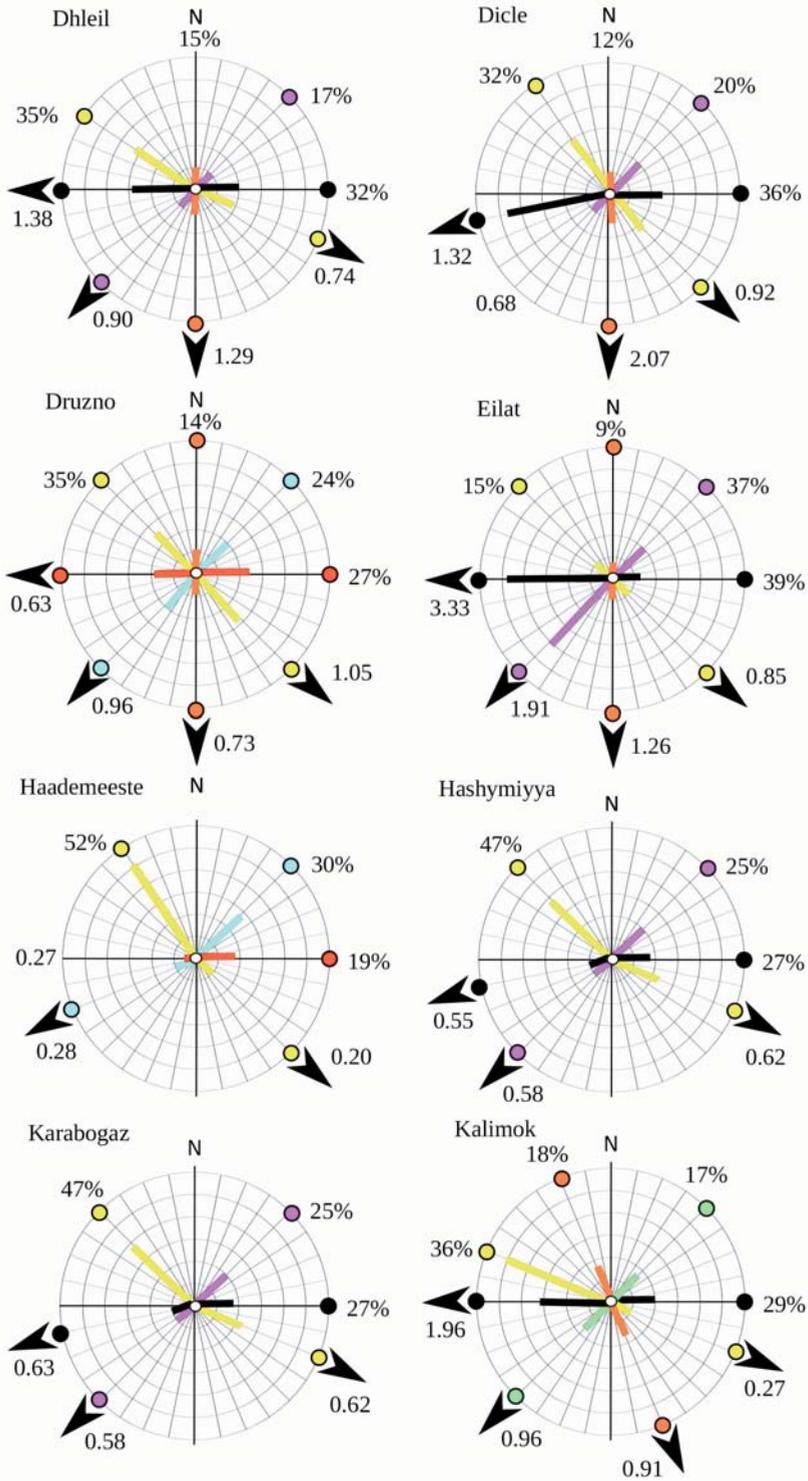
Evaluation of the local heading patterns began with procedures described in earlier papers (Busse 2019, 2020). The results are presented in Figure 7 and documented in the *Appendix*, where basic data are given about the local patterns at each ringing site: (1) classification of the local headings to one of eight migration streams defined in the general passerine migration pattern presented by Busse (2019) and designated with colour names (see *Methods*, pp. 12–13); (2) heading directions (sectors of the local wind-rose) of arrival and departure; and (3) indices of numbers of birds belonging to the stream groups. Values of derivative parameters used later in a detailed discussion of some aspects of the migration pattern are included. A summary for the migration streams is given in Table 1.

More than one stream of migration was found at all study sites (Fig. 7). The most commonly found was the *YELLOW* stream (27 of 28 sites), followed by *ORANGE* (17) and *BLACK* (12). The *WHITE* stream was found least often (2 sites), but this is because the eastern part of the study area was insufficiently covered by the study sites. The arrival and departure sectors of local distributions at the study sites are highly varied (Table 2). They do not occur in the same sector. This finding confirms that the local estimations differentiate streams well. Some doubts may arise from the separation of the *BLUE* stream from the *GREEN* and *VIOLET* ones (n.s. differences) as well as for the departure sectors of the *BLACK* stream. However, geographically the *BLACK* stream has a very unusual heading and must be discussed separately.

The arrival and departure tracks of the streams (from input to output sectors) show high linearity for the average spatial course; deviations from the average heading lines for separate streams range from 0.01 to 0.2 of the sector size, which is less than 2°. In general, the average deviation from the straight line is below 1°. **This strongly confirms the earlier finding that as a rule arrival and departure tracks are situated linearly.**

Average stream number indices are similar for arrival and departure headings (9.15 for arrival and 8.82 for departure headings), which means that the same number of birds depart the average site as arrive there, and the departure/arrival number ratio is close to 1 (0.99). However, it should be mentioned that this ratio varies for individual streams (from 0.80 to 1.61; $SD = 0.46$) and there is no correlation between streams in this parameter (Table 3). It seems that this variation is not a property of the streams, but possibly more of the geographic location of the study sites. This will be discussed later (p. 24 on). Total number indices representing numbers of birds using separate streams are similar for the *RED*, *BLUE*, *GREEN*, *VIOLET* and *ORANGE* streams (16.74 to 20.31 per stream) while the *YELLOW* group is the largest (27.18).





