RESEARCH ARTICLE

A new approach to evaluate multimodal orientation behaviour of migratory passerine birds recorded in circular orientation cages

Agnieszka Ożarowska[1,2,*], Mihaela Ilieva[3,4], Pavel Zehtindjiev[3], Susanne Åkesson[4] and Krzysztof Muś[1]

[1]Bird Migration Research Station, University of Gdańsk, Wita Stwosza 59, 80-308 Gdańsk, Poland, [2]Avian Ecophysiology Unit, Department of Vertebrate Ecology and Zoology, University of Gdańsk, Wita Stwosza 59, 80-308 Gdańsk, Poland, [3]Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 2 Gagarin Str., 1113 Sofia, Bulgaria and [4]Department of Biology, Centre for Animal Movement Research, Lund University, Ecology Building, SE-223 62 Lund, Sweden

*Author for correspondence (bioat@ug.edu.pl)

SUMMARY

Circular orientation cages have been used for several decades to record the migratory orientation of passerine migrants, and have been central to the investigation of the functional characteristics of the biological compasses used for orientation. The use of these cages offers unique possibilities to study the migratory behaviour of songbirds, but suffers from statistical limitations in evaluating the directions of the activity recorded in the cages. The migratory activity has been reported to vary, including complex multimodal orientation of migratory passerines tested in orientation cages irrespective of species studied. The currently applied circular statistical methods fail to describe orientation responses differing from unimodal and axial distributions. We propose for the first time a modelling procedure enabling the analysis of multimodal distributions at either an individual or a group level. In this paper we compare the results of conventional methods and the recommended modelling approach. Migratory routes may be more complex than a simple migratory direction, and multimodal behaviour in migratory species at the individual and population levels can be advantageous. Individuals may select the expected migratory direction, but may also return to safer sites en route, i.e. sites already known, which provide food and/or shelter in reverse directions. In individual birds, several directions may be expressed in the same test hour. At the species level, multimodal orientation may give an opportunity to expand the range or may refer to differential migration route preferences in different populations of birds. A conflicting experimental situation may also result in a different preferential orientation. In this paper we suggest a statistical solution to deal with these types of variations in orientation preference.

INTRODUCTION

Orientation cage experiments have been commonly used in studies on the mechanisms of orientation and navigation behaviour of songbird migrants (e.g. Gwinner and Wiltschko, 1978; Helbig, 1992a; Helbig, 1992b; Helbig et al., 1989; Munro et al., 1993; Åkesson, 1993; Åkesson, 2003; Wiltschko and Wiltschko, 1996; Wiltschko et al., 2002; Ritz et al., 2004; Åkesson et al., 2005), while this method has more rarely been applied in studies on species-specific migratory directions or to explore potential differences in orientation direction within populations (e.g. Rabøl, 1985; Sandberg et al., 1988; Hilgerloh, 1989; Ehnbom et al., 1993; Sandberg and Gudmundsson, 1996; Ożarowska et al., 2004; Zehtindjiev et al., 2010; Ilieva et al., 2012). In most studies, unimodal orientation may be the expected outcome. However, in several situations where for instance species or population preferences have been studied, or when compass cues were set in experimental conflict, bimodal or multi-modal orientation may be expected. For example, in one of the most well-known studies investigating the genetics of bird migration, Helbig (Helbig, 1991) applied calculation procedures assuming unimodal orientation in his experimental birds. Nevertheless, Helbig did not give a clear explanation for the hereditary mechanism of the migratory direction under study and this was not the purpose of his study at the time. In fact, the gene expression encoding this feature has still not been well studied, so researchers need to be careful when applying current statistical procedures to actual biological data because the resulting orientation responses of birds may be expected to express more than one direction.

To date there is only one example of multimodal orientation behaviour commonly accepted, i.e. axial orientation behaviour (Batschelet, 1981). Despite this, a number of researchers have already noticed that the behaviour expressed by birds tested in orientation cages can be complex and generate multiple orientation preferences deviating less than 180 deg from each other (Holmquist and Sandberg, 1991; Rabøl, 1993; Busse, 1995; Busse and Trocińska, 1999). In his monograph on the ecology of bird migration, Newton (Newton, 2008) also points to this complexity. Moreover, there is growing evidence for more complex migratory routes (within the same population) revealed by tracking studies and of new evidence for individually distinct migratory strategies (Åkesson et al., 2012; Guilford et al., 2011; Vardanis et al., 2011).

The aim of this study was to analyse the behavioural patterns of songbird migrants tested in the most common type of orientation cage, the so-called Emlen funnel (Emlen and Emlen, 1966), and to propose a statistical method to analyse the data and to identify multimodal orientation responses.

MATERIALS AND METHODS
Study species
The data set consisted of N=139 orientation cage tests with nocturnal songbird migrants of four different species; no tests repeated on the same individuals were included in the analysed data set. The birds were tested at the Biological Experimental Station Kalimok, NE Bulgaria (44°00′N, 26°26′E) in autumn 2001. Studied species included long-distance migrants wintering in Africa: the great reed warbler, *Acrocephalus arundinaceus* (Linnaeus 1758) (N=41), the sedge warbler, *Acrocephalus schoenobaenus* (Linnaeus 1758) (N=45), the willow warbler, *Phylloscopus trochilus* (Linnaeus 1758) (N=39) and the whitethroat, *Sylvia communis* Latham 1787 (N=14). The experiments were conducted in accordance with the national animal welfare legislation of Republic of Bulgaria.

Field methods
Standard SE European Bird Migration Network working procedures were applied (Busse, 2000), such that the bird migrants were caught with mist-nets, ringed and measured (including fat score determination). Birds captured during the day were kept together in a large cage (2.5×1×1 m) with free access to mealworms and water. Orientation experiments were performed in modified Emlen funnels (Emlen and Emlen, 1966). The experiments were initiated shortly after sunset and lasted for 60 min.

Data analysis
Definitions
Modality refers to the number of directions/headings preferred by an individual bird tested in the orientation cage, i.e. showing no (0='disoriented'), one or more preferred directions.

Unimodal behaviour refers to the situation when a tested individual preferred only one direction (Fig. 1). Multimodal behaviour refers to when a tested individual preferred more than one direction (i.e. bimodal, trimodal etc.; Fig. 1), and axial behaviour when the two
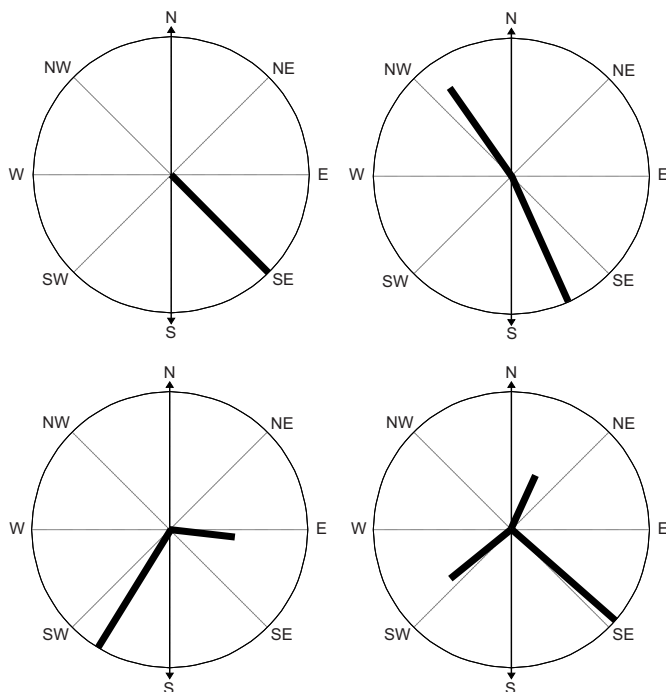
directions were 180 deg (±30 deg) apart. Activity was recorded during a 60 min period as the number of scratches left on the correction paper covering the walls of the cage, and tested individuals were classified as inactive when the total activity was less than 40 scratches (e.g. Helbig, 1992a; Korner-Nievergelt et al., 2002).

