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Anschrift des Verfassers: R. Schlenker, Vogelwarte Radolfzell, D-7760 Schloss Moeggigen

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Max-Planck-Institut für Verhaltensphysiologie, Seewiesen

## Selected Aspects of Migratory Orientation in Birds

By Hans G. Wallraff

### 1. Introduction

A migrating bird must know the direction it has to fly, and it needs some mechanisms enabling it to determine and to maintain this direction. Thus, one may ask the following questions: Which intended direction<sup>1)</sup> is given? How did it originate? With respect to which environmental cues is it given? And finally, how is the bird able to select it?

Under the key-word “compass orientation“ we will shortly deal with the last question first. Thereafter, some problems concerning intended directions and the relationship between different compass mechanisms will be discussed, and finally we will stress the orientational aspects of the more complicated routes followed by several species. In this context, then, we will deal in more detail with classic as well as more recent studies on migratory orientation of the White Stork (*C. ciconia*) in Europe.

The aim of this essay is a discussion of not yet clarified questions rather than a review of established results.

### 2. Compass Orientation

The term “compass orientation“ may be used if an animal maintains, over a longer distance, a straight-lined course which is set as an angle to some environmental parameter. The course must not be related to a goal to which the animal is in sensory contact, and it has to be independent of the manifold structures of the immediate environment, such as landscape features, etc.

It follows that the animal has to use reference cues to which it does not change its angle while it is moving straight ahead over a greater distance. Thus, the cues must be far away, i. e. some orders of magnitude farther than the distances covered by the animal, or there must be a wide-range field with parallel structure. The latter often follows from the first: The rays of the far distant sun are parallel over a wide range, and the same is true of the field lines to the far distant magnetic pole.

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<sup>1)</sup> As “intended direction“ (*Sollrichtung*) I designate a hypothetic direction that an animal tends to select in idealized surroundings. Its realization in actual bird migration corresponds roughly to what is called standard direction or primary direction (GEYR VON SCHWEPENBURG 1949).

Herewith, the parameters being *a priori* best suited for compass orientation have already been mentioned: (a) astronomical cues and (b) the magnetic field of the earth. These two sorts of parameters have mutually different advantages and disadvantages:

(a) It is an advantage of celestial cues that they can easily be localized by use of conventional sensory equipment. But there are several disadvantages, too: Relevant information can only be deduced if considerable knowledge is available concerning time of day and year, celestial movements, distribution of stellar configurations, etc. No particular compass direction stands directly out from the others. Furthermore, celestial cues are not always available as they are often obscured by clouds.

(b) In case of the magnetic field, perception is more likely to be the problematic part. Neither the physics nor the physiology of magnetic perception in organisms is understood as yet. However, once an animal is able to perceive the alignment of the geomagnetic field, no further problems need be raised, for it has already all that is required. It has a complete compass with its scale adjusted to the north-south axis, being permanently available and well-suited for global use without additional knowledge.

There is sufficient evidence available to state that birds are able to choose and to maintain a compass direction by using either the sun, the stars, or the geomagnetic field as reference cues. But neither the experiments by which the existence of these capabilities was proven nor the specific problems being solved or unsolved within each compass system shall be reported here (see, e. g., EMLÉN 1975, SCHMIDT-KOENIG 1975, WALLRAFF 1972b, WILTSCHKO & WILTSCHKO 1976b). However, we will come back to the compass mechanisms on p. 66.

### 3. On the Origin of Intended Directions and on their Reference Cues

A bird may be able to distinguish between compass directions — but how does it know which of these directions to choose?

PERDECK (1958) has most clearly shown that juvenile and adult Starlings (*Sturnus vulgaris*) behave differently: When displaced perpendicular to their autumnal migratory route by several hundred kilometers, the juveniles continued flying the normal compass course thus reaching winter areas dislocated by the respective amount. But the adults changed their direction toward the normal wintering grounds, and some of them were actually found there.

From this experiment as well as from several others (e. g., SCHÜZ 1951, BELLROSE 1958, EMLÉN 1969, WILTSCHKO & GWINNER 1974) one may conclude that an intended direction can have been evolved phylogenetically, i. e. that it can be innate<sup>2)</sup> in an individual. But obviously, the birds are also capable of getting some idea of their respective position by individual experience. Once they have had such experience, they are capable to determine, even in an unknown environment, a new direction to be intended in relation to a place where they had been in earlier times.

The way in which this relation might be achieved and the physical parameters involved could be discussed in a separate chapter under the heading "navigation". But this chapter has to be omitted here. (For detailed information see, e. g., KEETON 1974, WALLRAFF 1974, SCHMIDT-KOENIG 1975, PAPI 1976.) The problem of navigation is not at all solved, but it should be stressed that the capability of finding an experienced goal from an unexperienced area is well established.

Every direction being in some way related to the environment has to be given as an "angle to something". When training an animal, the experimenter can determine the reference cue, and it has been shown that both the sun and the starry sky are suited for this purpose (e. g., KRAMER 1952, 1953, WALLRAFF & KLEBER 1967, WALLRAFF 1972a). In the case of navigation (goal orientation, homing) the intended direction seems primarily to be determined as an angle to the sun's azimuth (e. g., KRAMER 1961, KEETON 1974, WALLRAFF 1974, SCHMIDT-KOENIG 1975). If the sun is not available, the magnetic compass may be used (KEETON 1972, 1974, WALCOTT & GREEN 1974).

