METHODS

EVALUATION OF ORIENTATION EXPERIMENT DATA USING CIRCULAR STATISTICS – DOUBTS AND PITFALLS IN ASSUMPTIONS

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ABSTRACT

Busse P., Trocińska A. 1999. *Evaluation of orientation experiment data using circular statistics – doubts and pitfalls in assumptions*. Ring 21, 2: 107-130.

The paper is devoted to the methodical analysis of the „silent" assumptions that are the basis of application of the circular statistics to evaluation of bird orientation data collected in „orientation cages" of any design. The study is based on the analysis of available published description of the methods used in evaluation of bird orientation data. The theoretical discussion is followed by a detailed analysis of application of the discussed methods to the data on migrating Robins (*Erithacus rubecula*), collected at the Operation Baltic field station in autumn 1996. Two different models of approach: classic – one-vector model assuming only unimodal behaviour of migrating birds and multi-vector model that accepts all uni- and multimodal distributions of the registered signs of bird migration restlessness significantly different from the random one, are compared. Both methods can be applied at two different levels – for an individual bird and a group of birds. The assumptions of the methods, their consequences and evaluation procedures are presented and discussed in detail. In conclusion it appears that the classic computing routine: (1) is based on wrong biological assumption of unimodality of bird behaviour that is not a case for many tests, (2) when applying classic statistic procedures, it allows to include only unimodal and axial distributions into analysis, (3) biases the results giving strong influence to side vectors that should not be included into the result vector, (4) when studying the group of birds it should not be used in most cases, as the group of birds can show multimodal distribution, instead of only one resulting mean vector. In contrast, multi-vector model evaluation procedures allow finding and analysis of any existing vector pattern at both – an individual and a group – levels.

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Key words: orientation experiments, circular statistics, method evaluation.

INTRODUCTION

Since Kramer's (Kramer 1949) and Sauer's (Sauer 1957) studies on orientation abilities of night migrants made use of evaluation of migratory restlessness in

„orientation cages", the method became a standard one in the bird orientation studies. Technical design of experimental cages developed from the one with some perches inside (Kramer 1949, Sauer 1957) where bird hopping was evaluated by means of electric counters, counting of scratches on typewriter correction paper in Emlen's funnel cage (Emlen and Emlen 1966) to counting of dots made by bill of a tested bird on transparent plastic foil in Busse's flat cage (Busse 1995). All these technical methods give basic circular data: signs of the bird activity that are noted by sectors of a circle. Number of sectors varies from 6 (e.g. Kramer 1950) to 24 (e.g. Helbig *et al.* 1989).

Data collected, because of the nature of the study, must be evaluated using circular statistics. The routine of application of the circular statistics, as well as layout of data presentation, were established many years ago and all authors use the same standard. In most published papers description of the method is usually extremely short and is repeated one after another (Helbig *et al.* 1989, Helbig 1991, 1992a, 1992b, Berthold *et al.* 1992, Weindler *et al.* 1995, Wiltschko and Wiltschko 1995, Bletz *et al.* 1996). The only one exceptions were papers by Cherry and Able (1986) and Busse (1995). Cherry and Able (1986) stated that signs of the bird hopping are not distributed accidentally, so it is not allowed using circular statistics for the raw data. Busse (1995) presented new method of testing directional preferences of night migrants. There the method of evaluating the data was not a standard one. However, it was not discussed in details. This was because the main aim of the paper was to show that experiments with the night migrants could be performed during daytime with the use of method much simpler than the traditional experimental one. Collecting big samples of data (up to 1000 per season) and first evaluations of the results enabled more detailed analysis of the methods of evaluation of such kind of data.

Use of any statistical method for the analysis of a field data is based on a fundamental assumption that defined set of data could be correctly analysed using defined statistical method. There could be two kinds of doubts:

(1) whether the data fit the statistical constrains of the method (using simple example – the method requires continuous distribution of events while the data contain arbitrary defined groupings), and

(2) whether the particular statistics has application because of logical or biological constrains (e.g. calculation of average weight of caught birds while the birds caught belongs to several species – this is neither logically nor biologically sound).

It is a pity that in many papers such fundamental assumptions are not even listed or discussed. Because of that some methods applied are based on „silent" assumptions, which are not necessarily correct. This can lead to results, which only apparently are correct while in fact they are more or less artefacts rather than description of reality. It is especially dangerous when the calculation routine is followed by next authors who believe that the first application of the method is really sound and they do not check its assumptions.

This paper is devoted to the methodical analysis of the silent assumptions that are the basis of application of the circular statistics to evaluation of bird orientation data collected in „orientation cages" of any design.

MATERIAL AND METHODS

Methodological discussion takes into consideration available published descriptions of methods used in evaluation of data obtained using different kinds of orientation cages used in experimental and field studies on migratory restlessness of nocturnal migrants (Helbig *et al.* 1989; Helbig 1991, 1992a, 1992b; Berthold *et al.* 1992; Weindler *et al.* 1995; Wiltschko and Wiltschko 1995; Bletz *et al.* 1996). The theoretical discussion is followed by checking the methodical conclusions on real data on migrating Robins (*Erithacus rubecula*) collected in autumn 1996. Birds were tested in the Busse's cage at the Operation Baltic field station Bukowo/Kopań located at the Polish Baltic coast. Altogether 453 tests were performed. Only in 9 (2%) tests birds showed too little activity (less than 30 scratches per test) and were excluded from further analysis. In other 4 tests (1%), individuals showed no directionality in distribution of the signs of activity in the cage (after Chi-square test at 0.01 level).

THEORETICAL ANALYSIS OF METHODS

Data structure and presentation

There are two levels at which the orientation experiment circular data are evaluated:
1. individual behaviour,
2. group behaviour.

At the first level, individual behaviour, the raw data from every experiment are collected. The signs of the bird activity are counted by sectors and registered (Fig. 1A). Numbers are presented in a graphic form as vectors located radially from the centre of the graph in appropriate sectors (Fig. 1B). According to convention applied and software used, the graphic form can be different (Fig. 1C). In the classic routine an individual experiment vector is calculated from the raw data in the form [direction in degrees a_i- length of the result vector r_i] using standard calculation of a mean vector given in circular statistics. The second level of evaluation in the classic method is the calculation of the mean vector [a, r] for a group of birds from individual vectors. Then individual vectors are shown as separate signs located at the periphery of the circle and the result vector is located in the centre of the graph (Fig. 2). Group data can be, however, as it is used in the new method, presented as a sum of vectors grouped by narrow sectors (all vectors in every sector are added, but not summed up with the vectors from other sectors) – Figure 3. This is a graphic form giving presentation of distribution of individual vectors rather than average for the group.

