

The orientation of migrant birds following displacements by man or wind. A survey based on funnel experiments.

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Introduction

The system responsible for the spatial and temporal autumnal progress of juvenile, long-distance migrants has been a matter of discussion for many years. Primarily based on evidence on the temporal component the view has settled that a vector-orientation programme forms the basis of the inherited orientation system (reviews of e.g. Able & Bingman 1987, Wiltschko & Wiltschko 1988, Helbig 1990, Berthold 1990, Wallraff 1990). A vector-orientation migratory programme (i.e. a 'clock-and-compass' strategy) corresponds to a vector with a length and a direction, as the migratory programme is described as a number of migratory steps with an approximately constant compass course, where the length and number of migratory steps are defined by an endogenous circannual clock (Berthold 1996). The migratory programme may consist of one or more such vectors.

However, migrants in nature are influenced by exogenous factors experienced along the migratory route, such as wind, topographical features and available orientation cues, and migrants have been shown to respond to at least some of these (e.g. ecological barriers, coastlines and wind drift (Åkesson 1993, Fortin et al. 1999)) and Wehner (2001) recognise, that migrants combine all sorts of regionally specific geographical cues to ensure on-time arrival at their destination. The capability of coping with such factors lies 'on top' of the vector-orientation programme, and allows the migrant to compensate for displacements. The actual mechanism for such capabilities is, however, largely unknown. The proposed mechanisms range from birds only being able to compensate (partially) for wind drift while on migratory flights to birds being able to use navigation on site, the latter approaching the so-called goal area navigation system (which does not imply an underlying vector-orientation programme) (Rabøl 1969, 1970).

The most important distinction between the mechanisms proposed is between those involving navigational processes, and those who do not. The following hypotheses can thus be set up for the migratory orientation programme (ranging from the simplest to the most advanced additional orientation capability) (cf. further Rabøl 1994):

- (1) Systems not involving navigational processes.
 - (a) Simplest vector-orientation with no compensation ('One-direction orientation', Perdeck 1958).
 - (b) Vector-orientation with compensation for wind during migratory flights.
 - (c) Vector-orientation with compensation on site using reverse path integration (Wiltschko & Wiltschko 1976).
- (2) Systems involving navigational processes.
 - (d) Vector-orientation with compensation using navigation on site (W. Wiltschko in Rabøl 1972, Rabøl 1994 Fig.1D).
 - (e) Goal area navigation (Rabøl 1969, 1970).

As navigation involves processes that have not been documented in migrant birds, one should not accept these mechanisms before having excluded other possibilities as explanations of the results. It is therefore reasonable to test the results against hypothesis (a), which is the simplest mechanism. However, failure to reject the hypothesis in a certain case is not necessarily

evidence against other mechanisms being involved, as this might just mean that the birds are unable to express a certain behaviour in a particular set-up, and positive evidence in favour of a mechanism (rejection of the null-hypothesis) is thus much stronger than a negative result (failure to reject the null-hypothesis). This is comparable to the situation with homing birds, where we accept that birds are able to home from long distances – even when only single birds from a large sample return home. Even though navigational processes have not been documented in migrants (Berthold 1996, however, see Rabøl 1998), it is not unreasonable to assume such an additional orientation system, based on navigation, to be present: As we expect experienced birds to be able to navigate, a navigational system must be expected to be built up already in the pre-migratory period (from post-fledging) and along the route allowing juvenile migrating birds to compensate.

One way to test the hypotheses is by testing the behaviour of displaced migrants. Birds displaced by the wind can be used to test between (a) and more advanced mechanisms, while birds displaced by man and the reaction to 'displacement' under a planetarium sky can be used to test whether the behaviour involves navigational processes (test between (1) and (2) – or, in case of real displacements between (b) and (c), depending on how birds were transported). A difference in behaviour between tests under starry skies and in overcast can then indicate whether birds use the stellar sky as indicator of the displacement.

Recently, Mouritsen (1999) re-evaluated many displacement experiments described in the literature. In most single experiments he concluded that the clock-and-compass hypothesis is sufficient to explain the results. In the present paper we re-assess previous displacement experiments by using a 'community-wide' approach, i.e. by pooling the experiments contrary to just looking at single experiments. The systemic approach of ours is not influenced by our interpretation of the single experiment, but the weightings of the single experiments/samples could be challenged and bias could – in principle – arise from many experiments carried out on the same or the same few biased sites.

Material and methods

All experiments testing the orientation of displaced migrant birds in funnels are summarised in the appendices 1-4. App.1 includes birds displaced by man and tested under a natural starry sky, App.2 includes birds displaced by man and tested under an overcast sky, App.3 includes 'displacements' under a planetary 'starry sky' and App.4 includes tests of the orientation following natural displacements by the wind. The significance of any directional shift was tested using Watson-Williams or Mardia-Watson-Wheeler two-sample test when comparing with the control direction or confidence interval (CI) test when comparing with the expected standard direction) (Batschelet 1981). Furthermore, the significance of the 'sample' orientation was tested using Rayleigh test (Batschelet 1981). The orientational responses to displacements were considered both with and without the inclusion of insignificant 'sample' orientations, thus in general 'samples' with less than 4 individuals would thus be excluded.

In App.1, 2 and 3 we have included all published displacements – also minor ones. The unit in the appendices could be anything from a single bird tested a few times to a large sample of birds tested many times (e.g. App.1 no 33 and no.18, respectively). In the figures and Tab.1 all units are equalised, corresponding to the use of grand mean vectors.

For each 'sample' we evaluated the orientational response to the displacement. In each case the response was assigned to the following categories: (1) unaltered/standard, (2) between standard and compensatory, (3) compensatory, (4) reversed standard and (5) 'other' orientations. The assignment is illustrated on Fig.1 that shows the orientational response of a bird trapped in A and displaced to B. The direction of the displacement in Fig.1 in relation to the standard (or observed) orientation in A is approximately optimal for showing compensatory orientation. If the birds are displaced in about right angles to the standard direction the angular

sector of compensatory orientation (3) decreases. If the birds are displaced ahead in the migratory standard direction it is not possible to distinguish between reverse (4) or compensatory (3) orientation, and a displacement backwards on the migratory route renders it impossible to distinguish between standard/unaltered (1) and compensatory (3) orientation.

On the figures orientations shifts in a compensatory direction are calculated as positive numbers and therefore depicted as clock-wise shifts.

The principal focus is on the orientation of naïve migrants. In most autumn experiments only juveniles have been used, but in a few cases a few adults have been involved. In such cases no difference in orientation was observed. In the long-distance displacements to Kenya and the Canary Islands (Rabøl 1981a, 1993) substantial numbers of adults were included but these were considered separately.

Results

The number of 'samples' falling into each category for each experimental set-up (displacement under a starry sky (starry), displacement under an overcast sky (overcast), 'displacement' under a planetarium sky ('starry') and displacement by the wind (wind)) is summarised in Tab.1. Tab.2 shows the same when samples showing insignificant orientation are omitted. Overall the distribution on categories is not significantly different for the different experimental set-ups. However, contrary to the starry, 'starry' and wind distributions, the overcast distribution contains very few 'samples' considered compensatory and if considering the overall categories unaltered/standard (1), compensation ((3)+3) and other (4+5) the overcast distribution differs significantly from starry ($P < 0.001$, χ^2).