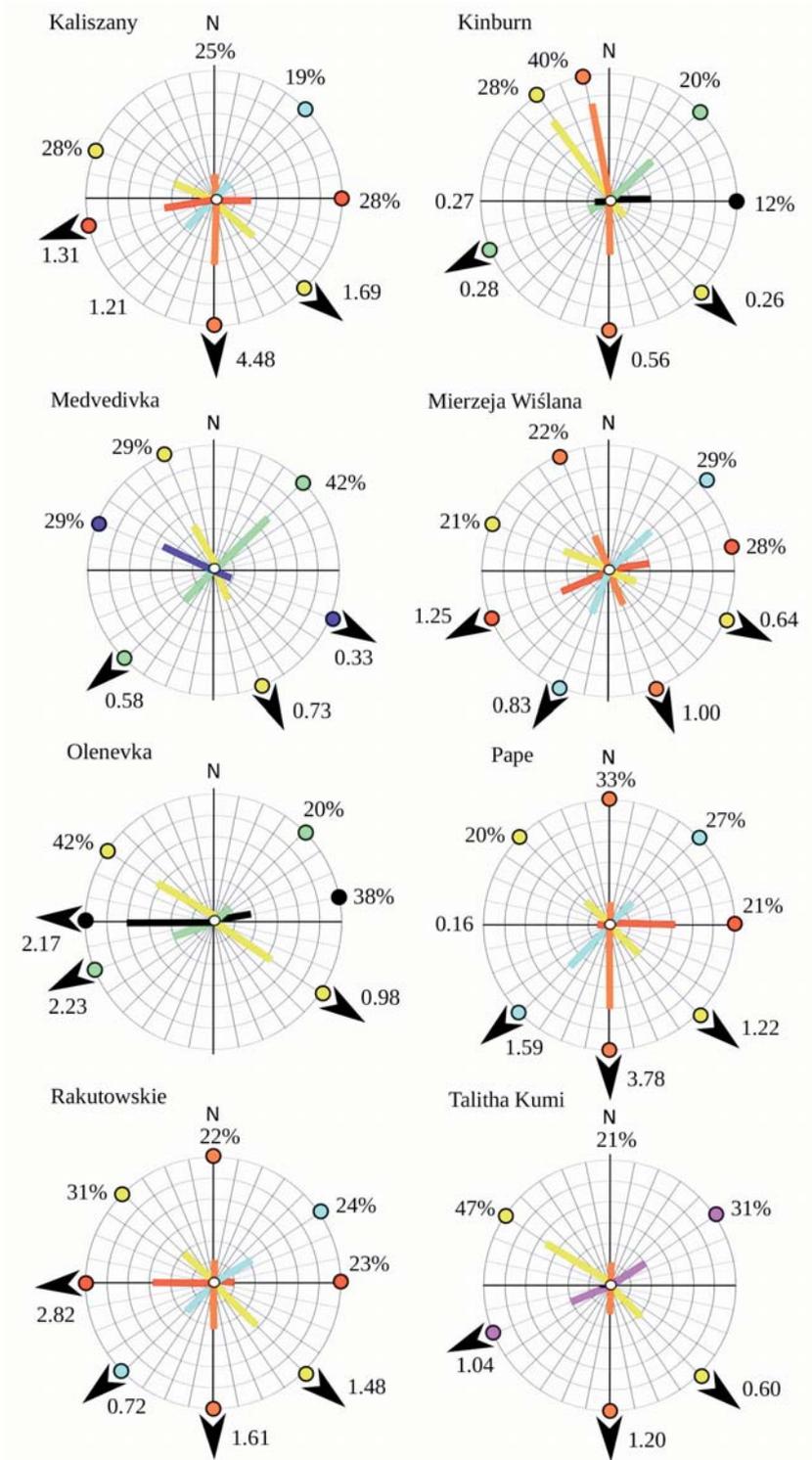


Table 3

Differences between average tracks of migration streams at study sites (see Table 1); p -values are given. *N.s.* differences are shaded.

	<i>RED</i>	<i>BLUE</i>	<i>GREEN</i>	<i>VIOLET</i>	<i>ORANGE</i>	<i>YELLOW</i>	<i>WHITE</i>	<i>BLACK</i>
<i>RED</i>	X	0.87	0.75	0.53	0.20	0.86	0.94	0.14
<i>BLUE</i>		X	0.54	0.47	0.08	1.00	0.86	0.05
<i>GREEN</i>			X	0.20	0.26	0.50	0.89	0.20
<i>VIOLET</i>				X	0.89	0.39	0.65	0.02
<i>ORANGE</i>					X	0.05	0.41	0.80
<i>YELLOW</i>						X	0.86	0.03
<i>WHITE</i>							X	0.34
<i>BLACK</i>								X

Spatial analysis of migration pattern

Starting maps for the spatial analyses of headings of Blackcap migrants were prepared as described by Busse (2019) and look like the example map for the Middle East (Fig. 8). Following this tradition, estimation of the general pattern for the Blackcap may look as presented in Figure 9. Generally speaking, it resembles the general passerine migration pattern presented by Busse (2019). This, however, is a very rough estimation of the pattern, and an attempt could be made to draw one with more detail and more accurate pictures.

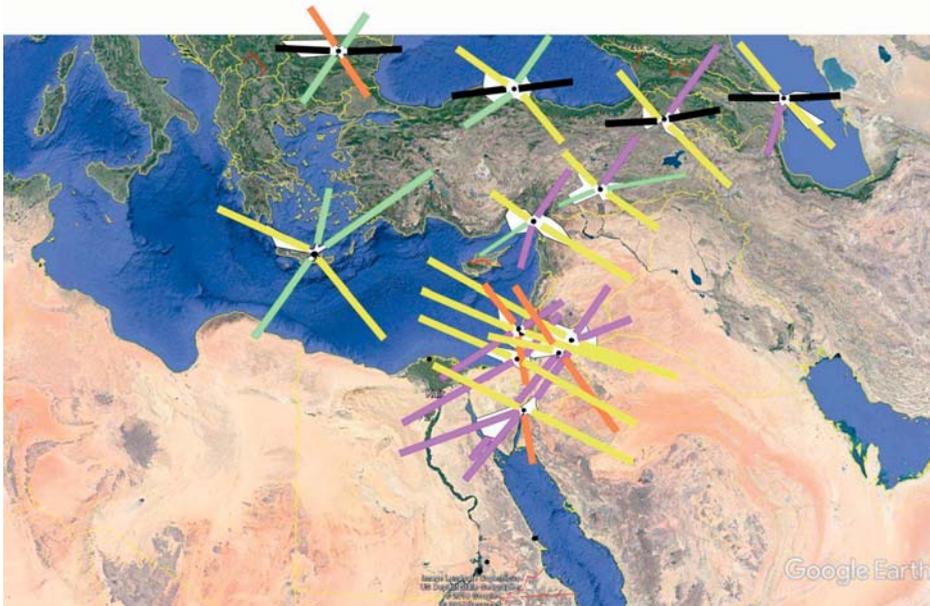


Fig. 8. Local heading patterns of Blackcap migration streams in the southern part of the study area, according to the style proposed by Busse (2019). White polygons – raw distribution patterns, bars – identified headings. Colours as defined in the text (pp. 12–13).

