

DIRECTIONAL PREFERENCES OF THE REED WARBLER
(*Acrocephalus scirpaceus*) AND THE SEDGE WARBLER
(*A. schoenobaenus*) ON AUTUMN MIGRATION
AT LAKE DRUŻNO (N POLAND)

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ABSTRACT

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In 2000, during the whole autumn migration period, Reed Warblers (212 indiv.) and Sedge Warblers (205 indiv.) were tested with Busse's method (Busse 1995) for directional behaviour at Lake Drużno ringing site. Distributions of scratches, reflecting cage activity of an individual, were tested for uniformity and more than 97% showed directional behaviour of tested birds. The data were elaborated using non-standard method for evaluation of circular data proposed by Busse and Trocińska (1999) that allows to show multi-modal distributions.

Results show that as much as around 55% of obtained headings point at directions reversed in relation to the normal direction of autumn migration. They suggest that pronounced number of individuals show axial behaviour in the cage. Causes of this phenomenon are still vague and it was decided that directional behaviour will be discussed after reversing northward headings by the doubling the angle method (adding 180°). Then main directions of headings were set as WSW, SSW and SE. They were confronted with available ringing recovery data and quite high (10-12° difference) or even very high (WSW "beam" of migration of Reed Warblers – 5° difference) accordance was found. Using, for the comparison, the same method to the Lesser Whitethroat (*Sylvia curruca*) data published elsewhere, an excellent agreement between cage data and ringing recoveries at the level 2° only was found. This can be treated as a check of the field and evaluation methods used for basic data presented in the paper. The heading pattern changed in the course of autumn migration and in subsequent periods different headings dominated. The most clear it was for the Reed Warbler data. However, this problem still needs further analyses.

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INTRODUCTION

Bird migration studies are among the most basic branches of contemporary ornithology. They contain research on migration patterns, population differentiation, orientation of migrants and physiology and strategy of migration (Busse 1991). The most popular and traditional method to study movements of nocturnal migrants is bird ringing and a large amount of data were collected on some of such species. However, ringing data sometimes show misleading patterns depending more on human distribution and education than on real distribution of migrants (*e.g.* Busse and Kania 1977, Spina 1999). The moon watching and radar studies can supply us with general patterns of nocturnal migration, but identification of species is usually impossible, thus information is very incomplete (*e.g.* Griffin 1964, Busse 1995, Zehtindjiev and Liechti in press). Nocturnal observations of birds in a strong beams of light or at illuminated greenhouses could be misleading too, as strong light at night attracts flying birds and they can change their standard direction of flight (Busse *et al.* 2001). A method of cage experiments as a tool of bird orientation study was developed in the 1940s and evolved as to techniques used. The basic assumption of the method is that caged migrants behave directionally because of strong internal urge. Kramer's and Sauer's cages were round structures with a system of horizontal sticks and differentiated electrical devices registering behaviour of caged birds. As very difficult to manage in the field conditions, those experiments were usually performed in laboratories and birds used were caged for a long time. A simpler design was proposed by Emlen and Emlen (1966) – birds were tested in a round conic cage where a bird jumped against a slope wall and fell down after every jump. The procedure was still stressing the bird much and evaluation of results was time-consuming, but widely used in field experiments (*e.g.* Beck and Wiltshko 1981, Rabøl 1985, Hilgerloch 1989 and others). Cage experiments were, however, criticised (*e.g.* Gerard 1981) because of caging stress, that could influence the birds behaviour shown in the cage. Experiments on nocturnal migrants were performed at night, frequently quite a long time after catching. During daytime only diurnal migrants were tested (*e.g.* Munro *et al.* 1993). On the contrary, Busse (1995) stated that cage experiments could be an useful method if the stress was reduced as much as possible. His cage design (flat cage, where the bird can move on foot without falling down) and performing the experiments just after catching a bird (instead of caging it till the night). These novelties allow to perform many experiments on the nocturnal migrants that are mist-netted in the morning and then not caged before the experiments. The method was used for collecting of the field data on several species of nocturnal migrants (Nowakowski and Malecka 1999, Busse *et al.* 2001, Trocińska *et al.* 2001) and results are encouraging for the continuation of data collecting in a larger scale. This is a case within SE European Bird Migration Network (SEEN). The method was also used in Morocco (Zehtindjiev pers. comm.) and Canada (Yosef pers. comm.).