We used ORIANA software (version 3; http://www.kovcomp.co.uk/oriana/) to analyse the data according to conventional methods applied in circular statistics, and ORIENT software (available from the Bird Migration Research Station, University of Gdansk, Poland, sbwp.ug.edu.pl; as this program requires specific data format, please contact K.M. before use) for the modelling based on Bayesian statistics. Both methods enable the analysis of individual tests in the first stage and analysis of the group of tests in the second stage. As we used this novel modelling procedure, as opposed to the conventional one, below we give a more detailed description of the method.

Modelling procedure: analysis of an individual test
In the modelling procedure, the results of an individual test (scratches counted in each of eight sectors) were given as a histogram and each mode of cage data distribution was modelled as a wrapped (circular) Gaussian distribution (Fig. 2, Table 1) with the maximum likelihood method.

For each individual, several models were tested: isotropic (disoriented bird), unimodal, bimodal, trimodal and four-modal. This limitation is due to the number of sectors (i.e. eight) in which scratches were counted. The Bayesian information criterion (BIC) (see Schwarz, 1978) was applied to quantify the goodness of each model. Lower BIC scores indicate better models. The BIC values were recalculated into posterior probabilities of the models (Eqns 1, 2):

$$\text{Weight (model)} = \exp\left[-0.5\text{BIC (model)}\right], \quad (1)$$

$$P\text{ (model)} = \text{weight (model)} / \text{sum (weights)}. \quad (2)$$

Fig. 1. Examples of a unimodal (no. of directions, N_{dir}=1; top left), bimodal (N_{dir}=2; top right: axial, bottom left: non-axial) and trimodal (N_{dir}=3; bottom right) pattern of directional behaviour of birds tested in orientation cages.
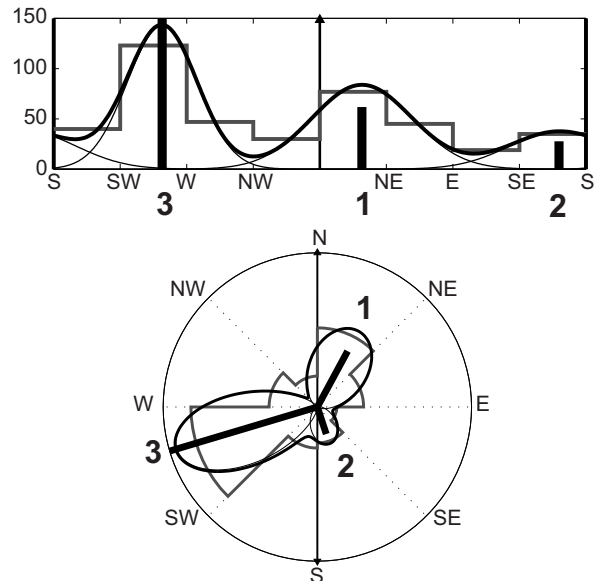
Fig. 2. Final result of the modelling procedure for one individual showing three preferred directions. Top, histogram showing the number of scratches counted in each sector; solid thin lines show single fitted modes; solid bold line shows angular probability distribution of the analysed data; bars show central values of each fitted mode with length proportional to their precision, i.e. activity divided by the mode's variance. Bottom, graphical presentation of the same data and information given in the upper graph but on a circular scale. Table 1 shows the revealed modes in the data, their standard deviation and the part of the total activity covered by a given mode.

Table 1. Results of the modelling procedure

Direction no.	Direction (deg)	s.d. (deg)	Activity
1	28.5	34	158
2	161.8	34	70
3	253.4	24	188

See Fig. 2 for description.

Table 2. Model quality scale (Jeffreys, 1961)

Evidence	Model quality
≤0	Bad
>0 and <1	Not substantial
≥1 and <2	Substantial evidence
≥2 and <3	Strong evidence
≥3 and <4	Very strong evidence
>4	Decisive evidence

A selection criterion of a final model for the individual was a maximum posterior probability among tested models. The odds of the selected model were calculated as:

$$\text{Odds} = P\,(\text{model}) \,/\, [1 - P\,(\text{model})] , \qquad (3)$$

i.e. the probability of the model against the sum of probabilities of all remaining models (Eqn 3).

We defined evidence of the best model as (Eqn 4):

$$\text{Evidence} = 2\log_{10}\,(\text{odds}) , \qquad (4)$$

and applied the model quality scale given in Table 2 (after Jeffreys, 1961). According to this scale 'bad' model quality means that none of the analysed models was favoured, 'not substantial' means that one of the analysed models was favoured but at a non-significant level, and 'decisive evidence' means that all the remaining models can be rejected.

Modelling procedure: analysis at the group level

The modelling procedure at the group level is shown in Fig. 3. Calculations at this level were performed following the methodology given above, except for the input data, where in place of the number of scratches by the individual bird, the directions estimated in the individual tests were used (Fig. 3A). In polar plots, the continuous curve is the angular probability distribution of the group direction (Fig. 3B,C), while bars indicate the central values of each fitted mode with length proportional to the relative weight of each direction (Fig. 3C) in the sense outlined above.

To optimise calculation efficiency, model fitting was performed in two steps: (1) initial fit to the smoothed distribution of input data – the common standard deviation (s.d.) was used as a smoothing parameter, (2) final fit to the 'raw' input data. The weight of each group direction in the fitted model is proportional to the number of contributing individual directions. Consequently, as at the group level there are more data than in the individual test, the number of resulting directions for the analysed group is no longer limited to four. The number of these directions is in practice limited by the BIC criterion, in which with increasing BIC values the posterior probability of the model systematically decreases, although the goodness of fit of the model increases.

