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METHODS

DIRECTIONAL BEHAVIOUR OF THE SEDGE WARBLER (*Acrocephalus schoenobaenus*) STUDIED IN TWO TYPES OF ORIENTATION CAGES DURING AUTUMN MIGRATION – A CASE STUDY*

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ABSTRACT

Zehtindjiev P., Ilieva M., Ożarowska A., Busse P. 2003. *Directional behaviour of the Sedge Warbler (Acrocephalus schoenobaenus) studied in two types of orientation cages during autumn migration – a case study.* Ring 25, 1-2: 53-63.

Migratory directions of Sedge Warblers tested in the Emlen funnel and Busse's flat cage during autumn migration in the Balkan region were studied. Some methodological aspects of orientation data analysis were discussed as well. According to orientation data at least two populations of the Sedge Warbler migrate in NE Bulgaria: one in SW direction *via* Greece, crossing the Mediterranean Sea to Libya, and then Central Africa and second one through Turkey, (Cyprus?) and the Middle East to the eastern parts of winter quarters (SE direction). This pattern is clear when a calculation method that assumes reverse and axial behaviour of birds (*i.e.* reversing vectors from northern sectors) is applied. Nature of "reverse migration" is still not well recognised and seems to be very interesting for further studies.

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INTRODUCTION

During migration birds behave directionally flying from breeding grounds towards winter quarters. Direction of bird migration is genetically fixed and modified by physiological and environmental factors (Gwinner and Wiltschko 1978, Akesson 1993, Bruderer and Liechti 1998). Since papers by Kramer (1949) and Sauer (1957), researchers often use registration cage experiments to determine migratory activity and direction. At the beginning orientation cages were heavy and complicated and they were applied to laboratory experiments on orientation cues used by migrants. Since simpler Emlen funnel cages were designed (Emlen and Emlen 1966) some field experiments on birds during their real migration have been performed. With very simple experimental cage and simple procedures proposed by Busse (1995) the field experiments became more popular in Poland and SE Europe (Nowakowski and Malecka 1999, Busse *et al.* 2001, Trocińska *et al.* 2001, Formella and Busse 2002). Theoretical problems on evaluation of orientation data were discussed by Busse and Trocińska (1999). However, there are still some problems that have to be discussed when extensive field data are evaluated. One of them is how to handle and interpret reverse directions frequently observed in orientation cages. Another question is whether results of two different experimental methods and procedures – Emlen funnel cage and night tests *versus* Busse's cage and daytime tests – are compatible.

The present paper focuses on some methodical aspects of orientation data evaluation, *i.e.* comparison of results obtained with different techniques (Emlen funnel cage / Busse’s flat cage) and interpretation of orientation data as a consequence of calculation procedures used.

Another aspect of the research is to investigate innate migratory directions of a trans-Saharan migrant – the Sedge Warbler – during autumn migration in the Balkan region (NE Bulgaria). This species is included in a large-scale program of orientation studies at several stations working within SEEN network and the results could be compared with the data from larger area of SE Europe. Moreover, a coordinated moon-watching study of nocturnal bird migration in the Balkan area described prevalence of the S-SSW directions in autumn suggesting that the majority of trans-Saharan migrants intend to cross eastern Mediterranean Sea between Greece and Egypt/Libya on a broad front (Zehtindjiev and Liechti 2003), thus, the comparison of these studies results could reveal more details on bird migration in the region.

MATERIAL AND METHODS

Orientation tests data on the Sedge Warbler from Kalimok ringing station (41°00’N, 26°26’E, located near the Danube river-bank, NE Bulgaria), autumn 2001 and 2002, were analysed. Two types of registration cages were used in following years: Emlen funnels (Emlen and Emlen 1966) and Busse’s flat cages (Busse 1995). In autumn 2001 (6 August – 10 October) all individuals (N = 45) were tested only in Emlen funnels. Birds were trapped in mist-nets in resting habitats 2-14 hours before the experiments and caged in the large aviaries in natural conditions. All birds were ringed and measured according to the SEEN standards (Busse 2000). Only individuals that were not in moult and of which fat score was at least 3 (fat classes after Busse 1983) were selected for the experiments. Tests were made during the first hour after sunset and lasted 60 minutes. Bird activity was recorded as a number of claw marks on the typewriter correction paper (Tipp-ex®) attached to the funnel cage walls (Akesson 1993). Afterwards, scratches were counted in 45 degrees sectors. Next year (1 August – 30 October 2002) birds (N = 121) were tested in Busse's cages during the daytime, immediately after trapping. Bird activity was recorded as a number of holes and scratches on transparent foil covering the side wall of the flat cage. The wall was divided into 8 sectors (45 degrees each).