But if the intended direction is "innate", it must be related to some concrete cue of reference, too. From the results of WILTSCHKO & GWINNER (1974) with hand-raised Garden

<sup>2)</sup> Without a discussion of controversial points of view, the term "innate" is used here in the sense in which K. LORENZ (1961) uses and defends it.

Warblers (*Sylvia borin*) one may conclude that an intended angle to the geomagnetic field vector is determined phylogenetically. SAUER (1957, 1971) claims the same with respect to the stars, and EMLEN (1970, 1972) asserts that Indigo Buntings (*Passerina cyanea*) are capable to evaluate empirically the rotational axis of the stellar sphere, and then set their migratory course at a certain angle to this axis.

Recent experiments of WILTSCHKO & WILTSCHKO (1975a, b, 1976a), however, raise some doubt whether there really exist two or more independent reference systems. Namely, it was possible to reorient the direction chosen with respect to the stars by shifting the relations between the North Star and magnetic north. In the view of WILTSCHKO & WILTSCHKO (see also 1976b), the magnetic compass is the basic system that is necessary for adjusting the star compass to geographically meaningful directions. Also EMLEN's experiments might have been influenced by the geomagnetic field in some uncontrolled manner so that perhaps no definite conclusions can be drawn from them. It should be added, however, that a considerable number of experiments conducted in our planetarium did not lead to clear and unequivocal results so far with respect to the questions involved. The problem is still under investigation and cannot yet be taken as being definitely clarified.

#### 4. Possible Peculiarities of and Connections between Different Compass Mechanisms

It might be difficult to believe that the magnetic compass could play a key role in direction finding since experiments with orientation cages ("Kramer cages") in visually cueless conditions always result in nearly randomized movement patterns within each night (e. g., WILTSCHKO 1968, EMLEN 1975). The fact that second-order tests nevertheless reveal remarkable consistency of the directions which are minimally preferred, and the fact that this consistency is statistically well established, cannot eliminate the fact that the birds obviously are not able to maintain a direction in the cage over several hours by using only magnetic information (as they can do, in the same cages, if visual cues are available). If one would directly transfer the birds' behaviour to natural conditions, erratic movements would result instead of the rather straight flight courses which are mostly observed even under overcast skies (e. g., BELLROSE 1967, STEIDINGER 1968, GRIFFIN 1973).

The inconsistency might be resolved by assuming that in the cage merely small rudiments of the orientational capabilities can be observed while in natural conditions the magnetic compass works rather precisely, too. Thus, one might assume that movements in and through the magnetic field are important for the physics of perception. Movements, however, are highly restricted in the cage situation.

If the problems are only due to the experimental procedures, assuming that in nature the magnetic compass does not work less precisely than the astronomical compasses, then, however, the question arises why the latter compasses exist at all. If both types would work at the same level of accuracy, the magnetic compass should be superior (cf. p. 65), and there would be no need of another.

The picture might be clarified somewhat if certain assumptions concerning the mechanism of magnetic orientation are made. The basic assumption is that the birds do not possess an equivalent of a magnetic needle by which the direction of the horizontal field vector can directly be read. Instead, they have to scan the magnetic intensities in different directions by respective body movements and may not be able to measure absolute field strength but only its first derivative, i. e. rate of change, or even no more than its sign of change. Thus, the birds have to discover the direction of the maximum (or minimum) intensity by successive measurements.

When trying to determine a weakly marked maximum, it might be helpful for a bird to memorize some optical cue in the direction it believes to have found it or in a certain angle to this direction. In several repetitions it may check the position of this cue and, if necessary, correct it. In this way it can fit the direction of the magnetic maximum into an optical scale of reference. Later, then, it can refer easier, faster, and more precisely to the secondary digital scale than to the primary analogue measurements. It may also be easier to determine a certain angle to this secondary scale than to the vague magnetic scale.

Without visual help, its own movements will lead the bird again and again away from the optimal setting which it is not able to maintain when depending only on the derivative of magnetic field strength with respect to its body turns. This holds true for the free flying bird, but it is even more easily to be expected in the cage. The confined bird, when trying to satisfy its locomotory drive, is forced to deviate from the preferred course as it cannot move forward in the desired direction. Thus, it has to scan the field gradient again and again. If it has visual reference cues, however, it can set its direction to these distinct stimuli immediately.

If these assumptions hold true, the different degrees of scatter in cage experiments without and with stars (or other visual cues) could be explained. In the open field without stars the bird is provided with better conditions than in the cage, since it can continue its course without bumping against walls. And very often it could make use of visual terrestrial cues, even at night time (cf. BELLROSE 1971), and/or of some acoustical signals (GRIFFIN & HOPKINS 1974) and/or of wind gusts or other kinds of air currents (cf. BELLROSE 1967, 1971, GRIFFIN 1969) providing some reference cues at least transitionally for a period of time. Also vestibular mechanisms might be used for stabilizing the flight course (cf. DRURY & NISBET 1964), and it should be stressed again that movement through the magnetic field (cf. p. 66) really might be an important factor.

