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BUSSE'S FLAT ORIENTATION CAGE VS. EMLEN'S FUNNEL – COMPATIBILITY, DIFFERENCES AND CONCLUSIONS

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ABSTRACT

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This paper focuses on field practice using different types of orientation cages. The two orientation cage designs most commonly used in field work, i.e. Emlen's funnel and Busse's flat orientation cage, are described in detail and compared for compatibility of results, simplicity of use and time effectiveness. Apart from cage designs and field procedures (60-min nocturnal tests in Emlen's funnel vs. 10-min diurnal tests according to Busse's procedure), the standard data evaluation procedures are compared and discussed. The data used in the discussion were collected for four species of nocturnal migrants (the Reed Warbler, the Sedge Warbler, the Willow Warbler and the Whitethroat) at the Kalimok Bird Station (Bulgaria): altogether 141 individuals were tested in Emlen's funnel in 2001 and 788 in Busse's cage in 2001-2007.

The following conclusions were drawn: (1) Busse's flat cage design and its standard procedures yield results fully compatible with those obtained using Emlen's funnel and the associated procedures; this means full compatibility in terms of the directionality of tested birds in the diurnal and nocturnal tests; (2) the procedures compared have distinct differences in terms of constraints on the methods:

– Emlen's cage is extremely stressful for the bird and should be avoided as much as possible in practice due to animal welfare concerns;
– Emlen's standard procedure of testing the bird for 60 minutes is completely useless, as this is inefficient in terms of quality of results and causes more stress to the bird than is necessary;
– Busse's 10-minute standard makes it possible to collect a vast amount of data (12 birds per hour and person) in real field work, even performed in wilderness areas;

(3) At the stage of evaluation of raw data it is essential to use evaluation tools which take into account the fact that raw data items show a high percentage of multimodal distributions, and therefore tools assuming unimodal distribution are unsuitable.

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Keywords: orientation cages, directionality, nocturnal migrants, field tests, circular data, bird migration

INTRODUCTION

Technical design of the orientation cages

Since 'orientation cages' were first introduced in research on the directional behaviour of birds (Kramer 1949, Sauer 1957), their design, experimental procedures and handling of data has evolved significantly. The first were fairly large constructions with perches and various types of mechanical or electric, and then electronic counters. They were mainly used as laboratory tools in studies on the orientation abilities of nocturnal migrants. Orientation cues were manipulated and the orientation cage was used to document changes in the birds' behaviour. Due to their size and construction, and often the need for electricity, the experiments were done either in laboratories or outdoors, but close to laboratories or field bird stations. The basic procedure was to work with caged birds, frequently hand-reared, caged for a long period, and tested several times in a changing environment. Such studies can provide answers to various questions associated with bird migration, but the answers were highly conditional on the bird manipulation procedures. More in-depth research and studies on the migration patterns of actual migration required tests to be conducted outdoors, in field conditions, in various localities that were frequently far from laboratories and an electric power supply. Due to these constraints such studies were uncommon in Europe (Evans 1968). In 1966 Emlen and Emlen (1966) offered a new, much simplified design of the orientation cage, commonly known as Emlen's funnel (Fig. 1). The main feature of the construction was an inverted, truncated cone covered with a net and placed with its smaller surface on an ink-pad. During the test the bird located by the handler jumps from the bottom onto the wall of the slope and leaves footprints pointing in the direction in which the bird has moved. After each attempt to jump the bird fell back down onto the ink-pad. The authors showed exam-

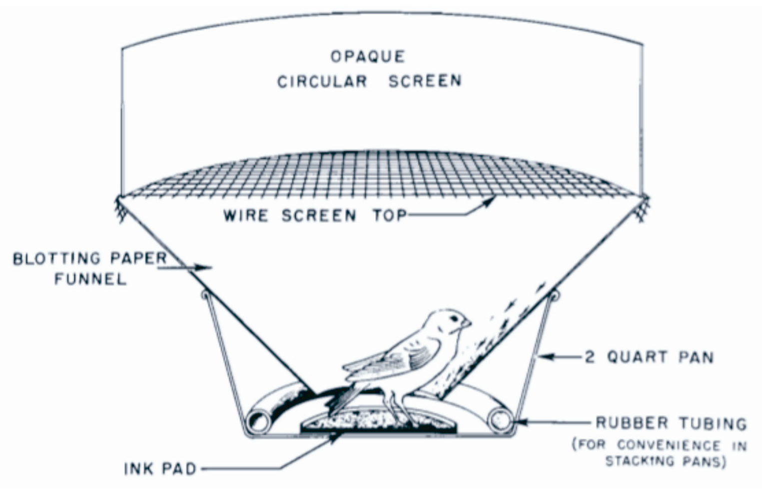

Fig. 1. Emlen's orientation cage original design. From Emlen and Emlen, 1966.

ples of the resulting pictures with their interpretation as fans of directions shown by the bird (Fig. 2). For statistical purposes, after the test the wall was divided into 24 sectors within which the number of footprints was estimated visually. In the examples given in this picture the interpretations on the right of the ink patterns on the left were clearly made 'by eye' and were of very limited documentation value. Many years ago, a Latvian ornithologist using this method commented that: '*after the experiment the robin was black, the paper was black, I was black and after one hour of counting jumps I had little useful information*'. These properties of the original design discouraged the use of the funnel as a working tool or forced the introduction of upgrades to the procedure. The first upgrade was the use of Tipp-Ex correction paper to cover the slope wall, eliminating the ink-pad. This solved the problems of ink on the bird and estimation of bird activity by eye alone, but created a new one: the new slope cover