The raw data set was computerised with ORIENTIN program available from the Bird Migration Research Station, University of Gdańsk, Poland. The evaluation of orientation experimental data followed multi-vector model described in details by Busse and Trocińska (1999). Inactive individuals (less than 30 scratches/holes in total) and disoriented individuals (nondirectional distributions compared with equal frequency distribution by χ^2-test) were excluded from further analysis. The standard presentation of results is given as QUATTRO PRO radar graphs. Individual vectors are summed up in 6° sectors to show total distributions of headings (*e.g.* Fig. 1). These graphs show an overall pattern of directional preferences of tested birds, but as they represent sum of all final vectors shown by each individual, they give much details and are rather difficult to compare and to discuss differences and/or similarities of distributions, thus we used simplified pictures – we summed up final, ***basic*** data within each 45° sector, representing cage sectors. This type of presentation is used at most graphs. ***Reversed*** data patterns were obtained by adding 180° to the vectors from northern sectors – seasonally "inappropriate" directions – as we studied autumn migration. If there were axial vectors, then the length of the northern one was added to its southern counterpart, thus *e.g.* the NNE vector was added to SSW one and the sum was drawn as SSW heading. This presentation of data was already used in some papers, but not discussed in detail, nevertheless, axial distributions are the rule in this kind of data. The mean angles were calculated according to standard circular statistics (Batschelet 1981).

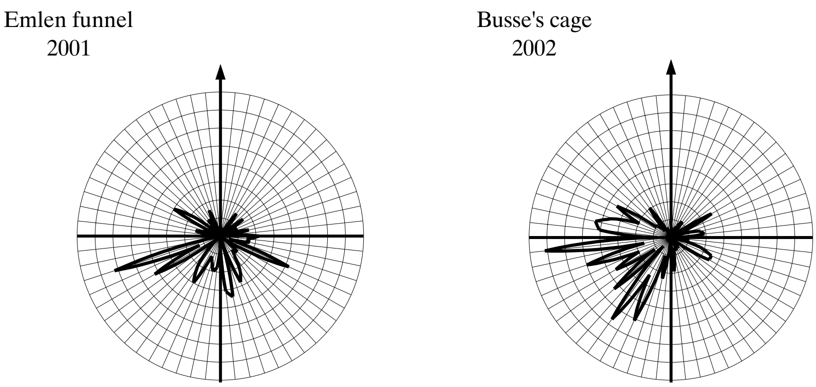

Fig. 1. Total distribution of headings at Kalimok station as found in 2001 and 2002

RESULTS AND DISCUSSION

In all data sets the number of inactive and disoriented individuals was low. Most of those behaving directionally showed only one preferred direction (unimodal distribution) – Table 1.

Figure 1 shows basic data distributions in subsequent years. Two field methods were used (Fig. 1 – left: Emlen funnel; right: Busse's cage), but data were elaborated according to the same procedures. For better data presentation, as it was mentioned earlier, results are given in a simplified way (Fig. 2). Basic distributions