Our goal in the paper is to follow directional preferences of Reed Warblers and Sedge Warblers during autumn migration through Lake Drużno ringing station, situated in northern Poland.

MATERIAL AND METHODS

The data were collected at the ringing station situated in southern part of the “Drużno Lake” nature reserve (54°05’N, 19°27’E) near village Żółwiniec. Lake Drużno is a big, shallow lake, that is overgrown much by reedbeds and swampy vegetation. It is a good breeding and resting place for the birds connected with wet biotopes.

Birds were mist-netted within reedbeds (*Phragmitetum communis*) and willow thickets (*Salix spp.*). Caught birds were ringed, measured using the Operation Baltic standards (Busse 1983) and then tested for directional behaviour using the Busse’s cage (Busse 1995).

The experiment cage is a rather flat (10 cm height, 36 cm in diameter) cage made of two wire circles connected by eight vertical sticks that divide vertical side-wall into eight sectors. Top surface is covered by netting while side wall by exchangeable transparent plastic foil. During experiment, the cage is situated in the centre of a bigger (120 cm in diameter) not transparent screen, that does not allow the bird to see any visual cues for orientation (*e.g.* trees, reeds *etc.*) – the bird can see only the sky. A bird is put into the cage for 10 minutes and then released instantly. All birds were put into the cage from the same side – from the north. After release of the bird, the cage was taken into laboratory and dots and scratches made by the bird were counted sector by sector.

The field data were elaborated using the special computer software ORIENTIN 4.0 (designed by P. Busse). It bases on non-standard evaluation of circular data (Busse and Trocińska 1999), that allows for multi-modal distributions frequently observed among the data collected in orientation cages. In this method a result for an individual is presented as one or more vectors that have their azimuths and lengths (the maximum length is 100 for a single vector). Cases when less than 20 scratches were found were eliminated from the sample (such birds were called “inactive”) and others were tested for randomness of distribution using χ^2 -test. Rare cases of distributions not significantly different from random ones were eliminated from samples, too. Directional preferences of birds are illustrated using a radar graph technique within QuattroPro 8.0 software, where sample headings are obtained by combining all individual vectors of birds belonging to the sample. Vectors that fall into the same 6°-sector are added and their total length represents this sector in a general picture. This gives an idea about dispersion of obtained individual headings within the group of headings. The sum of lengths of all vectors belonging to the group is called an index of directionality.

Following other papers (Busse and Trocińska 1999, Busse *et al.* 2001), the northern directions (a nonsense with regard to the autumn migration) found here were

corrected into the southern ones by “doubling the angles” method (adding 180° to the obtained azimuth – e.g. Helbig *et al.* 1989) at most of presented graphs. Thus, headings are discussed as WSW, SSW, SSE and ESE only.

The fieldwork was performed from 1 August to 16 September 2000. Catching dynamics (Fig. 1) was a basis for the division of this time into the periods used for the analysis of time-dependent changes in directionality of birds behaviour. Numbers of birds tested in subsequent periods are presented in Table 1 and 2.