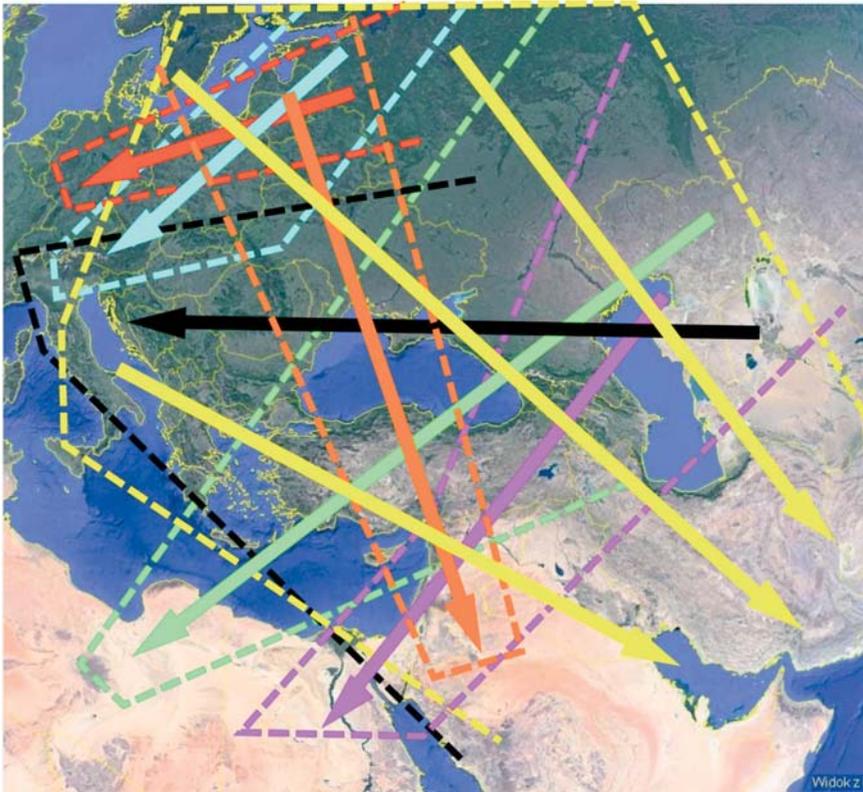


Fig. 9. General Blackcap migration pattern according to the style proposed by Busse (2019). Broken lines – borders of areas where a given migration stream was identified at the study sites; Arrows – estimated general directions of the streams. Colours as defined in the text (pp. 12–13).

A more exact graphical procedure was tested. Figures 10 (A, B) to 12 illustrate successive steps: (1) the traditional (Busse *op. cit.*) presentation of the local headings (Fig. 10A) is transferred to the pattern in Figure 10B by extending the local headings far from the site location (arrival tracks backward to the north and departure tracks forward to the south); this operation is based on the confirmed linearity of the tracks and the assumption that these headings are stable over long distances; (2) the tracks are extended to the borders of the map, and then the average crossing coordinates are calculated and drawn as in Figure 11 (example for two streams); (3) average tracks for the streams are presented in Figure 12, where the width of the lines is proportional to the numbers of the site where this stream was found. This pattern seems to clearly confirm the conclusion that the *YELLOW* stream is the most common in the study area.

The next procedure, based on some calculations, takes under consideration not only data for local headings at the study sites (*Appendix*) but the geographic co-ordinates of the sites as well. This locates the pattern more precisely in a geographical space, so the picture presented is more realistic than the patterns shown in Figures 9 and 12.

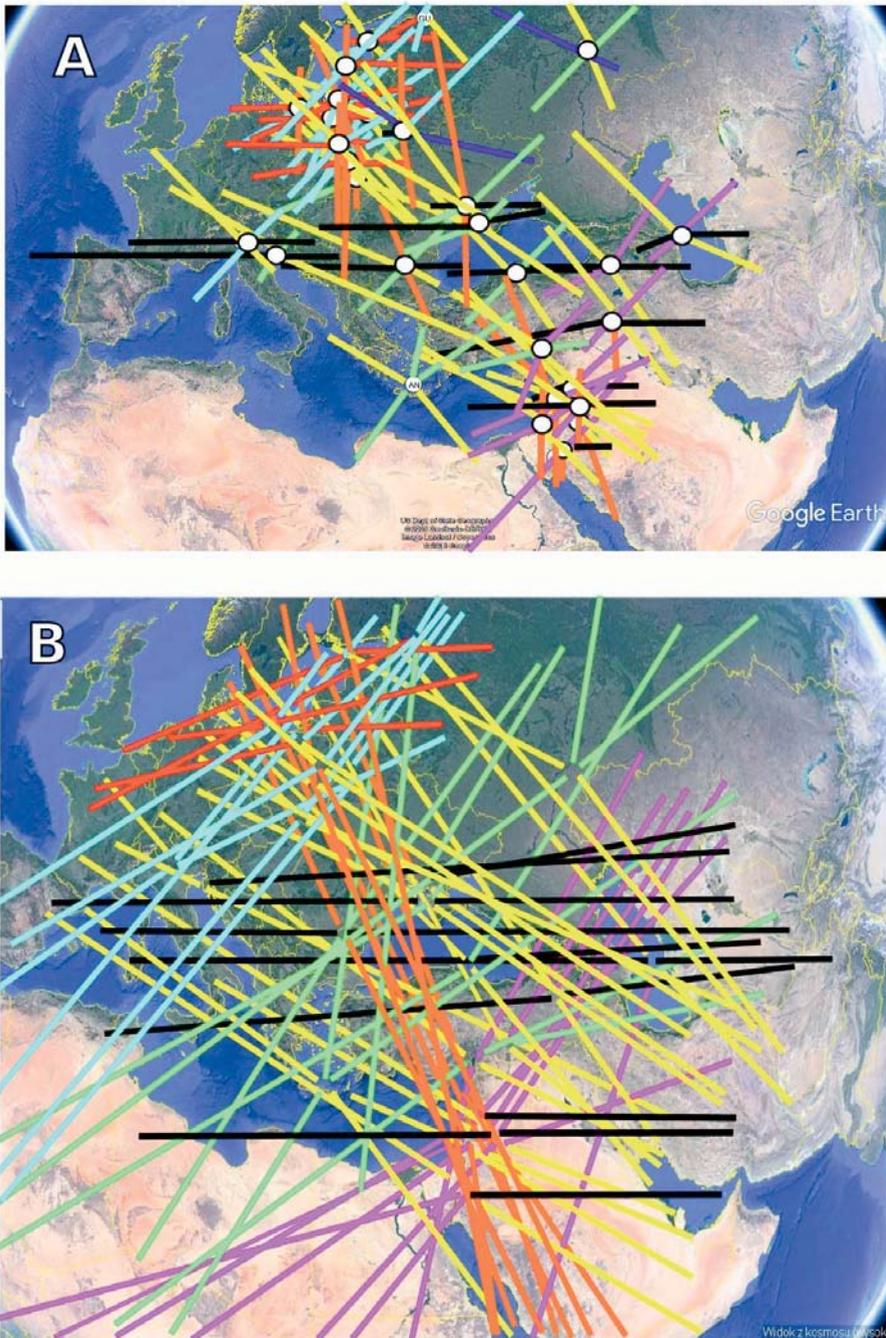


Fig. 10. First two steps in estimation of the general heading pattern from several local heading distributions. A. Determination of local heading distributions - local heading bars could be standardized (as in Fig. 7) or not standardized (as in Fig. 8). B. Local heading bars extended northwards (arrivals) or southwards (departures), even to the borders of the map (see Fig. 11).