Thus, the difference between cage and natural conditions might be plausible. But nevertheless, one might expect, also in free flying birds, some minor difference in the ability to maintain a straight course under clear and overcast skies, respectively. There are at least some radar observations indicating different amounts of scatter under both conditions (BELLROSE 1967, STEIDINGER 1968), but there are also contradicting reports (ABLE 1974). In homing pigeons, even if they show rather good homeward orientation under overcast, the angular variance of initial bearings seems to be commonly somewhat greater than with the sun being visible (KEETON 1969, see EMLÉN 1975, Fig. 21; BALDACCINI *et al.* 1971).

Thus, direction finding in birds might be considered as an integrated system in which the specific advantages of various environmental factors (see p. 65) are adequately utilized (see also WILTSCHKO & WILTSCHKO 1976b). The migratory birds would not have to take into account the seasonal and latitudinal changes of the stellar sky, since they could readjust their orientational system continuously by using magnetic information. These considerations, however, are still at a rather speculative stage.

### 5. Intended Directions in Case of Routes with Directional Change

Not all the migratory routes can be understood as a maintenance of just one invariable intended direction. In several species the routes include one or more directional changes and are commonly well fitted into the morphological structures of the earth, avoiding unfavourable areas (cf. SCHÜZ 1971, ZINK 1977). But even in these more complicated cases one may ask for the phylogenetically determined direction(s) which a juvenile bird being isolated from conspecifics might try to select. Several possibilities are listed in Table 1, and possible consequences leading to the actual routes are indicated.

The types listed under B may require some comment (see Fig. 1). It is assumed that there is an ecological barrier blocking the direct passage from the birth place B to the wintering grounds W. Actual flight directions could result then in different ways:

B—I) The intended direction points directly to the wintering grounds. The barrier, however, forces the bird into another direction. After it has reached the flank of the barrier, it has to compensate for the deviation. This could be done either by (1) quantitative measurement and integration of the deflection itself, or by (2) determining the difference to the intended course by means of position dependent coordinates in relation to its place of origin or to the undisturbed part of its path. In both cases, the bird is able to determine a new, secondary direction leading it back to the air line between B and W (see also p. 69).

B—II) The compensation of the deflection caused by the barrier has not to be performed by the individual bird, since evolution has already taken it into account. By the barrier the course is displaced to a parallel line, but just this line leads to the "goal".

B—III) The barrier does not act as a proximate, but as an ultimate factor (cf. IMMELMANN 1972), for the bird does never touch it, as its intended direction points directly to the flank of the

obstacle. The bird arrives at the mouth of a funnel at which the migratory routes of several populations converge. This results in a considerable concentration of individuals. If there is enough intraspecific interaction, the further flight direction reflects some compromise between diverging tendencies and depends on the quantitative composition of the sample. Furthermore, the resulting course should be influenced more by those individuals that tend to a certain direction most resolutely and these should be mainly the adult birds. Thus, as far as both age groups are represented, tradition should participate at least as a partial component.

If the apparent picture of a migratory route corresponds to type B—III, the phylogenetic basis might nevertheless be represented by either B—I or B—II. Leading by adults could prevail so that juvenile birds normally do not follow their “innate” intended direction.

Table 1: Phylogenetically determined intended directions in migratory routes with directional change.

The juvenile bird in its first autumnal migration tends toward:

A. *no* direction: leading by adults (tradition).

B. *one* direction; this points

I. to the wintering grounds: passive deflection, active compensation

- (1) by integration of the amounts of deviation,
- (2) by position dependent navigation;

II. neither to the wintering grounds nor to the flank of the barrier: passive parallel displacement precalculated;

III. to the flank of the barrier: concentration effect, directional change caused by social influences.

C. *varying* directions; controlled by

I. time dependent program:

- (1) season (circannual periodicity),
- (2) duration of flight;

II. distance dependent program:

- (1) physiological measurement of distances,
- (2) navigational measurement of distances;

III. position dependent program:

- (1) by topographic cues: (a) types of landscape,  
(b) local criteria,
- (2) by navigational coordinates: (a) relative to starting point,  
(b) absolute.

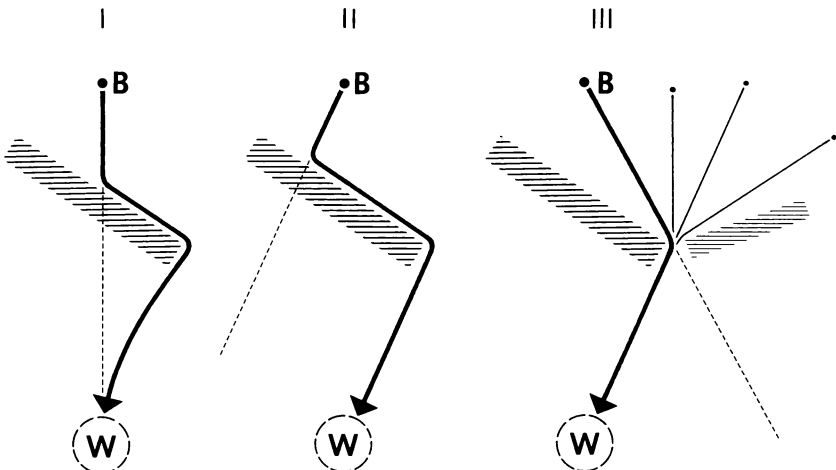


Fig. 1. Orientation types B-I, II, and III according to Table 1. Explanation in the text.