According to the fit quality of the final angular probability distribution to the initial distribution of all individual directions, the researcher is able to control the resulting number of directions. At the present moment it is recommended to use about a dozen different values of standard deviation and analyse corresponding BIC values and the number of directions of the resulting model. The comparison of the results of orientation tests and the recovery distributions of passerine migrants showed that a smoothing parameter standard deviation of about 10–15 deg is adequate (A.O. and K.M., unpublished data). Still, the BIC criterion based on the total number of directions is applied as a supporting criterion. The Matlab R20011b (MathWorks Inc., Natick, MA, USA) was used to create the models and to perform the calculations. ORIENT software is available as detailed above. All data used in the present study are available at either the Bird Migration Research Station (sbwp.ug.edu.pl) or the Biological Experimental Station Kalimok (Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Bulgaria; www.iber.bas.bg).
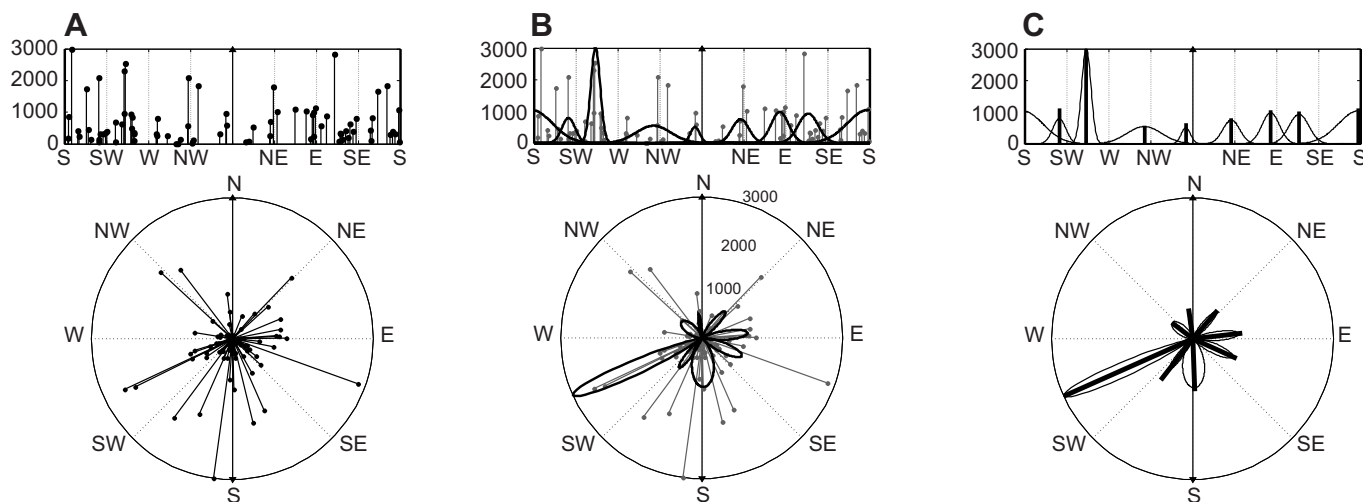

Fig. 3. Modelling procedure at the group level: (A) directions estimated in the individual tests (lines with a dot at the end) comprise the analysed group and are used in the modelling; (B) the modelling procedure applied to the directions estimated in the individual tests (given as background) results in angular probability distribution (solid curved lines) reflecting the directions (here, eight) estimated for the analysed group of tests; and (C) final results of the modelling procedure at the group level, where solid curved lines show the angular probability distribution of the group directions estimated for the analysed group of tests, while bars show central values of each fitted mode, with length proportional to the relative weight of each direction.

Table 3. Proportion of different patterns of behaviour of migrants tested in the orientation cage

A. Conventional procedures

Species	Number of tests	Included	Disoriented	1 direction	Axial
A. arundinaceus	41	41	0	38	3
A. schoenobaenus	45	43	0	42	1
P. trochilus	39	35	0	32	3
S. communis	14	14	0	13	1
Total	139	133	0	125	8

B. Modelling procedure

Species	Number of tests	Low evidence (<1)	Included	Disoriented	1 direction	2 directions	3 directions	4 directions
A. arundinaceus	41	6	35	0	12	20	2	1
A. schoenobaenus	45	5	38	0	8	22	8	0
P. trochilus	39	2	33	1	8	21	3	0
S. communis	14	2	12	0	6	5	1	0
Total	139	15	118	1	34	68	14	1

(A) Conventional methods applied to data; (B) modelling procedure applied to data.
Study species: *Acrocephalus arundinaceus*, *Acrocephalus schoenobaenus*, *Phylloscopus trochilus* and *Sylvia communis*.

RESULTS

In total, 96% of the orientation tests were included in further analyses when applying conventional circular statistical methods (Batschelet, 1981), while in our modelling procedure 85% were included (Table 3). Six individuals (4.3%) were classified as inactive. According to the modelling procedure, in 10.8% of the tests the model quality was too low (evidence<1). These tests were not included in further analyses. According to conventional circular statistical methods, in most (94%) of the tests the birds showed a unimodal pattern of orientation, while in 6% of the tests their directional behaviour was axial (Table 3). When applying the modelling procedure to the same available data set, the observed proportion of the different patterns of bird behaviour in the cages was far more complex (Table 3, Fig. 4).

Depending on the species, either unimodal or bimodal orientation dominated, while trimodal directional behaviour (Table 3) was observed in 12% of the tests. Moreover, when analysing bimodal orientation responses, i.e. when the two directions were within 150–180 deg of each other, they were axial in 36.8% of all tests (Table 4). This proportion varied across the four species from 20% to 45%.

The final results of both calculation methods applied to single tests can be compared in Figs 5–8.

When analysing unimodal distributions, the two methods were in good agreement (Fig. 5). All tests classified as unimodal based on the modelling procedure represented unimodal distributions according to the conventional procedures (Table 5). Most axial distributions according to the conventional procedures also represented this category when the modelling procedure was applied (Fig. 6, Table 5).

For the purposes of illustration, the calculations were applied to bimodal and trimodal distributions and the results of these calculations are given in Figs 7 and 8. The assumption of unimodality was not fulfilled; still, statistically significant results are obtained based on the conventional circular statistical methods. According to our modelling procedure, bimodal (excluding axial), trimodal and four-modal distributions comprise as much as 49.2% of all tests included in the analyses, so excluding them from the data set would not be advisable.

While at the individual level the two methods, when applied to certain types of distributions, show similar results, at the group level the observed pattern is different between the two methods because of the larger number of modes in the latter (Fig. 9, Table 6).

Conventional calculation procedures applied either to a single test or to the group of tests result in one, average direction, while the modelling procedure enables, at both levels, the analyses of far more complex patterns describing in more detail the directional preferences shown in the circular cages. With the latter method the only criterion for including the test in the sample set is whether the tested bird was active or not, while the researcher does not make any preliminary assumptions as to the distribution pattern, which is mandatory in the conventional statistical methods. Consequently, we avoid the risk of unintentionally breaking basic assumptions of some statistical tests and getting false results, and finally we are not
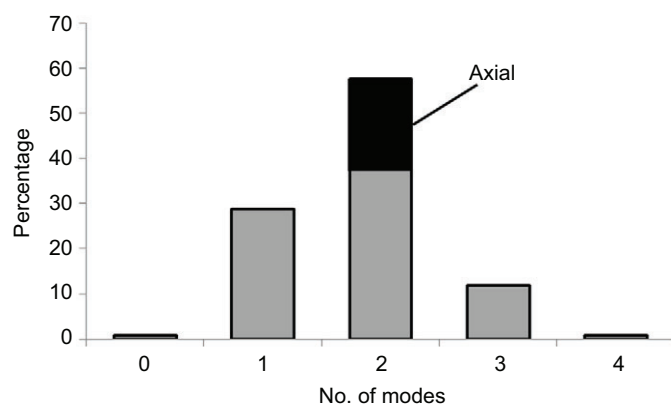

Fig. 4. Modality distribution in a group of birds tested in orientation cages during migration (modelling procedure applied). Black section of the bar shows the percentage of axial distributions within bimodal ones. *N*=118.