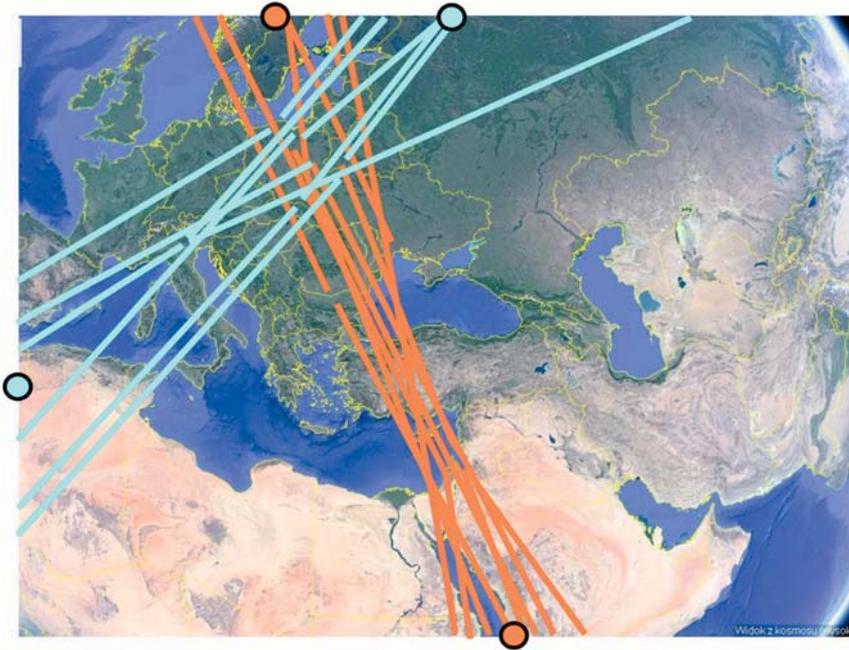


Fig. 11. Final step in estimation of the general heading pattern from several local heading distributions. Calculation of average co-ordinates at the edges of the map enabling estimation of the general heading axis of the stream (here example for the *BLUE* and *ORANGE* streams).

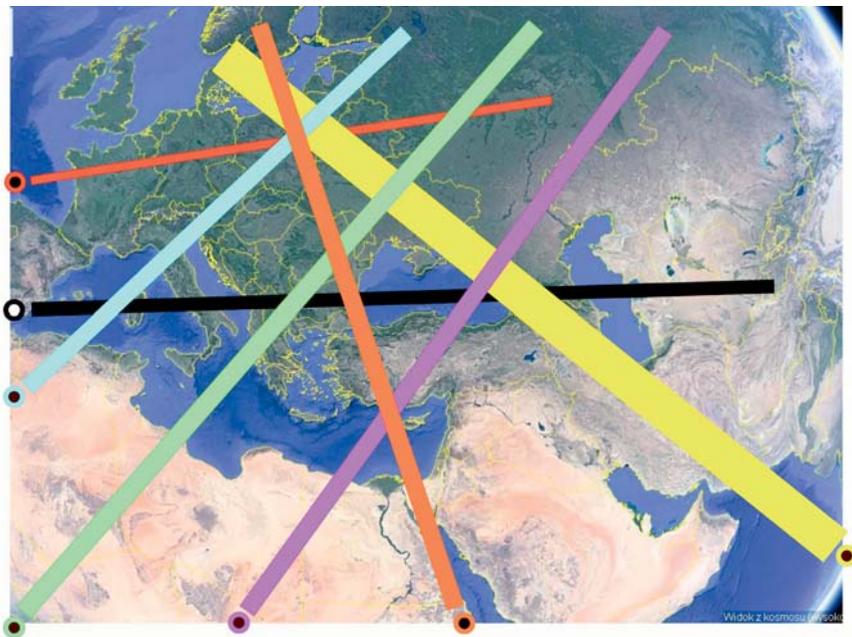


Fig. 12. General migration pattern estimation using the graphical method. Width of axes depends on the number of study sites where the stream was found. Colours as defined in the text (p. XX).

Details for the Blackcap migration streams are given in the maps in Figure 13, while a synthetic picture is shown in Figure 14. Comparison of the results from the three different procedures strongly suggests that the general picture of the Blackcap migration in Central/Eastern Europe and the Middle East is clear and coherent. This could enable comparison of the migration patterns of species representing different migratory habits and expansion histories. In the case of the Blackcap, it seems that one could try to connect migration streams to different winter quarters, as shown on distribution maps similar to that presented in Figure 1 (Moreau 1972).