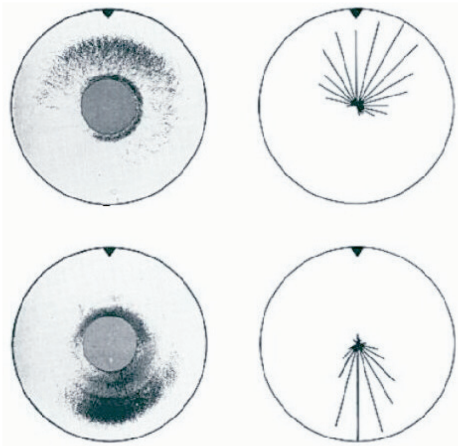

Fig 2. Emlen's original examples of results (left) and their interpretations (right). From Emlen and Emlen 1966.

shows scratches made by the bird claws, and to obtain numerical data to evaluate them statistically the number of scratches per sector must be counted. Originally this was extremely time-consuming, as a bird has two legs and four claws on each leg. Thus one jump could potentially make eight scratches in one slip back from the jump, or even more if the starting flutter was close to the wall and the bird were to use his legs to help himself when starting; Bianco *et al*. (2016) claim that from 5 to 159 scratches could be counted for just one jump. To reduce counting time, simplified counting methods have been developed, as described in the cited paper and shown in its Figure 3. The next step towards simplifying the use of Emlen's funnel was the use of thermal paper for the slope (*op. cit*.) and technically supported counting of scratches from the wall paper. The most sophisticated methods are video-tracking software for interpretation of video files (Muheim *et al*. 2014) and visual annotation of these files (here, Bianco *et al*. 2016 report that annotation of 12 h of video 'took several days'…). Due to the constraints of these last-mentioned methods, they are only suitable for solving special problems using limited numbers of individuals, in laboratory or quasi-laboratory conditions. Thus, it seems that the procedures involving the use of thermal paper are the most practical tools within applications of Emlen's funnel. The high coherence of the traditional manual counting, visual estimation and automatic evaluation of directionality is pointed out by Bianco *et. al.* 2016 in their Figure 5 (three individuals). However, in this example the same bird (2KG36809) showed very different directions. This peculiarity will be discussed later.

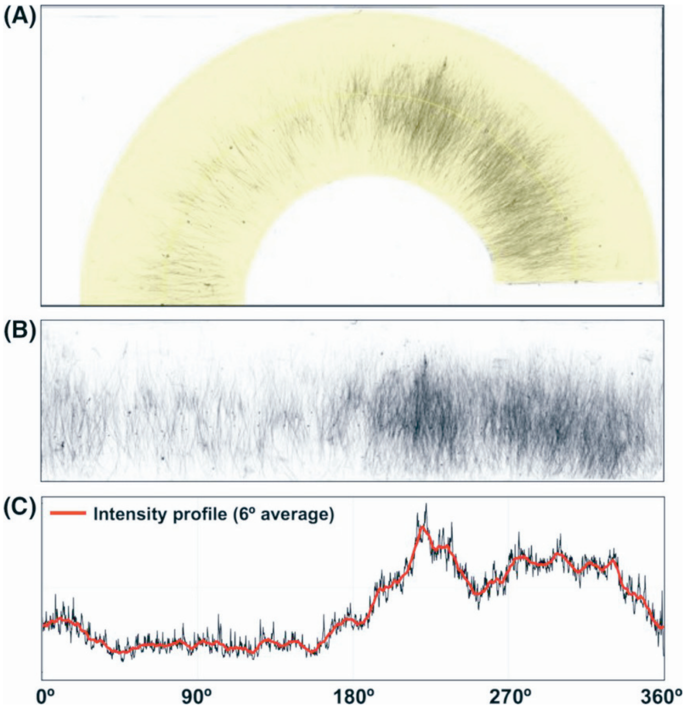

Fig. 3. Examples of modern procedures in presentation of Emlen's funnel raw results: A – original look of flattened cage wall paper, B – linearised picture of the wall shown in panel A, C – the same example as seen on thermal paper. From Bianco *et al.* 2016.

A totally new design of an orientation cage was proposed by Busse (1995) and presented in the abstract of the paper as follows: '*Proposed new method to study directional preferences of the night migrants comprises a new field technique … The advantages of the field technique allows to use it in real field conditions both by the professionals and amateurs: the equipment is simple and cheap, the technique is very easy to learn in a standard form, the experimental routine allows to collect really big amount of data …*'. The construction was based on observations of the actual behaviour conditions of birds in Emlen's funnel: the small bottom of the funnel meant that the bird had to jump onto the slope wall and then slip down back to the bottom, falling on its tail or even its back (Fig. 4). This is a highly unusual movement for a bird and causes it considerable stress. To avoid such stressful situations, Busse's cage is flat and placed on a flat ground plate (Fig. 5 here), so that the bird can walk or run up against a cylindrical wall (covered with a transparent, thin plastic foil). It could also attempt