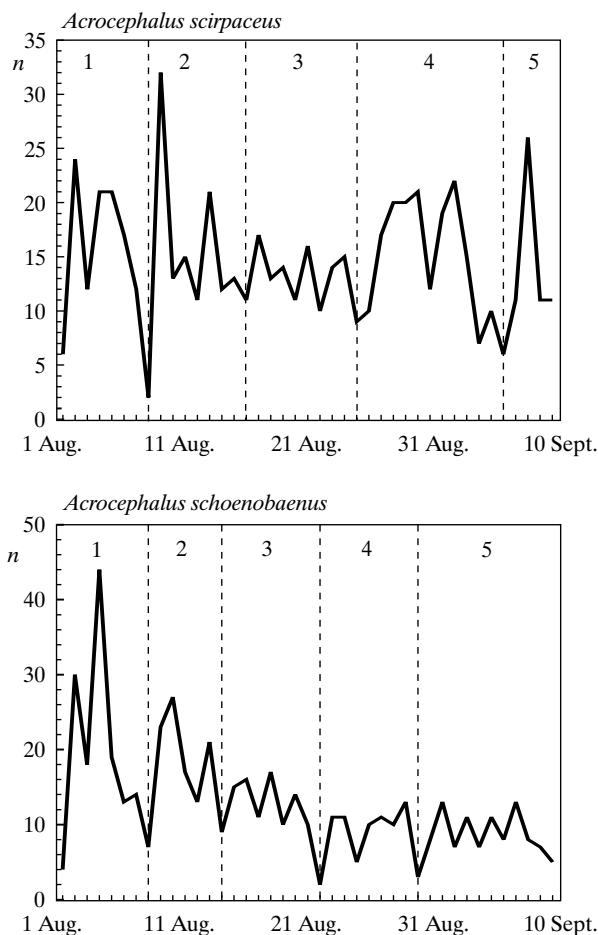


Fig. 1. Catching dynamics of the Reed Warbler ($N = 600$) and the Sedge Warbler ($N = 526$) at Lake Družno in 2000. Vertical lines show division of the season into subsequent periods (numbers above).

For checking the results obtained by using the orientation tests method, we analysed ringing recoveries from Reed Warblers (46) and Sedge Warblers (12) ringed at Družno and at Mierzeja Wiślana Operation Baltic station and collected during period 1968-2000. Presented maps were drawn using RECRING 2.0 software by P. Busse.

Table 1
Sample sizes for subsequent periods. Reed Warbler.

Period:	1	2	3	4	5	Total
Dates:	1-8 Aug.	9-16 Aug.	17-25 Aug.	26 Aug.-5 Sept.	6-16 Sept.	
$n =$	44	56	42	50	14	209

Table 2
Sample sizes for subsequent periods. Sedge Warbler.

Period:	1	2	3	4	5	Total
Dates:	1-8 Aug.	9-14 Aug.	15-22 Aug.	23-30 Aug.	31 Aug.-16 Sept.	
$n =$	47	39	48	35	31	200

RESULTS

Orientation experiments

Out of 212 tests performed on Reed Warblers, 209 distributions were significantly different from random (at the level $p < 0.01$). 200 of 205 tests performed on Sedge Warblers had non-random distributions. Total distributions of headings of both studied species are presented at Figure 2. High share of northern headings, opposite to actual autumn migration directions, is visible. Altogether, as much as 55.3% of the Reed Warbler headings were directed to the north and 57.7% of the Sedge Warbler ones. However, the share of northern headings were differentiated much when three axes were analysed separately: reverse headings on NNE-SSW axis were around twice stronger than on NW-SE and ENE-WSW axes. This phenomenon is visible in both species to a similar degree. After the reversing of north-

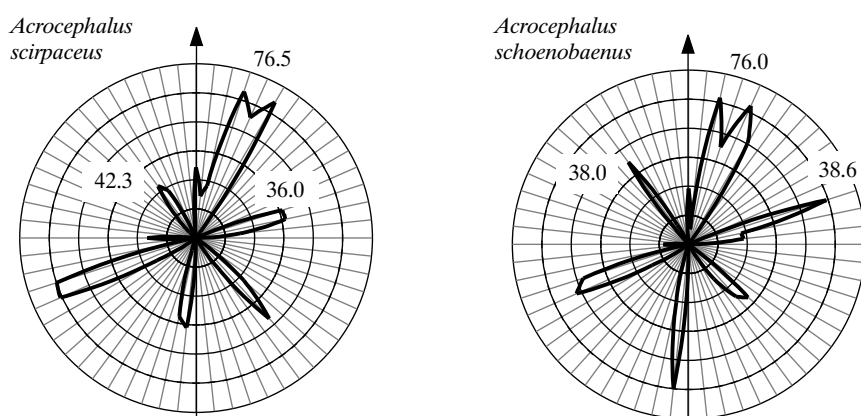


Fig. 2. Total distribution of the headings of Reed Warblers ($N = 209$) and of Sedge Warblers ($N = 200$). Numbers show percentage of headings directed to the northern part of the compass rose along different axes.