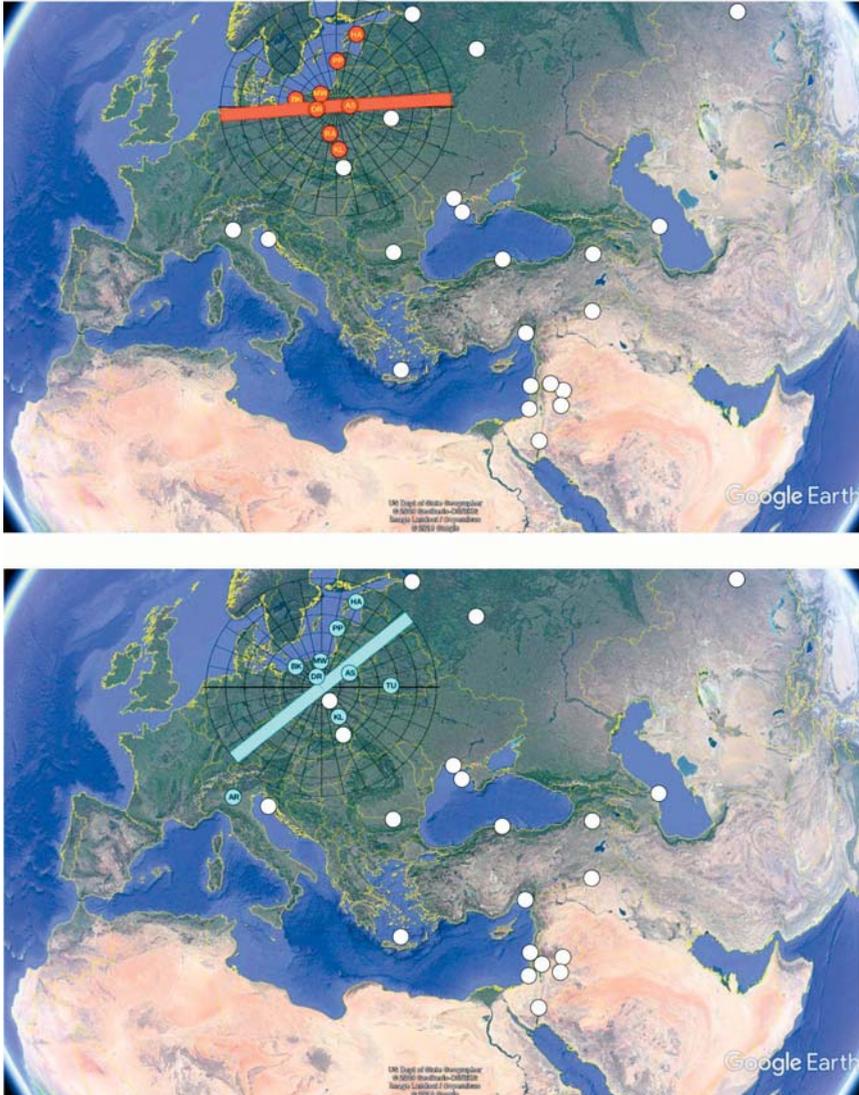


Fig. 13-1. Geographic location for *RED* and *BLUE* migration streams according to average coordinates of the study sites where the stream was found (coloured circles) and average headings of that stream at the sites.

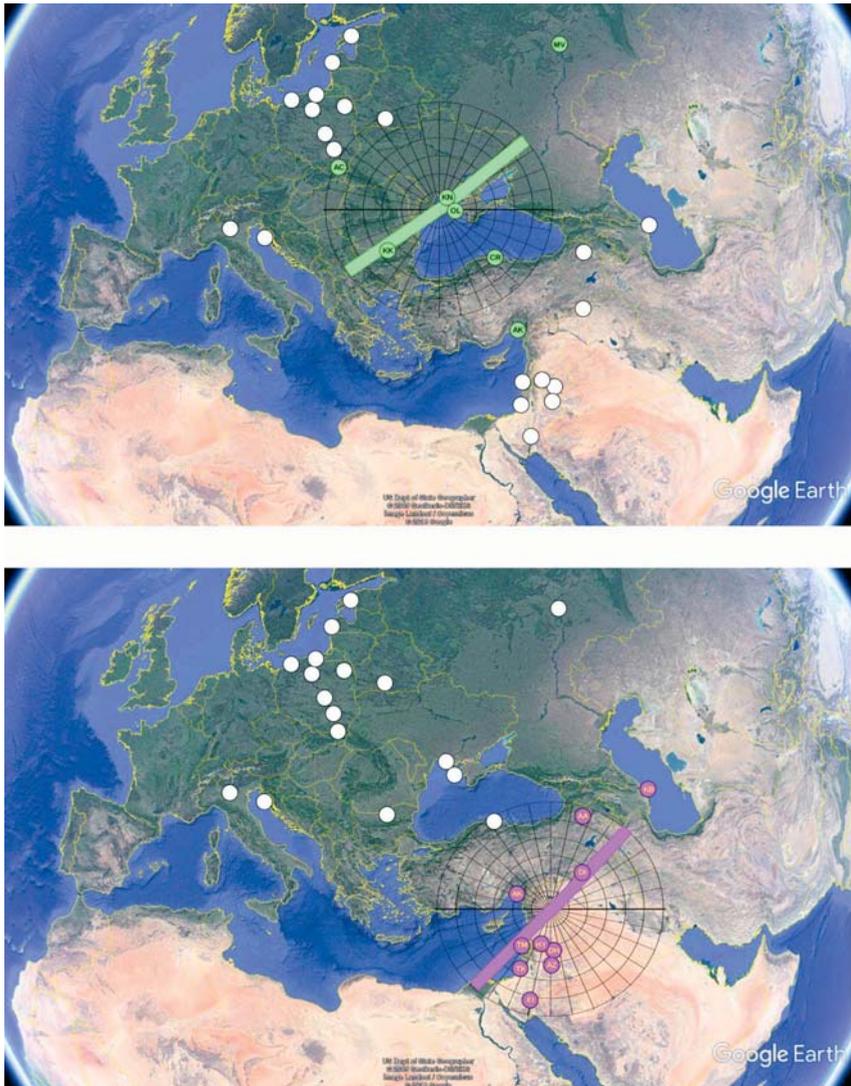


Fig. 13-2. Geographic location for GREEN and VIOLET migration streams according to average coordinates of the study sites where the stream was found (coloured circles) and average headings of that stream at the sites.