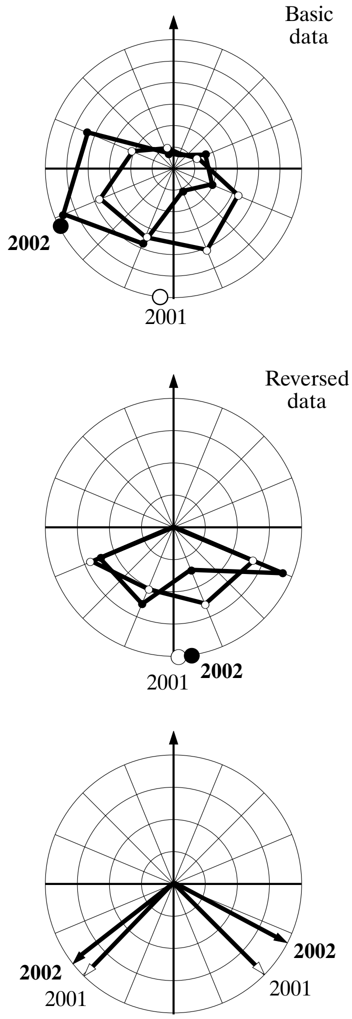

Fig. 2. Simplified distributions of headings at Kalimok station in 2001 and 2002 (basic – top panel and reversed data – middle panel) and interpretation of these data (bottom panel). Average azimuths are shown. For more explanations see the text.

Table 1
Number of orientation experiments

	2001	*2002*
Total number	45	121
Significantly directional	43 (95.6%)	109 (90.1%)
Unimodal	60.5%	55.0%
Reversed headings	27%	37%

and the result azimuths are quite different (Watson-Williams test, $p << 0.001$). It is worth to note that in both samples birds demonstrated also northward headings (WNW-ENE): 27 and 37%, respectively, of birds tested in 2001 and 2002. As the Sedge Warbler's winter quarters are in Central Africa, these are absurd headings in view of the species autumn migration. Northward headings can be treated as a random scatter within circular normal distributions or "reverse orientation/migration" as it was suggested in some papers (Akesson *et al.* 1996, Phillips 2000, Komenda-Zehnder *et al.* 2002, Zehnder *et al.* 2002). The second panel of the figure shows what happened when we used the alternative method assuming reverse migration and axial behaviour of birds – reversing vectors from northern sectors. The result mean angles for samples from 2001 and 2002 become nearly identical (176° and 172°, respectively), while distributions still differ.

The problem of distribution analysis in cage experiments seems to be crucial in the field studies of migrant directional preferences. In classic studies when an individual is considered, calculation of the mean angle and applying Rayleigh test will exclude most multimodal distributions from the analysis as non-significant – with an exception of axial distribution when special procedure (doubling the angles) is applied; at the group level – again there is an assumption of only one migratory direction as calculation of the mean angle and Rayleigh test will allow only to accept unimodal distributions. This can be the truth if we assume that all tested individuals represent the same population *e.g.* birds taken as nestlings, kept in aviaries and then tested during the migratory period. But if we handle birds that are caught during migration, we do not know which population they represent, we do not have homogenous data, thus we cannot apply simple averaging. This problem was discussed in detail in a previous paper (Busse and Trocińska 1999) and the necessity of taking into account multimodal distribution was claimed. Also Phillips (2000) found that "any experimentally tested group of migrants exhibits a very wide range of orientation directions. (...) One cannot accept the mean direction as being valid while selectively ignoring individual data points from which it is derived." It is crucial at the localities where other data suggest that a stream of migrants could consist of birds originating from different breeding grounds and heading to different winter-quarters (Högstedt and Persson 1971, Scebba and Olivieri del Castillo 1983, Busse and Maksalon 1986, Busse 1987, Pettersson *et al*. 1990, Remisiewicz 2002). When we look at our results one can easily see that the distributions, as shown in Figure 2, are not unimodal de Mise's circular distributions describing unidirectional migration. 2001 sample shows very wide range of variation that can put a question mark as to orientation abilities of this species (that in fact is able to reach Central African winter-quarters). A shape of 2002 distribution suggests, however, that it is really bimodal one with SW and SE components – there is clear deficit of birds heading SSE. This could justify next step: we "cut" 2001 and 2002 distributions along N-S axis (we had no other possibility if we apply eight sector grouping). Results of this procedure are shown in Figure 2 (bottom panel): mean angles of two studied samples – 2001 (Emlen funnel, night tests: 134° and 228°) and 2002 (Busse's cage, daytime tests: 124° and 223°) do not differ between corresponding vectors (Williams-Watson test, $p > 0.05$). We can conclude that Sedge Warblers migrating through Kalimok comprise two migrating groups that choose different directions and that this pattern is observed in both types of orientation cages.