The orientational responses for the experimental set-ups are shown on Figs.2-4.

For man-made displacements under a natural starry sky (Fig.2) the mean vector is $59^\circ - 0.488^{***}$ ($n=51$) and it deviates significantly from 0° ($P < 0.01$, CI test (29°)), i.e. the direction is significantly turned in the compensatory direction. Excluding insignificant sample orientations still results in a significantly clock-wise turned mean vector ($61^\circ - 0.481^{***}$ ($n=46$)). Using 'expected' instead of 'actual', in the 11 cases where both 'expected' and 'actual' orientation are given, results in a mean vector of $56^\circ - 0.510^{***}$ ($n = 51$) (or $57^\circ - 0.505^{***}$ ($n=46$) excluding insignificant samples), which is still being significantly turned clock-wise. If the orientation is shown in relation to the orientation expected in relation to navigation towards a 'goal area' somewhere ahead on the migratory route the sample mean vector does not deviate significantly from 0° .

The orientation under an overcast sky (Fig.3) is bimodal ($-44^\circ/136^\circ - 0.308$ ($n=19$, $P > 0.05$) or $-33^\circ/147^\circ - 0.415$ ($n=13$, $P > 0.05$)) and quite different from the orientation under a natural starry sky (Fig.2).

Discussion

For birds tested under a natural starry sky and under a planetarium sky a significant shift in orientation was found in the direction expected for a compensatory movement. An equal but not significant shift (the number of experiments smaller) was shown by wind drifted migrants. The degree of compensation in birds tested under an overcast sky was low and reversed/other orientations high.

The significant shift in orientation, found in displaced birds tested under a natural starry sky, indicate that migrants need at least to use reverse path integration for compensation (hypothesis c) or a navigational mechanism (hypothesis 2). This is further supported by the 'goal area' directed orientation of displaced migrants. The pattern shown by wind drifted migrants is equal but the number of experiments is smaller.

Though the way of treatment (and the use of different species) undoubtedly influences the degree of compensation there seems to be a tendency for more clearcut compensations in the

short-distance displacements compared with long-distance displacements (Figs.4-5). This could be indicative of problems using reverse path integration on this scale, a less than global navigation system or conflicting information from different cues in a multifactor orientational system

There seems to be no differences between birds tested under a natural starry- or a planetarium 'starry' sky – in both the degree of compensation is high and significant. This indicates that birds use some kind of navigational process for compensation (hypothesis 2), and reverse path integration cannot explain these results. Results from the most extensive 'displacement' experiment performed under a planetary sky is shown in Fig.6, which shows the sample mean directions from 14 positions to which Pied Flycatchers (trapped on Christiansø) were displaced in the planetarium experiments of Rabøl (1998). When compensatory directions are shown clock-wise, the mean vector of the orientation in relation to the previous orientation in the field on Christiansø, is $97^\circ - 0.542^*$ ($n=12$) and it deviates significantly from 0° ($P<0.01$, CI test (70°)), i.e. it is compensatory. The mean vector of the orientation in relation to the planetarium orientation on the positions of 'Christiansø' or 'Oslo/Stockholm', is $102^\circ - 0.711^{**}$ ($n=12$) and it deviates significantly from 0° ($P<0.01$, CI test (43°)).

Stars on the southern sky resembles the sun in 'moving' 15° clock-wise per hour, and birds using a time-compensated southern sky star compass are thus expected to shift their orientation accordingly when displaced east or west (but not north or south) or when their circadian clock has been reset (so-called clock-shift experiments). This shift in orientation will be in the direction expected of compensatory movements (hence called 'pseudo-navigation' by Rabøl 1997, 1998). However, the observed shifts in orientation in planetary E/W 'displacements' (Rabøl 1998) are larger (though not significantly so) than expected from this, and it cannot explain the observed shifts in north and south displacements. Perhaps surprisingly, the course was unchanged southerly following the 'displacement' in the only real clock-shift experiments performed on long-distance migrants (Rabøl 1970), i.e. there was no sign of compensation based in true or pseudo-navigation. In these experiments Rabøl (1970) simulated a 'displacement' 8 hours clockwise (from Denmark to about Chabarowsk in easternmost Russia) in an autumn sample of Redstarts and Garden Warblers. However, the experimental treatment in clock-shift experiments might cause the birds to recalibrate their compasses using rotational or magnetic north.

The orientation of migrants trapped in coastal areas often deviates significantly from the supposed (standard) direction resulting from e.g. wind drift compensation or temporary reverse migration (e.g. Sandberg et al. 1988, Åkesson et al. 1996, Rabøl 1995, Åkesson 1999) and most of the experiments (Apps.1-2 and 4) are carried out with migrants trapped at coastal sites. This kind of orientational response will not cause bias in the results. However, excess of SE-orientation under influence of a local anomaly in the Blåvand/Skallingen area is claimed by Mouritsen (1999). This pattern is normally prominent in autumn and in birds trapped locally – not in birds trapped in another place and displaced to the area. Almost all arrivals of migrants to the Blåvand-area take place in easterly winds which – obviously – more or less displaced the birds some of which are of Norwegian origin with a standard direction E of S. This has been known for many years (e.g. Rabøl 1969, 1995), and there is no reason to consider the SE-orientation influenced by some local anomaly.

The orientation experiments following a displacement – real or simulated, by man or wind – suggests that migrant birds are able to compensate a displacement, and possibly that some sort of navigational mechanism is involved.

At least some simple form of sign navigation system (Wallraff 1974) must be involved in the orientation following the planetarium "displacements" because in these experiments no real

transports are carried out and therefore compass based reverse path integration cannot be the explanation. Furthermore, the lack of compensation under an overcast sky is indicative of a central role of a stellar-based system.

There are other indications that the simplest vector-orientation system (hypothesis a) is not sufficient. Very often also the orientations in funnels of birds not displaced are deviating significantly from the standard direction, e.g. Pied Flycatcher SE autumn (Beck & Wiltschko 1982, Bingman 1984), Goldcrest SE autumn (Weindler 1994), and the general NW/SE-axis of orientation (e.g. Bingman 1981, Beason 1987, 1989, Able & Cherry 1986) in several North American birds with a standard axis NE/SW (as shown by ringing recoveries). These deviations are probably not just stochastic noise or deviations caused by the conditions or experimental set-up. Probably, they arise in a system which is not just the simplest vector-orientation. Furthermore, modelling studies indicate the use of more mechanisms (Thorup et al. 2000, Thorup & Rabøl 2001; However, see Mouritsen 1998, 2000). Clearly, time has come for a fruitful hybridisation of the fields of migratory orientation and optimal migration.

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Tab.1

Number of experiments in each category. The number in parenthesis includes cases when the category is shared equally with another category.

Category	Starry	Overcast	'Starry'	Wind
Standard/unaltered 1	9(14)	5	3(6)	2
Unaltered/compensatory 2	5(9)	0	3	1
Compensatory but insignificant (3)	11(13)	0	2(5)	3(4)
Significantly compensatory 3	10(12)	2	4(5)	3
Reversed standard 4	2(5)	5	0(2)	0
Other 5	4	7	1	0
Total	41(57)	19	13(22)	9

Tab.2

As Tab.1 except that insignificant sample orientations are omitted

Category	Starry	Overcast	'Starry'	Wind
Standard/unaltered 1	7(11)	3	2(4)	2
Unaltered/compensatory 2	4(8)	0	1	1
Compensatory but insignificant (3)	10(12)	0	1(4)	3(4)
Significantly compensatory 3	10(12)	2	4(4)	3
Reversed standard 4	1(3)	5	0(1)	0
Other 5	4	3	1	0
Total	41(57)	19	13(22)	9

Appendix 1

Man-made displacements tested under a natural starry sky.