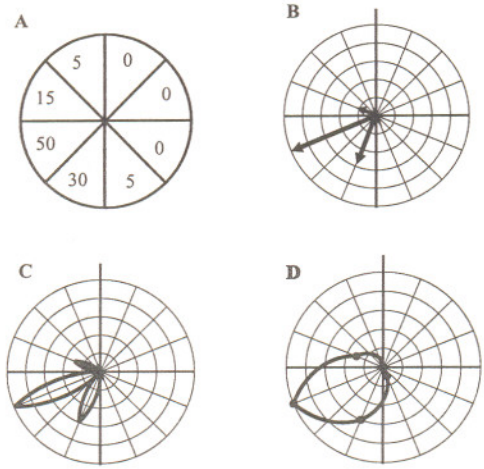


Fig. 1. Presentation of data collected using orientation cages. A – raw data noted (8 sectors), B – data presented as vectors, C, D – two versions of presentation using Quattro Pro for Windows „radar graphs".

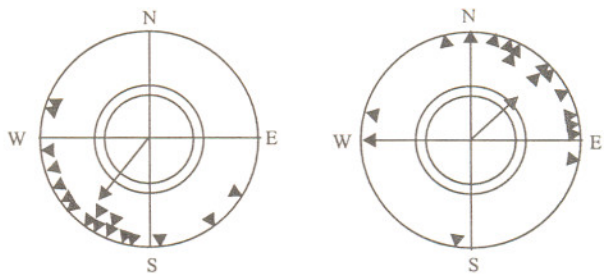


Fig. 2. Classic layout of data presentation: „Orientation behaviour of young blackcaps hand raised and tested without ever seeing the sky... Triangles at the periphery of the circle, directions of individual birds...; arrows, mean vector based on these mean directions drawn with respect to the radius of the circle = 1. Two inner circles, the 5% (dotted) and the 1% significance border of the Rayleigh test.". After Berthold (1996).

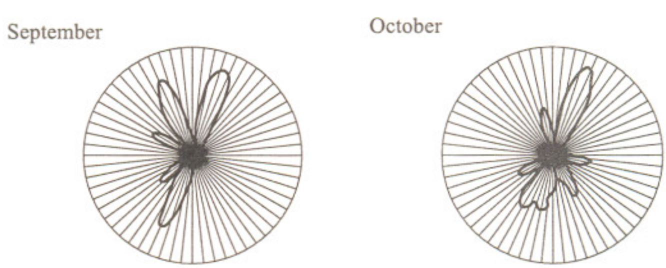


Fig. 3. Presentation method used by Busse (1995): „Local vectors in the sample of the Song Thrush, Bukowo-Kopań 1995: ... distributions for September and October caught birds.". After Busse (1995).

Basics of the circular statistics calculations

As it was mentioned earlier numbers of signs of the bird activity are expressed in the raw orientation data as vectors located in the sectors around all circle (Fig. 1). Despite any assumptions of the method, the result vector is defined with the use of procedure of adding the vectors that is also the basis of any other calculations on vectors. The rules of adding the vectors are shown at Figure 4. In practice the rectangular co-ordinates are used in calculations (Zar 1984) instead of geometrical adding of vectors as shown on the figure:

(1) if we add n vectors, denoted as a_i though a_n and vector length 1, we first consider the rectangular co-ordinates of the mean angle a:

$$X = \frac{\sum \cos\alpha_i}{n}, and\ Y = \frac{\sum \sin\alpha_i}{n}$$

(2) then length of the vector is computed:

$$r_1 = \sqrt{X^2 + Y^2}$$

(3) the mean angle is defined by:

$$\cos\alpha = \frac{X}{r_1},\ \ \sin\alpha = \frac{Y}{r_1}$$

In the first level of evaluation of orientation data when counting signs of activity by sectors, in fact we group all single vectors into subsequent sectors. If the vectors are grouped the formulas for X and Y are modified:

$$X = \frac{\sum f_i \cdot \cos\alpha_i}{n},\ and\ \ Y = \frac{\sum f_i \cdot \sin\alpha_i}{n},$$

where f_i values are frequencies in subsequent intervals.

At the second level of evaluation of orientation data individual vectors that are added differ in length, so other modification of formulas for X and Y is used:

$$X = \frac{\sum r_i \cdot \cos\alpha_i}{n},\ and\ \ Y = \frac{\sum r_i \cdot \sin\alpha_i}{n},$$

where r_i values are lengths of subsequent vectors.

For the data distributed axially (this will be discussed below) a special procedure called „doubling the angles" is usually applied and the length of axial vector r_2 is calculated. The procedure contains two steps:

(1) all angles are multiplied by two and if the result angle is greater than 360° then value 360 is subtracted from the doubled angle value,

(2) the standard computing procedure is applied, but the r_2 value is obtained instead of r_1.

The most basic examples of computing are shown at Figure 5. V_x is the result vector when the distribution is unimodal (A), while if it is bimodally axial (B) there is computation problem as direction (a) is indeterminated and the lenght of vector is 0. Doubling the angles procedure allows to compute axial a and r (C). It must be, however, stressed that although this procedure overcomes computation problem, r_2 value is not equal to r_1 obtained from the same raw data when axially opposite vec-

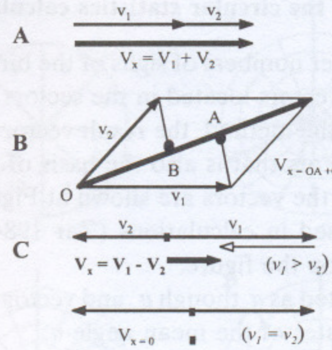


Fig. 4. Basics of vector adding. A – sum of vectors of the same axis and pointing the same direction. B – geometrical sum of vectors at angle ($OA = v_1 * cos\ a_{v1}$, $OB = v_2 * cos\ a_{v2}$), C – sum of vectors of the same axis but directed opposite equals subtraction of their lengths.