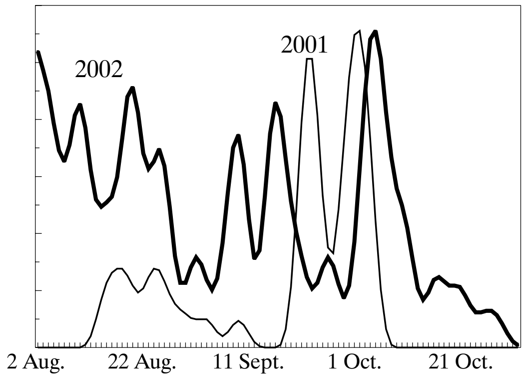

Fig. 3. Seasonal distribution of performed experiments (smoothed)

This pattern stresses the problem of understanding biological sense of reversed headings: two hypotheses should be checked – (1) northward headings are reversed directions within the same axis of migration, or (2) the birds show their arrival direction – however, solving this problem is not a topic of this paper. The reason for some variation in the results can be different relative distribution of performed tests in 2001 and 2002 (Fig. 3).

Changes of directional preferences with a progress of migration were discussed in earlier papers (Busse *et al.* 2001, Formella and Busse 2002). These findings encouraged us to study this aspect at Kalimok as well. We analysed only 2002 data, as only this sample was large enough to look for seasonal differentiation. 2002 season was divided into three periods on the monthly basis – results for both basic and reversed data are given in Figure 4. It is worth to stress that reversed data are clearly bimodal in all analysed periods. This supports our previous presumption about bimodality of distributions. Basic data distributions show quite pronounced headings around W-E axis – directional preferences in the second migration period are particularly interesting but difficult to explain. All these are rather strange and should