A and S designate autumn and spring, respectively. In autumn all birds are juv. if nothing else denoted. The two sites – e.g. Blåvand and Ottenby (no.1) – designate the site of trapping and the site to where the birds were displaced, respectively. If the displacement distance is more than 1,000 km the distance is indicated. The number and direction following a site – e.g. 8 SSE* – gives the number of birds tested (and displaying oriented activity), the mean direction of the bird/group/sample, and * and ** signal $P < 0.05$ and $P < 0.01$, respectively (Rayleigh test). Sometimes the number is given as – e.g. – 5(45), which means that 5 birds produced a total of 45 directions/directional bird-nights. If no controls at the site of trapping the presumed orientation (standard direction) is denoted (as e.g. ‘SSW’). When the presumed and actual orientation differ both are given. NC, C, and CC means no controls, controls (other individuals than displaced), and controls (same individuals), respectively. Considering the final digit-code 1 designates unaltered/standard orientation following the displacement, 2 unaltered/compensatory, i.e. it is not possible to make a distinction, (3) is (compensatory), i.e. it looks like compensation but it is not statistically significant, 3 is compensatory (based on Watson-Williams or Mardia-Watson-Wheeler two sample tests or confidence interval test), 4 is reverse, i.e. opposite 1 and 5 is ‘others’ (cf. Fig.1). ‘NS’ marks insignificant sample orientations.

1. Rabøl (1969), Garden Warbler, A, Blåvand 8 (last two nights, individual concentrations (r) > 0.20) SSE* – Ottenby 5 (first night, $r > 0.20$) SSW, C, 3. Blåvand 13 (last two nights, $r > 0$) SSE* - Ottenby 7 (first night, $r > 0$) SSW, C, 2/(3). Overall (3).
2. Rabøl (1969), Lesser Whitethroat, A, Ottenby 22 S – Blåvand 7 SSE, C, 2
3. Rabøl (1969), Redbacked Shrike, A, Ottenby 15 S – Blåvand 5 SE, C, 2
4. Rabøl (1970), Willow Warbler I, A 1969a, Hanstholm 12 (‘SSE’) ENE** – Dueodde 12 NNE(SW), C, ‘5’, (3)
5. Rabøl (1970), Willow Warbler II, A 1969b, Hanstholm 14 (‘SSE’) ESE** – Dueodde 4 SSE, C, ‘1’, 5
6. Rabøl (1970), Garden Warbler, A, Hanstholm (‘SSE’) 12 E* – Dueodde 7 SW*, C, ‘3’, 5
7. Rabøl (1970), Redstart/Garden Warbler I, A 1969a, Skagen (‘S’) 15 SE – Langeland 7 NNE, C, ‘4’, (3)
8. Rabøl (1970), Redstart/Garden Warbler II, A 1969b, Skagen (‘S’) 17 SE* – Langeland 8 ENE, C, ‘5’, 3
9. Rabøl (1970), Garden Warbler/Redstart, A, Skagen (‘S’) 9 SE* – Tisvilde 13 SSE*, CC, ‘1’, 1
10. Rabøl (1972), Garden Warbler/Redstart, A, Akerøya (‘S’) – Blåvand a) 7 NNE*, shifting b) 19 ENE**, finally c) 7 SE, NC, a) ‘4/3’, b) ‘3’, c) ‘(3)’
11. Rabøl (1972), Redstart/Whinchat, A, Akerøya (‘S’) – Chr.ø 18 W**, NC, ‘3’
12. Rabøl (1972), Redstart, S, Chr.ø 15 (‘N’) NW** – Tisvilde first a) 12 SE CC/C, then b) 6N CC/C, a) ‘(3)/5’, 4), b) ‘1’, (3)
13. Rabøl (1975), Redstart, S, Chr.ø 16 NNW – Tisvilde 11 ENE**, C/CC, 3
14. Rabøl (1975), Robin, S, Chr.ø (‘N’) 21 NW** – Blåvand 8 E, C, ‘(3)’, (3)
15. Rabøl (1975), Garden Warbler/Redstart, S, Chr.ø 27 N* – Blåvand 9 NNE**, C, 3
16. Rabøl (1975), Robin, A, Chr.ø (‘SW’) 11 W* – Blåvand 6 SE, C, ‘(3)’, (3)
17. Rabøl (1981),
 - a) Robin juv., A, Chr.ø (‘SW’) – Gomera (4,000km) 6(38) ESE**, NC, ‘3>1/2’
 - b) Robin ad., A, Chr.ø (‘SW’) – Gomera (4,000km) 5(31) S**, NC, ‘2/1’
18. Rabøl (1993),
 - a) Pied Flycatcher juv., A, Chr.ø (‘SW-SSE’) – Kenya (7,000km) 10(106) WSW**, NC, ‘1>3’
 - b) Pied Flycatcher ad., A, Chr.ø (‘SW-SSE’) – Kenya (7,000km) 10(96) WSW**, NC, ‘1/3’
19. Rabøl (1993), Lesser Whitethroat, A, Chr.ø (‘SE-S’) – Kenya (7,000km) 7(39) NNW*, NC, ‘3>4’
20. Rabøl (1993), Garden Warbler ad./juv., A, Chr.ø (‘S’) – Kenya (7,000km) 17(85) SW**, NC, ‘1>(3)’
21. Rabøl (1994), Pied Flycatcher, A 1986, Chr.ø (‘SW’) – Skallingen 8 ESE, NC, ‘(3)’
22. Rabøl (unpubl.), Garden Warbler, S, 1989, Chr.ø (‘NNW’) – Sæby 11N**, NC, ‘1/2’
23. Rabøl (1994), Pied Flycatcher, A 1989a, Chr.ø (‘SW’) – Skallingen 14 S, NC, ‘2’
24. Rabøl (1994), Pied Flycatcher, A 1989b, Chr.ø (‘SW’) – Skallingen 12 S**, NC, ‘2/(3)’
25. Rabøl (1994), Mou 22, Pied Flycatcher, A 1990, Chr.ø 10 SW**/13 SSW* – Skallingen 14 S*, CC, 3
26. Rabøl (1995), Mou 23, Redstart/Garden Warbler, A, Blåvand (‘SSE’) 10 ESE**/17 E** – Chr.ø 10 SW**/15SW*, CC, ‘3’, 3
27. Mouritsen & Larsen (1998), Pied Flycatcher, A, Chr.ø 14 SW/19(34)SSW** – Czech Rep. 16(31) S**, CC/C, 1
28. Mouritsen & Larsen (1998), Pied Flycatcher, A, Chr.ø 14 SW/19(34)SSW** – Klelund 16(29)S**, CC/C, 1
29. Rabøl (unpubl.), Robin, A, Akerøya (‘SSW’) – Chr.ø first a) 16 ESE*, later b) 16 WSW, NC, a) ‘5’, b) ‘2’
30. Rabøl (unpubl.), Garden Warbler/Redstart, A, a) Blåvand 11 SSE – Stensoffa 14 W*, CC, then later (same birds) b) Stensoffa (‘SW’) 14 W* – Blåvand 14 SE**, CC, a) (3), b) ‘3’, 3