Table 4. Proportion of axial behaviour of migrants tested in the orientation cage

Species	2 directions	Axial	Proportion (%)
A. arundinaceus	20	9	45.0
A. schoenobaenus	22	7	31.8
P. trochilus	21	8	38.1
S. communis	5	1	20.0
Total	68	25	36.8

Modelling procedure applied.
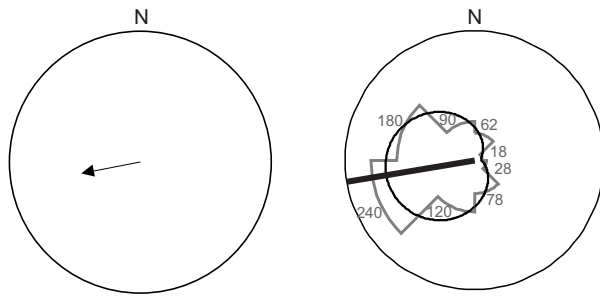
Acrocephalus arundinaceus Ring no. 482442	
Conventional	Modelling
259.5 deg	**260.3 deg** (s.d.=71 deg)
r=0.46 P=4.65E−77	Evidence=5.5 P=0.9982

Fig. 5. Unimodal distributions analysed with two methods: the conventional (left) and modelling (right) procedure. Left plot: a mean vector is shown (*r*), the length of which gives an indication of the degree of concentration of the scratches. Right plot: circular histogram showing the number of scratches (given on the plot) counted in each sector; the solid black line shows the angular probability distribution of the analysed data; the bar shows the central value of the fitted mode with length proportional to its precision, i.e. activity divided by the mode's variance. The data below show the mean direction (including s.d. for the modelling procedure); length of the mean vector (*r*) and *P*-value for the conventional procedure; and evidence and probability of the best model for the modelling procedure.

ignoring the complexity of the behaviour of birds tested in the orientation cages.

DISCUSSION

Experiments for which migratory activity has been recorded for songbirds in circular cages or analysed by ringing recoveries often show unimodal expected migratory preferences, but also differential migratory orientation in individual experiments as well as at the group level (e.g. Sandberg et al., 1988; Busse, 1987; Åkesson et al., 1996; Mouritsen, 1998; Muheim et al., 2002; Remisiewicz, 2002). In most studies, standard procedures are deployed to treat the circular cage data from individuals for further statistical analyses (e.g. Sandberg et al., 1988; Helbig et al., 1989; Åkesson, 1994; Wiltschko and Wiltschko, 1996; Muheim et al., 2002; Wiltschko et al., 2002; Ilieva et al., 2012). After initial treatment of individual test data it is often valuable to compare mean orientation between groups. The conventional procedures of a single cage test data analysis include the Rayleigh test application in the first step, as outlined elsewhere (Batschelet, 1981), to find out whether the tested individual bird was disoriented or showed directional behaviour, i.e. one migratory direction. This is a suitable approach as long as the distribution does not have more than one mode, as the Rayleigh test requires unimodality (Batschelet, 1981). Currently, the only exception to this procedure is treatment of an axially bimodal distribution with the 'doubling the angles' procedure, after which the Rayleigh test can be employed. However, when circular data on the individual level are neither unimodal nor axially bimodal, Zar (Zar, 1999) recommends applying the 'Rao spacing test' (Batschelet, 1981; Zar, 1999). The problem is that there is no conventional circular statistical tool available for testing hypotheses on multimodal distributions. Therefore, it could happen that when following the conventional procedures, a researcher will not be able to identify that the orientation cage results show a multimodal pattern. Some multimodal distributions analysed with conventional methods, not appropriately applied, will thus give significant but false results. The problem could be overcome by excluding multimodal distributions from further analyses, but then in some cases, as in our study presented here, we would exclude nearly 50% of all tests and more importantly develop false results and interpretations.

Axial orientation behaviour needs special attention as this is the only example of a multimodal distribution when a conventional approach, the Rayleigh test, can be applied after the doubling angles procedure. However, when analysing the bimodal pattern of our experiments in detail we found that the experimental birds showed axial behaviour in only 36.8% of tests. This proportion differs
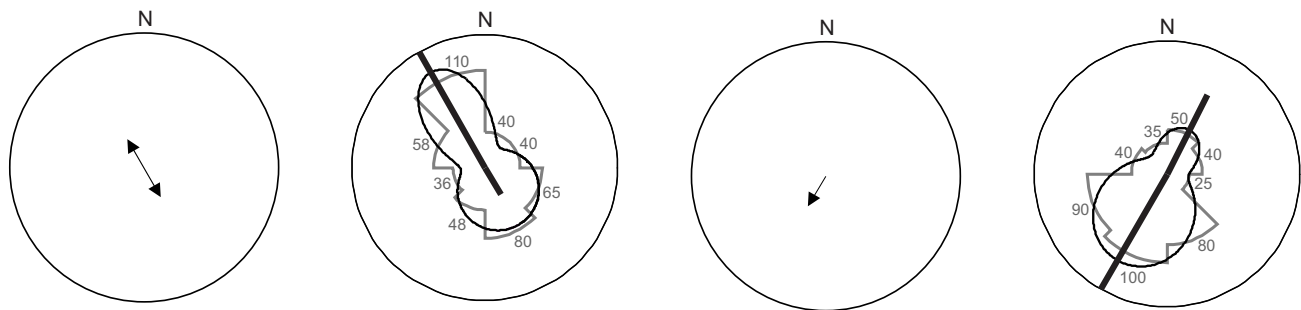
Phylloscopus trochilus Ring no. 4	
Conventional	Modelling
149.0 deg **329.0 deg**	**148.8 deg** (s.d.=72 deg) **330.5 deg** (s.d.=27 deg)
r=0.25 P=1.13E−13	Evidence=8.0 P=0.9999

Phylloscopus trochilus Ring no. 23	
Conventional	Modelling
211.4 deg	**210.0 deg** (s.d.=54 deg) **27.0 deg** (s.d.=40 deg)
r=0.26 P=5.16E−14	Evidence=6.5 P=0.9994

Fig. 6. Axial distributions analysed with two methods: the conventional (left) and modelling (right) procedure. Abbreviations and details as in Fig. 5.

Fig. 7. Bimodal distributions analysed with two methods: the conventional (left) and modelling (right) procedure. Abbreviations and details as in Fig. 5.