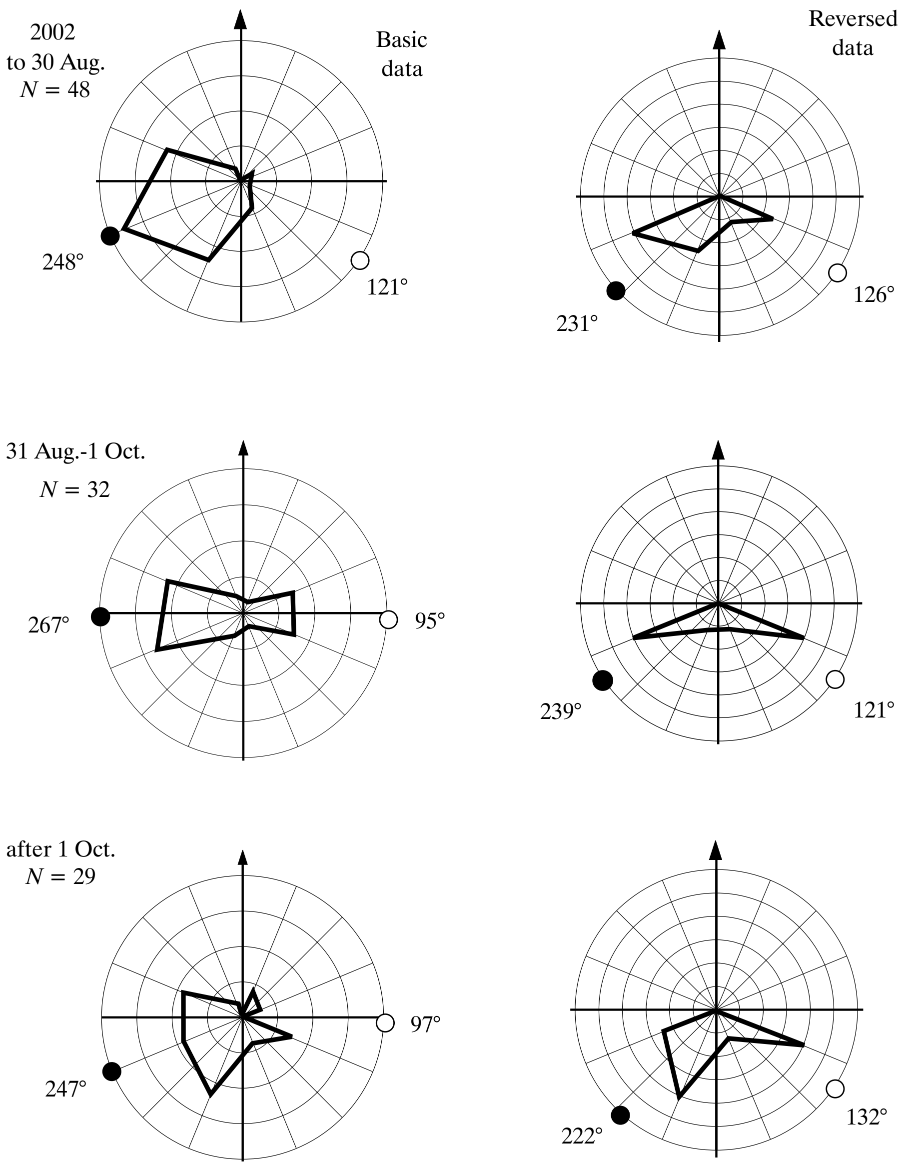

Fig. 4. Basic and reversed data distributions at Kalimok station in subsequent periods. Average azimuths for western and eastern beams are shown.

be discussed in detail. First, they could illustrate only a local migration route, which at Kalimok is rather improbable, because this is an inland station and there are no strong guiding lines for nocturnal migration – the Danube seems to be definitely not a guiding line for the nocturnal migrant that uses long-step migration strategy (Gyuracz *et al.* 2003). Also in a paper on nocturnal bird migration in SE Europe based on a moon-watching study, no influence of this river on the bird migratory direction could be found (Bolshakov *et al*. 1998, Zehtindjiev 2001; *cf.* Fig. 2 and 4 in

Zehtindjiev and Liechti 2003). Second, assuming that these distributions are based on a real long-distance orientation one must accept migration much closer to the west (Fig. 4, left panels). Third, unlike basic ones, reversed data stress occurrence of two azimuths of migration (Fig. 4, right panels). Comparing mean headings in all three periods (Fig. 4) we can say that reversed data pattern is much more probable if the species migration is taken under consideration.

Figure 5 shows migration pattern at Drużno ringing station (54°07'N, 19°24'E, located in the Lake Drużno reserve, N Poland). In Figure 6, the results from Kalimok are compared with that data. In both cases an assumption was made that birds should show a distant migration goal in the cage (although not excluding loop migration) rather than a local one, thus accepting reverse migration and axial behaviour of birds as a normal feature of bird migration, and a method of reversing vectors of seasonally "inappropriate" directions as valid. This pattern fits quite well to general pattern shown in Figure 7 based on ringing recoveries given in Zink (1973-1985) and summarised by Busse (Busse 1987, 2001). If we accept straight western direction, as it is suggested by basic data, we obtain migration pattern that is not consistent with general one. The eastern beam of the basic data pattern is even less acceptable. The suggestion based on reversed data seems to make sense considering the bird final destination: one direction *via* Greece, crossing Mediterra-