31. Dolnik & Shumakov (1967), Barred Warblers, Scarlet Grossbeaks, A, Rositten SE – a) Dushanbey (4,000km) S, and later b) Chabarowsk (8,000km) NE/(SW), C, a) (3)/2, b) 5>3
32. Potapov (1966), Garden Warblers, Barred Warblers, Scarlet Grossbeaks, A, Rositten SE? – a) Dushanbey (4,000km) SE?, and later b) Chabarowsk (8,000km) SE?, C, a) 1, b) 1
33. Hamilton (1962a), Bobolink, A, North Dakota ('SE') – San Francisco (2,000km) (1 NE – E - SSE, NC, '(3)'; NS
34. Hamilton (1962b), Bobolink, A, North Dakota ('SE') – San Francisco (2,000km) ad. 2(14) SE**, NC, '1'; NS
35. Hamilton (1962b), Bobolink, A, North Dakota ('SE') – San Francisco (2,000km) juv.2 (3) NW/(SE), NC, '4>1'; NS
36. Hamilton (1962b), Bobolink, S, Florida ('NW-NNE') – San Francisco (4,000km) ad. 4(?) NNE/(SSW), NC, '1>4'; NS
37. Hamilton (1962b), Bobolink, A, New York ('SSW') – San Francisco (4,000km) 1 ad./2 juv. N/S, NC, '1/4'; NS
38. Sauer & Sauer (1959), Sylvia-warblers, A, Germany ('SE/SSW') – Namibia (9,000km) 5(21) S**, NC, '1'
39. Sauer (1963), American Golden Plover, S, Alaska (displaced previous autumn) ('N') – San Francisco (4,000km) 1 NW, NC, '2'; NS
40. Åkesson et al. (1995), Wheatear, A, Tiksi (Siberia) ('SW/W') – Site 6 (Kola) (3,500km) 20 S/(N)*, NC, '(3)'
41. Emlen (1967a), Indigo Bunting, S, Alabama ('N') – Michigan (3,000km) 7(>30?) NNE/SSW*, NC, '1/4/3'

Appendix 2

Man-made displacements tested under a natural overcast sky. For explanations see App.1.

1. Rabøl (1975), Redstart, S, Chr.ø 16 NNW – displaced to a) Hansthalm 13 SSE**, CC/C (same as starry 13), and then to b) Tisvilde 3 N CC. a) 4, b) 1
2. Rabøl (1975), Redstart, Garden Warbler, S, Chr.ø 27 N** – displaced to Blåvand, a) first night, 9 NNW*, C, and b) second night, 20 S*, CC, a) 1, b) 4
3. Rabøl (1975), Robin, A, Chr.ø 11 ('SW')W* – Blåvand 13 ESE**, C (same birds as Tab.1 16.), '3', 4>3
4. Mouritsen & Larsen (1998), Pied Flycatcher, A, Chr.ø 14SW/19(34) SSW** – Klelund 12 SW, CC/C (same birds as Tab.1 28.), 1
5. Rabøl (1994), Pied Flycatcher, A, Chr.ø 10 SW**/13SSW* – Skallingen 13 NE*, NC (same as Tab.1 25.), 4
6. Rabøl (1975), Robin, S, Chr.ø ('N') 21 NW** – Blåvand 17 SW, C (sub-sample to Tab.1 14.), '5', 5
7. Rabøl (1969), Garden Warbler, A, Blåvand 8 SSE* – Ottenby 8 S/(N), C, (same birds as starry 1) 1
8. Åkesson et al. (1995), Wheatear, A, Tiksi (Siberia) ('SW/W') – site 4 (Petchora) (3,000km) 20 NW*, NC (same birds as Tab.1 40.), 5
9. Rabøl (1993), Pied Flycatcher, Garden Warbler, A, Chr.ø ('SW/S') Kenya (7,000km), previous starry orientation 26 SSW/(NNE)** - 13SE/NW* (same birds as Tab. 1 18 and 20) CC, right angle
10. Rabøl (unpubl.), Robin, A, Akerøya ('SSW') – Chr.ø 8 NNW, NC (same as Tab.1 29.), '4>(3)'
11. Sauer & Sauer (1959), Whitethroat, A, Germany ('SSW') – Namibia (9,000km) 1(2) S, NC, '1'; NS
12. Sauer (1963), American Golden Plover, A, Alaska S – San Francisco (4,000km) 2 E, NC, right angle/5; NS
13. Sauer (1963), American Golden Plover, S, Alaska N – San Francisco (4,000km) 1 W, NC, right angle/5; NS
14. Hamilton (1962b), Bobolink, A, North Dakota ('SE') – San Francisco (2,000km) ad. 1 SSW/NNE, NC, 5; NS
15. Hamilton (1962b), Bobolink, S, Florida ('NW-NNE') – San Francisco (4,000km) 3 WNW, NC, 5>1; NS

Appendix 3

Planetary 'displacements'. For explanations see App.1.

1. Emlen (1967b), Indigo Bunting, S, controls 8 N** - +/- 45°/90° E/W 8(18 N**, 4 ENE/WNW*), CC, 1>(3)
2. Emlen (1975), Indigo Bunting, S, controls 5 N* - +/- 45°/90° E/W 5(14) N**, CC, 1
3. Emlen (1967b), Indigo Bunting, A, control 1 SSE - +90° E 1 SSW, CC, 2; NS
4. Rabøl (1992), Pied Flycatcher, Redstart, A, controls 9 SSW – longitude-shifts (1,500-9,000km) 12 (30) comp.**; CC, 3
5. Rabøl (1997, 1998), Pied Flycatcher, Redstart, A, controls 11(22) SSE - longitude/latitude-shifts (1,000-4,500km) 12(41) comp.*; CC, 3
6. Rabøl (1997, 1998), Pied Flycatcher, A, controls 9 SSE - longitude/latitude-shifts (1,300-5,400km) 11(32) comp.**; CC, 3
7. Rabøl (1997), Pied Flycatcher, Redstart, S, controls 8 ('Christiansø') NNE** - 'Lofoten' (70°N, 10E°) 10 (17) ESE/(N), CC, (3)>1
8. Rabøl (1997), Pied Flycatcher, Redstart (same birds as 7.), S, controls 8 NNE** - 'Ural' (70°N, 60°E and 55°N, 60°E) 11(19) ENE**, CC, 5>1
9. Rabøl (1981), Redstart, Garden Warbler 1977, S, 63°N(10 E/4 WSW), 49°N (4 ENE/5 WNW), more northerly orientation on the southerly 'latitude' of 49°N, C, 2
10. Rabøl (1981), Redstart, Garden Warbler 1978, S, latitudes 49°N (12 NNE*), 56°N (controls, 11 NNE-NE*) – 'displaced' a) 49°N (12 NNE*) and b) 63°N (11 ESE*), C, a) 1/2, b) 3
11. Rabøl (1981), Redstart, Garden Warbler 1978, S, a) controls 4 E – 'displaced' 20°E 6 E, b) controls 4 W – 'displaced' 20°W 3 E, CC, a) 1, b) (3)
12. Rabøl (1990), Pied Flycatcher, A, controls 56°N 4(20)S** - 'displaced' 30°N 4(42) N/S**, CC, 1, (3/4)
13. Sauer (1957), Lesser Whitethroat ('Müllerchen'), A, controls 50°N 1(7) SSE** – latitude-shifts 45°N-10°N 1(7) SSE**, CC, 1; NS
14. Sauer (1957), Lesser Whitethroat ('Müllerchen'), A, control 1 SSE – a) longitude-shifts towards E 1(5) W*, b) longitude-shifts towards W 1(3) SE*, CC, a) (3), b) 1; NS
15. Sauer&Sauer (1960), Blackcap (632), A, control 1(2) SSW – a) longitude-shifts towards E 1(6) WSW, b) longitude-shifts towards W 1(6) SE, CC, a)(3), b) (3); NS
16. Sauer&Sauer (1960), Garden Warbler (637), A, control 45°-50°N 1(2) SSW – 30°N 1(6) NNE*, CC, 3/4; NS
17. Sauer (1963), American Golden Plover, S, Alaska ('N') – exp.s in San Francisco but apparently exposed under the planetary sky of 20°N, 89°W 1 NW/(SE), NC, 2; NS