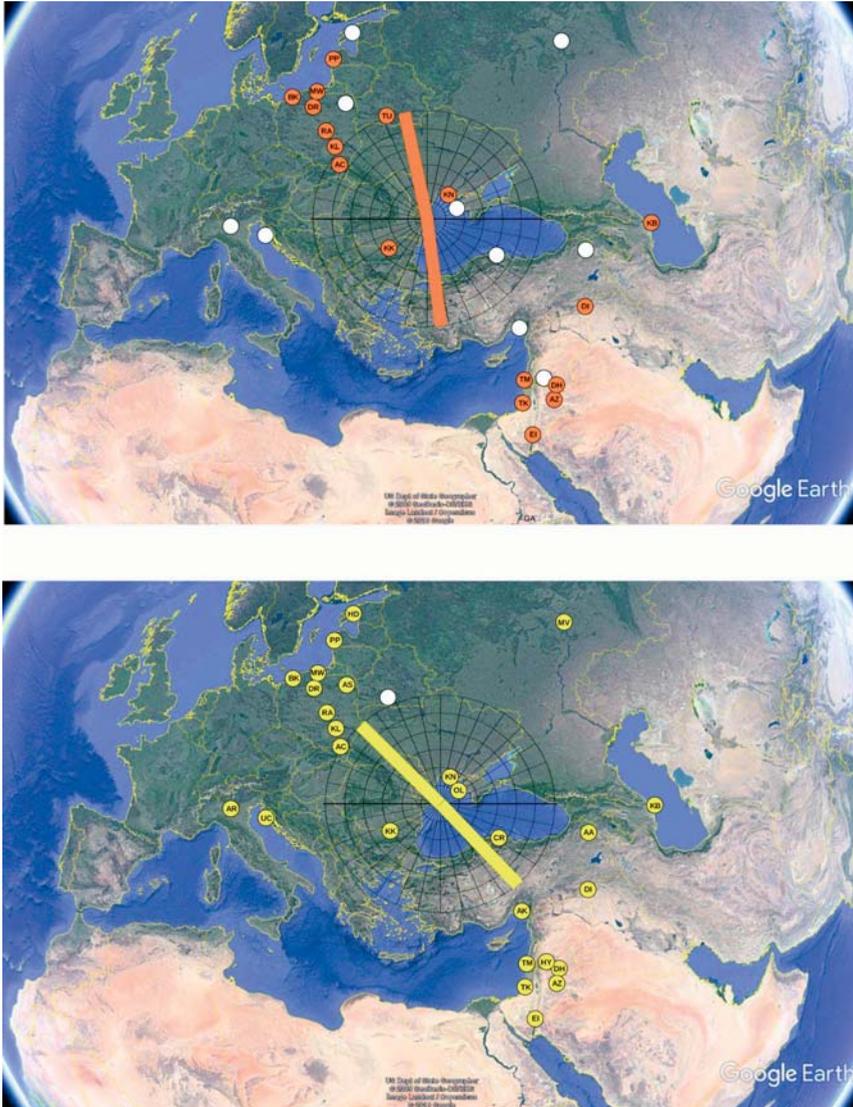


Fig. 13-3. Geographic location for *ORANGE* and *YELLOW* migration streams according to average coordinates of the study sites where the stream was found (coloured circles) and average headings of that stream at the sites.

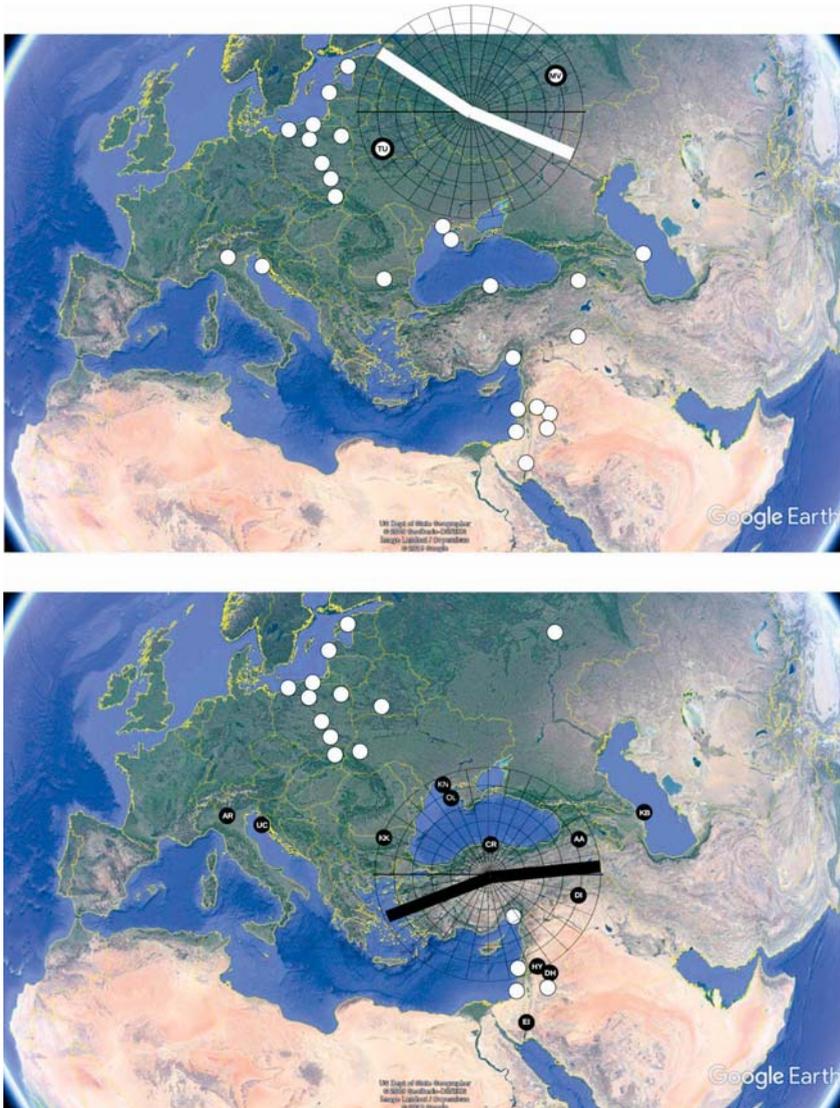


Fig. 13-4. Geographic location for *WHITE* and *BLACK* migration streams according to average coordinates of the study sites where the stream was found (coloured circles) and average headings of that stream at the sites.

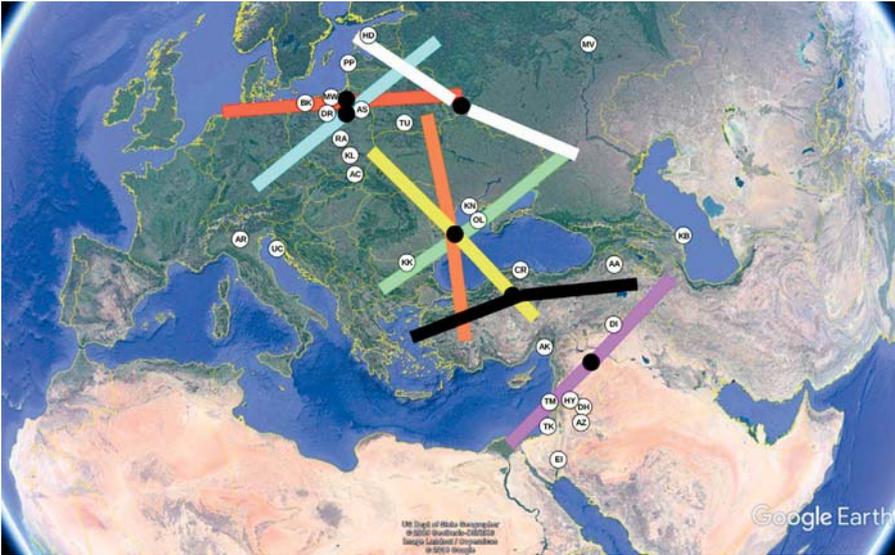


Fig. 14. General migration pattern estimated using the calculation method. Colours as defined in the text (pp. 12–13).