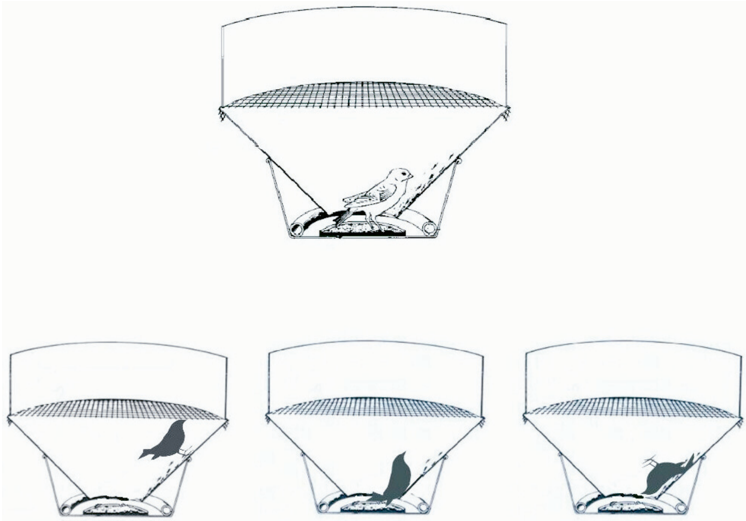

Fig. 4. Emlen's funnel original design showing the starting position of the tested bird (top) and actual situations of the bird tested – jumping on and falling down the slippery wall.

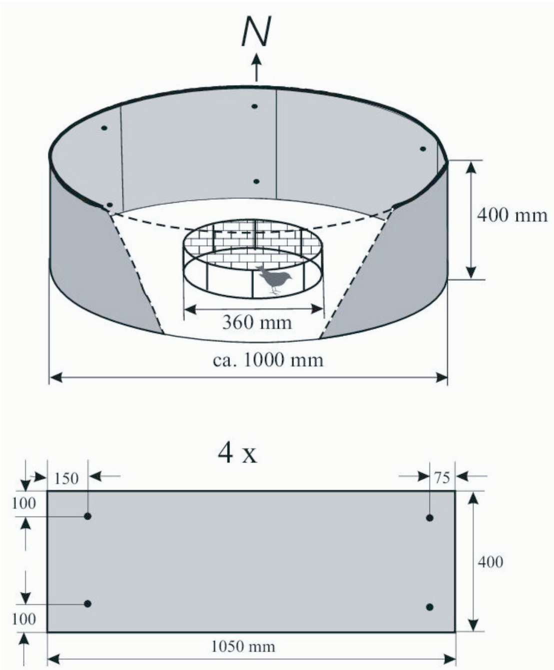

Fig. 5. Busse's flat orientation cage (upper panel): the bird in the flat cage covered with netting in front of a vertical side wall covered with transparent plastic foil. The cage of 80-120 mm height is surrounded by an opaque screen protecting the bird from visual cues (in this picture the front part of the wall is 'cut off' to show the cage inside. Lower panel: one of 4 (4x) segments of the screen surrounding the cage during work; segments are fixed together with screws. From Busse and Meissner 2015, modified

to start to fly. As in most cases the bird hits the wall with a usually pointed bill, the bird leaves a number of well visible dots on the foil, which can easily be counted. They are counted in 8 sectors. If the bird jumps up it can make scratches with its claws as well, and these can be identified and counted together with the marks made by the beak. It takes less than 10 minutes on average to count the dots on the foil, and an experienced person working simultaneously on two orientation cages could test 12 birds per hour. This makes it possible to collect a vast amount of data, e.g. Stępniewska *et al.* 2011 (1,344 tests of 34 species of the 2,767 birds caught in the spring in Azraq, Jordan).

The orientation cage (Fig. 6) is surrounded by an opaque wall to protect the bird from any visual cues apart from the sky (Fig. 7). Dimensions are given in the original article (Busse 1995) as well, with some explanations in the manual by Busse and Meissner (2015). This design can be used for testing waders as well (A. Ożarowska – pers. comm.); the only difference is in the height of the cage.

Fig. 6. Demonstration of the flat cage. Photo P. Busse

Working procedures

From the early days of orientation cage experiments it was accepted that the experiments must be conducted at a time of day when the birds migrate in nature, which for most species tested is at night, usually starting about one hour after sunset.

Fig. 7. Work in the field with Busse's cage: a Sedge Warbler in the cage (top), changing the tested birds (bottom) – two stands are served by one person (day-time tests). Photo P. Busse

Thus, the regular practice was to experiment on birds which were caged for some time: in true orientation experiments the birds were caged for a long time, even hand-reared in the laboratory. In tests on the directionality of migrants in field conditions, the birds are usually caught in the morning and caged till the night in a single small cages or in larger common aviaries. These birds usually have access to food and water, but they are under stress for some hours due to being caged.

The duration of testing in the orientation funnel was established as one hour, after which this time-span was in most cases treated as a standard. This, obviously, resulted in a great number of scratches to be counted after the test was finished. This standard limited the number of performed tests or required the use of numerous funnels for simultaneous testing of several birds.

A completely new, revolutionary procedure is used with Busse's standard of work using flat orientation cages: the bird is put into the orientation cage immediately after ringing/measurements, and thus usually in full daylight (most migrants are caught in the morning), and it is tested for only 10 minutes and then released. This reduces stress on the bird to an absolute minimum. For special experimental designs the procedure can be used during the night or for repeated testing as well. Compatibility of day and night testing has been checked directly (Busse 1995) and indirectly (Zehtindjiev *et al.* 2003), and both studies found the results to be compatible.