Appendix 4

Orientation following displacement by the wind. For explanations see App.1.

1. Rabøl (1985), A, Faeroes, overcast/cloudy, E-S-winds
 - a) Blackcap ('SSW') 8(9) WSW**, '1,5'
 - b) Garden Warbler ('S') 4(7) SSW*, '1'
 - c) Garden Warbler ('S') 1(4) ESE, '(3)'; NS
 - d) Barred Warbler ('SSE') 1 E/(NW) '(3)'; NS
 - e) other warblers ('S') 8 S/(NW), '1>4'
2. Evans (1968), chats and warblers, A, Northumberland, starry, E-winds ('SSE>SSW') 12 SSE/(NNW)**,
'(3)'
3. Moore (1990), American warblers, S, US golf coast 'controls' (S-winds) 28 N** - E-wind arrivals 12 ENE*,
morning (twilight), (3)
4. Rabøl (1995), Garden Warbler/Redstart, A, Blåvand, starry, ENE-wind 17 ('SSE') E**, '3'
5. Rabøl (1975), Garden Warbler/Redstart, S, Chr.ø, starry/overcast ('NNE'), E-wind arrivals 44 NE* contra W-
wind arrivals 50 N**, '2/(3)'
6. Rabøl (1994), Pied Flycatcher, A 1976, Chr.ø, starry ('SW'), NE-wind arrivals 20 ESE**, '3'
7. Rabøl (1994), Pied Flycatcher, A 1991, Chr.ø, starry ('SW'), NNW-wind arrivals 8 WNW, '(3)'
8. Rabøl & Mouritsen (unpubl.), Pied Flycatcher, A 26 Aug., Chr.ø, starry ('SW'), SE-wind arrivals 43 S/(N)*,
'3'
9. Mouritsen & Larsen (1998), Pied Flycatcher, A 27 Aug. Chr.ø, starry ('SW'), SE-wind first 39 SW* shifting
to 16 SSW** and finally 15 S**, '1' shifting to '(3)'

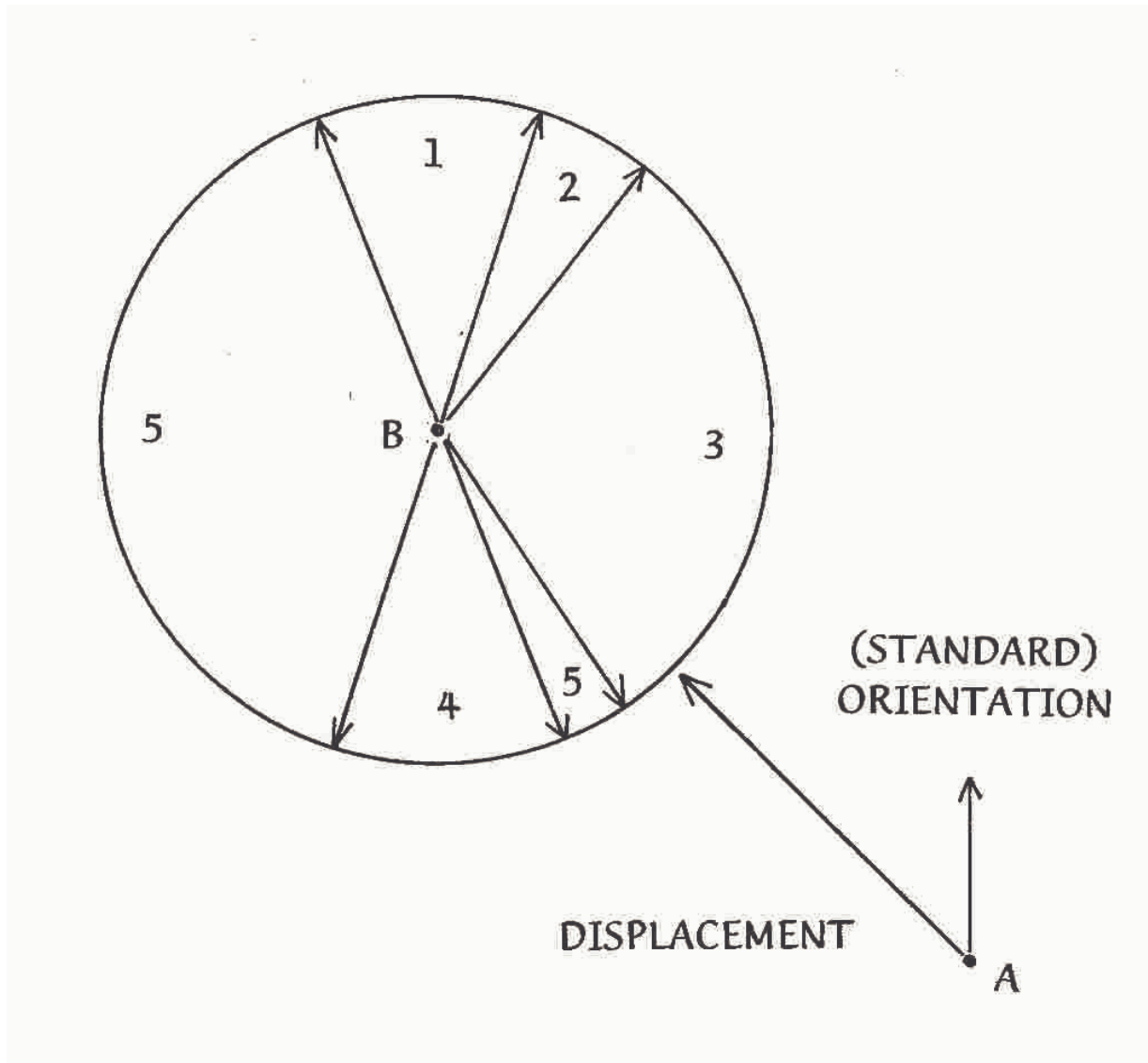


Fig.1. The meaning of the categories. The birds are trapped in A and displaced to B. The orientation in A (or the presumed orientation) is shown by the arrow '(Standard) Orient.'. In B the orientation could fall within the whole circle. 1 is designated 'unaltered/standard', 2 'unaltered/compensatory' (i.e. the orientation is between 1 and 3), (3) is 'compensatory' though statistically insignificant, 3 'compensatory' (sign. at the 0.05 level as revealed by Watson-Williams, Mardia-Watson-Wheeler or confidence interval tests), 4 is 'reverse' (i.e. opposite 1.), and 5 'others'.