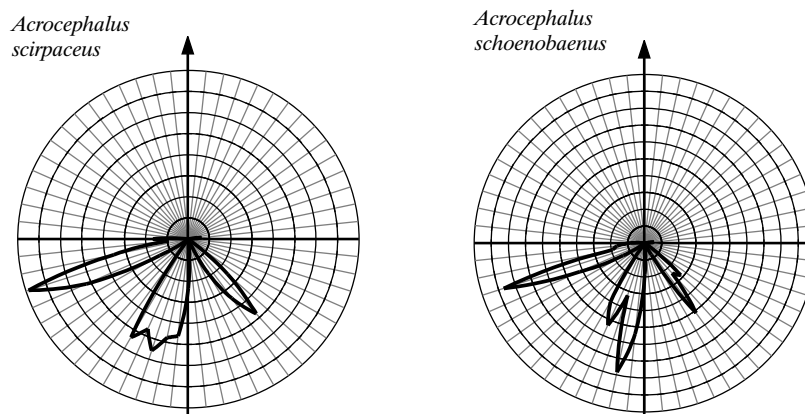


Fig. 3. Total distribution of the headings of Reed Warblers and of Sedge Warblers with northern headings reversed into actual direction of the autumn migration

ern directions the patterns become more clear and in both species similar picture is presented: WSW, SSW directions dominate and SE direction is visible (Fig. 3).

In subsequent periods of migration (see Figure 1), the patterns of birds headings are differentiated rather much (Fig. 4). The analysis of data presented as the radar graphs is difficult and we tried to find more convenient methods of presentation. Presentation of all period's distributions at one linear axis (Fig. 5) shows that despite the fact that the pictures for subsequent periods are differentiated as to a scatter of the headings, these are grouped around the same directions, namely WSW, SSW and SE. Relations between frequencies of these collective azimuths will be discussed in the following text.

A general pattern of headings in subsequent periods is presented at Figure 6. One can notice that the headings have their periods of dominance and periods when they are less represented. However, the picture is biased by different frequencies of azimuths in the total sample, e.g. shares of WSW-SSW-SE headings of Reed Warblers are 34-45-21 percent, respectively. To have less number-dependent picture, theoretical random distributions were calculated according to rules of χ^2 -testing. Results are presented as Tables 3 and 4, while Figure 7 shows how much observed distributions are different from the random ones (both observed distributions are significantly different from the random ones – $p < 0.0001$). It is much more clear here that for the Reed Warbler three subsequent periods (2 to 4) are strongly dominated by WSW, SSW and SE headings, respectively, and periods 1 and 5 are the most balanced (the beginning and the end of migration of three discussed groups). Migration of the Sedge Warbler is more differentiated as to headings and heading WSW dominates in period 3, while SSW – in two periods 2 and 5 that are not subsequent. Heading SE is strongly pronounced in 5 period only.

Ringling recoveries

Ringling recoveries from Reed Warblers and Sedge Warblers ringed at Lake Družno and its vicinity (Mierzeja Wiślana) or recovered there and ringed more to