The study area covers wide ranges of both latitudes and longitudes of ringing sites. It might be reasonable to study whether within this wide area local values of parameters – linearity of arrival-departure headings and number ratios between arrival and departure headings presented in the test cage – are geographically variable. The general rule that departure headings (to the south) follow the straight course of the arrival headings was mentioned above (p. 15). However, some peculiarities were found when the correlation of the deviation from the straight line against the latitude and longitude was checked. Table 4 presents the results of this analysis. Within the *RED*, *BLUE*, *GREEN* and *VIOLET* streams, the deviations observed are positively correlated with the latitude (the more northern the location, the higher the value of the deviation parameter), but Pearson's r values are not statistically significant. Within the *YELLOW* and *BLACK* streams, the correlations are negative (still n.s.), while for the *ORANGE* stream the correlation is not only high ($r = -0.65$), but statistically significant at 0.05. In contrast, the correlations with longitude are only positive (for the *YELLOW* stream with even a significant r -value = +0.40, $p = 0.05$); the correlation for all sites together is positively correlated (+ 0.53) at $p = 0.01$. For most of the streams, the departure/arrival number ratio seems to be negatively correlated with both the latitudes and longitudes of the locations, but none of the r -values there are significant. However, the *ORANGE* and *YELLOW* streams show positive values of the r coefficient (also not significant). As the results are difficult to explain without too much speculation, the comments must wait for more species to be studied in this respect.

Table 4

Correlation (Pearson's r -values) of the stream parameters (linearity and departure/arrival values) with the geographic location (coordinates) of the study sites.

In brackets – p -values; statistically significant values in bold.

Results of sign-test are added.

Stream	Deviation		Departure/Arrival	
	N	E	N	E
RED	+0.32	+0.22	-0.57	-0.33
BLUE	+0.15	+0.21	-0.52	-0.53
GREEN	+0.03	+0.08	-0.45	-0.41
VIOLET	+0.20	+0.31	-0.29	-0.41
ORANGE	-0.65 (0.05)	+0.40	+0.24	-0.03
YELLOW	-0.32	+0.40 (0.05)	+0.19	-0.23
WHITE				
BLACK	-0.10	+0.44	-0.04	-0.51
Total	-0.42 (0.05)	+0.53 (0.01)	-0.03	-0.23
Sign-test	$p = 0.77$	$p < 0.001$	$p = 0.23$	$p < 0.001$

CONCLUSIONS

1. The hypothesis put forth by Busse (2019) that arrival/departure heading axes are generally linear is accurate to within about one 10° sector. It was confirmed here at the level of local patterns for the study sites. In general, the average deviation from the straight line is below 1° . However, there is some geographical variation, and this problem could be discussed when many more results of this kind become available for a few more species.

2. The *YELLOW* stream seems to be the most common in the study area in terms of both the number of sites where it occurs and the numbers of migrants following it. The *BLACK* stream has a rather curious, longitudinal direction that could be investigated in further studies.

3. Comparison of the patterns obtained from three different procedures strongly suggests that the general picture of Blackcap migration in Central/Eastern Europe and the Middle East is clear and coherent. This encourages evaluation of data collected for other species.

4. Some variation in migration stream parameters (linearity and reversed heading share) suggests that further study in this direction could be undertaken using data from other species.

ACKNOWLEDGEMENTS

The data were collected from 1995 to 2016 during field work at 28 sites in 14 countries by dozens or even hundreds of professionals and volunteers. This makes it impossible to thank them individually, but they can all feel that this paper has been

completed thanks to their hard work. We all participated in the network activity, as Operation Baltic, SEEN or individual projects, by collecting the data and discussing the method of applying and interpreting the results during numerous meetings and e-mail contacts. Thank you all, indeed.

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Appendix

AA Aras	Sector			Index				Departure
	Arrival	Departure	Deviation	Arrival	Departure	Axes	Axis %	Arrival
<i>RED</i>								
<i>BLUE</i>								
<i>GREEN</i>								
<i>VIOLET</i>	4.1	22.0	2	14.5	8.0	22.5	31	0.55
<i>ORANGE</i>								
<i>YELLOW</i>	27.9	13.0	1	13.0	15.0	28.0	39	1.16
<i>WHITE</i>								
<i>BLACK</i>	7.9	24.2	0	10.3	10.7	21.1	29	1.04
<i>N = 38</i>			3	37.8	33.7	71.5	100	0.89
AC Carpatica	Sector			Index				Departure
	Arrival	Departure	Deviation	Arrival	Departure	Axes	Axis %	Arrival
<i>RED</i>								
<i>BLUE</i>								
<i>GREEN</i>	4.0	20.0	0	10.0	11.5	21.5	34	1.16
<i>VIOLET</i>								
<i>ORANGE</i>	0.0	15.9		11.6	3.8	15.4	25	0.33
<i>YELLOW</i>	28.1	10.0	-2	10.8	15.1	25.9	41	1.40
<i>WHITE</i>								
<i>BLACK</i>								
<i>N = 247</i>			-2	32.4	30.4	62.8	100	0.94
AK Akyatan	Sector			Index				Departure
	Arrival	Departure	Deviation	Arrival	Departure	Axes	Axis %	Arrival
<i>RED</i>								
<i>BLUE</i>								
<i>GREEN</i>	7.1	23.0	0	6.8	11.4	18.2	27	1.66
<i>VIOLET</i>	4.0	18.1	-2	7.5	7.1	14.6	22	0.95
<i>ORANGE</i>								
<i>YELLOW</i>	27.0	12.0	1	13.3	20.4	33.7	51	1.54
<i>WHITE</i>								
<i>BLACK</i>								
<i>N = 117</i>			-1	27.6	38.9	66.5	100	1.41
AR Arosio	Sector			Index				Departure
	Arrival	Departure	Deviation	Arrival	Departure	Axes	Axis %	Arrival
<i>RED</i>								
<i>BLUE</i>	4.1	20.1	0	6.5	10.0	16.4	25	1.54
<i>GREEN</i>				0.0				
<i>VIOLET</i>				0.0				

CR Cerneq	Sector			Index				Departure
	Arrival	Departure	Deviation	Arrival	Departure	Axes	Axis %	Arrival
<i>RED</i>								
<i>BLUE</i>								
<i>GREEN</i>	4.1	20.1	0	8.8	8.4	17.2	27	0.95
<i>VIOLET</i>								
<i>ORANGE</i>								
<i>YELLOW</i>	27.9	13.0	1	15.0	8.5	23.5	37	0.56
<i>WHITE</i>								
<i>BLACK</i>	8.0	24.0	0	14.0	9.6	23.7	37	0.69
<i>N = 858</i>			1	37.9	26.5	64.4	100	0.70

DH Dhleil	Sector			Index				Departure
	Arrival	Departure	Deviation	Arrival	Departure	Axes	Axis %	Arrival
<i>RED</i>								
<i>BLUE</i>								
<i>GREEN</i>								
<i>VIOLET</i>	4.0	20.0	0	7.3	6.6	13.9	17	0.90
<i>ORANGE</i>	0.0	16.0		5.2	6.8	12.0	15	1.29
<i>YELLOW</i>	27.0	10.0	-1	16.1	11.9	28.1	35	0.74
<i>WHITE</i>								
<i>BLACK</i>	8.1	24.1	0	14.8	10.7	25.5	32	0.72
<i>N = 539</i>			-1	43.5	36.0	79.4	100	0.83