Evaluation procedures

Orientation cage tests yielded, naturally, circular data sets. At first these data were evaluated 'by eye', which provided a rough estimation of directions shown by the bird and of its activity. Once numerical data became available (counting of scratches on the Tipp-Ex correction paper) and the first circular statistics were proposed (Batschelet 1981), a new standard was adopted to evaluate orientation cage test data: calculation of a directional vector for all the scratches counted and a Rayleigh test for uniformity. The *r*-value was a measure of the directionality of the result vector. After these standard calculations the researcher decided, based on the *r*-value, whether the tested individual behaved 'directionally' or was 'disoriented'. The results were classified as coming from disoriented and 'oriented' individuals, acting directionally according to the *r*-value, and only the latter were discussed as experimental results. This 'philosophy' was based on the ***hidden assumption*** that the bird will always show a direction towards the winter quarters of the species (southerly from the testing site) in autumn and towards the breeding grounds (northerly) in spring. The assumption was so natural (like testing a nocturnal migrant during the night) that no one questioned it, and the procedure was established as the standard and not discussed further. This assumption was not questioned because it was hidden and because the number of tests performed was relatively small, so it did not seem unreasonable to accept that there were a few disoriented individuals among tested birds. However, when the number of tested birds rose and sometimes the number of disoriented individuals became too high for a conscientious scientist to accept, a correction to the standard was proposed, whereby cases were accepted in which there were double-mode distributions in the individual data. A special 'doubling the angles' procedure was included in the standard and these individuals were shifted from the 'disoriented' class to acceptable as 'oriented'. The growing number of tested birds, however, showed that not all bimodal distributions of raw data are linear, and thus they do not fit the 'double angle' procedure. Holmquist and Sandberg (1999) presented the approach of a 'broken axis' to analyse bi-directional circular data, but they found no followers among traditionalists.

In 1995, the paper cited above (Busse 1995), in addition to proposing a new orientation cage design, discussed the problem of modality of the raw data from orientation tests, and showed that only 22% of 273 tests presented unimodal distribution, while 54% had bimodal distributions (most of them not linear) and as many as 22% had trimodal distribution. Moreover, Busse (*op. cit.*) documented that the distribution of numbers of modes was not different when the birds were tested at night ('Emlen's standard') and during the day ('Busse's standard'). As a result it was concluded that standard Batschelet calculations cannot be correctly applied to bird cage orientation data, because the condition for using Batschelet calculations is unimodal distribution. Busse (*op. cit.*) proposed a simple estimation of directionality where the number of possible modes is limited only by the number of sectors in which the data numbers are given (four modes in the case of a standard Busse's cage with 8 sectors). This was discussed in greater detail in a subsequent paper by Busse and Trocińska (1999). In all studies together using data from several thousand tests, the distribution of modality of results was compatible with those mentioned above; the dominance of unimodal distribution was never more than slightly over 50 percent (e.g. Ożarowska *et al.* 2013 and for the data from this work see p. XXX – Tab. 2). Finally, Ożarowska *et al.* (2013) devoted their paper exclusively to this problem, using a sophisticated statistical discussion of the problem of modality in orientation cage data. The general conclusion is clear: the traditional 'standard' procedure is invalid for actual data from bird orientation cages.

The aim of the paper

This paper focuses on field practice using different types of orientation cages. As cage orientation data provide important input for the description and understanding of migration patterns of nocturnal migrants (alongside testing the influence of orientation cues), the orientation cage method should be discussed in depth and any doubts resolved. It is especially important that it can be used in mass ringing programmes and when field stations require that the standards set are easy to apply, minimally stressing the birds tested and sufficiently cost/time-effective in real field conditions. For small passerines and for studying population differentiation of migrants the method is really more cost-effective than any radio transmitters or geolocators, while incomparably more time-effective than following bird migration on the basis of ringing recoveries. The problem of ornithological interpretation of the results obtained using orientation cages will be discussed in a future publication.

COMPARISON OF BUSSE'S AND EMLEN'S TEST RESULTS

A comparison of the results of tests performed using Busse's and Emlen's cages and procedures has already been published using data collected for the Sedge Warbler, *Acrocephalus schoenobaenus*, at the Kalimok (Bulgaria) bird station in 2001-2002 (Zehtjindiev *et al*. 2003). According to this paper, in 2001 45 individuals were tested using the Emlen's funnel procedures: '*the birds were caught with mist-nets 2-14 hours before the experiments and caged in the large aviaries in natural conditions.*'; the individuals selected '*… were not in in moult and [their] fat score was at least 3 (fat classes after Busse 1983); 'Tests were made during the first hour after sunset and lasted 60 minutes.*'. For comparison, 121 individuals were tested using Busse's procedure in 2002 at the same location. They were tested during the day for 10 minutes, just after ringing, and released immediately after the test. Although the samples were treated differently in terms of important test parameters, i.e. daytime vs. night-time, 10 minutes vs. 60 minutes, and 2001 vs. 2002, the conclusion of the paper was as follows: '*results in Emlen funnel cage and Busse's flat cage are coherent.*'

Material and method

In the study presented here much more numerous data are used, originating from the same station as presented above. The data cover four nocturnal, long-distance migrants representing both reed-bed inhabitants, i.e. the Great Reed Warbler, *Acrocephalus arundinaceus* (the acronym used through this paper: ACR.ARU) and the Sedge Warbler *A. schoenobaenus* (ACR.ENO), and birds characteristic of wooded habitats, i.e. the Willow Warbler, *Phylloscopus trochilus* (PHY.LUS), and the Whitethroat, *Sylvia communis* (SYL.COM) – Table 1). There were 141 individuals tested according to Emlen's procedure in 2001, while Busse's method was used to test 196 individuals in 2001 and 733 in 2002, 2004 and 2007. For direct comparisons only individuals tested in 2001 were used, thereby eliminating one of the parameters (season) that could potentially influence the results (see below for some comments on variance between season – p. XX). Other data were used to present the level of inter-seasonal variation.