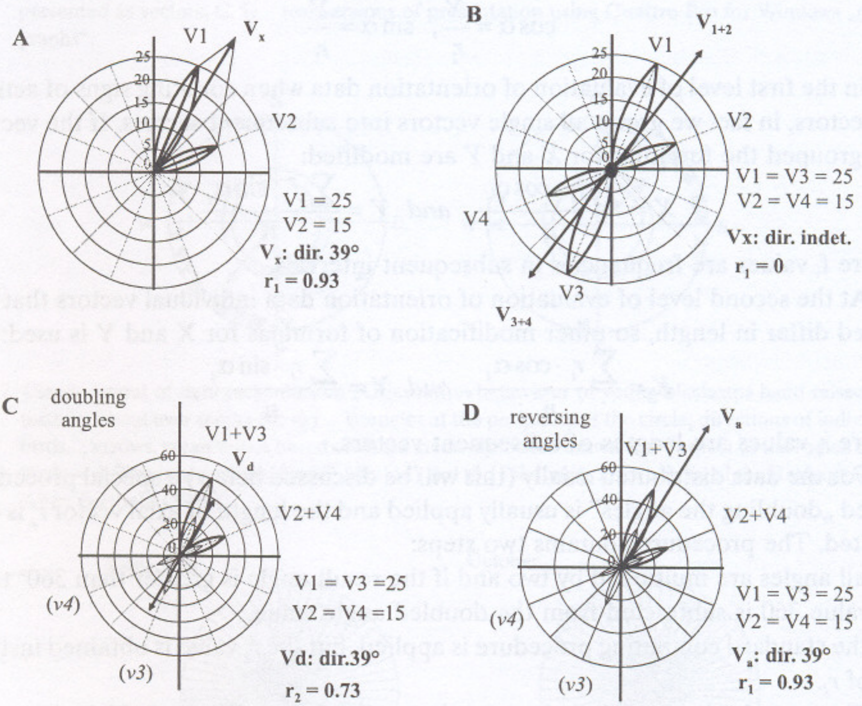


Fig. 5. Evaluation of the data using classic method. A – unimodal distribution: vector direction and r_1 are calculated, B – axial distribution, standard calculations: vector direction is indeterminate, $r_1 = 0$, C – „doubling the angles" procedure: axial vector direction and r_2 are calculated, D – logical operation „reversing the angles", not used in the classic method: opposite vectors are added after reversing (adding 180°), note that obtained $r_1 \neq r_2$ in procedure C.

tors are added – reversing of angles (D). The reversing of angles procedure is not used though it is logically and biologically more correct (see later). If we accept that the data are axial (the bird behaviour is along the line) the vectors at both sides of the centre are of the same logical and biological value, so they can be added instead of being statistically manipulated.

Assumptions in evaluation of orientation data

In orientation studies, as in other applications of statistics in evaluation of biological data, the results depend not only on computing procedure but, sometimes even more, on assumed model of the biological process studied. The data collected using orientation cages were evaluated assuming different models of bird behaviour in the cage. They can be called „classic", one-vector model (used in most publications since beginning of evaluation of orientation data) and multi-vector model (used recently in interpretation of field experiments – Busse 1995, Nowakowski and Malecka 1999, Trocińska *et al.* in press).

One-vector model

The model is based on two **assumptions**:

1. Because bird on migration behaves unimodally (it migrates towards winter-quarter in autumn and breeding ground in spring), so in the orientation cage it must show the same. This unimodal behaviour must be represented by one direction only and any deviations from the unimodality must be treated as accidental deflections being a kind of an information noise.
2. Computing the mean vector using the standard circular statistics procedure is a correct method to show directional preferences of the bird defined as above.

Let us to look more carefully at **consequences** of these assumptions.

(1) As only unimodal behaviour is expected all registered signs of migration restlessness must be reduced to one vector only. This means that all multimodal distributions are *a priori* not allowed and they must be removed by the statistical procedures. So, because of such assumption there is no possibility to discover multimodal behaviour of birds, which is not impossible. Moreover, many authors (e.g.; Helbig *et al.* 1989, 1992b, Berthold *et al.* 1990) found that some of data patterns were better described by axial distribution that means that they found bimodal distributions in their data and applied special statistical procedure allowing to include such birds into evaluated data set. Thus they use unimodal and bimodal distributions together (despite r_1 *and* r_2 values are not comparable – see above) and, additionally, accepting arbitral levels of axiality (this is discussed later). By this operation they do not follow the first assumption of the model. Such situation is methodically at least doubtful.

(2) Standard procedure of computing the mean vector includes adding all single vectors together. Logically that means that we treat all signs of the bird activity

as having the same calculation value, but earlier we assumed that this was not the case and that only one direction is correct while other vectors are the information noise, which should be removed. So, both assumptions are not observed.

(3) Basing on the first assumption we accept that by adding opposite vector (i.e. subtracting its length) to the longer one we remove a „noise" on that direction (in practice we assume that within the longest vector a part of its value is the noise as big as opposite vector is). However, some other vectors do not have opposite ones or they have quite different length – and we have fundamental question: what is the level of noise, which should be removed? Figure 6 illustrates the problem how much the standard procedure biases the raw data produced by the bird when computing the mean angle – both distributions shown there (lower one obtained silently during computation procedure – adding opposite vectors) give the same mean vector, though they look completely different. Resulting direction is much influenced by the vector perpendicular to the longest one (Fig. 6B), while, basing on assumption 1., it should be treated rather as „noise" only.

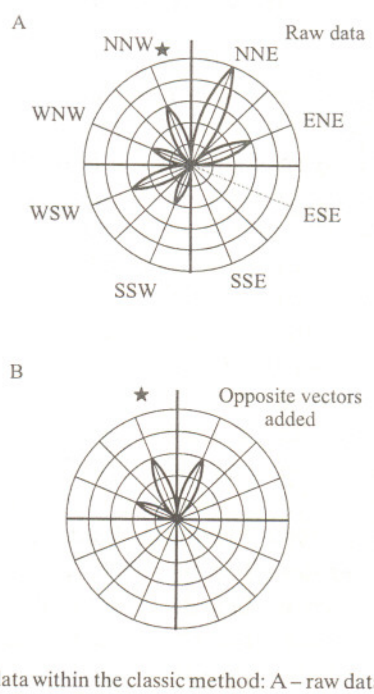


Fig. 6. Hidden manipulation of data within the classic method: A – raw data distribution, B – the same data when opposite vectors are added as it is a case within computing process (adding all vectors together). Asterisk – mean heading obtained by the standard classic procedure.

(4) Computing the mean vectors for a number of individuals using the standard circular statistics procedure gives vectors required by the model that are inter-

preted basing on the first assumption: if the vector points towards expected winter-quarter the birds are called „correctly oriented" and if not – they are „disoriented", because of any reason. This, once more, eliminates possibility to find differentiation within the studied group. One can claim that this is very strong limitation of the model, especially if it is applied to the evaluation of experiments made during a real migration in the field. In that case we must take into consideration possibility that within a sample there are individuals migrating towards different winter-quarters as it was shown in many papers (e.g. Zink 1973-1985, Glutz and Bauer 1991).

The **evaluation procedure** using one-vector model:

(1) Computation of vector parameters for the raw (a, r_1) [and doubled angles (a, r_2)].

(2) „In cases of axially bimodal distributions..." (e.g. Helbig 1992) or „...if the bimodal vector length r_2 exceeded the unimodal one r_1 by at least 0.10." (Weindler *et al.* 1995) or more than 0.01 (Helbig 1991) it is decided whether standard or bimodal vector is accepted. If the bimodal vector is further used its direction is decided basing on direction of the longer raw data vector or using the direction that was „proper" to the season (e.g. Helbig 1991).

Multi-vector model

The model is built on the **assumption** that we are not allowed to decide *á priori* on the bird behaviour directionality. That means that we have to accept any distribution significantly different from the random one. The bird can show one-vector directionality as well as axial or multi-vector tendencies. The aim of analysis is to find which kind of behaviour the bird shows. This assumption is based on hypothesis presented earlier by Busse (1992), who suspected that the individual bird, which is an inter-population („population" – in migratory sense) hybrid can have two (or even more) navigational programmes and, additionally, reversed ones. That means, as well, that reversed directions giving axial distributions are of a special biological value. Summarising – the bird can show multi-vector behaviour and we should accept this possibility.

