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ESTIMATION OF LOCAL HEADING PATTERNS OF NOCTURNAL MIGRANTS USING ORIENTATION CAGES

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ABSTRACT

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The main aim of this paper is to compare the results of two data evaluation procedures used for presenting the data from the orientation cage field tests. Both procedures accept multimodality of the data and multimodality of the headings of an individual bird as well as migrating population. The goal is to reach acceptable level of migration patterns presentation in biological sense, taking under consideration a flexibility of the real movements, depending on specific weather and landscape parameters. Such knowledge is absolutely necessary for estimating migration bottle-necks and the long-term studies on influence of the climate changes on migration patterns. The material used for the comparison of the procedures was collected in years 2001-2007 by the team of the Bulgarian Ringing Station Kalimok (44°00'N, 26°26'E) within the frame of the SEEN (SE European Bird Migration Network) activity and kindly shared for evaluation. The data were obtained using the standard SEEN methods, with the standard Busse's cage working procedure of the field tests. The material contains data on four species of nocturnal migrants living in different habitats: the Great Reed Warbler, *Acrocephalus arundinaceus* (ACR.ARU), the Sedge Warbler, *A. schoenobaenus* (ACR.ENO), the Willow Warbler, *Phylloscopus trochilus* (PHY.LUS) and the Whitethroat, *Sylvia communis* (SYL.COM). There are confirmed earlier conclusions that so called „classic" unimodal procedure is not applicable to the orientation cage data resulted from any field procedure. There are available two evaluation procedures that base on the same general assumptions: multimodality of distributions that reflects combination of several unimodal partial distributions, that can be described both using sophisticated Bayesian „*Calculation*" method and much simpler „*Estimation*" procedure. Results of both procedures are enough close to each other that they can be used for describing local and general heading patterns of migration of the nocturnal migratory movements studied using orientation cages.

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INTRODUCTION

The studies on bird orientation using orientation cages have a quite long history since mid of the XXth century (Kramer 1949, Sauer 1957). At the beginning, these were laboratory experiments devoted to solving the questions connected with orientation cues and orientation/navigation mechanisms. At the beginning using the cages in a field conditions was scarce as the cages were complicated, heavy and the technique used was electric power connection dependent. Field studies came later and still they were not too popular, despite new design of the cages was developed that was electricity independent and relatively simpler to use (Emlen and Emlen 1966). That type of the cage was then improved in relation of the original design, but commonly the same „standard" procedure was used: birds were tested by night and „orientation session" lasted 1 hour per bird. This procedure in the field was still not very popular as both the test and evaluation of the raw results was time consuming. Despite of a number of improvements of the design and the adopted procedure they could be strongly criticized as discussed in detail in the paper by Busse (2017) who compared this cage and the testing procedure with a new design and different procedure developed in 1995 by Busse (1995) and used in a mass field studies at the stations participating in the SEEN (SE European Bird Migration Network) network and sometimes elsewhere. There are more than 50 000 tests performed at a number of stations in several countries (Ożarowska and Muś 2008). Detailed description of the cage (so called „Busse's cage") and the procedure used could be found in Busse (2000, 2017) and Busse and Meissner 2015. In the paper by Busse (2017) the results obtained using these two field procedures were discussed as to compatibility and differences. The data used were collected at the Bulgarian Kalimok Station (44°00'N, 26°26'E) where in the same season both methods were used paralelly for four species of nocturnal migrants. There was shown that both methods are fully compatible as to results used as estimates of directionality of the bird headings in the field conditions.

Apart of the field collection of the data an another aspect of the cage studies play an important role in work on the directional preferences of studied migrants. It is a procedure of data evaluation. In the procedure accepted by the Emlen's funnel using students the scratches made by the bird claws were visually estimated as to intensity in the sectors. In the later years the scratches were simply counted and, finally, complicated methods were proposed as by Muheim *et al.* (2014) and Bianco *et al.* (2016). In the procedure developed in connection with the use of Busse's cage a simple counting of defined dots on a transparent foil in 8 sectors of the cage is used. Independently of the study technique (Emlen's funnel or Busse's flat cage), the raw result of the test in the orientation cage is always a set of numbers located in the circular sectors of the cage.

The first important and a not avoidable problem of the use of the cage data is an evaluation of the circular data for the tested individual and transform the obtained numbers into biologically interpretable picture of the bird behaviour – estimation of the direction/directions (see below) shown by the bird in the test. As the single individual heading is not enough for estimating populational picture of migration, the number of tests of many individuals must be evaluated to be allowed to draw more general picture of the migration at the study site. Then we have a second problem – how to combine a set of individual headings into estimated picture for the population studied.

Here lies the key problem of the cage style studies: how to evaluate obtained set of the circular data from a number of tests. At least since the Emlen's funnels were introduced the estimations were performed „by eyes" – direction shown by the individual was set as direction in which most of scratches were visible. When, in a development of the Emlen's funnel, the scratches become countable and the first circular statistics was proposed (Batschelet 1981), the „classic standard" evaluation of the cage data was adopted. It contains calculation of directional vector for all the scratches counted and performance of a Rayleigh test for uniformity (*r*-value as an uniformity index). In this standard, on the *r*-value basis, the bird is classified as „oriented" or „disoriented" and for the next step – a group presentation only vectors of „oriented" birds were taken under consideration and presented at the „radar" graphs as dots or triangles at the circle. The resulted vector is drawn inside and this inside located circle represents *„a level of statistical significance"*. The excellent example is presented at the Figure 1 left panel (after Hilgerloh 1989): this graph means that presented group of the Garden Warblers, *Sylvia borin*, tested in southern Spain, is totally *„disoriented"* – that is obvious wrong, as this species is a long-distance African migrant. The procedure is incorrect, because the basic condition of its use for the set of circular data is unimodality of the distribution. In bigger raw data sets there is clearly visible that distributions are frequently bi- or tri-modal, thus the „classic" calculation procedure is inapplicable. Exceptionally bi-modal distributions were handled by Holmquist and Sandberg (1991) in a *„broken axis approach"* and later, linear bi-modal cases were accepted. Unfortunately, described basic statistical routine is still in common use, despite the problem was already stressed and discussed many years ago by Busse (1995), Busse and Trocińska (1999). Multimodality of distributions in the cage studies

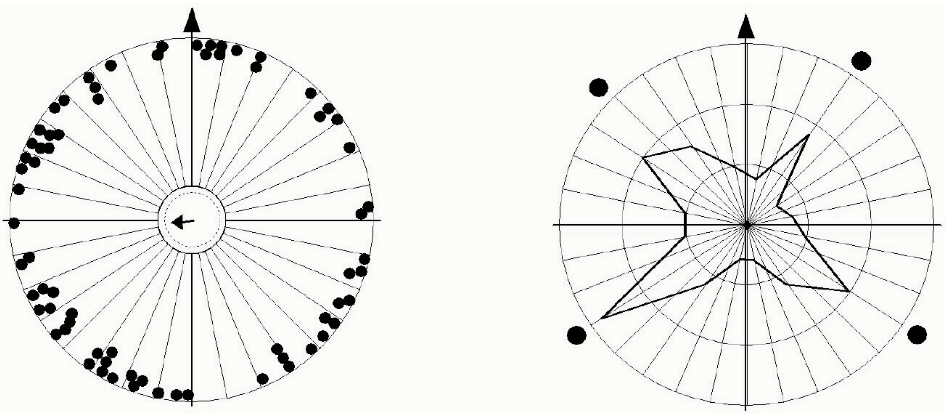

Fig. 1. Example of a difference in results from the orientation cage tests (Emlen's funnel) field procedure according to classic elaboration methodology and the estimation procedure discussed here. Left panel (after Hilgerloh 19XX) – dots – individual headings, arrow – result heading (as calculated classic): $\alpha = 250°$, $r = 0.14$, $p > 0.05$ (n.s.); Right panel (estimation procedure – the same field data), dots – average group headings, polygon – headings distribution.

was presented in several papers (e.g. Busse 1995, Nowakowski and Malecka 1999, Ożarowska and Yosef 2004, Ożarowska *et al*. 2013, Busse 2017). The multimodality was accepted as a basis for evaluations of all results of real data from Busse's cage since the beginning of that standard. A simple assumption was made as a basis for evaluations: „under" the multimodal distribution there are „hidden" wrapped Gaussian, von Mises distributions. These were roughly estimated in the simple DOS software created under the name ORIENTIN, used up to 2001 (Trocińska *et al*. 2001), and developed later as ORIENT software mentioned in number of papers evaluating the orientation tests collected. From 2005 the Bayesian statistics based on the same general assumption was introduced (Muś 2005, 2008, Ożarowska and Muś 2008), Deeper statistical discussion of the problem, using the Bayesian statistics, can be found in the paper by Ożarowska *et al*. (2013) and the conclusion of this paper is clearly eliminating classic unimodal procedure from analyses of the cage data. The example of comparison of results (from the same raw data) of the classic procedure and the Bayesian modelling is shown at the Figure 2 (left panel – classic, middle panel – modelling; both after Ożarowska *et al*. 2013) – in the model based picture there are a few vectors and the classic vector does not follow the model strongest one.