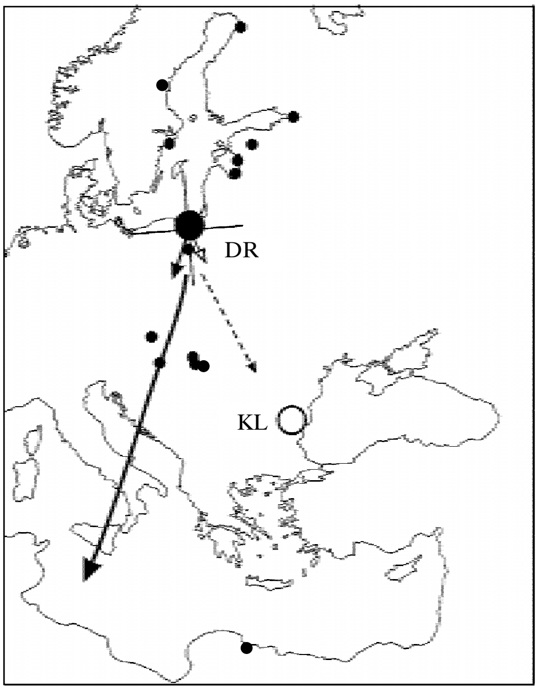

Fig. 5. Migration pattern of the Sedge Warbler at Drużno station (DR) after data from Trocińska *et al.* (2001) and Formella and Busse (2002); small black dots – ringing/recovery localities of birds caught at or in the neighbourhood of Drużno station. Localisation of Kalimok station (KL) is shown as well.

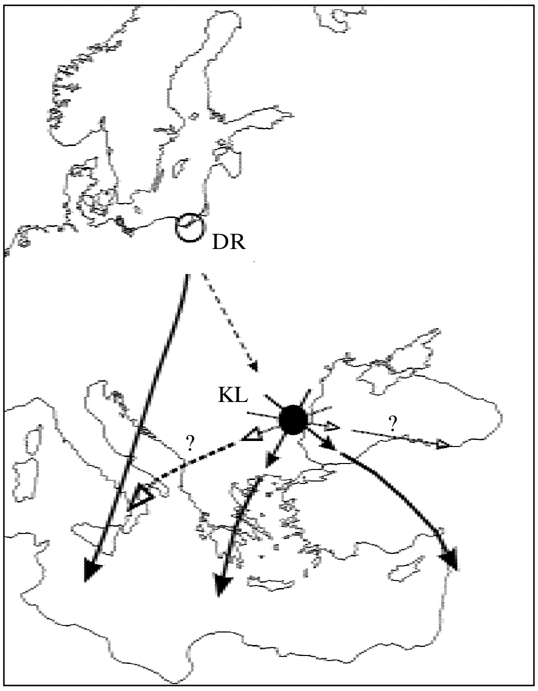

Fig. 6. Migration pattern of the Sedge Warbler in the area (DR – Drużno, KL – Kalimok). Discussion in the text.

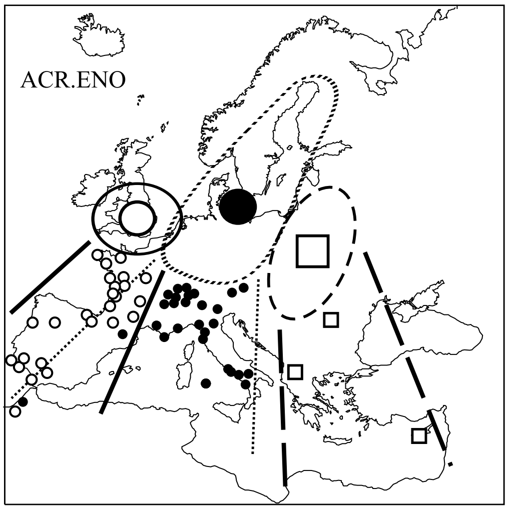

Fig. 7. European migration pattern of the Sedge Warbler (after Busse 2001) – breeding areas and recovery places (small signs) of ringed birds are shown

nean to Libya, and then Central Africa and second one through Turkey, (Cyprus?) and the Middle East to the eastern parts of winter quarters. Prevalence of the SW (but not WSW) directions in autumn is in agreement with the moon-watching study of nocturnal bird migration in the Balkan region (Zehtindjiev and Liechti 2003) but, interestingly, southeastern directions in this study were not common.

CONCLUSIONS

For the Sedge Warbler (at least):

1. results in Emlen funnel cage and Busse's flat cage are coherent, despite the tests were performed in different conditions (night-day) and in different years,
2. orientation data interpretation procedure has to assume multimodal distribution of bird headings as preferred directions could be hidden within abnormally wide spread of grouped individual azimuths,
3. reversing of seasonally "inappropriate" headings enables clear data interpretation and final patterns are in agreement with actual bird migration; nature of reversed headings is still obscure and seems to be very interesting topic for further studies,
4. it seems that at least two different populations migrate in SW and SE directions in NE Bulgaria; as there are some other possible data interpretations further studies should be conducted.

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