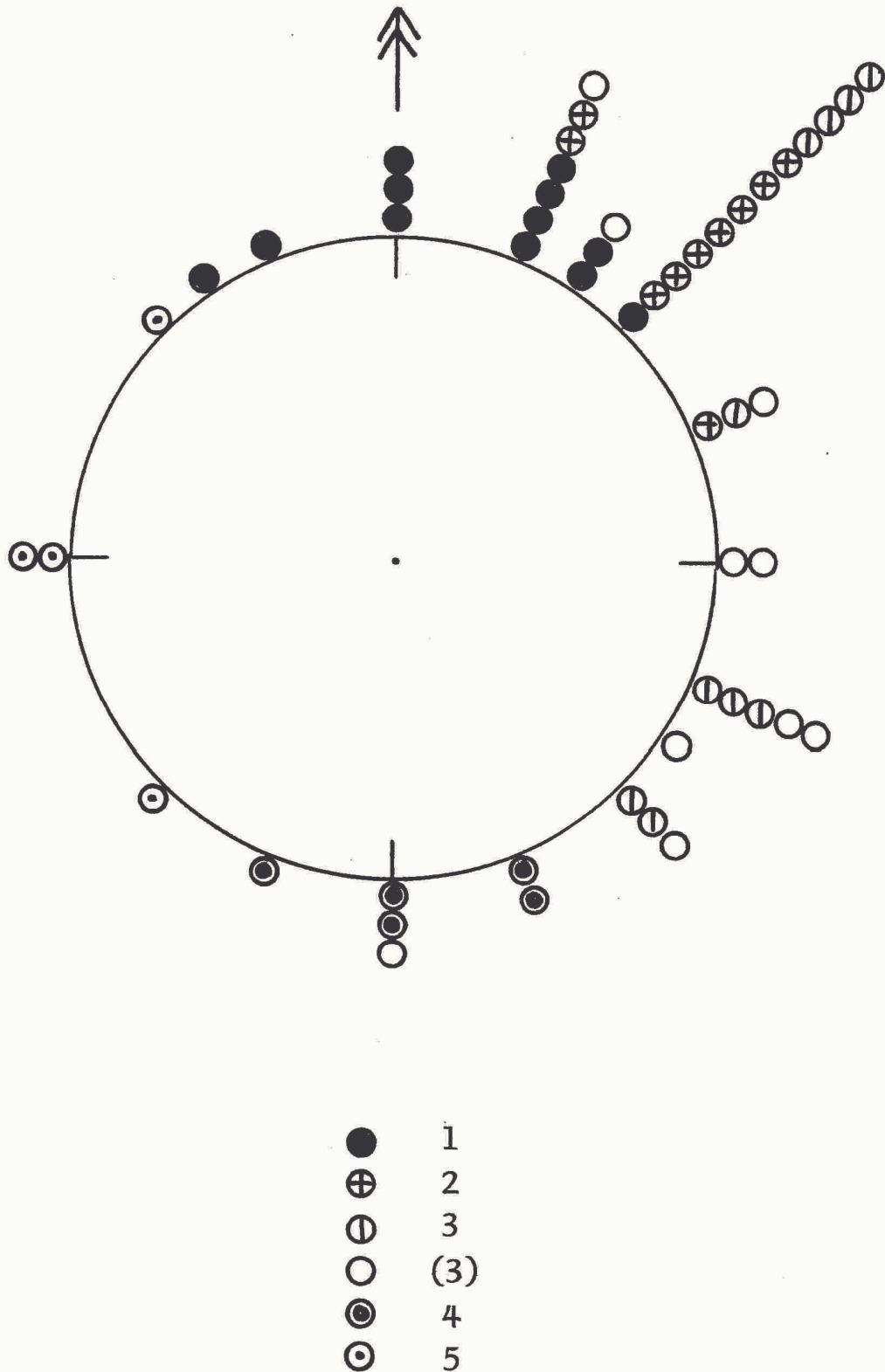


Fig.2. The outdoor orientation on starry nights following a real displacement (App.1). On the figures orientations shifts in a compensatory direction are calculated as positive numbers and therefore depicted as clock-wise shifts. For designation of numbers cf. Fig.1. In the 11 cases where the orientation is found in relation to both 'actual' and 'expected' orientation at the site of trapping only 'actual' is denoted. The mean vector is $59^\circ - 0.488^{***}$ ($n=51$).

