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Magnetic orientation and celestial cues in migratory orientation

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Summary. Young birds on their first migration possess innate information on the direction of their migration route. It is present in two forms, using celestial rotation and the geomagnetic field as references. These two systems, together with information provided by factors associated with sunset, interact in a complex way to establish the migratory direction. During ontogeny, celestial rotation appears to be dominant; during migration, however, celestial cues appear to be controlled by the magnetic field. The factors associated with sunset – the view of the setting sun, the characteristic pattern of polarized light – are important secondary cues which seem to derive their directional significance from the magnetic field. Their role appears to be more variable, with possible species-specific differences. During spring migration and later autumn migrations, flying in the migratory direction is complemented by navigational processes which enable the birds to return to a specific home site known from previous stays.

Key words. Migration; magnetic compass; star compass; celestial rotation; polarized light; navigation.

Every year, in late summer and autumn, myriads of birds leave their breeding areas and migrate in order to spend the winter in regions which offer more favorable environmental conditions. These migrants include many young birds on their very first migration; those birds face the task of reaching a distant area hitherto unknown to them – their species-specific wintering range.

Innate information

In species that migrate in flocks, old, experienced birds may guide the young ones on traditional routes, as has been documented for storks[52] and many species of waterfowl[34]. Yet in many other species, among them most of the familiar passerines like the robin *Erithacus rubecula*, the warblers and the flycatchers, the individual birds migrate alone. Here the young birds on their first migration must possess innate information on how to find the wintering areas of their species.

Large-scale displacement experiments with migrating birds revealed the nature of this innate information. The most prominent experiment was conducted by the Dutch Vogeltrekstation[47] with starlings, *Sturnus vulgaris*, that pass through Holland in large numbers on their way from their Baltic breeding areas to wintering grounds in southern England and northern France. Thousands of these transmigrants were caught and transported at right-angles to their normal migration route to Switzerland, where they were released. Ringing recoveries told about their later whereabouts. The majority of the recoveries of young birds came from the southern French Atlantic coast and northern Spain, indicating that these birds had continued on the west-southwesterly course which had brought them to Holland – and which, under normal circumstances, would have brought them to their traditional wintering range.

These findings, together with some earlier ones[21] suggest that young birds on their first migration fly fixed courses – the innate information they possess on the position of their species' wintering range seems to be given in 'polar coordinates', namely as a direction and a distance to be travelled. This is also indicated by the well-documented fact that hand-raised birds show spontaneous directional tendencies in their species-specific migratory direction[9, 13, 15, 20, 24, 50, 51, 61, 66]. The distance of migration is controlled by an endogenous time program and the amount of migratory activity[30] (for discussion see Berthold[11]); this paper is devoted to the question of how birds localize their migratory direction.

Methods used to analyse orientation

The mechanisms used for directional orientation have been a subject of intensive research during the last 30 years. The experimental procedures have been based on analyses of the behavior of caged migrants. For methodological reasons, most authors focussed on the orientation of night migrating birds, because these birds exhibit nocturnal Zugunruhe that can be recorded in appropriately designed cages.

Two such cage types are in common use: an octagonal cage with 8 radially positioned perches developed by Merkel and Fromme[38] in which the bird's activity is recorded by microswitches, and a funnel cage developed by Emlen and Emlen[28]. The latter records the traces left by birds on the inclined walls when they try to escape from the center, either as inky marks or as scratches on typewriter correction paper. From the distribution of activity, the bird's bearing is determined, and from several of these bearings, a mean vector is calculated which represents the direction the birds preferred. This direction can be compared with the natural migratory direction as known from ringing recoveries and with any manipulations of environmental factors to be tested.

The findings have shown that migratory orientation is a highly complex system where factors of different natures interact to enable the young birds to find the species-specific wintering range.

Compass mechanisms

Two compass systems have been described so far for nocturnal migrants – a magnetic compass and a star compass. But also the sun and sun-related cues may be of great importance, since most birds start their nocturnal flight at dusk when the setting sun provides a prominent mark in the western sky. We will begin with the magnetic compass, because it represents the simplest mechanism of direction finding.