All original data for both methods of field work were the numbers of scratches/dots in 8 sectors covering the full wind-rose. The data from both methods were analysed according to the same procedure using ORIENT 4.6 software by P. Busse, available from the author. This programme is a simple means of evaluating circular orientation cage data, taking into account the fact that this type of data is generally multimodal, as the data used clearly show: Table 2 – for the samples from 2001 the share of unimodal distributions from Emlen's and Busse's cages are very close (54.3% and 49.4%, respectively; 2-tailed t test for percentage shares– $p = 0.44$). This is similar to the level reported in earlier papers (Busse 1995, Busse and Trocińska 1999, Zehtindjiev *et al*. 2003). It is worth noting that Ożarowska *et al*. (2013), in an analysis using sophisticated statistics for the same Emlen's data, found a much lower share of unimodal distributions (28.8%). The fundamentals of the calculation method were given in previously cited papers by Busse (1995) and by Busse and Trocińska (1999).

Table 1
Statistics for the data used in the study. The following are given for each sample: total number of tested birds, number of tests used for evaluations, number of tests excluded due to low activity, and percentage of tests excluded. Species acronyms – see text p. XX.

		Emlen's	Busse's				
		2001	**2001**	2002	2004	2007	Total
ACR.ARU	Total	**43**	**96**	79	30	0	212
	Used	**36**	**79**	74	29	0	182
	Excluded	**7**	**17**	5	1	0	30
	% Excl.	**16.3**	**17.7**	6.3	3.3	0.0	14.2
ACR.ENO	Total	**45**	**46**	121	244	19	430
	Used	**28**	**43**	99	152	18	312
	Excluded	**17**	**3**	22	92	1	118
	% Excl.	**37.8**	**6.5**	18.2	37.7	5.3	27.4
PHY.LUS	Total	**39**	**39**	99	31	55	224
	Used	**19**	**36**	83	28	53	200
	Excluded	**20**	**3**	16	3	2	24
	% Excl.	**51.3**	**7.7**	16.2	9.7	3.6	10.7
SYL.COM	Total	**14**	**15**	25	23	0	63
	Used	**11**	**15**	23	22	0	60
	Excluded	**3**	**0**	2	1	0	3
	% Excl.	**21.4**	**0.0**	8.0	4.3	0.0	4.8
Total tested		**141**	**196**	324	328	74	929
Total excluded		**31.7**	**8.0**	12.2	13.8	4.4	14.3

According to the current standard presentation style, the results are illustrated in 'radar graphs' within spreadsheet programmes as polygons representing distributions of sums of vectors shown by all individuals from the sample that were active at the level chosen. In Busse's procedure this level is set at 20 dots, which usually means 20 strikes of the wall with the bill. For Emlen's data the level was set at 40 scratches, which is the level usually adopted by users of this procedure. However, the two levels are not comparable for the reasons presented in the section *Introduction – Technical design of the orientation cages*. For this reason this parameter will be not discussed; as will be seen later, the length of time during which the bird is treated in the cage does not influence the directionality of the bird's behaviour.

Results and discussion

Directions distribution patterns

The data obtained from Emlen's and Busse's procedures and analysed according to the same procedure taking into account multimodality of distributions showed the patterns presented in Figure 8. A direct comparison was made only between tests performed in one season, 2001, so fluctuations between seasons are eliminated. Results from other seasons are only used to show that there is variance between seasons