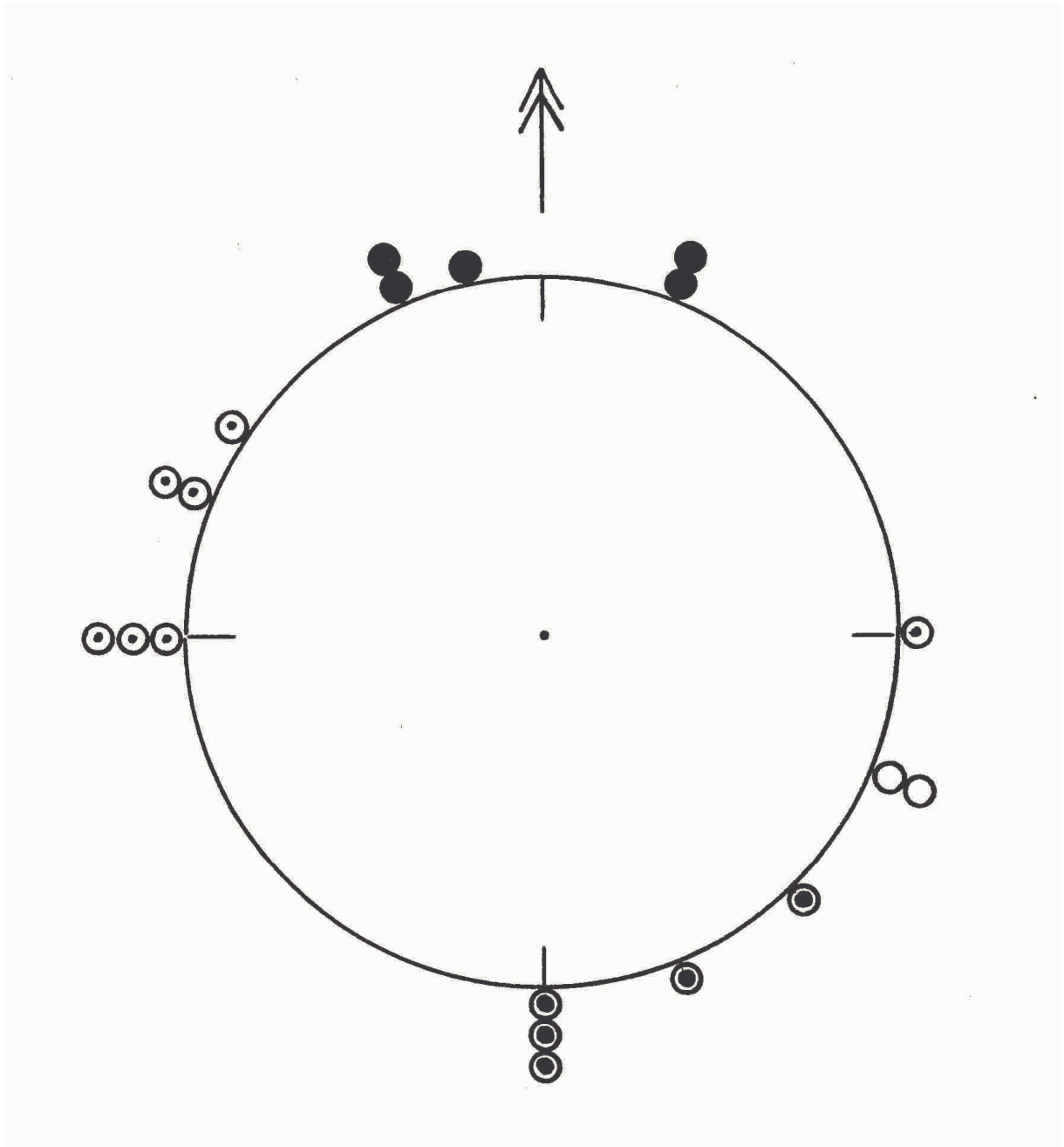


Fig.3. The outdoor orientation on overcast nights following a real displacement (App.2). For designation of numbers cf. Fig.1. The sample mean vector is $-73^\circ - 0.107$ ($n=19$). Doubling the angles leads to an axis $-44^\circ/136^\circ - 0.308$ ($n=19$).

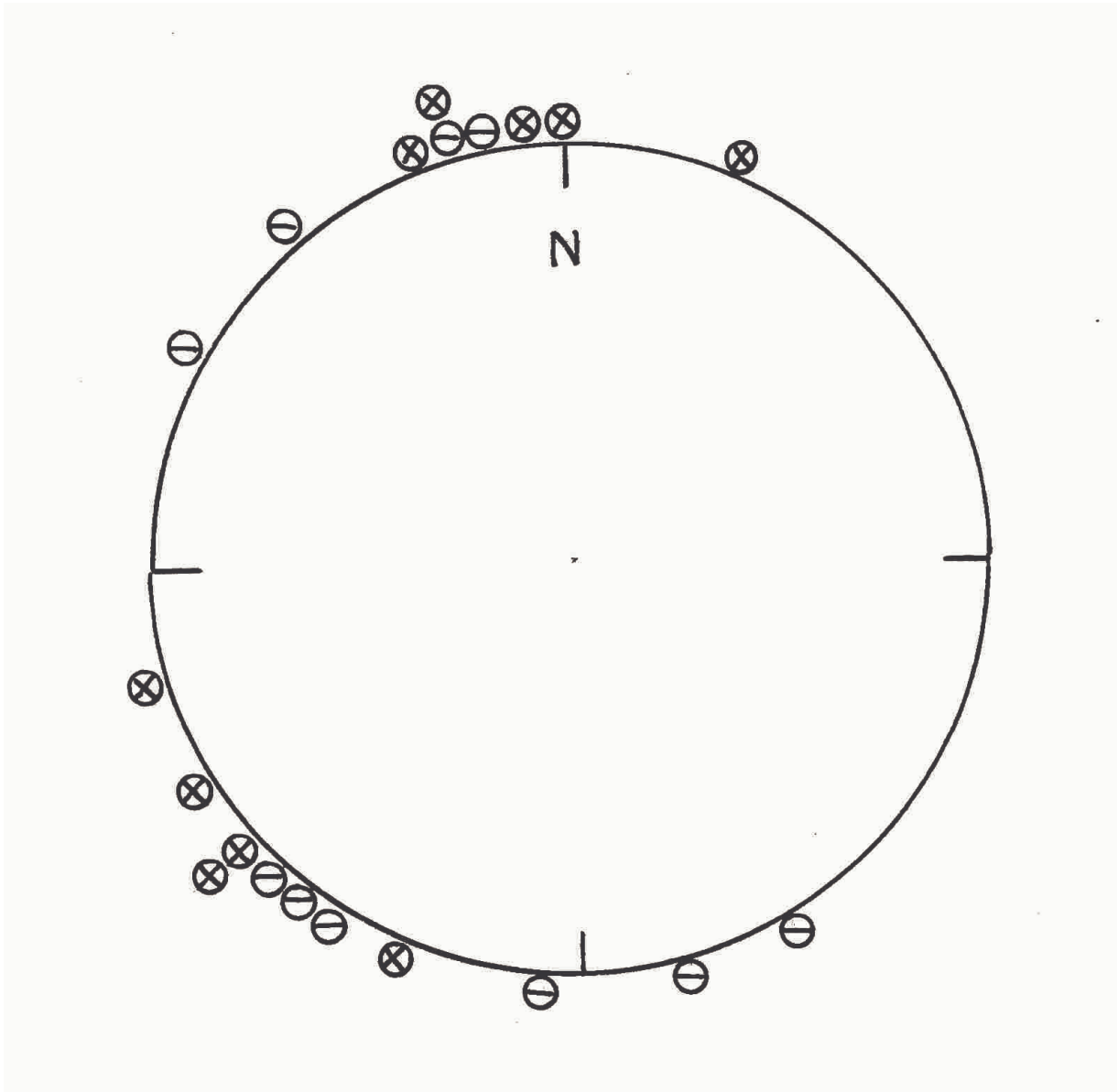


Fig.4. Pied Flycatchers *Ficedula hypoleuca*. The first night orientation after displacement from Denmark to Kenya (Rabøl 1993). Juv. is designated by a crossed dot, and ad. by a dot with a bar. Bimodal peaks are found at 345° (n=9) and 213° (n=11).