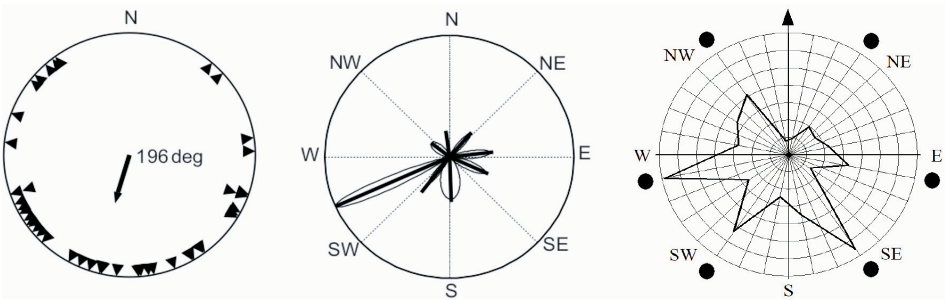

Fig. 2. Example of a differences in results from the orientation cage tests (Emlen's funnel) field procedure according to classic elaboration methodology (Left panel – explanation see Fig. 1), modelling procedure offered in the paper Ożarowska *et al*. 2013 (Middle panel) and the estimation procedure discussed here (Right panel – explanations see Fig. 1).

The right panels at Figures 1 and 2 show the same raw data evaluation results as that evaluations done using the earlier presented procedures, but obtained from the ORIENT based procedure, proposed by Busse (1995), but presented in the graphic format used contemporaneously. The last procedure application resulted in the directional distribution of estimated vectors, that seems similar to the pattern obtained using the Bayesian modelling, while very much different from the classic one-vector picture.

The Bayesian modelling procedure is well grounded as a statistical tool useful for presenting of the orientation cage data (Ożarowska *et al*. 2013), but rather complicated for use by a common student working on such data sets: input format to the ORIENT(KM)[1] software used in the paper by Ożarowska *et al*. (*op. cit*.) *„requires spe-*

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1 the name „ORIENT software" was incorrectly used in that paper as the original ORIENT (now in version 4.6) name was in use by its author – P. Busse – and others already since 2001 (Trocińska *et al*. 2001). To avoid misunderstandings in following text K. Muś software will be called „ORIENT (KM)".

cific data format… please contact K.M. before use". This „*specific data format*" needs preliminary calculations in the MatLab very much sophisticate package. The Busse's procedure based on the simple DOS original ORIENT (PB) software needs as an input only a simple linear data vector with numbers representing 8 or 16 cage sectors The basics of the software are explained in the first papers presenting the procedure (Busse 1995, Busse and Trocińska 1999). After receiving the output file, importable to the any common spreadsheet, the results can be presented as the radar graphs in preferred layout (see examples at Figures 1 and 2 – right panels).

The main aim of this paper is to compare the results of two evaluation data procedures both accepting multimodality of the data and multimodality of the headings of individual bird as well as migrating population. The statistically well grounded Bayesian procedure presented and discusssed in comparison with the classic statistical method in the paper by Ożarowska *et al.* (2013) will be called „the ***Calculation*** procedure" while the Busse's procedure – „the ***Estimation*** procedure" and, consequently, results described as „*calculated*" or „*estimated*", despite that estimation bases on some calculations as well. Simplicity of the procedure preferred here and an acceptable level of agreement with potentially most precise results of the calculation procedure can encourage students to work in the field with the orientation cages for solving the mysteries of migratory patterns of many nocturnal migrants. **The goal** is to reach biologically acceptable level of migration patterns presentation, taking under consideration a flexibility of the real movements, depending on specific weather and landscape parameters. Such knowledge is absolutely necessary for estimating migration bottle-necks and the long-term studies on influence of the climate changes on migration patterns.

MATERIAL

The material used for the comparison of the procedures was collected in years 2001-2007 by the team of the Bulgarian Ringing Station Kalimok (44°00'N, 26°26'E) within the frame of the SEEN (SE European Bird Migration Network) activity and kindly shared for evaluation (Zehtindjiev *et al.* 2003, Busse 2017). The data were obtained using the standard SEEN methods, with the standard Busse's cage working procedure of the field tests (Busse 2000) – Table 1. The material contains data on four species of nocturnal migrants living in different habitats: the Great Reed Warbler, *Acrocephalus arundinaceus* (ACR.ARU), the Sedge Warbler, *A. schoenobaenus* (ACR.ENO), the Willow Warbler, *Phylloscopus trochilus* (PHY.LUS) and the Whitethroat, *Sylvia communis* (SYL.COM). All the data evaluated here using „*Estimation*" and „*Calculation*" procedures were the same raw data, that allows a direct comparisons. From the same station there were originated the data used in the paper by Ożarowska *et al.* (2013), but they were collected in the field using Emlen's funnel procedure. Compatibility of results from both field procedures was set as the conclusion in the paper by Busse (2017).

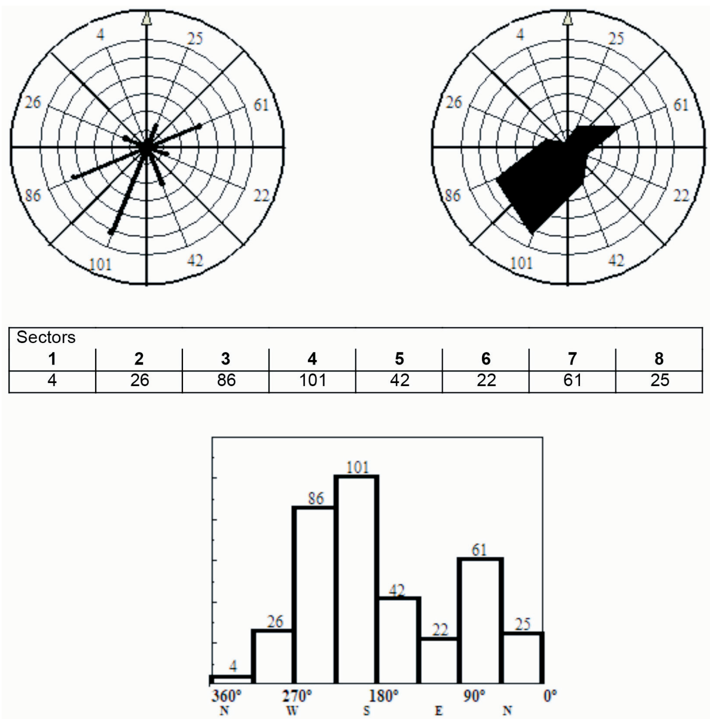
Table 1
Numbers of individuals tested in the Busse's flat orientation cage

	ACR.ARU		ACR.ENO		PHY.LUS		SYL.COM	
	Active	Inactive	Active	Inactive	Active	Inactive	Active	Inactive
2001	79	17	43	3	36	3	15	1
2002	74	5	99	22	83	16	23	2
2004	29	1	152	92	28	3	22	1
2007			18	1	53	2		
Total	182	23	312	118	200	24	60	4

METHODS, RESULTS AND DISCUSSION

Basics of the estimation of the heading patterns

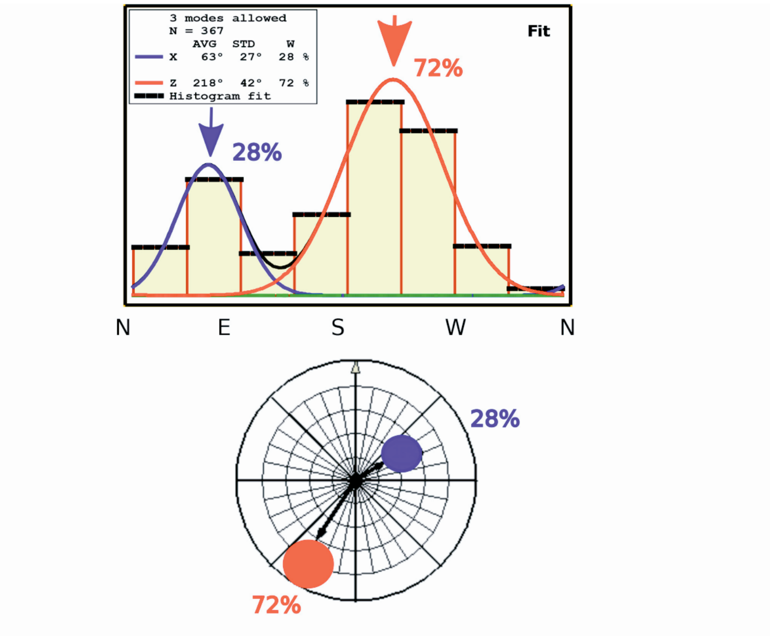
The course of obtaining the raw data from the orientation cages of both main types was described and discussed several times in publications (especially in detail in Busse 2017). The basic raw data set for an individual bird is always the row of values representing sectors of the wind-rose and optionally some other data according to



Sectors							
1	2	3	4	5	6	7	8
4	26	86	101	42	22	61	25

Fig. 3. First step of the estimation procedure – presentation of the raw data (individual test): the Table – numbers of scrathes in eight sectors; Left panel – numbers of scratches shown as vectors, Right panel – the same presented as distribution polygon; Lower panel – the same distribution shown as the bar graph.