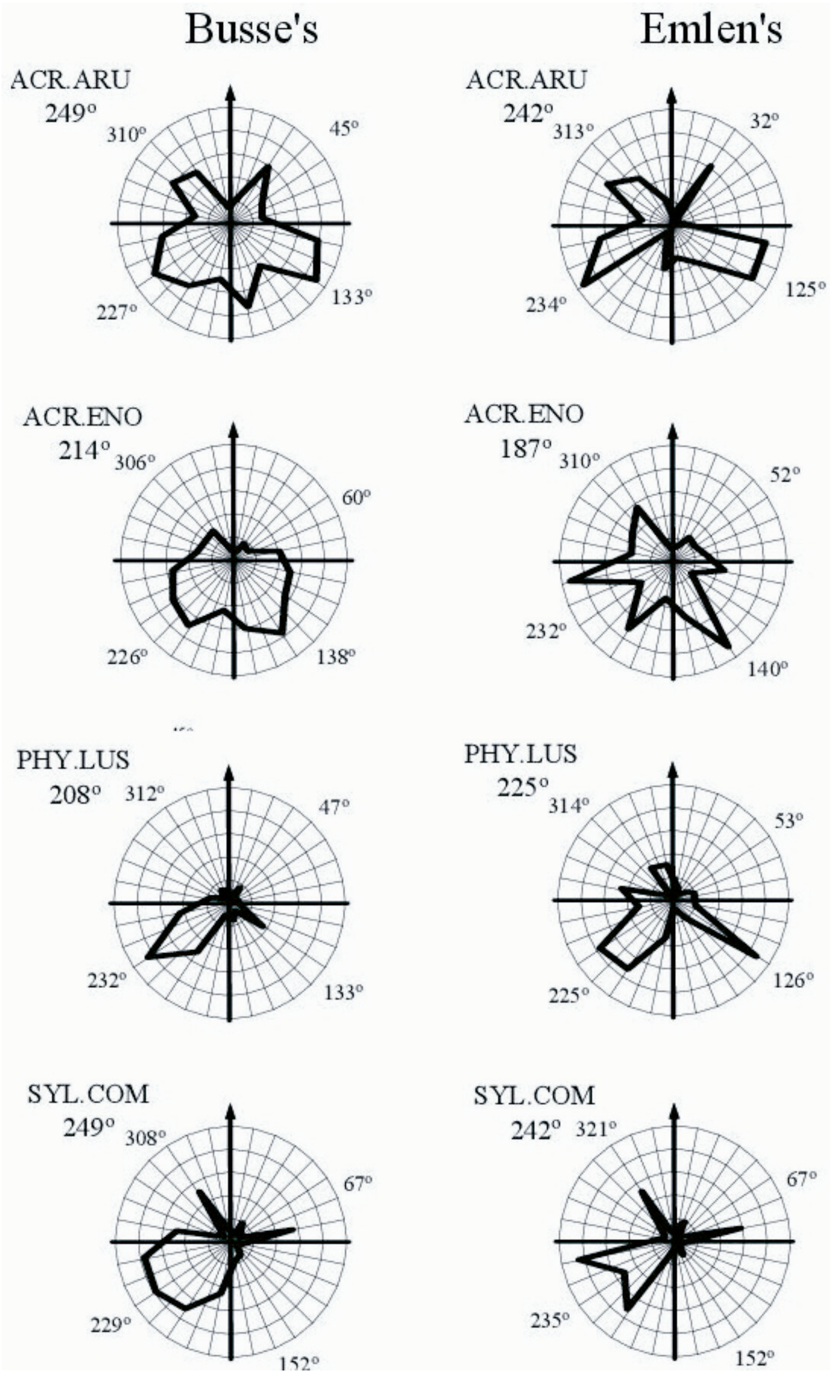

Fig. 8. Comparison of heading patterns of four species (see text for species acronyms) samples tested in 2001 in Busse's (left) and Emlen's (right) cages. In each panel: number below the species code – average direction calculated traditionally for the whole sample, outside the radar graph – average headings as calculated from quarters of the wind-rose. For sample sizes see Table 1.

within data collected using the same procedures. The patterns for Emlen's and Busse's procedures were compared in four different ways: (1) general vector direction, (2) four basic quarters of the wind-rose, (3) Pearson's correlation coefficient (*r*) and (4) *chi*^{2} of distributions. It must be stressed that the first, traditional method is totally unsuitable, as these distributions are all multimodal. The same applies in part to the distributions of the quarters; most distributions within quarters are unimodal or close to unimodal, while some of them are clearly bimodal, and thus calculations must lead to a situation in which the calculated direction lies between two modes, which is the fundamental flaw of the traditional calculation procedure. The other two means of comparison are sufficiently robust to be used for this kind of data.

Table 2
Numbers of modes in individual tests

2001

Emlen's	ACR.ARU		ACR.ENO		PHY.LUS		SYL.COM		TOTAL	
Modes	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
1	19	52.8	16	57.1	10	52.6	6	54.5	51	54.3
2	14	38.9	9	32.1	4	21.1	3	27.3	30	31.9
3	3	8.3	3	10.7	1	5.3	0	0.0	7	7.4
4	0	0.0	0	0.0	4	21.1	1	9.1	5	5.3
5	0	0.0	0	0.0	0	0.0	1	9.1	1	1.1
6	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Total	**36**		**28**		**19**		**11**		**94**	

Busse's	ACR.ARU		ACR.ENO		PHY.LUS		SYL.COM		TOTAL	
Modes	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
1	34	41.5	24	55.8	21	58.3	8	53.3	87	49.4
2	31	37.8	16	37.2	7	19.4	4	27.6	58	33.0
3	12	14.6	3	7.0	4	11.1	0	0.0	19	10.8
4	0	0.0	0	0.0	4	11.1	2	13.3	6	3.4
5	5	6.1	0	0.0	0	0.0	1	6.7	6	3.4
6	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Total	**82**		**43**		**36**		**15**		**176**	

All years

Busse's	ACR.ARU		ACR.ENO		PHY.LUS		SYL.COM		TOTAL	
Modes	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
1	166	91.2	153	48.9	86	43.2	25	41.7	430	57.0
2	12	6.6	111	35.5	66	33.2	26	43.3	215	28.5
3	4	2.2	39	12.5	37	18.6	3	5.0	83	11.0
4	0	0.0	9	2.9	8	4.0	5	8.3	22	2.9
5	0	0.0	0	0.0	2	1.0	1	1.7	3	0.4
6	0	0.0	1	0.3	0	0.0	0	0.0	1	0.0
Total	**182**		**313**		**199**		**60**		**754**	

The results of the first procedure are given as the total vector direction in degrees for the distributions (see Fig. 7 – bold numbers, below panel titles). No single pair of Emlen's and Busse's results significantly differs, although the average difference in the results reaches up to 15°.