Acrocephalus schoenobaenus Ring no. 483140	
Conventional	Modelling
169.8 deg	**116.2 deg** (s.d.=24 deg) **218.4 deg** (s.d.=24 deg)
r=0.56 P=2.02E−17	Evidence=6.1 P=0.9991

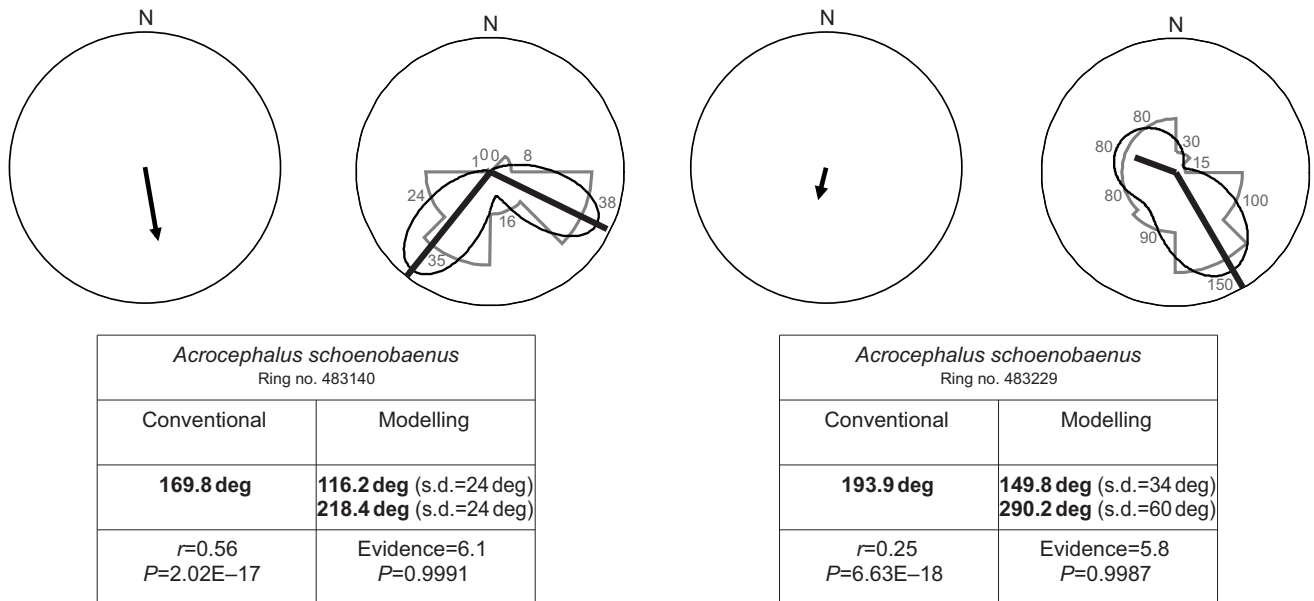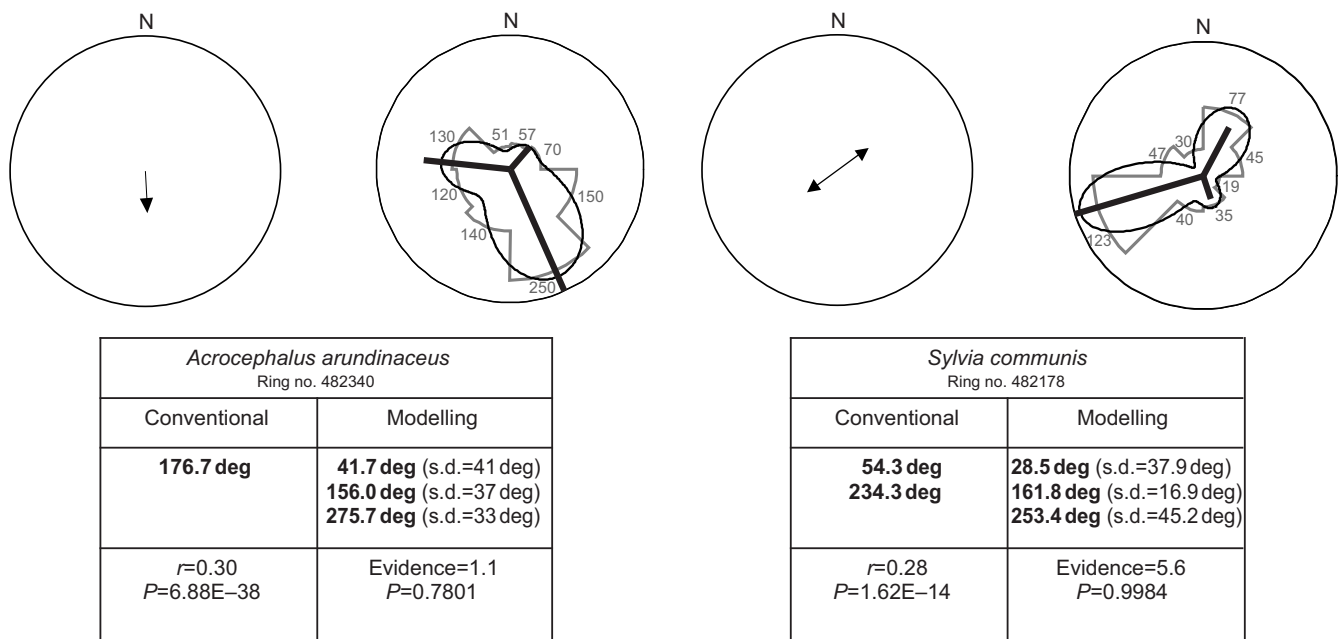| Acrocephalus schoenobaenus Ring no. 483229	
Conventional	Modelling
193.9 deg	**149.8 deg** (s.d.=34 deg) **290.2 deg** (s.d.=60 deg)
r=0.25 P=6.63E−18	Evidence=5.8 P=0.9987

Fig. 8. Trimodal distributions analysed with two methods: the conventional (left) and modelling (right) procedure. Abbreviations and details as in Fig. 5.

Acrocephalus arundinaceus Ring no. 482340	
Conventional	Modelling
176.7 deg	**41.7 deg** (s.d.=41 deg) **156.0 deg** (s.d.=37 deg) **275.7 deg** (s.d.=33 deg)
r=0.30 P=6.88E−38	Evidence=1.1 P=0.7801

Sylvia communis Ring no. 482178	
Conventional	Modelling
54.3 deg **234.3 deg**	**28.5 deg** (s.d.=37.9 deg) **161.8 deg** (s.d.=16.9 deg) **253.4 deg** (s.d.=45.2 deg)
r=0.28 P=1.62E−14	Evidence=5.6 P=0.9984

Table 5. Comparison of the results of two calculation methods when applied to the same data set

Conventional	Modelling							
	1 direction	Axial	2 directions	3 directions	4 directions	Disoriented	Low evidence	Total$_C$
1 direction	34	19	42	13	1	1	15	125
Axial		7		1				8
Total$_M$	34	26	42	14	1	1	15	133