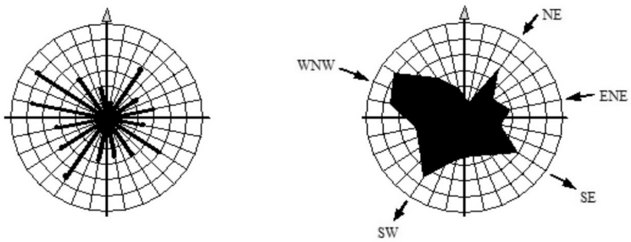
special needs of the student (these additions are not processed in the main calculations routine) – in ORIENT 4.6 the standard is 8 sectors, but 16 sectors is acceptable. The raw data can be presented graphically in a circular form (Figure 3 – upper panels) or, for easier perception, as a traditional linear bar presentation (Figure 3 – lower panel). The linear picture suggests that the distribution is not only bi-modal, but in these modes there are „hidden” normal distributions as this kind of distribution is the most common in natural, biological world (this idea was already used in modelling the „wave” pattern of the bird migration – Busse 1996 and followed papers as by Kopiec 1997, Kopiec-Mokwa 1999). Thus, presented raw distribution could be modelled and visualized as at Figure 4 (upper panel). There are two resulted distributions (despite three were allowed at the start) with their own parameters as the average, standard deviation and „the power” – the relative frequencies. The other graphical presentation of these properties are shown at the same Figure (lower panel) – in this individual data we have two heading vectors with lengths representing „the power” of these bird headings. The question *„why one bird could show more than one heading”* is not a question for this paper, but it was discussed several times in papers based on different orientation data, among others in the paper by Ożarowska *et al.* (2013). Any case that is the fact.



Sectors															
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
0	0	0	0	0	0	72	0	0	0	0	0	0	28	0	0

Fig. 4. First step of the estimation procedure – evaluation of the raw data (individual test): Upper panel – assumed normal distributions as fit to the data presented at the Figure 3: estimated average group headings and their relative weight (after Muś 2005 presentation, modified); the Table – resulted individual headings (shown in 16 sectors) as a part of the output table (see Fig. 5); Lower panel – a radar style presentation of the result.

The example output of the ORIENT 4.6, containing results for several members of the bird group, imported to the speadsheet looks like the Table 2 and it is presented at the Figure 5. On the left panel of the Figure there are shown resulted common, summarised vectors by 16 sectors, while on the right panel the same results using a graphic technique easier for perception by a human mind. The proposed style of the graphic presentation of the final results works very well for real heading distributions extracted from the weather radar as shown at the Figure 6. If one has in his mind the idea presented earlier at Figures 3 and 4 (hidden normal distributions) it is rather easy to ESTIMATE directions preferred by the studied group of birds, that is our goal. These estimations are presented by arrows headed according to the season, spring or autumn, as arrival and departure directions (see Chapter „*Reversed headings...*").



Vectors	Sectors 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
V-1	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0
V-1	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0
V-2	0	0	0	0	0	0	0	0	0	0	0	0	50	50	0	0
V-1	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0
V-1	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0
V-1	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0
V-1	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0
V-2	0	0	78	0	0	0	22	0	0	0	0	0	0	0	0	0
V-2	0	0	0	0	0	0	79	0	0	0	0	0	21	0	0	0
V-2	0	0	0	0	35	0	0	0	0	65	0	0	0	0	0	0
V-3	15	15	0	0	0	0	0	0	0	0	0	0	0	70	0	0
V-3	0	36	0	0	0	17	0	0	0	0	0	0	47	0	0	0
V-3	0	56	0	0	0	0	30	0	0	0	14	0	0	0	0	0
V-3	0	47	0	0	0	0	0	22	0	0	0	0	16	16	0	0
V-4	0	20	0	0	15	15	0	0	0	0	0	0	0	50	0	0
V-3	0	21	0	0	0	0	0	0	24	24	0	0	0	31	0	0
V-3	10	10	0	0	0	28	0	0	0	52	0	0	0	0	0	0
V-4	0	28	0	14	0	0	0	0	0	0	0	0	0	29	0	29
...	**...**	**...**	**...**													
...	**...**	**...**	**...**													
Sum	614	2274	1282	1732	1357	2396	1700	1505	1666	2797	2065	2719	2870	3180	1858	1169
Percent	**2.0**	**7.3**	**4.1**	**5.6**	**4.4**	**7.7**	**5.5**	**4.8**	**5.3**	**9.0**	**6.6**	**8.7**	**9.2**	**10.2**	**6.0**	**3.7**

Fig. 5. Second step of the estimation procedure – the group headings pattern in the 16 sector format. Left panel – sums of individual vectors (see Fig. 4) of the example group of birds from the table below; Right panel – polygon presentation of the headings pattern and estimated average group vectors (the heads of resulted arrows as for the autumn migration – northern part of the wind-rose – arrival headings, southern ones – departure headings).

Table 2
Sample output from the ORIENT (PB) software imported to the spreadsheet.
Shadowed are individual bird's heading vectors values
(sum values of an individual is always 100%).

Vectors	Sectors															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
V-1	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0
V-1	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0
V-2	0	0	0	0	0	0	0	0	0	0	0	0	50	50	0	0
V-1	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0
V-1	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0
V-1	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0
V-1	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0
V-2	0	0	78	0	0	0	22	0	0	0	0	0	0	0	0	0
V-2	0	0	0	0	0	0	79	0	0	0	0	0	21	0	0	0
V-2	0	0	0	0	35	0	0	0	0	65	0	0	0	0	0	0
V-3	15	15	0	0	0	0	0	0	0	0	0	0	0	70	0	0
V-3	0	36	0	0	0	17	0	0	0	0	0	0	47	0	0	0
V-3	0	56	0	0	0	0	30	0	0	0	14	0	0	0	0	0
V-3	0	47	0	0	0	0	0	22	0	0	0	0	16	16	0	0
V-4	0	20	0	0	15	15	0	0	0	0	0	0	0	50	0	0
V-3	0	21	0	0	0	0	0	0	24	24	0	0	0	31	0	0
V-3	10	10	0	0	0	28	0	0	0	52	0	0	0	0	0	0
V-4	0	28	0	14	0	0	0	0	0	0	0	0	0	29	0	29
...	...	...	...													
...	...	...	...													
Sum	614	2274	1282	1732	1357	2396	1700	1505	1666	2797	2065	2719	2870	3180	1858	1169
Percent	**2.0**	**7.3**	**4.1**	**5.6**	**4.4**	**7.7**	**5.5**	**4.8**	**5.3**	**9.0**	**6.6**	**8.7**	**9.2**	**10.2**	**6.0**	**3.7**

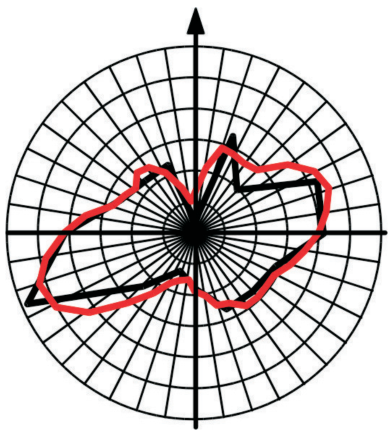


Fig. 6. Effectiveness of presentation of the migration headings of birds in 16 vs. 40 sectors using the real exact headings of birds as seen by the weather radar (the data from Świdwin weather radar, October 2013, supplied kindly by Dr. Anna Górska): black polygon – 16-sector pattern, red – 40-sector pattern (original data – 1°)

Results of the estimation of headings

Results of the estimation procedure applied to the Sedge Warbler data are presented at the Figure 7. The data of the Sedge Warbler for the years 2001, 2002, 2004 and 2007 are presented separately (four panels above) as well as all years data combined into the total distribution (the lowest panel). The between years variation of the heading patterns is the very well known phenomenon for the students working on this kind of data (e.g., Adamska and Filar 2005, Formella and Busse 2002, Ściborska and Busse 2004). This is caused mainly by unequal sampling of the species/popula-