The **consequence** of this assumption is that we must apply such evaluation procedure, which will not *á priori* eliminate multi-vector patterns. Because of the reasons explained above the standard calculation procedure could not be used for the full set of data.

The **evaluation procedure** using multi-vector model:

(1) Accepting the single experiment data set for evaluation –

- excluding low-active birds as in previous model; the procedure discussed was applied to data obtained by means of Busse's cage, where in general level of counted signs is much lower than in Emlen's cages, the minimum level was set to 30 (Busse 1995) or 20 (Trocińska *et al.* in press) signs;
- checking whether distribution is directional (data are compared with equal-frequency distribution by Chi-square test).

(2) Local vector number analysis – potential vectors are identified from the raw data distribution using the rule that if there are local maxima, defined as „values higher from both neighbouring ones", the local vector is suspected, e.g. at Figure 7 both A and C distributions are suspected to be three-vector ones. However, distribution A has the third maximum small and it can be an accidental deviation. To avoid such cases smoothing the data by means of moving average could be used. This operation „cleans" further pictures from some information noise, e.g. graphs B and D at Figure 7 (at graph D third suspected vector is still visible although the picture is less clear). Since that moment of the procedure single bird data can be evaluated using separately raw and/or smoothed data according to the needs of the analysis. The latter one gives more simplified pictures.

(3) Data are recalculated to percentages for graph and computing purposes („weight" of the vectors – see later).

(4) Computing the vector parameters. There are three parameters of the local vector: direction (a) and concentration (r), as in standard one-vector model procedure, and „weight" of the local vector (w). „Weight" is defined as a sum of values in sectors used in calculations expressed in percent of total number of signs of the bird activity (as computed in point 3 above).

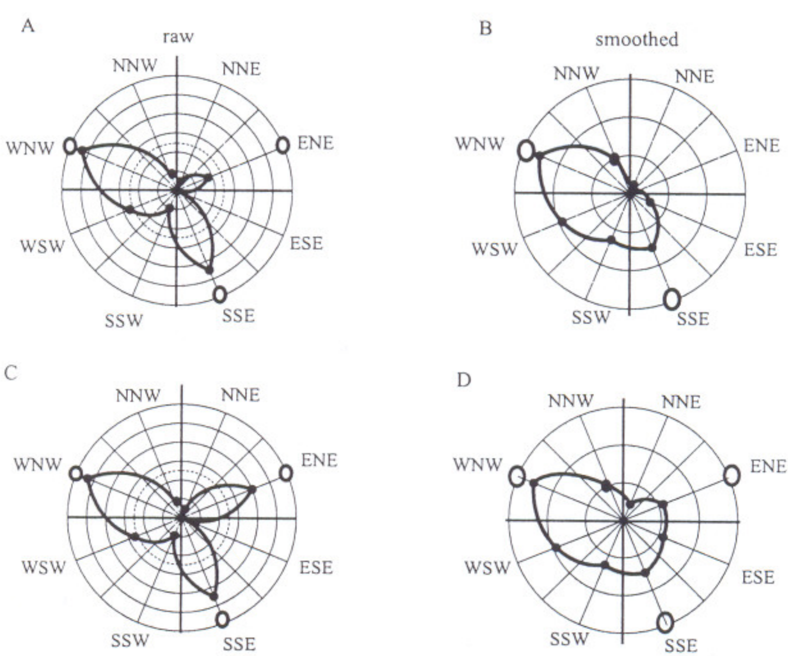


Fig. 7. Effects of smoothing procedure in the new method of calculations: A, B – distributions of raw and smoothed data: one of local maxima (circles) is lost after smoothing (ENE sector); C, D – the same for stronger third maximum (in ENE sector maximum is still visible after smoothing).

The local vector defining procedure is based on the rule that multi-modal distribution could be regarded as a mixture of a few one-modal ones (Mardia 1972). If the distribution contains vectors not grouped by sectors a special procedure called broken axis approach (Holmquist and Sandberg 1991) should be used to define local axes, but the data discussed here are grouped into sectors and results of local vector number analysis is used for evaluation of vectors parameters. Every local vector parameters are computed separately after dividing the data into groups of three sectors for each local vector. The group is defined as „sector with local maximum and two neighbouring ones". In many cases, when local maxima are two sectors apart, as it is shown at Figure 8A, grouping is simple, but if they have common neighbouring sector a procedure shown at Figure 8B, C is used as a best fit. Within every group of three sectors vectors are traditionally added - a and r_l parameters are calculated as well as third parameter w.

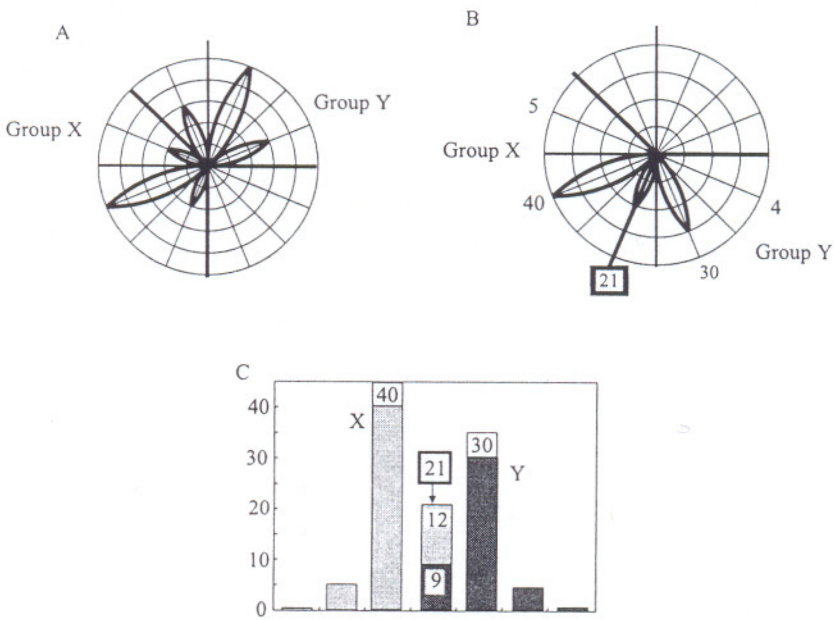


Fig. 8. New method procedures. Splitting the multimodal distribution into a few unimodal ones: A – distribution shown at Figure 6 is split onto groups X and Y, B – the procedure when local maxima share neighbouring sector; length of this vector (21) is divided into two vectors (9 and 12), which lengths are proportional to local maxims lengths (30 and 40), C – distribution B in linear form to illustrate the procedure explained in B.