Total$_M$, number of tests representing different categories according to the modelling procedure; Total$_C$, number of tests representing different categories according to the conventional methods.
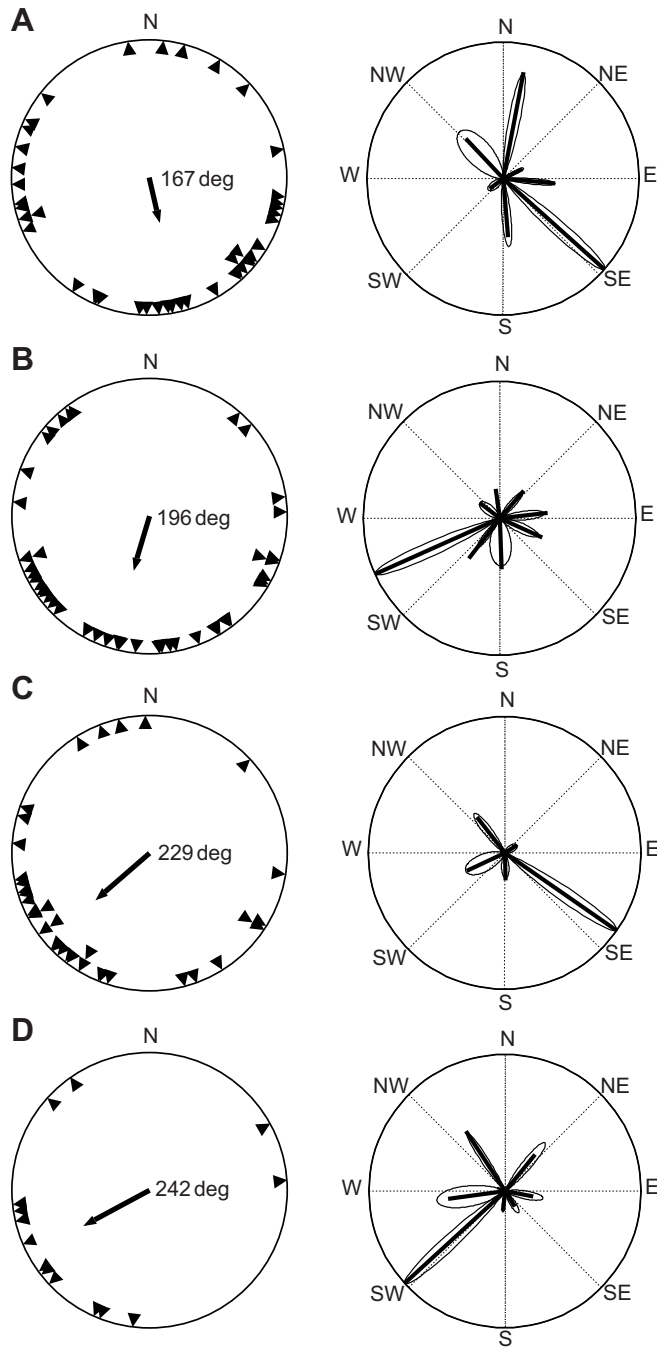
Fig. 9. Analysis of the circular data for the groups of tested songbird migrants: (A) *Acrocephalus arundinaceus*, (B) *Acrocephalus schoenobaenus*, (C) *Phylloscopus trochilus* and (D) *Sylvia communis*. The directional preferences of different species of long-distance migrants are given according to the conventional (left) and modelling (right) procedure (see Table 6 for details).

Table 6. Analysis of the circular data for the group of tested migrants with two methods: conventional and modelling procedure

Species	Conventional		Modelling	
	Direction (deg)	s.d. (deg)	Direction (deg)	s.d. (deg)
A. arundinaceus	164	88.9	11	5
			63.2	6.5
			95.4	5
			131.7	5
			174.8	6.2
			232.6	19.1
			316.8	19.4
A. schoenobaenus	196	77.8	41.5	9.1
			83.8	9.3
			114.1	10.6
			177.9	21.6
			217.1	7.1
			246.1	5
			308.4	18.6
			352.8	5
P. trochilus	229	67.3	57.1	21.6
			124.6	5
			177.7	14
			244.6	19.5
			322.2	8.3
S. communis	242	64.5	39.8	7.4
			100.7	9.9
			147.8	10.4
			186.4	5
			227.5	5
			262.1	14.4
			326.6	5

taken when evaluating orientation cage results such that analyses of multimodality should be included in the analyses of circular data as a standard method to investigate the pattern of distributions. Thus, we strongly recommend the modelling procedure applied in this study to orientation data analyses, which enables the researcher to distinguish among distributions differing in modality and subsequently to compare the probability of these distributions and thereafter to choose in an objective way the one that is the most probable. However, one disadvantage of such an approach is the problem of distributions in which none of the analysed models is favoured (evidence<1; in our study, 15 distributions). In future studies we plan to incorporate Bayesian model averaging (BMA), which overcomes this problem by conditioning not on a single 'best' model but on the entire ensemble of statistical models first considered (Kass and Raftery, 1995; Hoeting et al., 1999; Raftery and Zheng, 2003). The modelling procedure also offers alternative ways to analyse different aspects of birds' behaviour. For instance, the distributions can be analysed according to the number of individuals preferring a given direction, or the precision of their choice (based on standard deviation), or their activity (i.e. number of scratches) within the final direction. At the moment there is no software available that allow statistical comparison of two circular multimodal distributions. However, as the Orient program provides several parameters for each direction (e.g. angular value, standard error), contributing to the final pattern, we can compare two distributions by comparing pairs of corresponding directions.

There may be several reasons for the multimodal behaviour of migrants tested in orientation cages. Mechanisms controlling bird migration are necessarily conservative, but are under the influence of natural selection. Many features of migration, for example level and time of migratory restlessness and migratory direction, are

according to the species. Still, there could be a high proportion of bimodal tests, which should be excluded from the analyses according to the conventional statistical methods.

The results of our study show that multimodal orientation behaviour of migratory passerines tested in orientation cages dominates and is characteristic of these types of data. Moreover, modelling results show that conventional calculation procedures must not be used for multimodal distributions, with the exception of true axial distributions. We therefore propose that care must be

encoded genetically (e.g. Berthold, 1983; Berthold, 1993; Berthold, 1996; Berthold et al., 1990a; Berthold et al., 1990b; Berthold et al., 1992; Berthold and Helbig, 1992; Berthold and Pulido, 1994; Helbig, 1991; Helbig, 1992b). Furthermore, reverse migration is regularly shown at ecological barriers (Åkesson et al., 1996); all these are regulated by the biological compasses (e.g. Gwinner and Wiltschko, 1978; Gwinner, 1996; Weindler et al., 1996; Wiltschko and Wiltschko, 1996; Wiltschko and Wiltschko, 2003; Åkesson and Hedenström, 2007). All these phenotypic characteristics of the migration programme enable immature passerines to reach species- or population-specific wintering grounds during their first autumn migration. Visual observations and ringing results have further proved that birds show breeding site fidelity, but also fidelity to intermediate stop-over sites and wintering sites (e.g. Moreau, 1972; Salewski et al., 2000; King and Hutchinson, 2001). Shifts in migratory direction with progress of the season have also been observed (Gwinner and Wiltschko, 1978; Helbig et al., 1989). At certain stages of the migration, birds may show both prior and new migration route preferences when recorded in cages after range expansion of the species or corrections of previous drift during migration flights, depending on the ecological situation and stage of individual migration.

The problem was also addressed by Phillips in his study on the vagrancy of Asiatic warblers observed regularly in Europe (Phillips, 2000). He pointed out that a factor which had been widely overlooked was that any experimentally tested group of migrants exhibited a wide range of orientation directions and one could not accept the mean direction as being valid while selectively ignoring individual data points from which it was derived. He also concluded that the 'wrong' directions had to be derived genetically, from the birds' parents, though details of the genetic inheritance of orientation directions had not yet been worked out.

When considering these facts it seems logical that migrants should exhibit not just one migratory direction but several directions and that these preferences need to be handled statistically.