The earth itself is a huge magnet. The field lines leave the earth's surface at a pole close to the southern geographic pole and re-enter it at a pole near the north pole; in between they form varying angles of inclination with the horizontal, running parallel to the earth's surface at the magnetic equator (fig. 1 a). The total intensity of the geomagnetic field is around 60,000 nT at the magnetic poles and decreases to about 30,000 nT at the magnetic equator. At most locations, magnetic north does not coincide with geographic north; the deviation, called magnetic declination, is considerable near and between the geographic and magnetic poles, but it is small at lower latitudes, where the geomagnetic field is rather regular[53].

Any animal that is able to perceive the geomagnetic field will be provided with a means of distinguishing directions. Among birds, this ability appears to be rather widespread, as has been demonstrated in experiments with artificial magnetic fields[64]; altering the north direction of the ambient magnetic field by Helmholtz coils resulted in a corresponding change of the birds' directional preferences[59] (fig. 2).

When the functional characteristics of the birds' magnetic compass were analyzed in European robins, it was found to differ from man's technical compass in two important aspects. Firstly, its functional range is narrowly tuned to the total intensity of the ambient magnetic field, yet the birds could adapt to changing intensities within three days. Secondly, the birds' magnetic compass does not use the polarity of the magnetic field, but rather the axial course of the field lines and their inclination in space. Thus the birds do not distinguish between 'north' and 'south', but rather between 'poleward' and 'equatorward'; the 'birds' in figure 1b indicate what direction young birds take for their autumn migratory direction[64]. For long-distance migrants, this means that their magnetic compass will be able to adjust to the lower total intensities they encounter as they reach lower latitudes. When they cross the magnetic equator, however, the field lines run horizontally and the information from the magnetic compass becomes ambiguous. Two species of transequatorial migrants, the garden warbler, *Sylvia borin*[61], and the pied flycatcher, *Ficedula hypoleuca*[8], have been shown to possess a magnetic compass of the same type as the European robin; how they master this problem is still an open question.

Nocturnal migrants can also use the stars for orientation. Originally, Sauer[50, 51] believed that warblers could truly navigate to their winter quarters with the help of the stars, but a later analysis of stellar orientation in the indigo bunting, *Passerina cyanea*[22], revealed that stars give the birds information on direction rather than position.

In contrast to those from the magnetic field, stellar cues are not constant. The birds are faced with a multitude of stars that change their position in the course of the night (fig. 3). The position of stars at any given time of night also changes with season and geographic longitude. An analysis of the star compass showed that this does not interfere with orientation, as the birds seem to make use of the constant spatial relationship between stars. Emlen[23] suggested that they might derive directions from

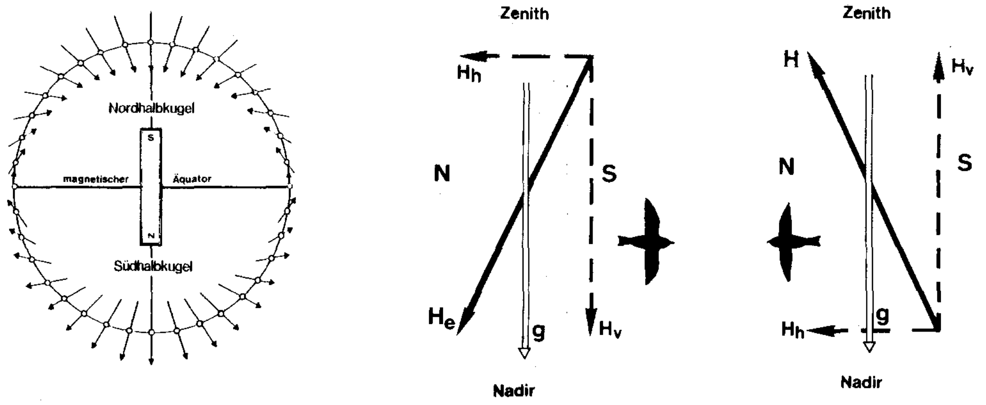
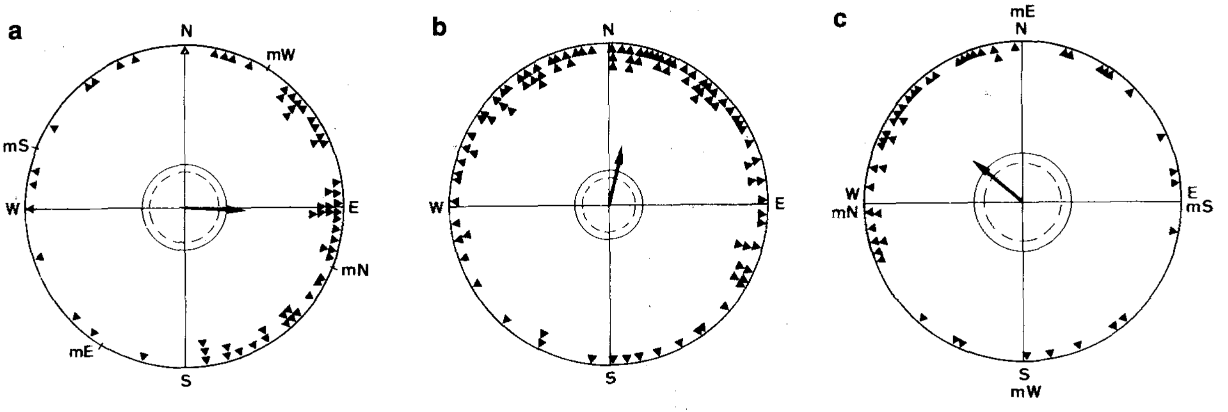