(5) The individual local vectors (from raw or smoothed data), as obtained in the point (4), can be used for further summarising analysis giving „raw" and „simplified" distributions for groups of birds. These are distributions obtained by adding w values of vectors located in narrow, 6° wide, sectors (e.g. Fig. 9 – above)

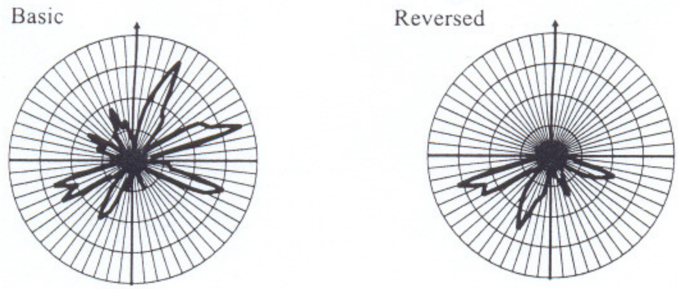


Fig. 9. Presentation of distribution of individual headings within a group. Basic distribution or raw headings and „reversed" distribution after reversing the headings pointing backward direction for a season.

and they are called „basic" („raw basic" from the raw data and „simplified basic" from the smoothed data) as they give not modified pictures (see point 6). Such distributions are not intended to be averaged in further analysis, as calculation of a mean value would break the general assumption that the group can be differentiated internally as to the direction of migration. The example presented at the Figure 9 shows well-pronounced axiality of elements of the distribution. This is caused by frequent axiality in individual distributions as well as by common reverse (in relation to seasonal direction of migration) heading of birds demonstrating one-vector pattern of activity. This problem will be discussed later.

(6) As the patterns obtained in the point (5) are not easy to be interpreted from the point of view of heading in a real migration the reversing of backward headings give more understandable patterns of migration to different winter-quarters. The procedure includes adding of 180° to the angle of the vector heading in backward direction to normal heading of migration in the season, i.e. northern in spring and southern in autumn. The result distribution looks like at Figure 9.

DISCUSSION OF RESULTS OBTAINED USING DIFFERENT MODELS

Individual tests

As an example, let us analyse distribution shown at Figure 10, which causes troubles when one-vector model is applied: despite of clearly visible bi-directionality of the original data results of the classic calculations are unsatisfactory and even doubling the angles does not describe the distribution well. Figure 11 demonstrates course of multi-vector analysis performed at the distribution shown at Figure 10 and compares final patterns obtained for this bird basing on two models.

Figure 12 contains some examples of the real distributions obtained when testing Robins by using Busse's orientation cage. It stresses differences between results

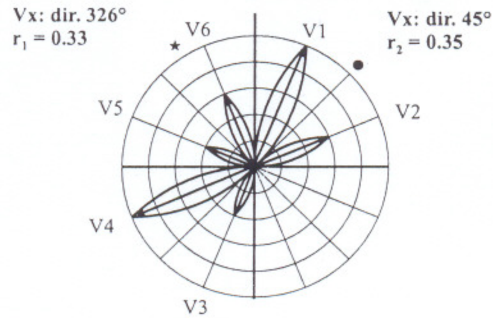


Fig. 10. Example of distribution that causes troubles when classic method is applied: direction obtained by the standard procedure (asterisk) and the doubling the angles procedure (black dot) are very different despite that difference between r_1 and r_2 is very small.

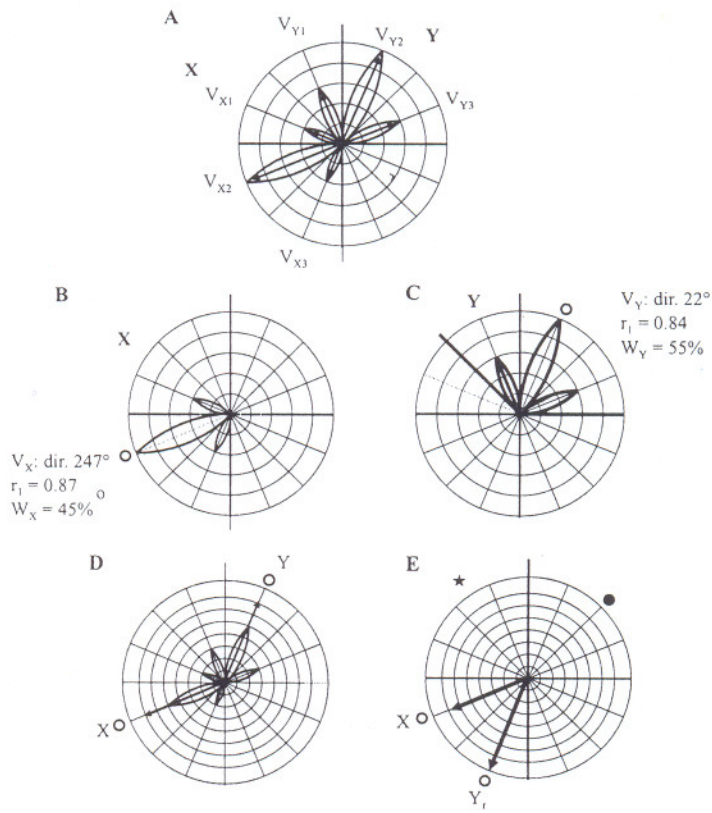


Fig. 11. The new method procedure: A – localisation of local vectors and splitting the distribution onto unimodal ones, B, C – computing directions, r and w values for local vectors, D – local vectors, basic presentation for an individual, E – local vectors, presented after reversing the backward vector; for comparison classic results are shown as asterisk for the standard classic procedure and black dot as the doubling of the angles procedure (the same as on Fig. 10).

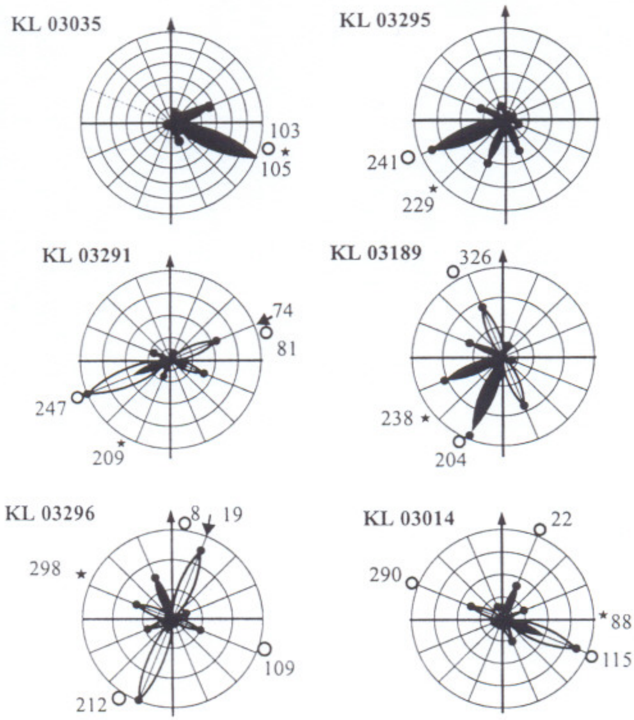
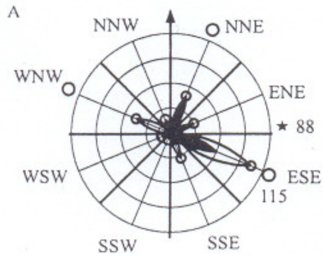