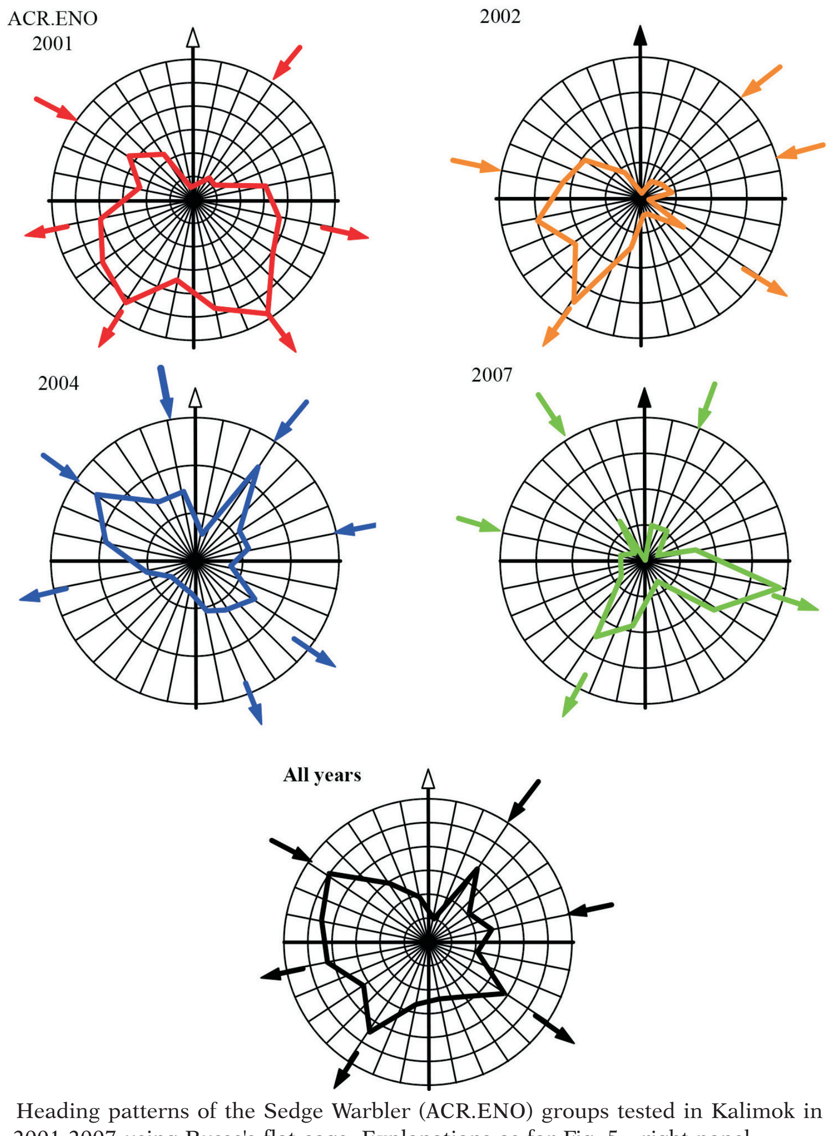


Fig. 7. Heading patterns of the Sedge Warbler (ACR.ENO) groups tested in Kalimok in years 2001-2007 using Busse's flat cage. Explanations as for Fig. 5 - right panel.

tion migrant flow during the season. However, the variation is usually much more expressed in „power” the result vectors than their directions (e.g., Formella and Busse 2002). The results of estimations for other species studied here are shown in the *Appendix*. The Figure 8 confirms this statement and the total distribution fits quite well to the yearly patterns and further confirm the above expressed opinion.

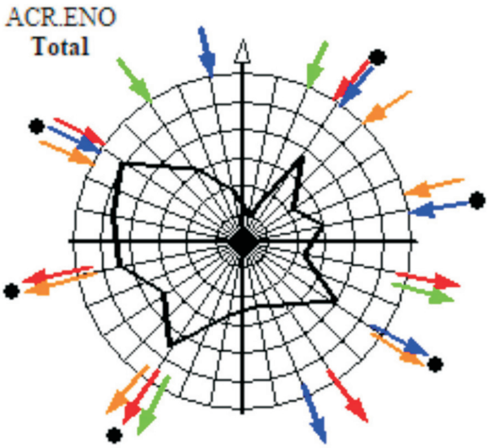


Fig. 8. Comparison of yearly heading patterns of the Sedge Warbler (ACR.ENO) groups presented at Figure 7. General pattern for all the data pointed as black circles.

Results of the calculation procedure

The basics of the „calculation procedure” at the level of the individual bird was enough well explained in the paper by Ożarowska *et al*. (2013). At the next level – the group analysis – the output of the ORIENT (KM) software contains a number of output parameters in numerical form (Table 3) and the graphic presentation of the heading pattern as linear and „radar” pictures (Fig. 9). In the present discussion only few of output parameters will be taken under consideration – they are (1) direction of the vector (*Dir. deg.*), (2) standard deviation of the vector (*SD*) and (3) relative size of the groups creating the vectors (*Group %* – expressed in percent of the whole activity of the birds belonging to). In the parameters calculated there is another estimation of the group size (*Ndir* – number of individual directions of birds – Table 3), but both distributions are highly correlated (Pearson's r at the level of 0.80, $p < 0.01$) and in the present paper presenting both of them could be repeating of the same.

The key problem with use of this procedure lies in a fact that there is no one model solution from a defined dataset: depending on one parameter, that **must be fixed** by the researcher **before running the programm,** the output parameters and the heading distributions are different. This key parameter is the basic sector for modelling (defined „window” or „sector” – expressed in degrees) which decides on the number of allowed distributions, namely – number of resulted directions, that defined other parameters as the vector (direction), standard deviations of resulted distributions and their volume. Thus full analysis of one group of birds gives several results as shown in the Table 4.

Table 3
Example output from the ORIENT (KM) software

Project		ACR-ENO_KK Total-4									
N birds		376									
...											
Total activity		51 342									
Mean activity		137									
Total dirs		615									
Mean dirs/bird		1.6									
Fitted sectors°		16									
Dir ID	*Dir deg.*	*SD deg.*	Activity	Activity %	Group %	SE	Prec.	Prob.	P/Pmax	*Ndir*	Pdir
1	24.0	24.4	6661	13.0	30	3.7E+04	0.1913	0.626	115.679	0.19	0.626
2	103.8	29.6	15068	29.3	24	5.6E+04	0.2933	0.960	165.061	0.27	0.893
3	210.9	32.8	13244	25.8	29	4E+04	0.2098	0.686	149.448	0.24	0.809
4	298.8	30.2	16367	31.9	24	5.9E+04	0.3057	1.000	184.812	0.30	1.000

where: *Dir. ID* – number of the direction group, *Dir deg.* – vector direction in wind-rose degrees, *SD deg.*– standard deviation within the direction group, Group % – group size in percent of the total sample activity, *Ndir* – group size based on individual birds headings; Shadowed are other derivative parameters not discussed here.

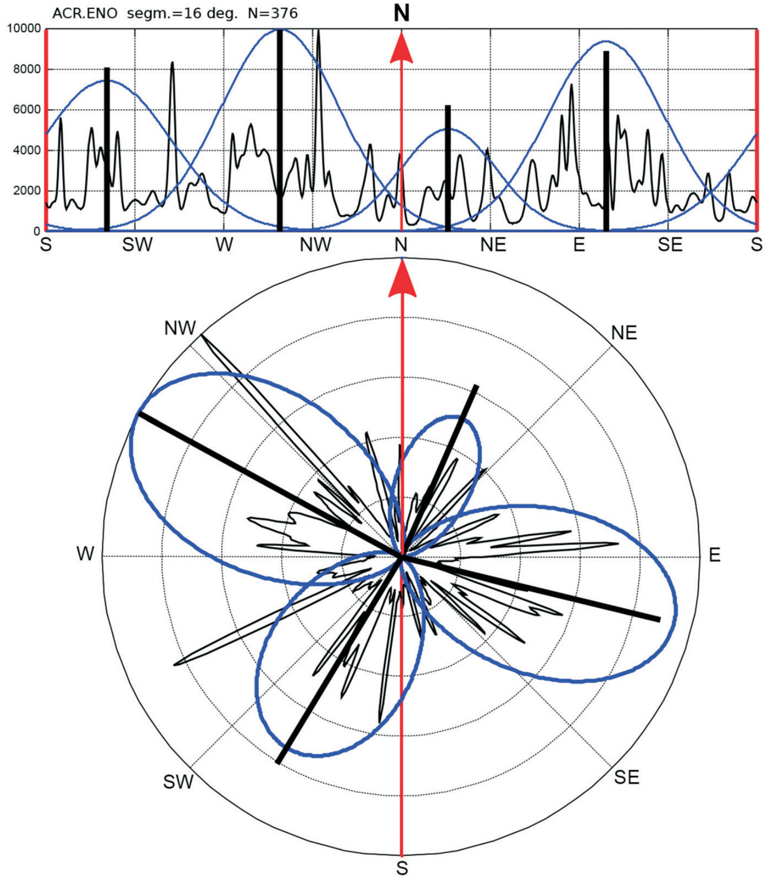


Fig. 9. Example graphical output from the ORIENT (KM). The same parameters presented in linear and circular format. Thin black line – distribution of individual birds headings, Thick black vectors – average group vectors, Blue – modelled distributions.