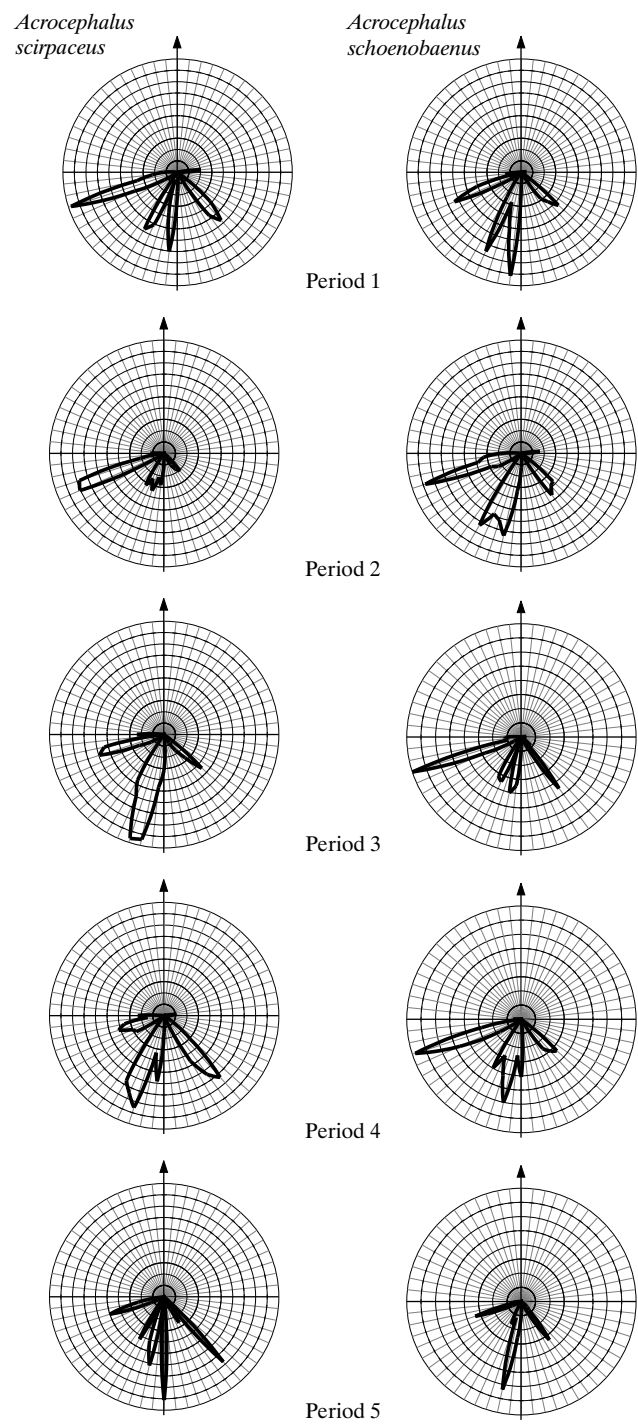


Fig. 4. Distributions of the headings of Reed Warblers and of Sedge Warblers in subsequent periods of the season. Northern headings reversed into actual direction of the autumn migration. For numbers of birds tested see Table 1 and 2.

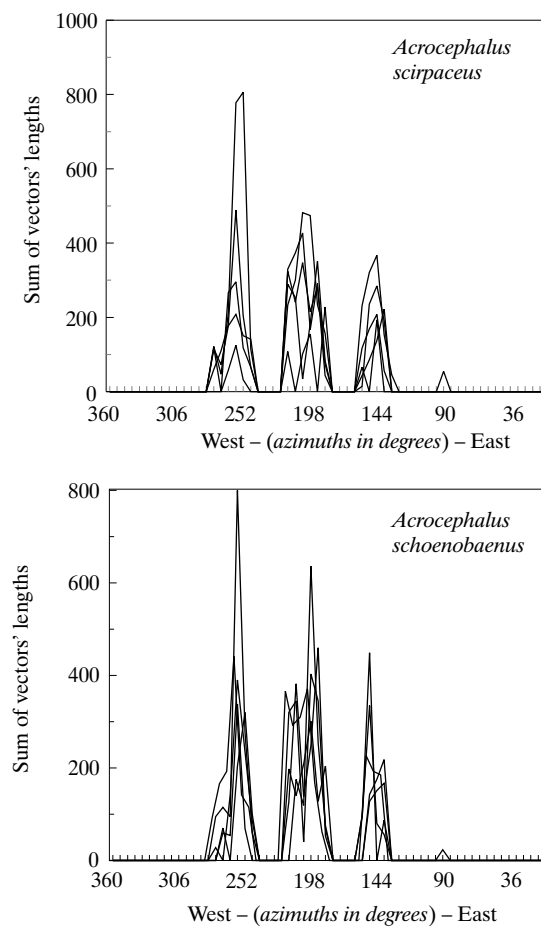


Fig. 5. Distributions of the headings of Reed Warblers and of Sedge Warblers combined from Figure 4. Northern headings reversed into actual direction of the autumn migration. Compass rose presented in a linear form from NW to NE.

the north are shown at Figure 8 and 9. Recoveries of Reed Warblers are concentrated mainly within WSW and SW directions (average directions for these groups are 254° and 223° , respectively) while those of Sedge Warblers more within SSW sector (an average direction – 197°). This is well visible at Figure 10, which was prepared using the technique of radar graph, that was used for presentation of orientation data in the previous chapter. The more westerly direction of two “beams” shown by recoveries at the graph for the Reed Warbler agrees surprisingly exactly with that shown by orientation experiments (259° – difference only 5° , cf. Fig. 3). The second beam of recoveries (an average – 223°) is shifted to the west in relation to azimuths shown by experiments. Recoveries of the Sedge Warbler are concentrated within southern directions similarly to the strongest concentration of headings shown by tested birds (209° – difference 12°), but WSW direction is lacking here. In both species, SE direction of migration was not confirmed by recoveries.