Fig. 12. Comparison of using different procedures for some real data on Robin (numbers of rings are given). Asterisk – standard classic procedure, arrow – doubling the angles procedure, circles – local vectors according to raw data new method procedure; numbers – exact location of signs (in degrees). Line with dots – raw data distribution, black pointers – classic equivalents obtained according to Figure 6.

obtained by means of two discussed methods and the problem of the influence of vectors perpendicular to the most pronounced one is pointed using the convention used at the Figure 6. Figure 13 contains analysis of the case of the individual with the ring KL 03014. It shows how much influence on final result of the classic procedure has side vector in the sector NNE, which is not balanced by an opposite one. This confirms clearly that such side vectors assumed to be the information noise influence the classic method results. Figure 14 compares results of multi-vector analysis of the same, as at Figure 12, birds when two variants of the new method were used. Raw data and smoothed data give very close results, but in some cases small vector registered in raw data disappeared after smoothing (e.g. birds KL 03189 – second vector, KL 03296 and KL 03014 – third vector).

Axial and multi-vector patterns in the individual data

Let us analyse multi-vector patterns shown within real data obtained during testing of Robins and look how the evaluation operations influence the original, raw



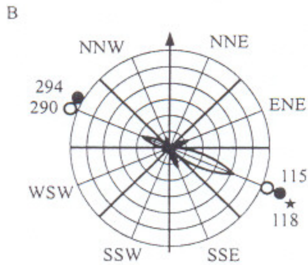


Fig. 13. Example of influence of the side vector (in the sector NNE) on result of standard classic routine applied for the Robin KL 03014 (above). For comparison, the same distribution is given below with side vector NNE removed. Asterisk – result according to the standard classic routine, circle – local vector for raw data version of the new method, black dot - local vector for smoothed data version; numbers – exact location of signs (in degrees).

data basic distributions. Multi-vector patterns are common in the raw basic data – there are only 26.8% of one-vector patterns (Table 1, Fig. 15). Smoothing the data changes this situation and one-vector patterns predominate (63.8%), but two-vector ones still cover 34.8% of individuals. Three-vector cases became rare (1.4%) and they can be treated as exceptions, esp. that three of six cases noted in the studied sample are close to be the axial patterns with one additional vector included. Reversing of vector procedure, when backward directions (opposite to the normal direction for the season) are reversed by 180° and added to the proper direction vectors if they are situated closer than 10°, results in reduction of multi-vector patterns by 14% for raw data and 23% for smoothed data. That means that within multi-vector patterns there is quite good bulk of birds showing axiality in behaviour, but this phenomenon does not explain all multi-vector patterns – within smoothed reversed patterns there are still numerous individuals showing bi-vector behaviour (26.8%). If we analyse localisation of the second (according to its weight w) vector in relation to the strongest one (Table 2) we can find that the birds with the strongest vector in NE quarter (NNE and ENE sectors) as well as vectors in SW quarter are accompanied by the second vector located more or less axially (resp. 86.8 and 67.3%). Those located in SE and NW quarters have counterparts located at angles 90-135° apart in 53.8 and 63.2% respectively. This distribution is, after Chi-square test, significantly different from the random ($p \ll 0.001$). Thus the birds migrating along NE-SW axis show higher axiality than these migrating SE.

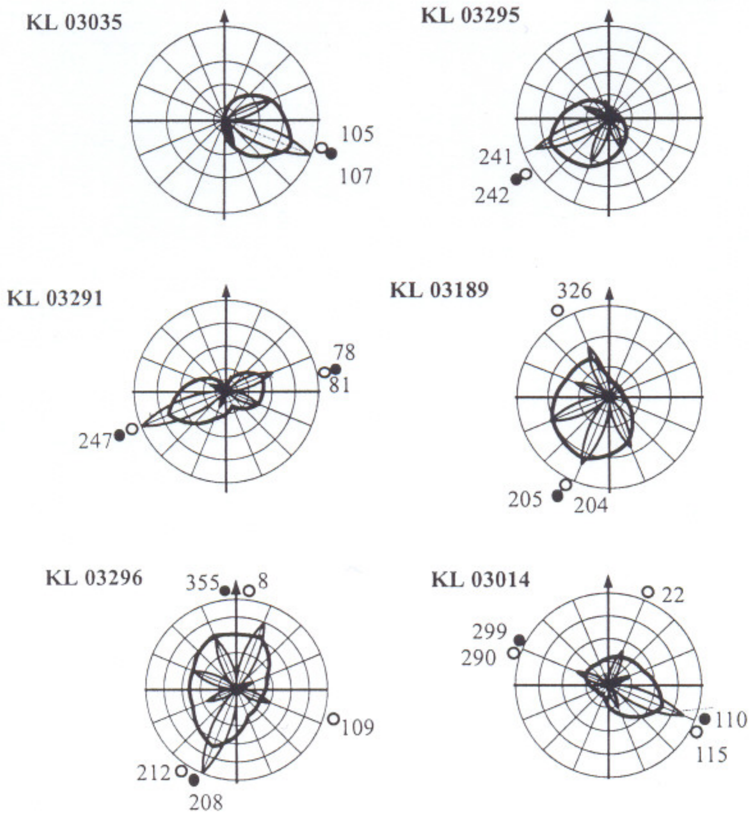


Fig. 14. Comparison of using different versions of the new method for the same birds as at Fig. 12 (numbers of rings are given). Thin line – raw data, thick line – smoothed data (note that two methods of presentation of the data are used together); open circle – local vector for raw data version, black circle – local vector for smoothed data version; numbers – exact location of signs (in degrees).

Table 1
Percentage distribution of numbers of local vectors

No of vectors:	1	2	3	4
Raw data				
Basic	26.8	53.6	19.1	0.7
Reversed	34.1	48.6	17.3	-
Smoothed data				
Basic	63.8	34.8	1.4	-
Reversed	71.8	26.8	1.4	-

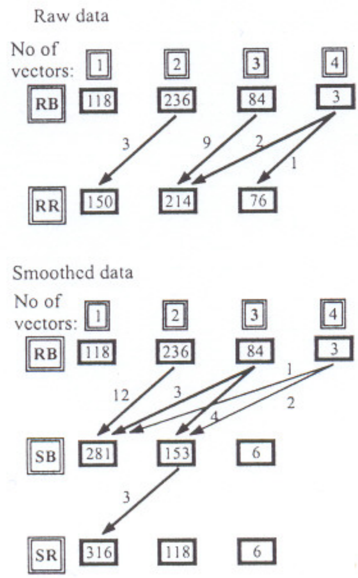


Fig. 15. Influence of procedures used in the new method on a number of local vectors found for individuals of Robins tested at Bukowo-Kopań (N = 440) in 1996. RB – raw data basic distributions, RR – raw data reversed distributions, SB – smoothed data basic distributions, SR – raw data reversed distributions. Arrows show how many distributions changed modality after smoothing (RB – SB) or reversing (RB – RR and SB – SR).