Although several studies have focused on the genetics of bird migratory behaviour (e.g. Berthold, 1983; Berthold and Helbig, 1992; Berthold and Pulido, 1994), only two have focused on the inheritance of a migratory direction. Berthold and colleagues (Berthold et al., 1990b) found that cross-breeding of individuals from migratory and sedentary populations resulted in axial behaviour of the offspring along the NE–SW axis, i.e. the characteristic migratory direction of the parents. Helbig studied the basis of migratory direction inheritance (Helbig, 1991) and found that cross-breeding of individuals from two populations showing highly different migratory directions resulted in an intermediate migratory direction of the F1 generation. Consequently, a general assumption has been that individuals tested in orientation cages could only show one migratory direction (with one exception of bimodal behaviour, i.e. axial behaviour). However, it was not the result of Helbig's study (Helbig, 1991) that explained and documented the hereditary mechanism of migration direction in such a way that could justify the common assumption of a unimodal pattern of bird behaviour. Multimodal behaviour of migratory passerines tested in the orientation cages probably shows that the mechanisms of bird compass orientation and navigation are complex and need special attention, but also that the physiology of individual birds has a strong effect on directional choices (Sandberg, 2003). There are several advantages of differential orientation such as returning to the protective sites en route, i.e. sites already known, which provided the migrant with food and/or shelter (Åkesson et al., 1996). Other examples deal with the opportunity to expand breeding and wintering

ranges (e.g. the blackcap, Asiatic warblers) (Berthold and Terrill, 1988; Busse, 1992; Berthold et al., 1992; Thorup, 1998; Phillips, 2000; Newton, 2008; Kopiec and Ożarowska, 2012). In this study we propose a way to objectively handle multimodal orientation responses in birds and to perform statistical evaluations of the data. Future evaluations of new results from light loggers (geolocators) currently applied in many studies and previously collected circular cage data will be important to further evaluate the modelling approach proposed.

AUTHOR CONTRIBUTIONS
A.O. was responsible for conception, data analyses, interpretation of the findings and writing the article; M.I. was responsible for conducting the orientation tests, data analyses, interpretation of the findings and writing the article; P.Z. was responsible for conducting the orientation tests; K.M. contributed statistical expertise, while all authors contributed to discussions, editing and revising the manuscript.

COMPETING INTERESTS
No competing interests declared.

REFERENCES

Åkesson, S. (1993). Effect of geomagnetic field on orientation of the marsh warbler, *Acrocephalus palustris*, in Sweden and Kenya. *Anim. Behav.* **46**, 1157-1167.

Åkesson, S. (1994). Comparative orientation experiments with different species of passerine long-distance migrants: effect of magnetic field manipulation. *Anim. Behav.* **48**, 1379-1393.

Åkesson, S. (2003). Avian long-distance navigation: experiments with migratory birds. In *Avian Migration* (ed. P. Berthold, E. Gwinner and E. Sonnenschein), pp. 472–491. New York, NY: Springer-Verlag.

Åkesson, S. and Hedenström, A. (2007). How migrants get there: migratory performance and orientation. *Bioscience* **57**, 123-133.

Åkesson, S., Karlsson, L., Walinder, G. and Alerstam, T. (1996). Bimodal orientation and the occurrence of temporary reverse bird migration during autumn in south Scandinavia. *Behav. Ecol. Sociobiol.* **38**, 293-302.

Åkesson, S., Morin, J., Muheim, R. and Ottosson, U. (2005). Dramatic orientation shift of white-crowned sparrows displaced across longitudes in the high Arctic. *Curr. Biol.* **15**, 1591-1597.

Åkesson, S., Klaassen, R., Holmgren, J., Fox, J. W. and Hedenström, A. (2012). Migration routes and strategies in a highly aerial migrant, the common swift *Apus apus*, revealed by light-level geolocators. *PLoS ONE* **7**, e41195.

Batschelet, E. (1981). *Circular Statistics in Biology.* New York, NY: Academic Press.

Berthold, P. (1983). Genetic basis of bird migration. *Ornis Fenn.* **Suppl. 3**, 14-16.

Berthold, P. (1993). *Bird Migration. A General Survey.* Oxford: Oxford University Press.

Berthold, P. (1996). *Control of Bird Migration.* London: Chapman & Hall.

Berthold, P. and Helbig, A. J. (1992). The genetics of bird migration: stimulus, timing and direction. *Ibis* **134 Suppl.**, 35-40.

Berthold, P. and Pulido, F. (1994). Heritability of migratory activity in a natural bird population. *Proc. Biol. Sci.* **257**, 311-315.

Berthold, P. and Terrill, S. B. (1988). Migratory behaviour and population growth of blackcaps wintering in Britain and Ireland: some hypotheses. *Ring. and Migr.* **9**, 153-159.

Berthold, P., Mohr, G. and Querner, U. (1990a). Steuerung und potentielle Evolutionsgeschwindigkeit des obligaten Teilzieherverhaltens: Ergebnisse eines Zweiweg-Selektionsexperiments mit der Mönchsgrasmücke (*Sylvia atricapilla*). *J. Ornithol.* **131**, 33-45.

Berthold, P., Wiltschko, W., Miltenberger, H. and Querner, U. (1990b). Genetical transmission of migratory behavior into a nonmigratory bird population. *Experientia* **46**, 107-108.

Berthold, P., Helbig, A. J., Mohr, G. and Querner, U. (1992). Rapid microevolution of migratory behaviour in a wild bird species. *Nature* **360**, 668-670.

Busse, P. (1987). Migration patterns of European passerines. *Sitta* **1**, 18-36.

Busse, P. (1992). Migratory behaviour of blackcaps (*Sylvia atricapilla*) wintering in Britain and Ireland: contradictory hypotheses. *Ring* **14**, 51-75.

Busse, P. (1995). New technique of a field study of directional preferences of night passerine migrants. *Ring* **17**, 97-116.

Busse, P. (2000). *Bird Station Manual.* Choczewo, Poland: SE European Bird Migration Network.

Busse, P. and Trocińska, A. (1999). Evaluation of orientation experiment data using circular statistics – doubts and pitfalls in assumptions. *Ring* **21**, 107-130.

Ehnbom, S., Karlsson, L., Ylvén, R. and Åkesson, S. (1993). A comparison of autumn migration strategies in robins *Erithacus rubecula* at a coastal and an inland site in southern Sweden. *Ring. and Migr.* **14**, 84-93.

Emlen, S. T. and Emlen, J. T. (1966). A technique of recording migratory orientation of captive birds. *Auk* **83**, 361-367.

Guilford, T., Freeman, R., Boyle, D., Dean, B., Kirk, H., Phillips, R. and Perrins, C. (2011). A dispersive migration in the Atlantic puffin and its implications for migratory navigation. *PLoS ONE* **6**, e21336.

Gwinner, E. (1996). Circannual clocks in avian reproduction and migration. *Ibis* **138**, 47-63.

Gwinner, E. and Wiltschko, W. (1978). Endogenously controlled changes in migratory direction of the garden warbler, *Sylvia borin*. *J. Comp. Physiol.* **125**, 267-273.