The deflections in types B—I and B—II need not to be caused by topographic features; they could also be caused by wind drift. Type B—I could react flexibly to various conditions, whereas in type B—II only rather regularly occurring cross winds could be “precalculated”.

In all the B types there is only one “innate” intended direction, but external influences superimpose another direction upon it, or the bird is at compensating such an enforced deflection by maintaining a secondary intended direction (B—I, third part of the route). It seems also possible, however, that the intended direction itself changes in dependence of endogeneous processes and/or external releasers which do not include, by themselves, directional information. Possibilities of that kind are listed in Table 1 under point C. Only a few additional remarks may be necessary:

*Ad C—II:* Point (1) means methods of physiological measurement, e. g. consumption of energy; point (2) means methods of using environmental cues for the measuring of distances. — *Ad C—III (1):* It is to be distinguished between (a) dependence on general characteristics of the landscape (as, e. g., land and sea) and (b) dependence on the characteristics of an individual location (e. g., the morphological appearance of a certain cape or bay).

The criteria listed under C are the same that have to be taken into account with respect to the termination of migratory movements (cf. GWINNER 1968, 1972, WALLRAFF 1972b). The picture of normal migration should scarcely be different from that according to type B—III.

None of the types might be realized in pure form. Any combination is possible, and evolution of migratory routes may have led to different solutions in different species.

At present, few results are available to answer the questions raised. The role of tradition should not be underestimated, especially in larger birds as, for instance, ducks and geese (cf., e. g., STERBETZ & SZIJJ 1968, BELLROSE & CROMPTON 1970). But whether the pure type A exists, i. e. whether juvenile birds spontaneously do not prefer any direction at all, remains doubtful. Type B—I has sometimes been favoured (cf. RÜPPELL 1937, WALLRAFF 1961), but its existence has not yet been proven. There is, at least, no doubt that landscape features as mountains, coasts etc. can deflect the directions otherwise taken over neutral areas (cf. SCHÜZ 1971). And with regard to compensation, not only in arthropodes (e. g., BURGER 1971, 1972), but also in birds (MERKEL & FISCHER-KLEIN 1973) compensatory turns have been shown even without use of external cues (“idiothetic orientation”, see MITTELSTAEDT & MITTELSTAEDT 1973). The dimensions in space, however, have been much smaller in these experiments than in those which occur in bird migration. Type B—I (2) is more thoroughly explained elsewhere (WALLRAFF 1972b, Fig. 5).

So far the best indications available support realization of type C—I (1): In cage experiments with Chaffinches *Fringilla coelebs* (PERDECK 1973) and with Garden Warblers *Sylvia borin* (GWINNER & WILTSCHKO in prep.) some shift of the preferred direction in the course of autumnal *Zugunruhe* could be observed that corresponded, at least in principle, with the directional change occurring in nature (cf. also GROOT 1965). It is difficult to believe, however, that a seasonal program alone is sufficient to explain all of the more complex migratory routes.

Several types of a position dependent program (C—III) are sometimes discussed, too. There are indications that migrating birds change their direction at dawn if they perceive that they are out at sea (MYRES 1964). It is, in general, not implausible to assume that birds prefer different directions when flying over different types of landscape, e. g. over land or sea. European populations, for instance, reaching Portugal on a southwesterly course, could follow the coast from there in a more or less zig zag manner if they head toward S or SE when flying over the sea (cf. WALLRAFF & KIEPENHEUER 1963). Hypotheses, however, assuming that juvenile birds in their first autumn might react to individual features of the landscape (C—III (1) (b)) or to absolute values of some navigational coordinates (C—III (2)(b)) should not be taken too seriously as long as they are not being supported by unequivocal experimental evidence. So far such evidence does not exist (cf., e. g., SCHÜZ 1950, 1964, 1971, SAUER 1957, WALLRAFF 1960, 1972b, SHUMAKOV 1967, RABÓL 1970, 1972, EMLÉN 1975).

### 6. Intended Directions in White Stork Migration

Finally, we will deal somewhat closer with an example of directional shift that leads back to the Vogelwarte Rossitten and herewith to the beginning of orientation research. One of the most spectacular directional changes occurs at the Gulf of Iskenderun at the southeastern corner of the Mediterranean Sea where masses of White Storks (*C. ciconia*) arriving from Europe turn from a southeasterly course to a southward direction (HECKENROTH 1968, SCHÜZ 1971). In 1926—33 the Vogelwarte Rossitten detained juvenile storks until all free-living conspecifics had left the area (THIENEMANN 1931, SCHÜZ 1949), and one may ask whether the data being available from these early experiments can contribute to solving the problems discussed in the foregoing chapter.

Fig. 2 shows the directions of the recoveries of these detained birds (B) in comparison with only banded, but not furthermore influenced juvenile storks (A), all of them having been hatched in East Prussia (Ostpreußen, abbreviated OP). The control birds (A) were found on the shortest way to the first point of concentration, i. e. to the Bosphorus, but the detained birds (B) preferred more southerly directions pointing to the African wintering grounds rather than to the Bosphorus. Though the difference between the means is only 11 degrees, it is statistically fairly significant (see Appendix). A greater difference cannot be expected anyway, as the potential goal directions are not farther apart from each other than about 11°.