Table 2

Axial second vectors and those at angle 90-135° to the longest one

Sectors	Axial vectors						At angle		Total
	stricte*		other**		All				
	N	%	N	%	N	%	N	%	
NE	19	35.8	27	50.9	46	86.8	7	13.2	53
SE	5	19.2	7	26.9	12	46.2	14	53.8	26
SW	8	14.5	29	52.7	37	67.3	18	32.7	55
NW	3	15.8	4	21.1	7	36.8	12	63.2	19
Total	35	22.9	67	43.8	102	66.7	51	33.3	153

* - within 10° limit, ** - within a quarter

REVERSE DIRECTIONS

Reverse, or backward, directions of local vectors of individual birds are common in the studied sample of birds – in total 48.9% of raw data vectors show these backward directions and 55.4% of smoothed ones (Table 3). This is totally against basic assumption of the one-vector model that the birds tested in orientation cages must show direction to the winter-quarters as the only one for birds, which are not called „disoriented". This could be a speciality of testing the birds during daylight (Nowakowski and Malecka 1999), but there were reported axial distributions in night-time experiments (e.g. Weindler *et al.* 1995 - „around 5 percent"). On the other side reverse directions are scarce in some samples of tests performed during the day (e.g. Trocińska *et al.* in press, for a number of species in Eilat, Israel), while very common in other localities (Trocińska *et al.* in press). In the sample studied here northern directions are significantly more represented within birds showing one direction of activity (for raw and smoothed data resp. 66.4 and 65.5% – Table 3). It is rather surprising and it suggests that the direction of the vector of the bird behaviour is less dependent on the orientation of the individual than on other, still unknown factors. On the contrary, axis of the vector is a better measure of orientation abilities of the bird.

Table 3
Distribution of directions of local vectors in the studied sample of Robins.
RB - raw data without smoothing; SB - smoothed data.
Data are grouped according to number of local vectors.

	RB 1		RB 2		RB 3		RB sum	
	n	%	n	%	n	%	n	%
NW	26	22.4	72	33.8	53	44.9	151	37
NE	51	44	141	66.2	65	55.1	257	63
N	**77**	**66.4**	**213**	**45.5**	**118**	**47.1**	**408**	**48.9**
SW	20	17.2	166	65.1	74	55.6	260	60.9
SE	19	16.4	89	34.9	59	44.4	167	39.1
S	**39**	**33.6**	**255**	**54.5**	**133**	**52.9**	**427**	**51.1**
Total	116*		468*		251*		835*	
	SB 1		SB 2				SB total	
NW	72	25.6	42	29.8			114	35.1
NE	112	39.9	99	70.2			211	64.9
N	**184**	**65.5**	**141**	**46.1**			**325**	**55.4**
SW	51	18.1	118	71.5			169	64.5
SE	46	16.4	47	28.5			93	35.5
S	**97**	**34.5**	**165**	**53.9**			**262**	**44.6**
Total	281		306				587	

* Some local vectors were located at W-E axis.

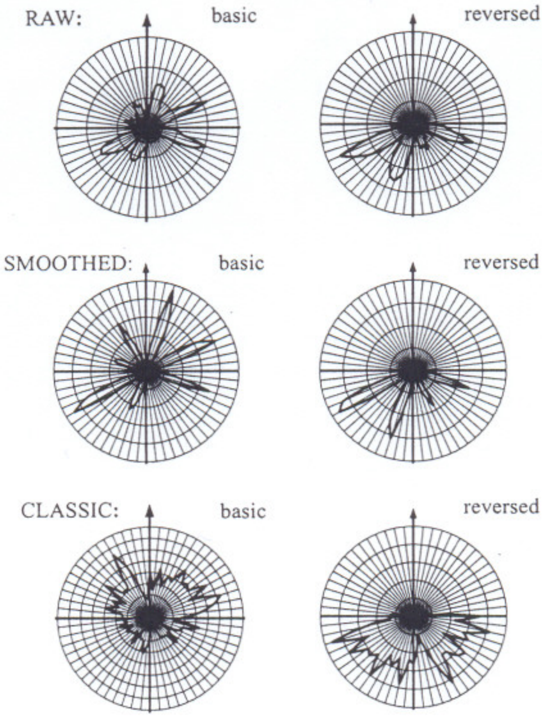


Fig. 16. Group distributions presented according to the new method procedure of showing the group headings. Basic and reversed distributions are shown for raw and smoothed data as well as headings obtained using classic procedure.

PRESENTATION OF RESULTS FOR GROUPS

In the classic treatment of group only one resulting mean vector is calculated as one direction for the group is assumed. For this reason the comparison is possible only if the classic individual data (one vector per bird) are presented in the form used within the new method of evaluation of data. That means that distribution of vectors by 6° sectors is used for individual vectors computed by the classic method. Distributions obtained using two versions (raw and simplified) of the new method and that classic one are presented at Figure 16. It is clearly visible that both natural and reversed data patterns for raw and simplified (smoothed) versions of the new method are similar while the graphs based on classic data are very different. Correlation coefficients between raw and simplified data are high (basic – r = 0.85, reversed – r = 0.89; highly statistically significant), while between raw data and classic one are not significant (basic – r = 0.17, reversed – 0.23). Similarly, correlation between simplified data and classic ones is low, and insignificant (basic – r = 0.24, reversed – r = 0.27). Thus distributions obtained basing on different models are incomparable. To check whether the difference depends on multi-vector individuals included in the sample of the data that were elaborated using the new method, only one-vector birds are used in comparison presented at Figure 16. Differences are on the same level.

SECTOR SIZE AND ACCURACY OF RESULTS

As it was mentioned earlier, the size of sectors in which signs of bird activity is counted varies from 6 to 24. It is obvious that the accuracy of obtained results depends on the size of sectors used in the data collection. However, it is not easy to estimate this influence and we did not find any discussion of the problem in the literature.