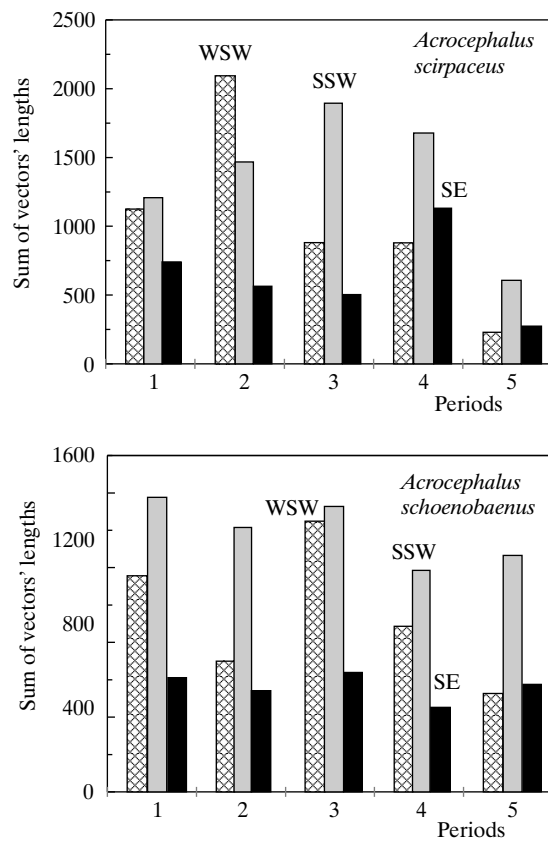


Fig. 6. Distribution of the headings of Reed Warblers and of Sedge Warblers in subsequent periods of the season. Northern headings reversed into actual direction of the autumn migration.

Table 3
Indexes of directionality of the Reed Warbler – observed and expected when assuming random distribution

Period	Indexes of directionality			
	WSW	SSW	SE	Total
Observed				
1	1110	1194	726	3030
2	2080	1453	550	4083
3	866	1880	489	3235
4	865	1664	1117	3646
5	215	593	259	1067
Total	5136	6784	3141	15061
Expected				
1	1033	1364	631	
2	1392	1839	851	
3	1103	1457	674	
4	1243	1342	760	
5	363	480	222	

Table 4
Indexes of directionality of the Sedge Warbler – observed
and expected when assuming random distribution

Period	Indexes of directionality			
	WSW	SSW	SE	Total
Observed				
1	1150	1570	605	3325
2	694	1409	536	2639
3	1443	1522	633	3598
4	880	1179	446	2505
5	521	1260	570	2351
Total	4688	6940	2790	14418
Expected				
1	1081	1600	643	
2	858	1270	510	
3	1169	1731	696	
4	814	1205	484	
5	764	1131	454	