Table4
Simplyfied output table presenting results of the ORIENT (KM) for ACR.ENO (all years)

Sector°	***Ndir***	*Dir deg.*	*SD dir*	Group *%*
19	**2**	95.8	44.0	36.3
		275.3	65.0	63.7
18...17	**3**	94.6	53.4	46,0
		212.6	22.4	13,0
		293.9	41.6	41,0
16	**4**	24,0	24.4	30,0
		103.8	29.6	24,0
		210.9	32.8	29,0
		298.8	30.2	24,0
15	**5**	16.5	29.9	15.5
		103.4	32.3	31,0
		205.8	29.2	18.6
		247.9	24.4	9.6
		299.8	24.9	25.4
14-13	**6**	28.1	26.4	15.4
		82.6	11.7	8.7
		121.4	25.6	20.5
		204.8	25.1	16.1
		248.6	26.5	10.8
		302.3	29.1	28.6
12...10	**7**	28.6	27.0	16.4
		81.9	7.3	6.4
		119.6	27.0	22.7
		206.7	22.6	18.2
		249.0	8.7	8.1
		281.2	7.1	7.8
		312.8	22.1	20.5
9-8	**8**	28.5	18.1	11.6
		81.3	7.6	5.6
		116.4	34.2	27.7
		208.3	19.5	16,0
		248.1	8.1	8.2
		284.2	11.1	14.9
		315.5	7.3	10.1
		346.6	8.2	5.9
7	**9**	29.9	22.8	14.9
		81.8	9.2	11,0
		116.3	11.1	11.2
		168.6	29.7	15.1
		210.9	7.3	7.4
		246.2	10.7	11.2
		284.3	9.9	13.8
		315.0	7.7	10.7
		345.4	7.0	4.7

One can see that setting the sector size defines the number of distributions acceptable as the procedure output. The narrower the fixed sector is the higher number of result headings is created. However, there are several cases where changing the sector size do not change the number of directions as well as some number of directions are „prohibited" and not accepted by the programm for defined sample studied. In the procedure there is no criterion that could help to find the best solution – the best number of heading directions. At the basis of analyses of all data sets available in this work it seems that formal measures used commonly in modelling and available within the procedure applied here – BIC (Bayesian Information Criterion) and QLN – are totally helpless: changes in their values show no properties selecting the point of the best „goodness of fit". More detail analysis of calculated directions resulted from fixing different modelling sectors (passes of the programm with the sector width set as shown in the Table 4) is presented at the example Figure 10.

At the beginning from the most wide sectors resulted directions are few and they have very high *SD*-values. During next passes with fixed narrower and narrower sector sizes the number of result directions grows – some of them are close to those at fixed at previous passes, while others change their position or, usually, they are two replacing one at the earlier passes. Using only calculations procedure one can reach ten or more result directions and still there is no clear suggestion which step gave the best fit to the real pattern. And here we are faced with necessity to make an ***estimation*** (arbitral choice) – within sophisticate calculation procedure. Such estimation was done eg. in the paper by Ożarowska *et al*. (2013), what was cited above at Figure 2 (central panel), where the authors arbitrally selected eight direction pass of the modelling, while more detail analysis after the estimation procedure (Fig. 11) suggested only six recognizable headings (with five vectors exception for the 2007 sample). The difference is well seen in comparison of central and right panels at the Figure 2. The suggestion of solving the calculation procedure problem with the choice of the number of directions as an accepted pattern is following the result pattern (number of directions) in the estimation procedure. Using this rule gives the best agreement between results of the two discussed procedures (Fig. 12 for the heading pattern of Sedge Warbler data from Kalimok Station discussed here in detail). Number of accepted directions is the property applicable only to one species in a certain locality. However, there is a good chance that at least some of „routes" (directions of headings) will be common for different species/populations passing the site of work (as is in the case studied here).

Applying the proposed rule of thumb to the all available data for four studied species seems to give acceptable level of agreement between procedures – in the most of headings estimated and calculated azimuths fall within the same or bordering sectors (of 11^{o} wide) – Table 5. Distributions of calculated and estimated headings are the same after chi^2 test at the level $p < 0.001$ for both – species distributions and distribution from processing all available data together. The last heading pattern could be compared with the data from the radar and moon observations where species of birds are not identifyable and all the birds must be treated „*bird sp.*" For a single species estimated and calculated patterns are less precisely fitted to each other than the total one (Table 6). Average differences between received directions in the most numerous

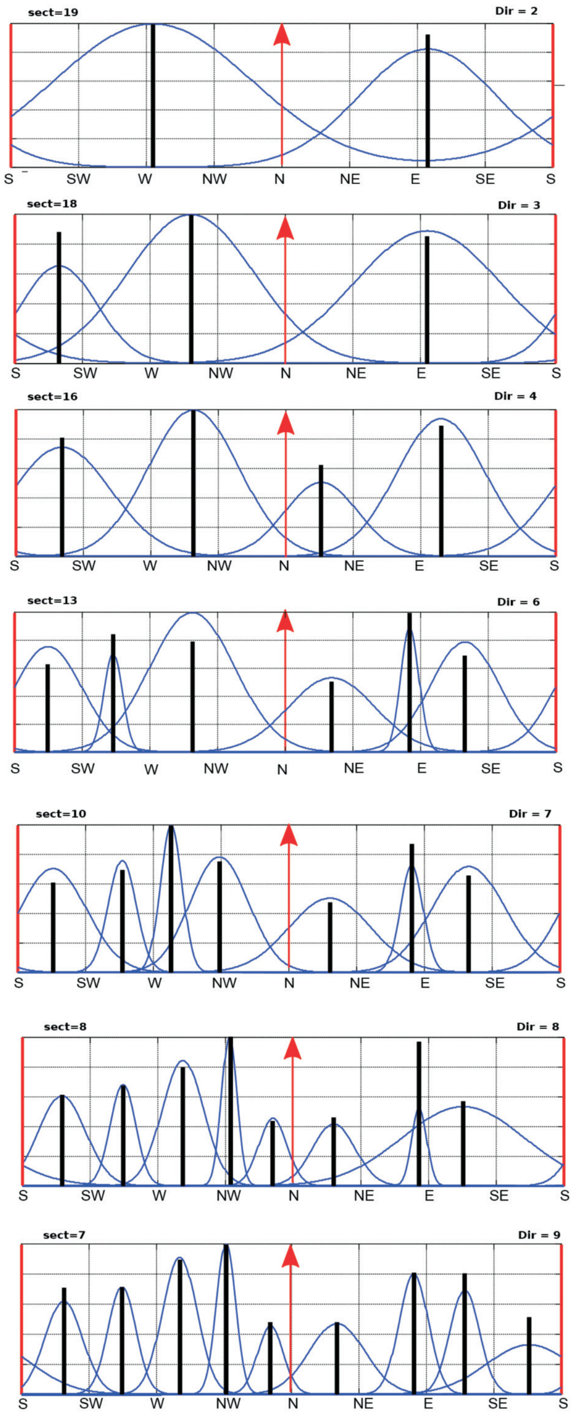


Fig. 10. Results of several runs of ORIENT (KM) using the same data, while different running sectors (sect) are set that resulted in different numbers of modelled distributions. Out of them the best model need to be chosen.