The numbers given around the radar graphs show the results of the calculations within the quarter. None of them is significant and the average difference between values for the two methods is only 6°. More details are given in Table 3. If we eliminate the two extreme differences (-13° and +13°) the average falls to less than 5° (4.75). These differences are biologically negligible.

Table 3
Average vector directions in the quarters of the wind-rose (in degrees, clockwise: see Fig. 7). Differences between Busse's and Emlen's results are listed, as well as their arithmetic and absolute means. Species acronyms – see text p. XX.

		Sample	NE	SE	SW	NW	Mean difference	
							Arithm.	Abs.
ACR.ARU	**Emlen's**	36	32°	125°	234°	313°		
	Busse's	70	45°	133°	227°	310°		
	Difference		-13°	-8°	7°	3°	-3°	**8°**
ACR.ENO	**Emlen's**	28	52°	140°	232°	310°		
	Busse's	43	60°	138°	226°	306°		
	Difference		8°	2°	4°	4°	4°	**4°**
PHY.LUS	**Emlen's**	19	53°	126°	225°	314°		
	Busse's	36	47°	133°	232°	312°		
	Difference		6°	-7°	-7°	2°	-2°	**6°**
SYL.COM	**Emlen's**	11	67°	152°	235°	321°		
	Busse's	15	67°	152°	229°	308°		
	Difference		0°	0°	6°	13°	5°	**5°**
Mean arithmetic difference		0°	-3°	3°	6°	1°		
Mean absolute difference		**5°**	**5°**	**6°**	**6°**		**6°**	

Table 4 clearly shows that the correlation coefficients between distributions of Emlen's and Busse's results in 2001 are very high (r = 0.70 to 0.88) and significant at levels of 0.01–0.001. In contrast, the correlations between results obtained for the same testing procedure in different seasons are low (on average r = 0.20 and insignificant in 26 of 28 cases). This last finding is in agreement with previously collected data on this matter. Sampling from different waves of migrants, which is usually the case in various seasons, has yielded differentiated distributions of headings (Formella and Busse 2002, Ściborska and Busse 2004, Adamska and Filar 2005). This, however, is a problem for another discussion.

Table 4
Correlation coefficients between Emlen's and Busse's distributions of bird headings in 2001 tests. Other comparisons – for results from Busse's tests performed in other years. r and p-values are given.

	Emlen's	**Busse's**			
	2001	**2001**	2002	2004	2007
ACR.ARU					
Emlen's 2001	X	***r* = 0.74**	0.27	0.28	
Busse's 2001	***p* 0.01**	X	0.18	0.06	
2002	ns	ns	X	0.51	
2004	ns	ns	0.05	X	
ACR.ENO					
Emlen's 2001	X	**0.70**	0.48	0.12	0.06
Busse's 2001	**0.01**	X	0.49	0.30	0.36
2002	ns	ns	X	0.03	0.05
2004	ns	ns	ns	X	0.38
2007	ns	ns	ns	ns	X
PHY.LUS					
Emlen's 2001	X	**0.75**	0.15	0.03	0.26
Busse's 2001	**0.001**	X	0.00	0.07	0.21
2002	ns	ns	X	0.01	0.57
2004	ns	ns	0.05	X	0.07
2007	ns	ns	ns	ns	X
SYL.COM					
Emlen's 2001	X	**0.88**	0.11	0.09	
Busse's 2001	**0.001**	X	0.37	0.16	
2002	ns	ns	X	0.05	
2004	ns	ns	ns	X	

The results of the analysis of the chi^2 values in the comparison of distributions are presented in Table 5. The chi^2 values for comparisons of the two methods are low (4.04 to 8.72), which means that the distributions are very close (p = 0.89 to 0.99); thus the result is in strong agreement with the conclusion from the correlation coefficients analysis. As before, the values for inter-season comparisons within one method are very different (chi^2 = 10.67 – 37.67, on average 21.25), which means that in some cases the differences are statistically highly significant.

Table 5
*Chi*² test between Emlen's and Busse's distributions of bird headings in 2001 tests. Other comparisons – for results from Busse's tests performed in other years. *chi*² and *p*-values are given.

	Emlen's	**Busse's**			
	2001	**2001**	2002	2004	2007
ACR.ARU					
Emlen's 2001	X	**chi2 = 8.44**	17.33	23.10	
Busse's 2001	**p = 0.90**	X	10.67	17.25	
2002	0.30	0.78	X	12.04	
2004	0.08	0.30	0.68	X	
ACR.ENO					
Emlen's 2001	X	**4.04**	13.90	13.00	17.00
Busse's 2001	**0.99**	X	12.50	15.03	12.21
2002	0.53	0.64	X	21.33	23.84
2004	0.60	0.45	0.13	X	22.68
2007	0.32	0.66	0.07	0.09	X
PHY.LUS					
Emlen's 2001	X	**8.72**	17.77	24.01	23.46
Busse's 2001	**0.89**	X	17.31	25.22	21.23
2002	0.27	0.30	X	10.76	11.89
2004	0.06	0.05	0.77	X	18.79
2007	0.07	0.13	0.69	0.22	X
SYL.COM					
Emlen's 2001	X	**6.27**	35.37	37.67	
Busse's 2001	**0.97**	X	23.87	34.54	
2002	0.002	0.003	X	34.35	
2004	0.001	0.007	0.003	X	