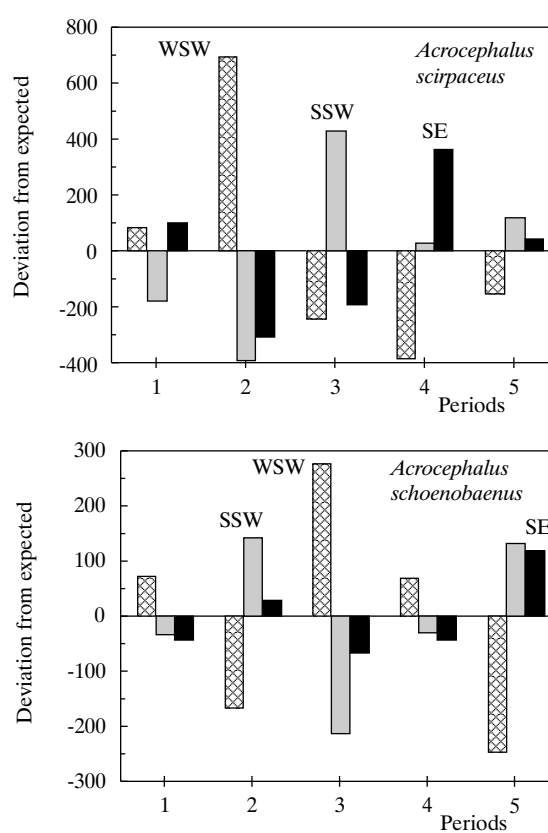


Fig. 7. Dominance of different headings of Reed Warblers and of Sedge Warblers in subsequent periods of the season. Deviations from expected random distribution are given.



Fig. 8. Ringing recoveries of Reed Warblers ringed in 1968-2000 at Drużno and Mierzeja Wiślana ($N = 46$)



Fig. 9. Ringing recoveries of Sedge Warblers ringed in 1968-2000 at Drużno and Mierzeja Wiślana ($N = 12$)

DISCUSSION

Analyses of cage tests performed using Busse's method are still not numerous (Nowakowski and Malecka 1999, Busse *et al.* 2001, Trocińska *et al.* 2001) despite the fact that the amount of collected data is quite large now. Nowakowski and Malecka (1999) concentrated rather on the testing the method on the Robins (*Erithacus rubecula*) migrating through the central Poland, while Trocińska *et al.* (2001) evaluated not too numerous data on the Reed Warbler and the Sedge Warbler collected at a few stations in central/eastern Europe, looking especially for differentiation of heading patterns between localities. Among others, rather poor samples of Reed and Sedge Warblers tested at Družno were evaluated. There were tested 37 Reed Warblers, of which 32 (86%) have shown statistically significant directionality, and 38 Sedge Warblers, among which 34 (89%) were significantly directed. These values were lower in comparison to our results (98 and 97% significantly oriented, respectively).

Since the beginning of evaluations of cage data, quite high number of reverse (in relation to migration direction normal for a season) directions shown by birds have been observed (Busse 1995, Busse and Trocińska 1999). These were treated as signs of axial behaviour and for discussion of migration patterns reversing of such headings was used (Busse *et al.* 2001, Trocińska *et al.* 2001). From rough evaluations of accessible data from many localities and for many species it is known that amount of reversed headings is very differentiated according to a locality and a season. The causes of the phenomenon are still vague, but our data in the present paper show that even for the same site and in the same season numerical relations between northern and southern directions can be different: as much as around 76% of birds headed northwards at NNE-SSW axis, while 36-42% only at NW-SE and ENE-WSW axes (Fig. 2). In further evaluation the northward headings are assumed to be signs of the axial behaviour and thus not discussed in detail. This problem needs to be studied separately.

In the paper by Trocińska *et al.* (1999) Reed Warblers showed mainly SSW headings – as in present study, but the second most numerous direction was SSE while in 2000 – WSW. Similar pattern was shown by Sedge Warblers. So, it can be concluded that the main direction of migration of these bird species at Lake Družno are SSW (both studies agree) and WSW, especially for the Reed Warbler, while differences in both studies can be explained by different distribution in time of tests performed in 1996 and 2000 (see later discussion).

The Reed Warbler is a trans-saharan migrant that winter mainly within area between Sudan and Zambezi. Birds from western Europe migrate WSW-SW while Czech and Hungarian birds move through the Middle East to SE (Zink 1973, Hage-meijer and Blair 1997). Following the SE flyway is confirmed by three recoveries of birds ringed in Eilat (southern Israel) and recovered in Central Europe and one more recovery in opposite direction (Yosef 1997). Figures 8 and 10 confirm migra-