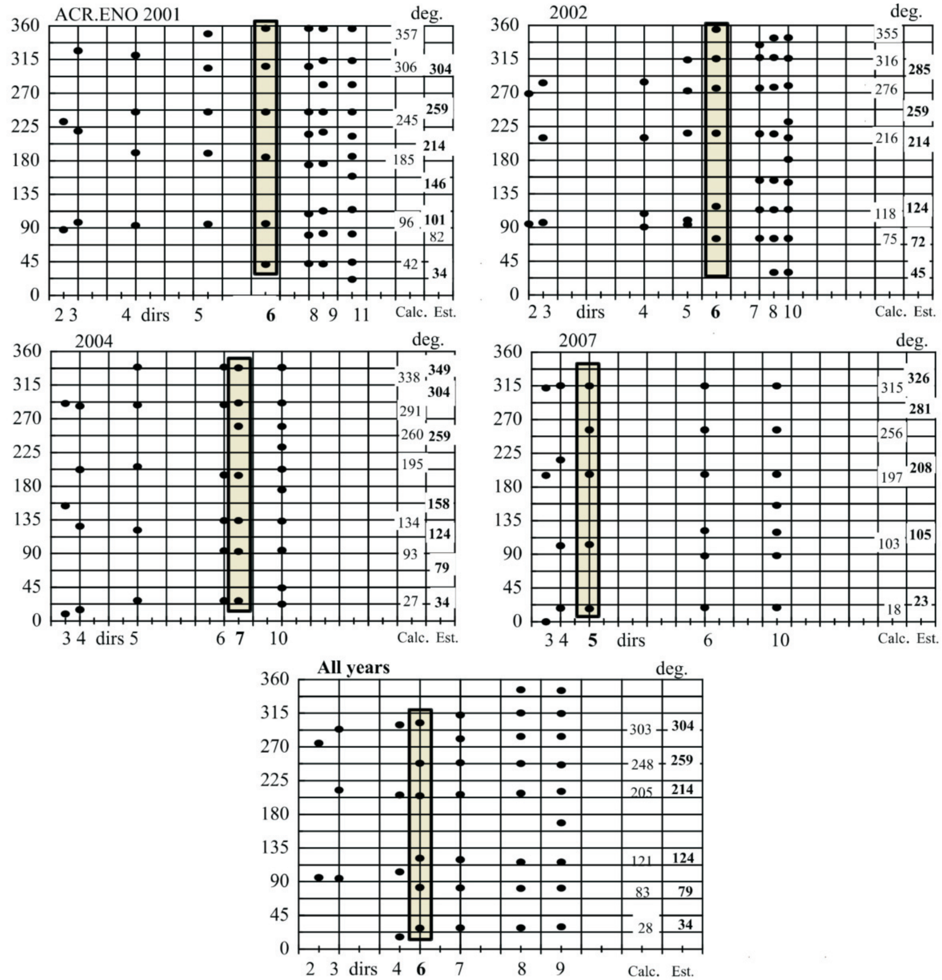


Fig. 11. Results of several runs of ORIENT (KM) using the same data. Every panel represent results from the Sedge Warbler tests for years 2001-2007 and for all data from this species (the lowest panel – All years). At the panel there are pointed (as dots) the calculated vectors values in relation to the vertically flattened wind-rose (in degrees); at the x-axis there are shown numbers of vectors (dirs) resulted in different runs of the programm, the shadowed rectangle points at the number of vectors selected as the best estimation; the right side of the panel contains values (*deg.* – degrees) of the vectors set as the best fit in *Calculation* (*Calc.*) and the *Estimation* (*Est.*) procedures.

species data sample (ACR.ENO – $N = 376$) are only 4° (arithmetic difference) or 6° (absolute difference), while those with the lowest sample size (SYL.COM – $N = 59$) – 13° (arithmetic difference) and 28° (absolute difference). For the total sample of all species these values are the smallest: 2° (arithmetic difference) and 6° (absolute difference). Differences in arrival directions seem to be lower than that of departure, with exception of Great Reed Warbler, but this should be cleared in the future studies of the problem. In presenting the patterns of migration differences found are negligible and could be accepted for discussion of local migration patterns (e.g., Fig. 13 – that quite well fits to the pattern of nocturnal passage as studied by moon watching method – Zehtindjiev and Liehti 2003).

Table 5

Distribution of vectors located by estimation and calculation procedures in sectors of the wind-rose (X). Green – both located in the same sector, yellow – located in bordering sectors. In „all species” columns – numbers of vectors located in different sectors; colors show the sectors prefered by the studied species, being common migration headings.

Sectors	ACR.ARU		ACR.ENO		PHY.LUS		SYL.COM		All species		
deg.	Esti-mated	Calcu-lated	Esti-mated	Calcu-lated	Esti-mated	Calcu-lated	Esti-mated	Calcu-lated	Esti-mated	Calcu-lated	Total
11									0	0	0
23		X					X		1	1	2
34			X	X	X	X		X	2	3	5
45									0	0	0
56	X								1	0	1
67						X			0	1	1
79		X	X		X		X	X	3	2	5
90				X					0	1	1
101						X			0	1	1
112									0	0	0
124	X		X	X	X				3	1	4
135		X							0	1	1
146									0	0	0
158							X		1	0	1
169	X				X				2	0	2
180		X						X	0	2	2
191						X			0	1	1
203									0	0	0
214			X	X	X				2	1	3
225									0	0	0
236									0	0	0
245	X	X			X	X	X		3	2	5
259			X	X					1	0	1
270								X	0	1	1
281									0	0	0
292					X		X		2	0	2
304	X		X	X		X		X	2	3	5
315									0	0	0
326									0	0	0
335									0	0	0
349									0	0	0
360									0	0	0

Table 6
Comparison of resulted vector directions (in degrees) after use the same raw data in an „estimation" and „calculation" procedures. All year data available for species used. *Arth. diff.* – arthmetic difference between values, *Abs. diff.* – absolute difference; *Arrival*, northern vectors are shadowed

ACR.ARU

Estimated	Calculated	Difference
	21	
56	69	-13
124	122	3
169	178	-9
240	248	-8
298	319	-21

Averages:	Arth. diff.	Abs. diff.
TOTAL	**-10**	**11**
Arrival	-17	17
Departure	-5	7

PHY.LUS

Estimated	Calculated	Difference
34	26	9
70	60	10
112	93	19
169	123	46
214	186	28
245	243	2
292	300	-8

Averages:	Arth. diff.	Abs. diff.
TOTAL	**15**	**17**
Arrival	4	7
Departure	24	24

ACR.ENO

Estimated	Calculated	Difference
34	28	6
79	83	-4
124	121	3
214	205	9
259	249	10
304	302	2

Averages:	Arth. diff.	Abs. diff.
TOTAL	**4**	**6**
Arrival	0	4
Departure	7	7

SYL.COM

Estimated	Calculated	Difference
17	24	-7
79	64	15
158	95	64
214	171	43
225	250	-25
292	303	-11

Averages:	Arth. diff.	Abs. diff.
TOTAL	**13**	**28**
Arrival	-1	11
Departure	27	44

All species

Estimated	Calculated	Difference
17	24	-7
79	72	7
124	121	4
169	176	-7
225	208	17
245	244	1
305	306	-1

Averages:	Arth. diff.	Abs. diff.
TOTAL	**2**	**6**
Arrival	0	5
Departure	4	7

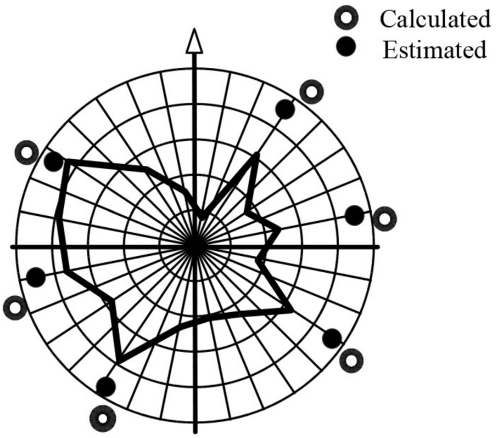


Fig. 12. Comparison of final results of evaluation of all the Sedge Warbler data from years 2001-2007 using the *Calculation* and *Estimation* procedures.

Fig. 13. The Sedge Warbler heading pattern at Kalimok Station as estimated using the *Estimation* procedure from the data of 2001-2007.

The obtained local patterns can be used in presentation of general migration patterns that could be created from the cage tests performed in the network of bird stations (e.g., Fig. 14 – modified after M. Filar unpubl., and Ożarowska and Muś 2008). The more general procedure for creating big scale patterns from the local heading patterns will be a task for further work.