Reverse headings in light of the methods compared

The reverse headings shown by birds tested in orientation cages were previously treated as unwanted 'exceptions', as a kind of experiment noise or symptoms of the 'disorientation' of the tested individual. Then they were forced into the assumed single-vector distribution using the 'double angles' procedure. Tens of thousands of tests thus far performed using Busse's cage have shown that this phenomenon is deeply built into the mechanism of orientation and is observed everywhere and in all circumstances. Some possible explanations for this were given by Busse (2006) in a presentation at the IOC Congress in Hamburg. The heading of the bird is a result of a combination of two processes: linear directionality of migration orientation (this is the basis for the 'doubling the angles' procedure) and the 'switch'—the process of establishing the correct seasonal direction during flight. In a cage, of any type, the bird is not in active flight, but only at the start of flight; the switch is not yet correctly set to 'ON' and is still flexible. The bird's behaviour in the cage is guided more by the linear directionality mechanism than by the 'switch' which decides whether the bird is heading north or south. The switch status is dependent on a number of parameters that we do not yet know. Thus we have either 'correct' (according to the season) or 'reverse' headings. According to current knowledge based on collected data, the share of reverse headings depends in part on the geographical location of the experimental site, and in some sites reverse headings can dominate over the correct ones. Here we have samples from a single station, and the question is whether the two methods reflect these processes in the same degree.

Comparison of the northern shares in directional distribution patterns between 2001 samples from Emlen's and Busse's methods are very similar (Tab. 6). The average difference for total north-south headings is only 3.7%, while it was 0.7% for the NE/SW axis and 5.5% for the NW/SE axis. This seems to be negligible, indicating that the shares do not depend on the method of study. However, the same comparison for Emlen's 2001 results and the 2001-2007 total for Busse's method suggest a clear tendency of more northern directions in the results from Busse's cage. This is in agreement with the discussion above—the cause of this phenomenon is that birds tested at night more frequently have their 'switch' set to the correct heading. This is a property associated with the time of testing, not the cage type. The table shows some additional interesting relationships: the share of reversed headings of birds that chose the NE–SW directional line is half of that noted in the case of the NW-SE line. Such differences are observed frequently in preliminary analyses done on a vast amount of available data. This problem is worth investigating, but is beyond the scope of this paper.

Table 6
Differences between percentage shares of reverse headings when Emlen's and Busse's methods were used. Species acronyms – see text p. XX.

		Emlen's	**Busse's**			
		2001	**2001**	Difference	Total	Difference
ACR.ARU	N/S	**35.1**	**35.5**	0.4	45.8	10.7
	NE/SW	**26.2**	**35.2**	9.0	39.7	13.5
	NW/SE	**41.1**	**35.7**	-5.4	51.4	10.3
ACR.ENO	N/S	**35.9**	**29.3**	-6.6	48.0	12.1
	NE/SW	**26.8**	**25.9**	-0.9	39.0	12.2
	NW/SE	**42.6**	**32.2**	-10.4	56.6	14.0
PHY.LUS	N/S	**31.3**	**23.7**	-7.6	48.1	16.8
	NE/SW	**19.0**	**15.4**	-3.6	38.1	19.1
	NW/SE	**44.2**	**40.0**	-4.2	58.7	14.5
SYL.COM	N/S	**39.6**	**38.5**	-1.1	53.7	14.1
	NE/SW	**27.3**	**21.9**	-5.4	41.5	14.2
	NW/SE	**78.4**	**76.3**	-2.1	68.0	-10.4
All	**N/S**	**35.5**	**31.8**	**-3.7**	**48.9**	**13.4**
	NE/SW	**24.8**	**24.6**	**-0.2**	**39.6**	**14.8**
	NW/SE	**51.6**	**46.1**	**-5.5**	**58.7**	**7.1**

CONCLUSIONS

The following conclusions can be drawn from the presented results and discussion:

1. Busse's flat cage design and its standard procedures yield results fully compatible with those obtained using Emlen's funnel and the associated work procedures, which means full compatibility in the directionality of tested birds in diurnally and nocturnally performed tests. Nocturnal tests seem to show a higher share of correct 'seasonal goal' headings, but this is a property of the practice of nocturnal testing of birds in Emlen's procedures, and not of the cage design.

2. The procedures compared have distinct differences in terms of the constraints of the methods:

– The Emlen's cage design forces the tested bird to jump onto a slippery wall, which causes it to slip backwards, contrary to usual bird movements, and to land on its tail or even its back. This is extremely stressful for the bird and, in my opinion, should be avoided as much as possible in practice due to animal welfare concerns.
– Emlen's standard procedure of testing the bird for 60 minutes is completely useless, as this is inefficient for quality of results, while stressing the bird more than necessary; Busse's standard 10-minute test yields the same results, as shown in point 1 of the conclusions.
– The 10-minute standard, owing to the simplicity of counting the signs of bird activity (dots or scratches), makes it possible to collect a huge amount of data (12 birds per hour and person) in actual field work, even performed even in wilderness areas.
– Most birds in field work are caught in the morning, and Emlen's standard procedure of testing them at night requires keeping wild birds for many hours in cages or aviaries, which causes them considerable stress and disturbs the migration process (stop/departure decisions); this is totally unnecessary (except for special experiments), as the same test, with the same quality of data, can be conducted according to Busse's procedure within a few minutes after catching and ringing.

3. At the stage of evaluation of raw data it is absolutely necessary to use evaluation tools which take into account the fact that raw data items show a high share of multimodal distributions; therefore tools assuming unimodal distribution are unsuitable and cannot be used.

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