DI Dicle	Sector			Index				Departure
	Arrival	Departure	Deviation	Arrival	Departure	Axes	Axis %	Arrival
<i>RED</i>								
<i>BLUE</i>								
<i>GREEN</i>								
<i>VIOLET</i>	4.1	20.3	0	9.6	6.5	16.2	20	0.68
<i>ORANGE</i>	0.0	15.9		3.1	6.4	9.4	12	2.07
<i>YELLOW</i>	29.0	12.0	-1	13.5	12.4	25.9	32	0.92
<i>WHITE</i>								
<i>BLACK</i>	8.0	23.0	1	16.6	12.6	29.1	36	0.76
<i>N = 76</i>			0	42.8	37.9	80.7	100	0.88

DR Družno	Sector			Index				Departure
	Arrival	Departure	Deviation	Arrival	Departure	Axes	Axis %	Arrival
<i>RED</i>	8.0	24.1	0	13.0	8.2	21.2	27	0.63
<i>BLUE</i>	4.1	20.0	0	9.5	9.1	18.7	24	0.96
<i>GREEN</i>								
<i>VIOLET</i>								
<i>ORANGE</i>	0.0	16.1		6.5	4.8	11.3	14	0.73
<i>YELLOW</i>	28.0	11.9	0	13.5	14.2	27.8	35	1.05

<i>WHITE</i>								
<i>BLACK</i>								
<i>N = 107</i>			0	42.6	36.3	79.0	100	0.85
EI	Sector			Index				Departure
Eilat	Arrival	Departure	Deviation	Arrival	Departure	Axes	Axis %	Arrival
<i>RED</i>								
<i>BLUE</i>								
<i>GREEN</i>								
<i>VIOLET</i>	4.1	20.2	0	10.0	19.1	29.2	37	1.91
<i>ORANGE</i>	0.0	15.9		3.3	4.2	7.5	9	1.26
<i>YELLOW</i>	27.8	11.8	0	6.2	5.3	11.5	15	0.85
<i>WHITE</i>								
<i>BLACK</i>	8.0	23.9	0	24.2	7.2	31.4	39	0.30
<i>N = 48</i>			0	43.7	35.9	79.6	100	0.82
HA	Sector			Index				Departure
Haade-meeste	Arrival	Departure	Deviation	Arrival	Departure	Axes	Axis %	Arrival
<i>RED</i>	7.9	24.1		8.9	2.5	11.4	19	0.27
<i>BLUE</i>	4.1	21.9	2	14.0	4.0	18.0	30	0.28
<i>GREEN</i>								
<i>VIOLET</i>								
<i>ORANGE</i>								
<i>YELLOW</i>	29.2	11.9	-1	26.2	5.3	31.5	52	0.20
<i>WHITE</i>								
<i>BLACK</i>								
<i>N = 32</i>			1	49.2	11.7	60.9	100	0.24
HY	Sector			Index				Departure
Hashimyyia	Arrival	Departure	Deviation	Arrival	Departure	Axes	Axis %	Arrival
<i>RED</i>								
<i>BLUE</i>								
<i>GREEN</i>								
<i>VIOLET</i>	4.0	20.0	0	10.2	6.0	16.2	25	0.58
<i>ORANGE</i>								
<i>YELLOW</i>	28.0	10.0	-2	18.8	11.7	30.5	47	0.62
<i>WHITE</i>								
<i>BLACK</i>	8.0	23.1	1	6.3	11.4	17.7	27	1.81
<i>N = 340</i>			-1	35.3	29.0	64.4	100	0.82

<i>ORANGE</i>	0.0	16.1		6.7	10.8	17.5	22	1.61
<i>YELLOW</i>	28.0	12.0	0	10.0	14.8	24.7	31	1.48
<i>WHITE</i>								
<i>BLACK</i>								
<i>N = 44</i>			-1	32.9	47.7	80.5	100	1.45
TK Talitha Kumi								
TK Talitha Kumi	Sector			Index				Departure
	Arrival	Departure	Deviation	Arrival	Departure	Axes	Axis %	Arrival
<i>RED</i>								
<i>BLUE</i>								
<i>GREEN</i>								
<i>VIOLET</i>	5.0	22.1	1	9.6	10.0	19.7	31	1.04
<i>ORANGE</i>	0.0	15.9		6.0	7.2	13.3	21	1.20
<i>YELLOW</i>	26.8	12.0	1	18.6	11.1	29.6	47	0.60
<i>WHITE</i>								
<i>BLACK</i>								
<i>N = 170</i>			2	34.2	28.3	62.5	100	0.83
TM Tulkarem								
TM Tulkarem	Sector			Index				Departure
	Arrival	Departure	Deviation	Arrival	Departure	Axes	Axis %	Arrival
<i>RED</i>								
<i>BLUE</i>								
<i>GREEN</i>								
<i>VIOLET</i>	6.0	21.9	-0	12.1	10.9	22.9	31	0.90
<i>ORANGE</i>	29.9	16.1	2	15.9	11.2	27.2	37	0.70
<i>YELLOW</i>	26.1	10.8	1	10.5	13.6	24.1	33	1.30
<i>WHITE</i>								
<i>BLACK</i>								
<i>N = 218</i>			3	38.5	35.7	74.2	100	0.93
TU Turov								
TU Turov	Sector			Index				Departure
	Arrival	Departure	Deviation	Arrival	Departure	Axes	Axis %	Arrival
<i>RED</i>								
<i>BLUE</i>	4.0	21.9	2	21.9	3.5	25.4	36	0.16
<i>GREEN</i>								
<i>VIOLET</i>								
<i>ORANGE</i>	0.1	15.0	-1	9.8	9.6	19.4	27	0.98
<i>YELLOW</i>								
<i>WHITE</i>	27.0	9.0	-2	9.8	17.0	26.8	37	1.74
<i>BLACK</i>								
<i>N = 18</i>			-1	41.5	30.1	71.6	100	0.73

UC Ucka	Sector			Index				Departure
	Arrival	Departure	Deviation	Arrival	Departure	Axes	Axis %	Arrival
<i>RED</i>								
<i>BLUE</i>								
<i>GREEN</i>	2.1	18.0	0	1.5	2.8	4.3	5	1.84
<i>VIOLET</i>								
<i>ORANGE</i>								
<i>YELLOW</i>	27.1	10.0	-1	15.0	28.9	43.9	53	1.92
<i>WHITE</i>								
<i>BLACK</i>	24.2	8.1	0	27.7	7.7	35.4	42	0.28
<i>N = 83</i>			0	44.2	39.4	83.6	100	0.89