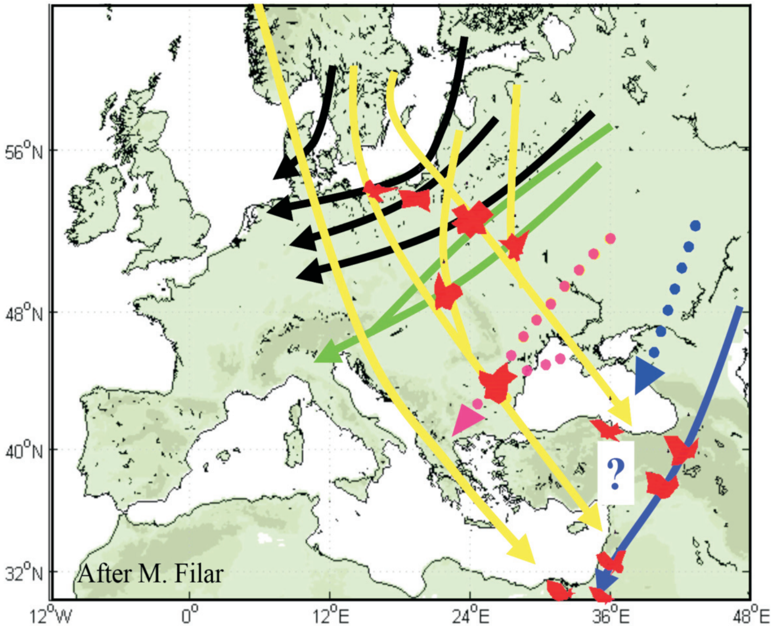


Fig. 14. Example of wide territory study based on results of the estimation procedure in number of bird stations. Data for the Chiffchaff *Phylloscopus collybita* tested at stations: Bukowo--Kopań, Mierzeja Wiślana, Siemianówka, Carpatica (Poland), Cholgyni (Ukraine), Kalimok (Bulgaria), Cernek, Aras, Dyiarbakir (Turkey), Azraq (Jordan), Eilat (Israel) and Burullus (Egypt).

Reversed headings – the axial or arrival-departure patterns

Practically all resulted orientation test patterns contain a number of headings in a „wrong" directions – northward in autumn while southward in spring. In spring reverse migration phenomenon is well known to all observers of the migration and simply explained as so called weather caused returns, while autumn reverse flights are less known, although regularly visible within moon-watching and radar studies (e.g., Alerstam 1978, Ehnbom *et al*. 1993, Akesson *et al*. 1996, Zehnder *et al*. 2002 as well as Fig. 6 cited above). In the cage studies, the reverse headings were frequently criticized as „a cage errors" caused by a testing stress. However, mentioned above visual, moon-watching and radar studies suggest that the reverse headings exist in the nature as a normal part of the migration behaviour. In some localities, as the Swedish Baltic coast, this phenomenon was explained as avoidance of overcrowding of migrants at the coast before crossing the sea barrier (e.g. Akesson *et al*. 1995). As the phenomenon is regularly observed inland (e.g. Adamska and Filar 2005, Adamska and Rosińska 2006, Stępniewska *et al*. 2011) it must be explained another way: as (1) simple axial behaviour – the headings will exactly reverse (by 180°) direction (Busse 2006), or (2) return heading to the earlier „known" place (e.g. last stop-over locality) when landing in a new „strange" landscape. At the beginning of estimation procedure application the first of listed explanations was accepted and even apart of the raw headings patterns the opposite „*reversed*” patterns were shown. In these graphs eg. autumn presented vectors were created as a sum of the „correct” southern directed vector and the opposite, northern vector situated plus or minus 180° (Busse *et al.* 2001, Trocińska *et al.* 2001, Rosińska and Adamska 2007). In fact, opposite vectors not always were different by exactly 180° and the obtained „corrected” pattern shown bigger variance, thus less precise estimation of departing direction. In the newer evaluations rather second of the above listed explanations is accepted (e.g. Stępniewska *et al.* 2011) and e.g. in the autumn northern directions are treated as „arrival directions” while southern ones as „departure directions”. However, it must be stressed that if the study site lies on a straight migration route both explanations are inseparable, but if over the study site migration corridor changes direction the results of orientation tests will reflect that property - arrival and departure vectors will be not opposite to each other.

In the data evaluated in the present paper most of deviations from the straight line are small (less than usual *SD* of distributions – within 10°) but five other are as big as 20–28° (Table 7). They could show that at the Kalimok some groups of migrants change their headings. This is, obviously, beyond of goals of the present paper, but could be an interesting area for the future studies.

Table 7

Linearity of the arrival-departure group vectors and their relative size. *Arrival* – northern vectors (shadowed), *Departure* – southern vectors; *Reversed* – direction opposite to departure vector (departure – plus or minus180°), *Observed* – arrival vector the closest to the *Reversed* one, *Rev. coeff.* – *RC* formula see text.

ACR.ARU

Direction	*SDdir*	*N*	Reversed	Observed	Difference	Arrival	Departure
deg.		%	*deg.*			N%	
21	8.9	10.5				10.5	
69	12.9	16.2				16.2	
122	23.1	13.5	302	319	17		13.5
178	20.6	14.7	358	21	23		14.7
248	29.6	20.3	68	69	1		20.3
319	21.5	24.8				24.8	
Avg. SD	**19.4**		Avg. absolute diff.		**14**	51.5	48.5
					Rev. coeff.	1.06	

ACR.ENO

Direction	*SDdir*	*N*	Reversed	Observed	Difference	Arrival	Departure
deg.		%	*deg.*			N%	
28	26.4	15.4				15.4	
83	11.7	8.7				8.7	
121	25.6	20.5	301	319	18		20.5
205	25.1	16.1	25	21	-4		16.1
249	26.5	10.8	69	69	0		10.8
302	29.1	28.6				28.6	
Avg. SD	**24.1**		Avg. absolute diff.		**7**	52.7	47.4
					Rev. coeff.	1.11	

PHY.LUS

Direction	SDdir	N	Reversed	Observed	Difference	Arrival	Departure
deg.		%	*deg.*			N%	
26	13.9	13.6				13.6	
60	7.7	4.9				4.9	
93	11,0	8.3	270	243	-27		8.3
123	7.8	7.3	303	300	-3		7.3
186	30.7	17.9	6	26	20		17.9
243	8,0	9.3	63	60	-3		9.3
300	23.3	38.9				38.9	
Avg. SD	**14.6**		Avg. absolute diff.		**13**	57.4	42.8
					Rev. coeff.	1.34	

SYL.COM

Direction	SDdir	N	Reversed	Observed	Difference	Arrival	Departure
deg.		%	*deg.*			N%	
24	16.8	24.7				24.7	
64	5.0	8.9				8.9	
95	10.7	10.3	275	303	28		10.3
171	23.8	14.1	9	24	15		14.1
250	26,0	19.7	70	64	-6		19.7
303	14.7	22.2				22.2	
Avg. SD	**16.2**		Avg. absolute diff.		**16**	55.8	44.1
					Rev. coeff.	1.27	

All species

Direction	SDdir	N	Reversed	Observed	Difference	Arrival	Departure
deg.		%	*deg.*			N%	
24	12.9	11.5				11.5	
72	15.8	13.9				13.9	
121	19.9	14.2	301	306	5		14.2
176	17,0	9.6	356				9.6
208	18.1	6.6	28	24	-4		6.6
244	19.1	11.6	64	72	8		11.6
306	27.2	32.7				32.7	
Avg. SD	**18.6**		Avg. absolute diff.		**6**	58.1	42.0
					Rev. coeff.	1.38	

Beyond the estimation procedure

The Table 7 contains some information that is beyond to be enough precisely studied using the estimation procedure. That is the problem of the migration group number volumes. In the parameters accessible from the calculation procedure there is percent share of the groups heading in different axes/directions. In the context of the axial interpretation of the headings (previous Chapter) this parameter can be useful for further, deeper studies of the migration pattern. At the moment there is possible to define the *„reversing coefficient” RC*, that is:

$$RC = N_A / N_D,$$

where: N_A – percent share of arrival vector value, N_D – percent share of departure vector value. In the Table 7 there are listed general *RC* values for species, but with the same formula local, for separate axes, values are possible to be defined. Within the estimation procedure only approximate relations can be valuated and the trials were done only for two axes pattern – NE-SW and NW-SE (e.g. Stepniewska *et al.* 2011, Busse 2017). Anyway the next problem is open for further studies.

CONCLUSIONS

1. There is confirmed earlier conclusions that so called „classic" unimodal procedure is not applicable to the orientation cage data resulted from any field procedure,
2. there are available two evaluation procedures that base on the same general assumptions: multimodality of distributions reflects combination of several unimodal partial distributions, that can be described both using sophisticated Bayesian „Calculation" method and much simpler „Estimation" procedure,
3. results of both procedures are enough close to each other that they can be used for describing local and general heading patterns of migration of the nocturnal migratory movements studied using orientation cages.