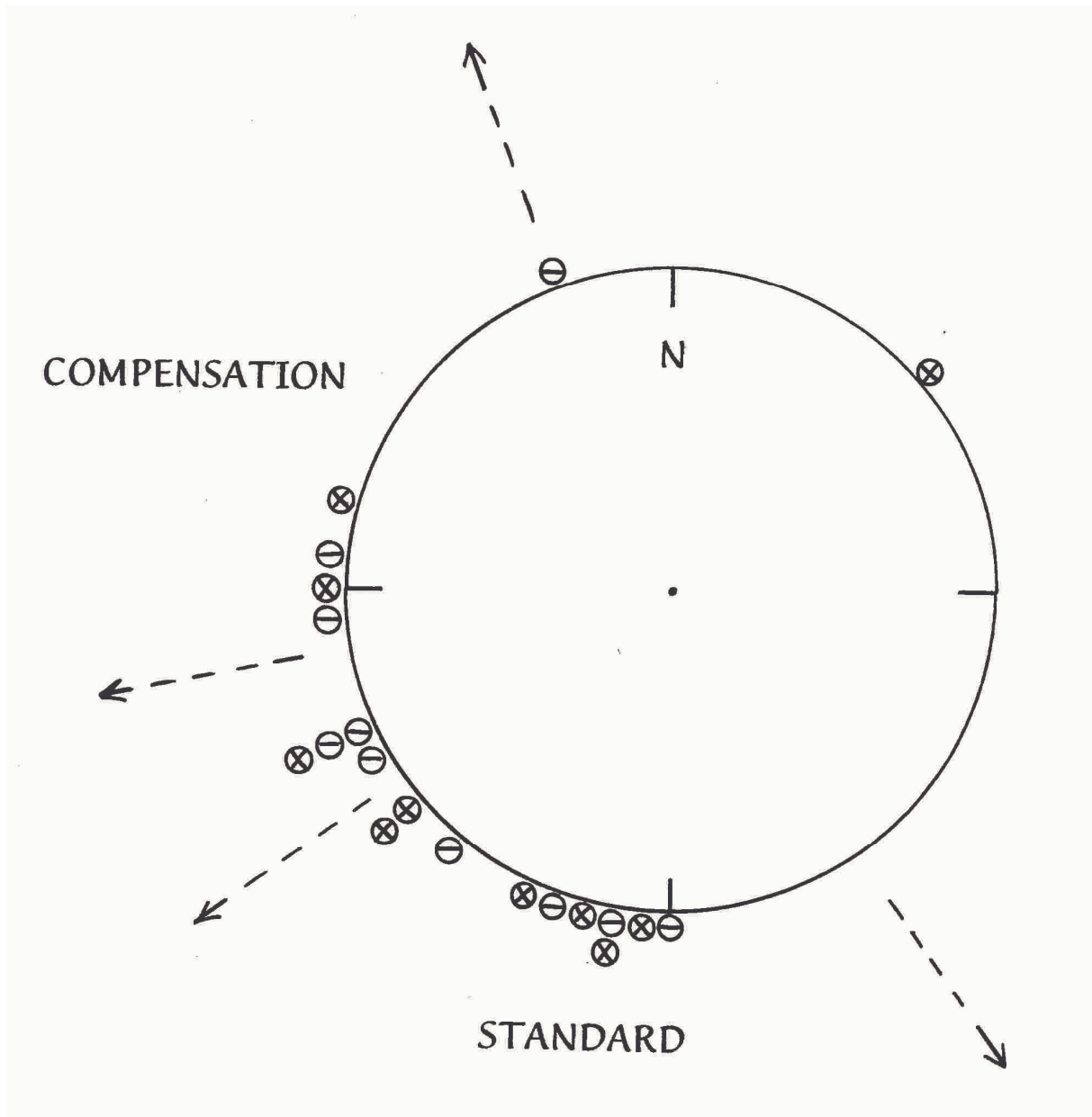


Fig.5. Pied Flycatchers *Ficedula hypoleuca*. Estimations of overall individual mean directions (Sep./Dec.) of 10 juveniles and 10 adults displaced from Denmark to Kenya (Rabøl 1993). Five birds show overall 'compensatory' orientation (towards the migratory route through Western Europe/Africa or the wintering area in Western/Central Africa). Ten birds show 'unaltered/standard orientation' (the migratory route shifts from about SW to SSE in course of the autumn). Four birds are in between, and a single bird falls outside the dichotomy.

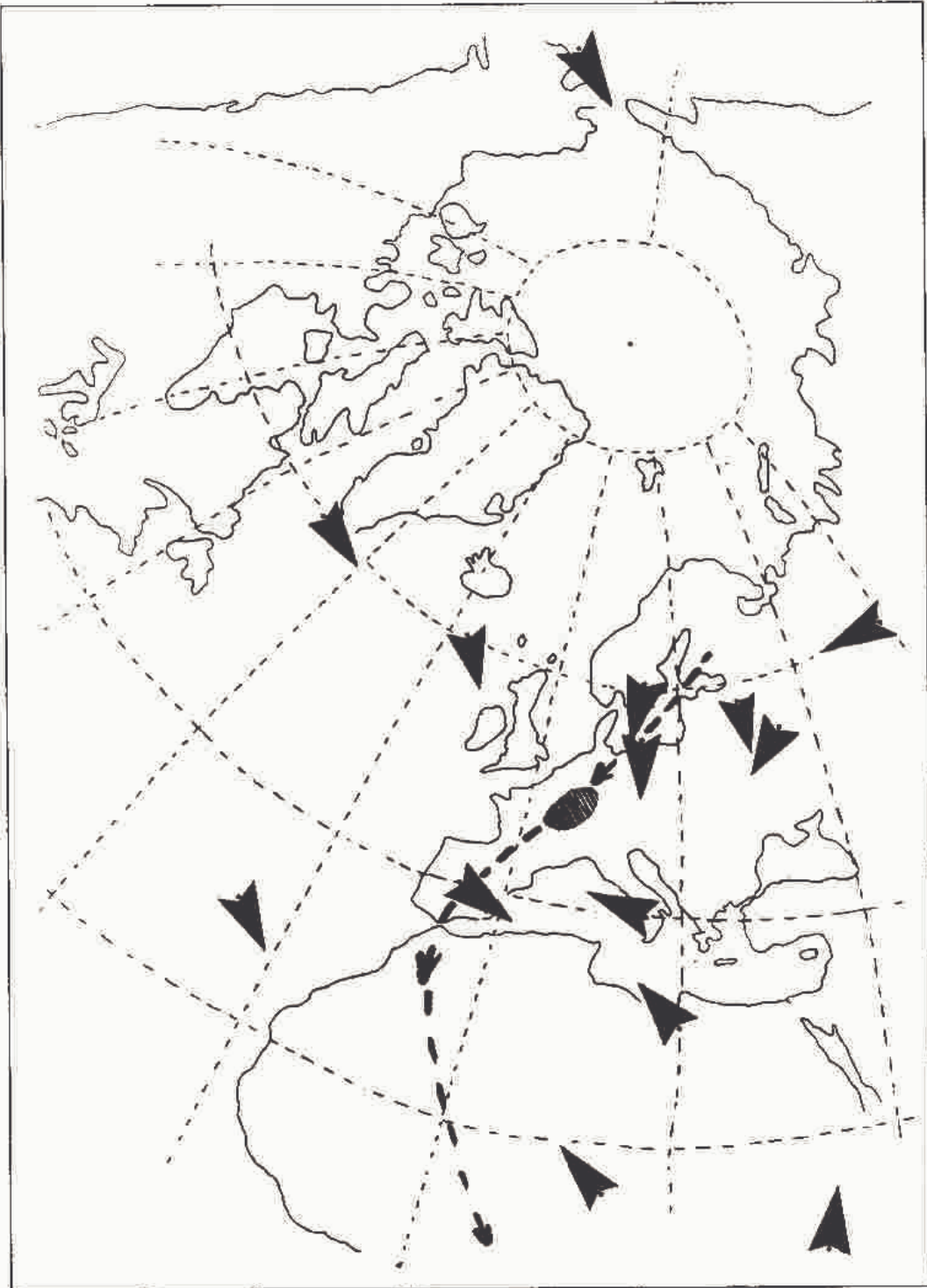


Fig.6. The sample mean directions from 14 positions to which Pied Flycatchers *Ficedula hypoleuca* were ‘displaced’ (three ‘Christiansø’ experiments are combined) under a planetary sky after being caught on Christiansø. Also shown are the autumnal migratory route (dotted line) and the presumed goal area (hatched in north-east France). From Rabøl (1998).