Let us look at this problem a little bit more in detail basing on the studied sample of Robins. The data on bird's activity were collected using 8 sectors by 45°. In further elaboration the number of all signs of the bird's activity counted within any sector was used as a length of the vector located in the middle of the sector. That means that number of all scratches in the NNE sector (1-45°) represent length of the vector located at 22.5° (see e.g. Fig. 1). This representation would be exact only if a real heading of the bird was exactly 22.5° and dispersion of scratches low enough to be limited to one sector only. The last condition is probably not fulfilled in the real data, as only in six cases of 854 local vectors defined, all scratches defining local vector were limited to one sector only. A scratch found just after the sector border is included in the data assigned to the middle of the next sector. Because of that in the new procedure applied two neighbouring sectors are used to define the local vector (some of the scratches in the neighbouring sector may belong to the heading located not in this sector). Depending on lengths of vectors in neighbouring sectors the local vector shifts out of centre of the sector with the longest vector but it stays within the sector. This shift towards the next strongest sector vector is balanced by the power of the third vector used in calculations. This means that the local vector has lower chances to reach position near the border of the sector. Thus they are located by the calculations closer to the centre of every sector – local vectors are not evenly distributed around the circle: concentrations of computed vectors can be visible on graphs illustrating distributions of vectors for groups of birds (e.g. Fig. 16 – raw and smoothed data). The smoothed data presentations have distributions closer to the centres of the sectors used, so they are called simplified distributions. Working with the data grouped into relatively wide sectors one must be aware that obtained „pointers" do not show exactly direction preferred by the group of birds but rather the general direction of the fan of local vectors. The narrower are the sectors used the more exact are the directions shown at graphs illustrating distributions. From the point of view of data collecting too many sectors are less easy to work with. It could be estimated that result-effort balance suggests 16 sectors as the best solution.

Concentrations of vectors obtained by traditional computing are not visible (Fig. 17). What does it mean? Is it an argument supporting this computation

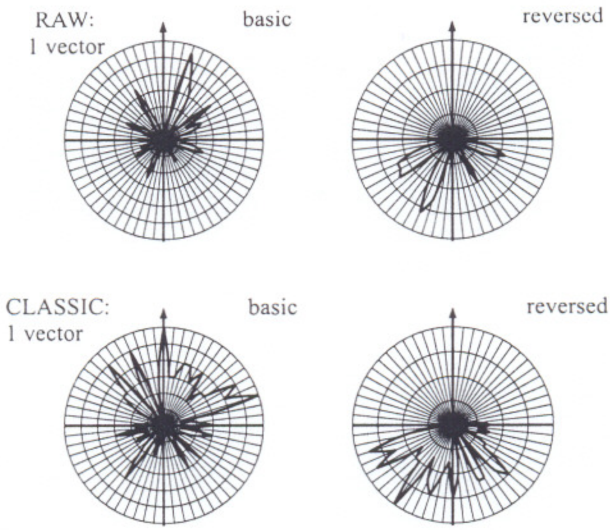


Fig. 17. Comparison of distributions of headings of birds that have shown unimodal distributions of the raw data (N = 118). Raw data basic and reversed distributions are compared with classic ones for the same sample of birds.

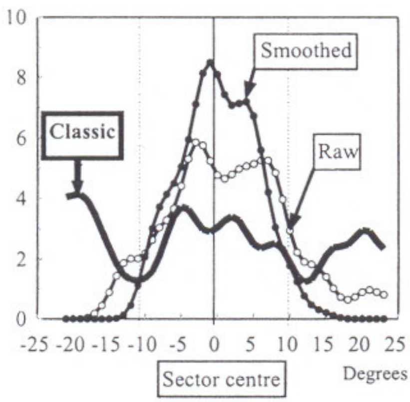


Fig. 18. Smoothed distributions of headings of Robins shown as deviations from the centres of sectors they belong to. Raw local vectors (N = 854), smoothed data local vectors (N = 605) and classic headings (N = 440) are compared.

model? Figure 18 shows smoothed distributions of local vectors in relation to the centre of sector in which they were found. Distribution of raw data vectors is relatively wide, but most of vectors were found within a limit of 10° (SD = 8.23, N = 281). Smoothed data vectors are more concentrated around the centre of the sector (SD = 5.16). Both distributions are bimodal, which suggests that source distributions of scratches exceed the borders of one sector – if all of them agree in the

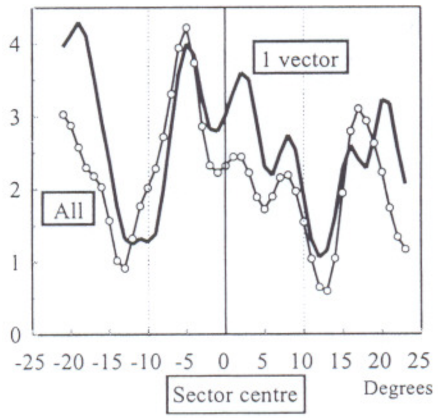


Fig. 19. Comparison of deviations from the centres of sectors for headings obtained using the classic method for birds that have shown unimodal distributions of the raw data and all individuals studied.

same sector unimodal distribution should be found. This confirms earlier observation that one-sector groups of scratches are rare. Distribution of vectors obtained by means of classic procedure is fundamentally different from these discussed above. Apart from that the central part of distribution is wide, but generally located within the same limits, as distributions obtained using the new method, there are two side peaks. They can be explained only as influence of side vectors in the original data that are located in sectors perpendicular to the sector with the strongest vector. These side peaks cause additional 40% of the basic variance shown by the raw data. This problem existing in one-vector model was discussed earlier (p. 120, Figs 12 and 13). Once more comparison of birds showing unimodal and multimodal activities (Fig. 19) suggests that this is a serious weakness of the model. Strange additional peaks in the distribution of the obtained vectors are the result of use in the computation procedure all vectors around the cage, including those being an information noise from the point of view of the calculated vector as well as those belonging to other vectors really existing. The side peaks in distribution are clearly artefacts caused by the computation routine.

CONCLUSIONS

Both theoretical discussion and the analysis of the real data strongly suggests that:

1. The classic computing routine based on automatic use of circular statistics procedures to evaluate the orientation data is based on wrong biological assumption of unimodality of the bird behaviour that is not the case of many tests. Limitation *á priori* of some of results by silent assumptions brakes the basics of the scientific research.

2. Classic computation procedure biases silently the results giving strong influence to side vectors that should be not included in the result vector obtained; it is, however, correct for unimodal source distributions.
3. Computing mean vectors from individual vectors is not allowed automatically as the group of studied birds can show multimodal distributions.
4. Evaluation of the orientation cage data should allow to study both axial and multi-vector patterns as they are common in the real data. The evaluation procedure proposed here allows finding any existing vector pattern. Some variants available allow concentrating on different aspects of the results.
5. Number of sectors used while collecting the data defines accuracy of the results.
6. Interpretation of multimodal patterns is the matter for further discussion. However, some hypotheses can be given:

6.1. The most basic in the bird orientation is the axial behaviour. It allows birds to find in autumn winter-quarters and return in spring towards breeding grounds.

6.2. Direction of migration is defined independently by the season, but in special situations the bird can show reversed directional behaviour. It could be suspected that the reasons of such behaviour could be of different origin both inherited (as observed in real migration, e. g. of Blackcaps) and caused by the time of experiment (night or day), caging stress or local habitat conditions that influence bird behaviour after landing at a place. So, reversed direction does not mean „disorientation", as the axis is still a correct one.

6.3. High share of individuals with two local vectors pointing at two different axes supports the suspicion that the individual that is an interpopulation hybrid can show more than one migration axis, which is expressed in the experiment as bi-vector individual pattern.

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