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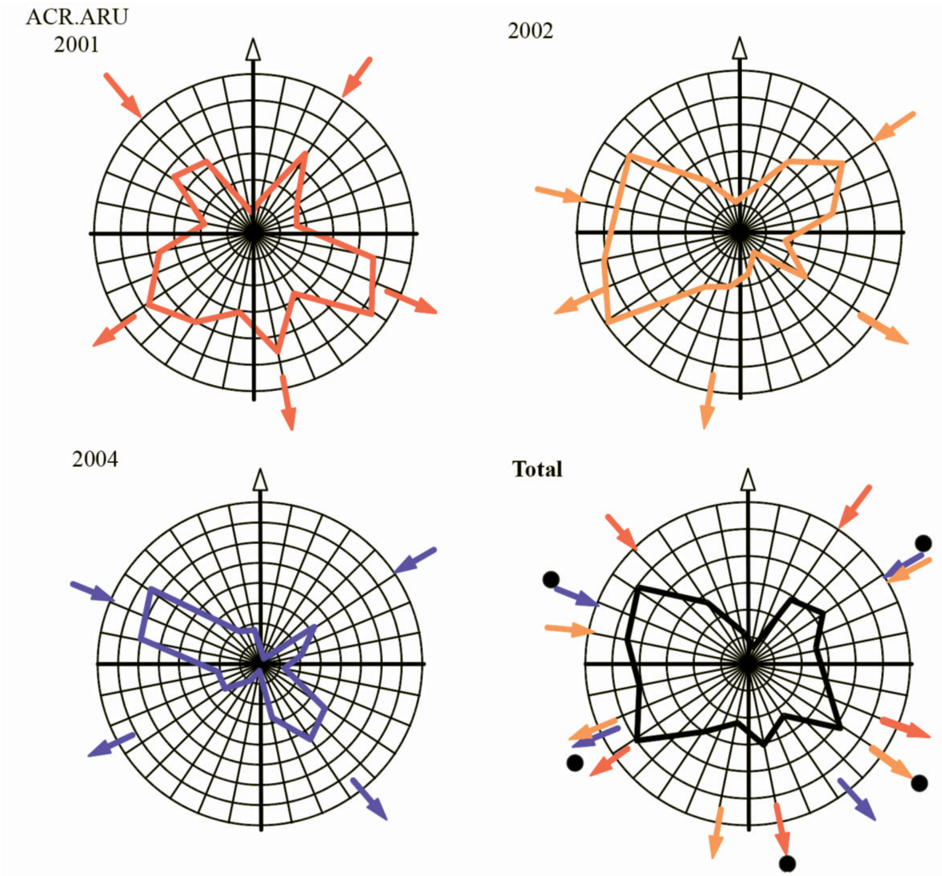
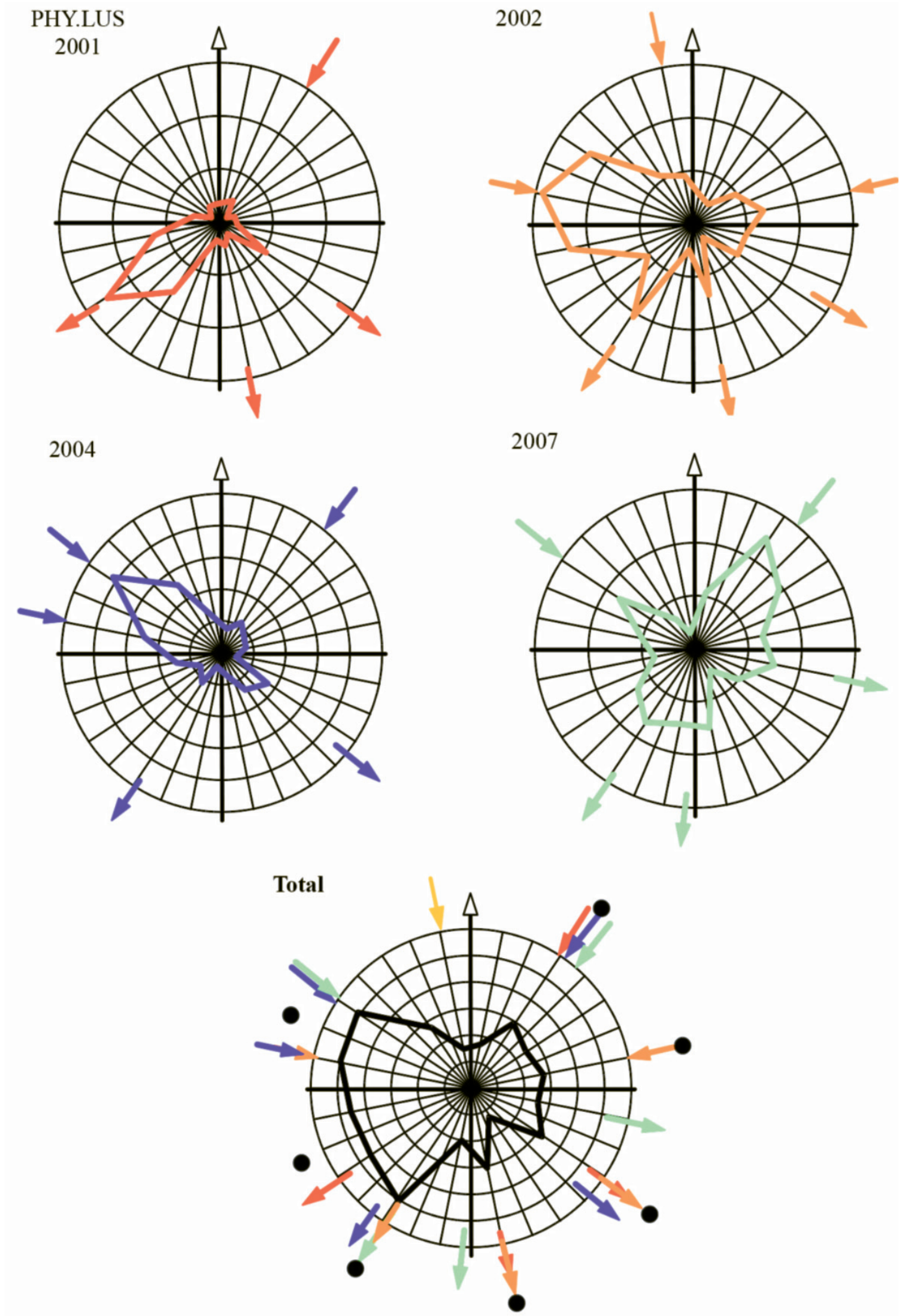
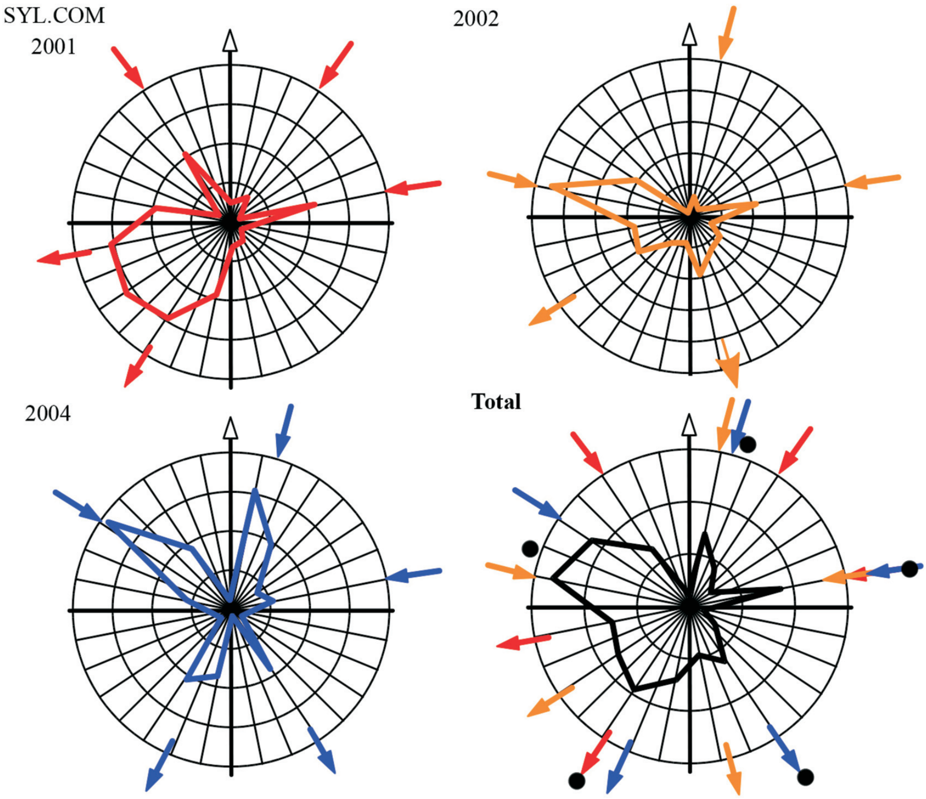
APPENDIX



AP-1. Heading patterns of the Great Reed Warbler (ACR.ARU) groups tested in Kalimok in years 2001-2004 using Busse's flat cage. Explanations as for Fig. 5 and 8.



AP-2. Heading patterns of the Willow Warbler (PHY.LUS) groups tested in Kalimok in years 2001-2007 using Busse's flat cage. Explanations as for Fig. 5 and 8.



AP-3. Heading patterns of the Whitethroat (SYL.COM) groups tested in Kalimok in years 2001-2004 using Busse's flat cage. Explanations as for Fig. 5 and 8.