Helbig, A. J. (1991). Inheritance of migratory direction in a bird species: a cross-breeding experiment with SE- and SW-migrating blackcaps (*Sylvia atricapilla*). *Behav. Ecol. Sociobiol.* **28**, 9-12.

Helbig, A. J. (1992a). Population differentiation of migratory directions in birds: comparison between ringing results and orientation behaviour of hand-raised migrants. *Oecologia* **90**, 483-488.

Helbig, A. J. (1992b). Ontogenetic stability of inherited migratory directions in a nocturnal bird migrant: comparison between the first and second year of life. *Ethol. Ecol. Evol.* **4**, 375-388.

Helbig, A. J., Berthold, P. and Wiltschko, W. (1989). Migratory orientation of blackcaps (*Sylvia atricapilla*): population-specific shifts of direction during the autumn. *Ethology* **82**, 307-315.

Hilgerloh, G. (1989). Orientation of trans-Saharan passerine migrants in Southwestern Spain. *Auk* **106**, 501-502.

Hoeting, J. A., Madigan, D. M., Raftery, A. E. and Volinsky, C. T. (1999). Bayesian model averaging: a tutorial. *Stat. Sci.* **14**, 382-417.

Holmquist, B. and Sandberg, R. (1991). The broken axis approach – a new way to analyze bidirectional circular data. *Experientia* **47**, 845-851.

Ilieva, M., Toews, D. P. L., Bensch, S., Sjöholm, C. and Åkesson, S. (2012). Autumn migratory orientation and displacement responses of two willow warbler subspecies (*Phylloscopus trochilus trochilus* and *P. t. acredula*) in South Sweden. *Behav. Processes* **91**, 253-261.

Jeffreys, H. (1961). *Theory of Probability. International Series of Monographs on Physics,* 3rd edn. London: Oxford University Press.

Kass, R. E. and Raftery, A. E. (1995). Bayes factors. *J. Am. Stat. Assoc.* **90**, 773-795.

King, J. M. B. and Hutchinson, J. M. C. (2001). Site fidelity and recurrence of some migrant bird species in the Gambia. *Ring. and Migr.* **20**, 292-302.

Kopiec, K. and Ożarowska, A. (2012). The origin of blackcaps *Sylvia atricapilla* wintering on the British Isles. *Ornis Fenn.* **89**, 254-263.

Korner-Nievergelt, F., Liechti, F. and Bruderer, B. (2002). How does age and body condition affect migratory restlessness and orientation in reed warblers *Acrocephalus scirpaceus*? *Ardeola* **49**, 29-37.

Moreau, R. E. (1972). *The Palaearctic-African Bird Migration Systems.* London: Academic Press.

Mouritsen, H. (1998). Modelling migration: the clock-and-compass model can explain the distribution of ringing recoveries. *Anim. Behav.* **56**, 899-907.

Muheim, R., Bäckman, J. and Åkesson, S. (2002). Magnetic compass orientation in European robins is dependent on both wavelength and intensity of light. *J. Exp. Biol.* **205**, 3845-3856.

Munro, U., Wiltschko, W. and Ford, H. A. (1993). Changes in migratory direction of yellow-faced honeyeaters *Lichenostomus chrysops* (Meliphagidae) during autumn migration. *Emu* **93**, 59-62.

Newton, I. (2008). *The Migration Ecology of Birds.* Amsterdam: Academic Press.

Ożarowska, A., Yosef, R. and Busse, P. (2004). Orientation of chiffchaff (*Phylloscopus collybita*), blackcap (*Sylvia atricapilla*) and lesser whitethroat (*S. curruca*) on spring migration at Eilat, Israel. *Avian Ecol. Behav.* **12**, 1-10.

Phillips, J. (2000). Autumn vagrancy: 'reverse migration' and migratory orientation. *Ring. and Migr.* **20**, 35-38.

Rabøl, J. (1985). The orientation of vagrant passerines on the Faeroe Islands, September 1984. *Dansk Orn. Foren. Tidsskr.* **79**, 133-140.

Rabøl, J. (1993). The orientation systems of long-distance passerine migrants displaced from Denmark to Kenya. *Ornis Scand.* **24**, 183-196.

Raftery, A. E. and Zheng, Y. (2003). Discussion: performance of Bayesian Model Averaging. *J. Am. Stat. Assoc.* **98**, 931-938.

Remisiewicz, M. (2002). The temporal pattern to robin *Erithacus rubecula* migration: evidence from ringing recoveries. In *The Avian Calendar: Exploring Biological Hurdles in the Annual Cycle.* Proceedings of the Third Conference of the European Ornithologists' Union, Groningen (ed. C. Both and T. Piersma), pp. 489-502. Groningen: Netherlands Ornithologists' Union.

Ritz, T., Thalau, P., Phillips, J. B., Wiltschko, R. and Wiltschko, W. (2004). Resonance effects indicate a radical-pair mechanism for avian magnetic compass. *Nature* **429**, 177-180.

Salewski, V., Bairlein, F. and Leisler, B. (2000). Recurrence of some palaearctic migrant passerine species in West Africa. *Ring. and Migr.* **20**, 29-30.

Sandberg, R. (2003). Stored fat and the migratory orientation of birds. In *Avian Migration* (ed. P. Berthold, E. Gwinner and E. Sonnenschein), pp. 515-525. New York: NY Springer-Verlag.

Sandberg, R. and Gudmundsson, G. A. (1996). Orientation cage experiments with dunlins during autumn migration in Iceland. *J. Avian Biol.* **27**, 183-188.

Sandberg, R., Pettersson, J. and Alerstam, T. (1988). Why do migrating robins, *Erithacus rubecula*, captured at two nearby stop-over sites orient differently? *Anim. Behav.* **36**, 865-876.

Schwarz, G. (1978). Estimating the dimension of a model. *Ann. Stat.* **6**, 461-464.

Thorup, K. (1998). Vagrancy of yellow-browed warbler *Phylloscopus inornatus* and Pallas's warbler *Ph. proregulus* in north-west Europe: misorientation on great circles? *Ring. and Migr.* **19**, 7-12.

Vardanis, Y., Klaassen, R. H. G., Strandberg, R. and Alerstam, T. (2011). Individuality in bird migration: routes and timing. *Biol. Lett.* **7**, 502-505.

Weindler, P., Wiltschko, R. and Wiltschko, W. (1996). Magnetic information affects the stellar orientation of young bird migrants. *Nature* **383**, 158-160.

Wiltschko, W. and Wiltschko, R. (1996). Magnetic orientation in birds. *J. Exp. Biol.* **199**, 29-38.

Wiltschko, R. and Wiltschko, W. (2003). Avian navigation: from historical to modern concepts. *Anim. Behav.* **65**, 257-272.

Wiltschko, W., Traudt, J., Güntürkün, O., Prior, H. and Wiltschko, R. (2002). Lateralization of magnetic compass orientation in a migratory bird. *Nature* **419**, 467-470.

Zar, J. H. (1999). *Biostatistical Analysis.* London: Prentice Hall.

Zehtindjiev, P., Ilieva, M. and Åkesson, S. (2010). Autumn orientation behaviour of paddyfield warblers, *Acrocephalus agricola*, from a recently expanded breeding range on the western Black Sea coast. *Behav. Processes* **85**, 167-171.