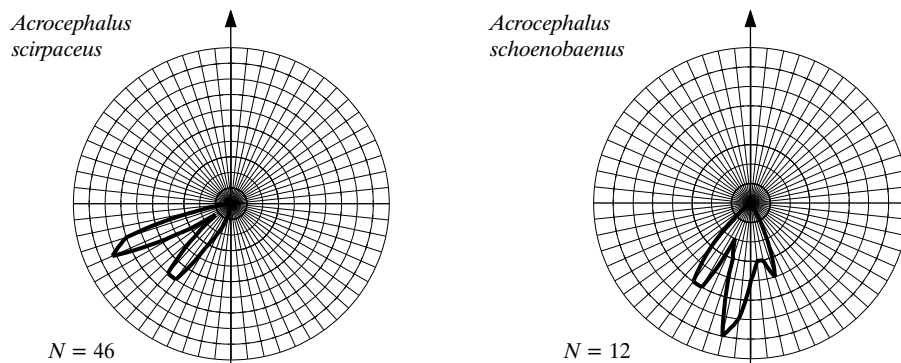


Fig. 10. Distribution of the azimuths shown by ringing recoveries of Reed and Sedge Warblers ringed in 1968-2000 at Družno and Mierzeja Wiślana (cf. Fig. 8 and 9)

tion of central European birds in south-western directions, but SE direction is shown by orientation experiments only (cf. Fig. 3). However, lack of Polish recoveries from the SE flyway can be caused by low recovery rate that is known from this region and lack of ringing stations in this area – apart from a single station in Israel (Eilat) that has been working for many years, the other stations in the region were established quite recently. The most interesting fact is so close agreement of average directions (5° difference only) for more westerly beams of recovery and cage data, while the difference for more easterly beams is as large as 20° with a shift of recoveries to the west in relation to cage data. This illustrates probably the problem of low recovery rate in eastern Europe (that apparently shifts azimuth of the recoveries to the west). The problem does not exist if the studied area is situated entirely, or at least mainly, on the territories with similar recovery rate, as it occurs in the case of the Lesser Whitethroat (*Sylvia curruca*), migrating through the Middle East to central and western Europe (a map shown in Busse 2000), where difference between recovery azimuth and the cage data azimuth is as small as 2° only (325° and 327°, respectively). These agreements support strongly the method of the cage orientation experiments as the source of valuable data on directionality of migrants.

The Sedge Warbler is a trans-saharan migrant, too. South Scandinavian and west European populations of this species migrate SW and winter in western Africa, while those breeding in Finland and eastern Europe migrate SE to central and eastern Africa. Recoveries of birds ringed at Družno and in its vicinity confirm this pattern (birds found in Austria, Hungary and Kenya). Sedge Warblers ringed in Czech Republic, on the way south, were then found in Hungary, Slovenia and Austria, that means in S-SSW directions (Literák *et al.* 1994). So, the heading pattern obtained from orientation tests agrees with this picture – difference between azimuth of recoveries and headings in the cage was only 12°, that is not too large as for a rather poor sample of recovery data.

As early as in the first paper on the topic, Busse (1995) mentioned differentiation of the heading patterns obtained in different parts of the migration period. Busse and others (Busse *et al.* 2001) beside territorial differentiation of headings

discussed temporal changes in the pattern of directional behaviour in the Robin and the Blackcap (*Sylvia atricapilla*). Having divided the whole period of migration into two-week-long subsamples, they showed that the heading pattern had been changing in the course of migration. Following this finding, we studied this problem more carefully, trying to establish samples according to migratory waves supposed on the basis of the catching dynamics. Such procedure seems to be more adequate to the structure of migration and gives chances for finding more clear results. Obtained differentiation in patterns is well pronounced (Table 3 and 4, Fig. 6 and 7) for both studied species. Changes of dominating directions were more clear for the Reed Warbler, for which more and more eastward directions were observed in subsequent periods of migration. In the Sedge Warbler, the dominance was the most pronounced for WSW headings in the period 3 and SE – in period 5, while SSW headings were more common in periods 2 and 5. This suggests different population structure of migrants, that is taken under consideration in many papers dealing with migration dynamics (e.g. Berthold and Helbig 1992, Remisiewicz and Baumanis 1996).

The method applied here for presentation of this type of data seems to be fruitful in pointing differences, but still the problem should be studied more in details, taking under consideration data from different stations and more dense sampling of the migration period. This needs very intensive fieldwork, that is, however, quite possible using the method applied in the study. For the most common migrants, sufficient samples could be collected even on a daily basis.

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