This result suggested the hypothesis that the White Stork belongs, according to its genetic equipment, to orientation type B—I (Table 1). The fact that juveniles flying in normal social contact approach the mouth of the funnel on the shortest way might then be explained by an influence of adult birds being superimposed. (That such influences can considerably take part in Storks results from other experiments of the Vogelwarte Rossitten; see SCHÜZ 1950.)

Granting this hypothesis to be true, some doubts may arise whether the dividing line (*Zugscheide*) between Stork populations in Middle Europe is really based on genetic differences

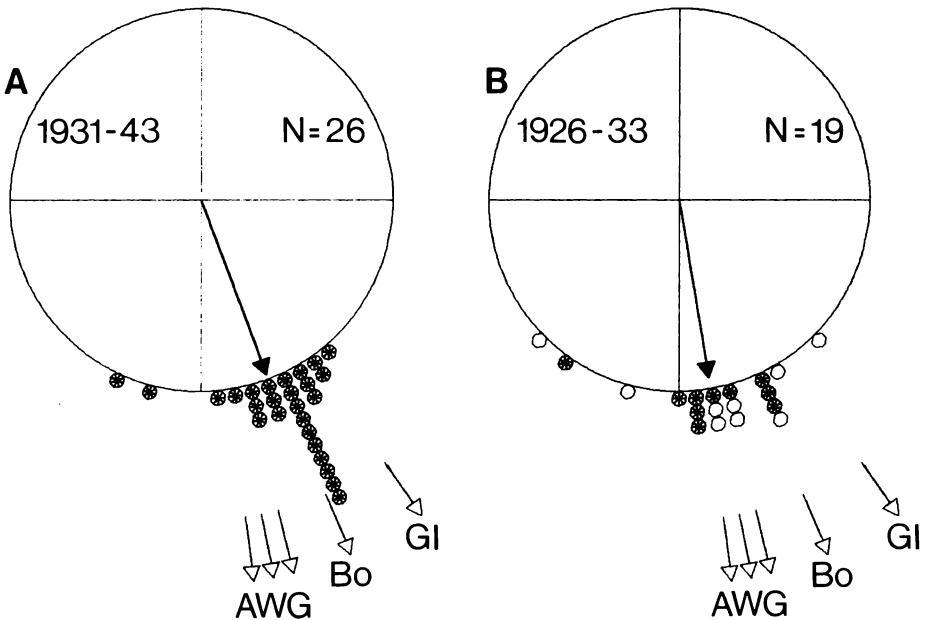


Fig. 2. Directions of autumn recoveries of juvenile White Storks hatched in East Prussia (OP). The recoveries are within Europe and at distances of more than 100 km. A: normally migrating birds. B: detained birds; dark dots: released at Rossitten (OP), white dots: released in western Germany. — Black arrow marks mean vector; white arrows indicate directions from OP to: AWG = African wintering grounds (SCHÜZ & BÖHRINGER 1950), Bo = Bosphorus, GI = Gulf of Iskenderun. [Data by courtesy of Vogelwarte Radolfzell (A), and from THIENEMANN (1931) and SCHÜZ (1949) (B).]

as SCHÜZ (1953, 1964) presumes. Rather than this idea the diagrams support RÜPPELL's (1937) assumption that the "genetically intended direction" of all populations point to the wintering grounds, and that deviations from this primary direction are based on secondary influences. The decisive experiment, i. e. releases of detained storks of the western populations, has not been made.

More than this working hypothesis could not be deduced from the Rossitten data. Therefore, a research program was started in 1963 that should lead to more definite conclusions. Storks hatched in Schleswig-Holstein (SH; northernmost part of West Germany, bordering Denmark) were used instead of OP birds, not only because of political reasons, but also because the two directions that might be intended diverge from this area by a greater angle, i. e. by about 25—35 degrees. Conclusive answers could be expected therefore from a smaller amount of data.

Unfortunately, after only two years the program had to be stopped, and it could not be continued later because of some technical reasons, not the least of which was the steady decline of population density. Thus, the results remained fragmentary. But at least their tendency looks quite clear, and as they constitute a late supplement to the classical Rossitten experiments, the anniversary of the Vogelwarte Rossitten/Radolfzell may be an adequate opportunity to publish them despite their fragmentary character.

For providing some background information, Fig. 3 shows the autumn recoveries of SH storks together with those ringed in Denmark up to 1960. In this reflection of normal migratory behaviour not even a rudiment of what might be expected on the basis of orientation type B—I can be detected. The main flyway neither "sags" nor seems to be influenced by geomorphological features, although by a slight southward bend the birds would avoid crossing the Carpathian Mountains and instead follow the Danubian valley. The main path, however, is on a straight line to the Black Sea and reaches it even somewhat north of the Bosphorus.

While in Fig. 3 southwesterly movements are only sparsely indicated, there is a conspicuous bipartition in Fig. 4 (white dots): more than a quarter of the storks was found in southerly to



Fig. 3. Autumn recoveries of White Storks of Denmark (triangles and squares) and of Schleswig-Holstein (circles) within Europe. Black symbols refer to juveniles in their first autumn, white symbols to adults from their fourth autumn onward. (Ages in between are omitted.) All available data from 1907 to 1960 are included (for sources see Appendix).



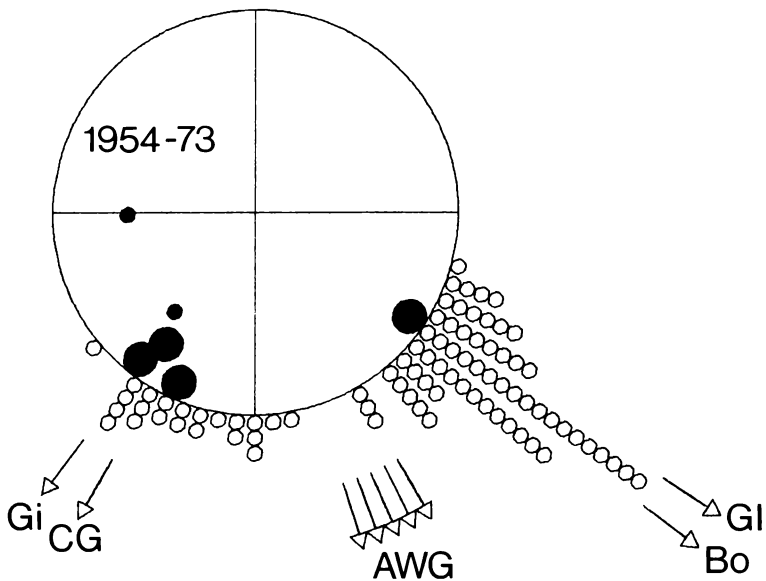


Fig. 4. White dots: Directions of autumn recoveries of juvenile White Storks hatched in Schleswig-Holstein (SH). The recoveries are within Europe and at distances of more than 100 km. The 20 years included (1954—73) are symmetrically placed around the experimental years 1963/64. [Data by courtesy of Institut für Vogelforschung, Wilhelmshaven.] — Black dots: Recovery directions of experimentally detained Storks (small dots: distances 50—100 km, large dots: 450—1150 km). — Gi = Gibraltar, CG = Cape of Gata (Spain), other abbreviations as in Fig. 2 (AWG is for eastern populations).

southwesterly directions. The percentage of SW recoveries increased from practically zero before World War II to 38% (13 out of 34) in 1964—73. Thus, the difference between Figs. 3 and 4 can be explained by the different years being included. It should be emphasized that in Fig. 4 the direction toward the African wintering grounds (AWG) falls into the gap between the two groups of recoveries.

In July of 1963 and 1964 10 and 11 young storks were brought from there nests in several villages between Friedrichstadt and Rendsburg to an aviary near Eckernförde. Between September 14 and 20 they were released in groups of two or three individuals at several places in SH, one group per day. Seven of the 21 storks were found at distances of more than 50 km from the site of release. Two of the recoveries concerned birds of the same group, and it was proven that they flew together (see Appendix). All others were of different release groups. When considering only the more distant recovery point of the pair mentioned, six recoveries can be thought of as being independent of each other. Their directions are shown as black dots in Fig. 4, the four large dots representing long-range recoveries at distances between 450 and 1150 km (see Appendix).

It is obvious that the detained storks preferred the two main directions of normal autumnal migration. They do not show any tendency toward the wintering grounds in Africa, although chances to get them reported in the respective direction should have been rather high (see Appendix).

If the results, despite the small numbers involved, would be taken seriously, just one conclusion could be drawn: Juvenile Storks of SH, migrating without contact to adults, do not tend to fly the shortest way to the wintering grounds, but they head for one of the two flanks of the Mediterranean Sea. Schleswig-Holstein (SH) seems to be a "mixed area" (at least nowadays) from which an individual stork may depart either toward SE or toward SW, but not toward some intermediate direction. Although it is still possible that the alternative between SE and SW is controlled by environmental and/or stochastic influences, it seems more likely that the

population consists of two genetically different types (cf. SCHÜZ 1953, 1964). This assumption is supported by the southeasterly recovery point (Fig. 4) which fits quite well to the normal flight path of SH storks, but not to the directions preferred by the detained OP birds (Fig. 2B). Thus, it seems probable that there is a progressive shift from SE to S between SH and the Baltic region, and this would suggest genetic rather than just modificatory differences.

In conclusion, the results do not support the hypothesis that was suggested by the Rossitten results (Fig. 2), i. e. they are not in accordance with orientation type B—I (Table 1, Fig. 1). But they are in accordance with either B—III or with one of the C types. The season dependent program C—I (1), however, can probably be excluded since the detained storks should have been in a time phase in which they, normally, would have already shifted to a southward course.

In a species in which individuals migrate in close social contact, as they do in the White Stork, type B—III should be sufficient. It ensures that a dispersed young bird can reach the area of concentration in which it gets contact with conspecifics. In the OP storks, some deviation to the south would at least not be detrimental, since they would nevertheless meet storks coming from more westerly regions. But the SH storks, starting at the edge of the funnel, would scarcely have a chance to find conspecifics when deviating to the south of the normal flyway.

Probably no further experiments with White Storks of Middle Europe can be conducted. Unfortunately, therefore, considerations have to stay at this stage of speculations.

## 7. Acknowledgements

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## 8. Zusammenfassung

### Ausgewählte Aspekte der Orientierung beim Vogelzug

Nach einem Hinweis auf die spezifischen Vor- und Nachteile einer Kompaßorientierung unter Zuhilfenahme der Gestirne einerseits und des Erdmagnetfeldes andererseits wird die Herkunft der beim Vogelzug wirksamen Sollrichtungen besprochen. Offenbar können sie phylogenetisch determiniert, also „angeboren“ sein, aber sie können auch unter Bezugnahme auf einen bekannten Zielort festgelegt werden. Einige Befunde (WILTSCHKO) legen den Schluß nahe, daß im Falle der „angeborenen“ Sollrichtungen dem Erdmagnetfeld als Bezugsgröße eine entscheidende Rolle zukommt. In diesem Zusammenhang wird die potentielle Funktionsweise des Magnetkompasses und sein Zusammenspiel mit der Sternenorientierung diskutiert.

Im Falle komplexerer Zugrouten, die Richtungswechsel einschließen, ist die Frage nach phylogenetisch determinierten Sollrichtungen differenzierter zu stellen. Potentielle Lösungswege sind in Tab. 1 aufgeführt. Am Beispiel des Weißen Storchs wird dieser Fragenkomplex eingehender behandelt. Die Versuche der Vogelwarte Rossitten mit verspätet abziehenden Jungstörchen legten die Hypothese nahe, daß unerfahrene Störche spontan die Richtung zum afrikanischen Winterquartier einschlagen (Fig. 2). Fragmentarisch gebliebene Versuchsergebnisse mit schleswig-holsteinischen Jungstörchen sprechen jedoch eher für ein Ansteuern der beiden Flanken des Mittelmeers (Fig. 4). Die Bedeutung dieser Befunde im Sinne der vorher erörterten Funktionsschemata wird diskutiert.

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## 10. Appendix

### White Stork Experiments: Details

In Fig. 2 only band recoveries (i. e., no observations of the painted experimental birds without band recovery) are included. Furthermore, if in the same year two or more storks were found less than 50 km apart from each other, only the farthest recovery point was used. Thus, statistical independence of the directional values may have been achieved with some approximation. (Not only the control birds surely migrated in flocks, but also the detained storks were released in smaller or larger groups consisting of up to a hundred individuals.) The resulting mean vectors are as follows (Co = controls = normally migrating storks; Ex = experimentals = detained storks;  $\bar{\alpha}$  = direction of mean vector clockwise from north;  $\bar{a}$  = length of mean vector in unit circle; z and p according to the Rayleigh test, see BATSCHLET 1965, 1972):

Co: n = 26 (birds),  $\bar{\alpha}$  = 159.3°,  $\bar{a}$  = 0.9737 (z = 24.65, p << 0.0001);

Ex: n = 19 (birds),  $\bar{\alpha}$  = 170.3°,  $\bar{a}$  = 0.9395 (z = 16.77, p << 0.0001).

The angular difference of 11.0° is significant with p < 0.05 (VWR test — BATSCHLET 1965, p. 33 — F = 4.55, B test — BATSCHLET 1972, p. 80 — U = 6.71), provided that the individual values are accepted as being independent of each other.

Definitely independent of each other are the mean directions of the single years. The means of these means are as follows:

Co: n = 11 (years),  $\bar{\alpha}$  = 158.2°,  $\bar{a}$  = 0.9870 (z = 10.72, p < 0.0001);

Ex: n = 4 (years),  $\bar{\alpha}$  = 171.3°,  $\bar{a}$  = 0.9995 (z = 4.00, p < 0.01).

The angular difference of 13.1° is significant with p < 0.05 (VWR test F = 6.81, B test B = 10.02).

No difference can be recognized between detained storks released in OP, i. e. their home area (n = 10 birds,  $\bar{\alpha}$  = 171.5°,  $\bar{a}$  = 0.9599), and those that had been displaced to and released in western Germany (n = 9 birds,  $\bar{\alpha}$  = 169.0°,  $\bar{a}$  = 0.9173).

In Fig. 3 all relevant recoveries that I could find are included, from the beginning of bird banding (first relevant record in 1907) up to 1960. The sources were as follows:

H. C. A. MORTENSEN: Dansk Orn. Foren. Tidsskr. 14: 91—156 (1920); 22: 126—132 (1928). — P. SKOVGAARD: Danske Fugle 4: 67—138, 165—211, 255—263 (1932—37). — H. JOHANSEN: Vidensk. Medd. Dansk naturh. Foren. 112: 119—132 (1950); 114: 309—339 (1952); 117: 349—397 (1955); 121: 75—139 (1959); and in litt. (recoveries 1955—60). — J. MÖLLER: Schr. naturw. Ver. Schlesw. Holst. 24: 39—52 (1949). — E. SCHÜZ: Bonn. zool. Beitr. 4: 31—72 (1953). — Institut für Vogelforschung "Vogelwarte Helgoland", Wilhelmshaven: unpublished recovery files.

The recovery data of the detained storks (Fig. 4, black dots), all of them hatched and banded in Schleswig-Holstein, are as follows (numbers refer to the "Helgoland" rings):

1. H 5698 o Klein-Bennebek, released 17-Sep-63 Klinkrade (53° 44.2'N 10° 35.3'E), Kr. "Ratzeburg" + dead (rotten) 5-Feb-64 Drochtersen (53° 42.8'N 9° 23.7'E), Kr. Stade. — 269°, 78 km.
2. H 5670 o Erfde, released 19-Sep-63 Kührsdorf (54° 10.0'N 10° 16.6'E), Kr. Plön + dead 21-Sep-63 Groß-Fredenbeck (53° 31.3'N 9° 24.4'E), Kr. Stade. — 219°, 92 km.

3. H 5673 o Meggerdorf, released 18-Sep-63 Moordorf (53° 53.4'N 9° 38.2'E), Kr. "Itzehoe" + 29-Sep-63 Gozdnic ( = Freiwaldau, 51° 26.3'N 15° 06.3'E), Kr. Zagań, Silesia, Poland. — 124°, 458 km.
- 3a. H 5671 o and released as 3. + dead 28-Sep-63 Rätzlingen (52° 58.6'N 10° 40.6'E), Kr. Ülzen, Bez. Lüneburg. — 145°, 123 km. — The stork flew in early morning hours against a high-tension line. Stork (3) has been observed nearby and departed after a few hours toward SE. It was found the following day at 118°, 347 km from this place. Both (painted) storks had been observed between Sep. 18 and 23 at Deichreihe near Glückstadt (213°, 22 km from release site).
4. H 5700 o Alt-Bennebek, released 20-Sep-63 Dellstedter Moor (54° 15.1'N 9° 21.4'E), Kr. "Heide" + 20-Dec-63 Aubenton (49° 50.4'N 4° 12.1'E), Aisne, France. — 218°, 603 km.
5. H 8275 o Meggerdorf, released 15-Sep-64 Moordorf (53° 53.4'N 9° 38.2'E), Kr. "Itzehoe" + dead 27-Sep-64 Houécourt (48° 17.7'N 5° 53.6'E), Vosges, France. — 204°, 674 km.
6. H 8258 o Bergenhusen, released 16-Sep-64 Kührsdorf (54° 10.0'N 10° 16.6'E), Kr. Plön + 6-Oct-64 Lamazière-Basse (45° 22.4'N 2° 10.0'E), Corrèze, France. — 214°, 1135 km.

The storks were painted for individual recognition, and they carried, in addition to the normal Vogelwarte ring, aluminium bands with labels attached. On the labels, reports were requested in German, Russian, French, and English, and addresses of institutes were given in Germany (FRG as well as GDR), in Hungary, and in Bulgaria. Thus, there should have been good chances for getting the storks reported without too much bias due to political reasons. To avoid an increase of such bias, no references were given to public media such as newspapers, broadcasting, or television.

All the directions and distances in this paper are calculated on the basis of great circle routes. Yet this was an arbitrary choice. Under some aspects the rhumb line (loxodrome) and under others the great circle fits better to potential expectations. The differences are rather small and do not affect the conclusions that can be drawn from the data. There are no apparent correlations between distances and directions of recoveries. Therefore, in Figs. 2 and 4 only directions are shown.

Author's address: Dr. H. G. Wallraff, Max-Plank-Institut für Verhaltensphysiologie, D-8131 Seewiesen

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Aus dem Fachbereich Biologie der Universität Frankfurt

## Der Magnetkompaß der Zugvögel und seine biologische Bedeutung

Von Wolfgang Wiltschko

Im Spätsommer und Herbst brechen die Zugvögel zum Flug in ihre Winterquartiere auf, unter ihnen auch die Jungvögel, die in diesem Jahr geboren sind. Für sie speziell stellt sich das Problem, die Überwinterungsgebiete ihrer Art aufzusuchen, ohne diese vorher zu kennen. — Bei einigen im Verband ziehenden Vogelarten spielen Traditionen beim Herbstzug eine wichtige Rolle, wenn beispielsweise aufgrund bestimmter ökologischer Ansprüche immer die gleichen günstigen Rastplätze aufgesucht werden — hier ist anzunehmen, daß die Altvögel die jungen Vögel zumindest teilweise führen. Auch die Verfrachtungsversuche der Vogelwarte Rossitten (SCHÜZ 1949, 1950) zeigen, daß bei Störchen das Verhalten der Jungvögel von Altvögeln beeinflußt wird. Bei vielen Singvogelarten aber verlassen die Jungvögel die Brutgebiete vor den Altvögeln und fliegen allein — sie müssen also von sich aus Informationen besitzen, die das Auffinden der arteilgenen Winterquartiere hinreichend genau gewährleisten.

### 1. Angeborene Richtungsinformation

Wir nehmen heute an, daß die dazu benötigte Information den Vögeln angeboren ist, und zwar in Form von „Polarkoordinaten“, nämlich als eine Richtungs- und eine Entfernungsangabe. — Bei der Entfernungsangabe handelt es sich, wie die Versuche von GWINNER (1968, 1974) zeigen, um ein endogenes Zeitprogramm, das die Vögel veranlaßt, für eine bestimmte Zeitspanne zu ziehen; diese Zeitspanne ist bei normaler Fluggeschwindigkeit so bemessen, daß der Vogel am Ende im Überwinterungsgebiet angekommen ist.

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