Figure 1. The magnetic field of the earth. Section through the geomagnetic field north of the magnetic equator: the polarity points downward; and south of the magnetic equator: the polarity points upward. N, S = north and south, respectively; g = vector of gravitation; H_e, H = vector of the geomagnetic field, H_h; H_v = horizontal and vertical component of the magnetic field.



43000 nT, mN = 112°, 42° Incl.

46 000 nT, mN = 360°, 66° Incl. (local geomagnetic field)

54000 nT, mN = 270°, 37° Incl.

Figure 2. Orientation of European robins (a) in a magnetic field with mN turned to ESE, (b) in the local geomagnetic field and (c) in a magnetic field with mN turned to W. In this and the following diagrams, each symbol at the periphery of the circle gives the mean of one test bird in one night. The arrows represent the mean vectors and the two inner circles mark the 1% and 5% (broken) significance border of the Rayleigh test[59].

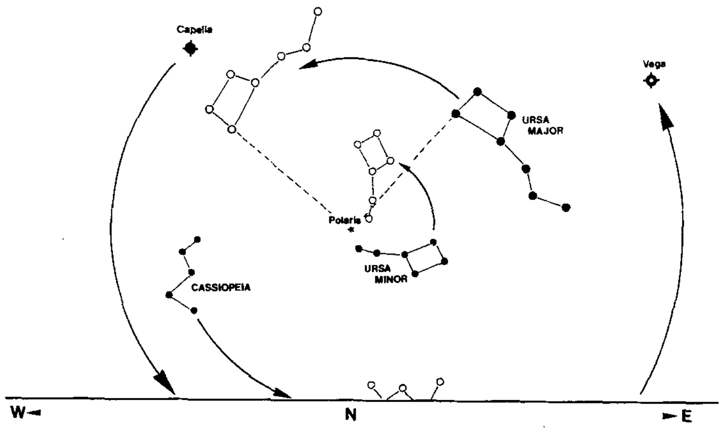


Figure 3. Changing star positions: view to the northern sky in spring from 30°N latitude. Solid star symbols: early evening, open star symbols: 6 h later.

the star patterns in a similar way to that in which we can find north from the constellation of *Ursa major*, regardless of its position (see fig. 3).

The factors associated with sunset may also provide directional information for nocturnal migrants. This possibility was first suggested by Vleugel[57]; cage experiments by Moore[39,40] and many other authors[17,35,37] confirmed their important role. Not only the view of the setting sun itself[41,42], but also the pattern of polarization[1,2,32,43,45] are used for orientation. The latter forms a band across the sky perpendicular to the position of the setting sun which is a prominent mark for animals such as birds that are able to perceive polarized light[20]. Several questions about the nature of the sunset orientation are still open, however; it is unclear whether the sunset cues are part of the sun compass or whether they represent an independent system indicating west to nocturnal migrants (see Moore[44] for discussion). Likewise, the significance of the orientation by polarized light is not clear yet; in experiments where polarizers were used to alter the position of the e-vector, the birds mostly oriented parallel to the e-vector axis[1,2,43,45], even if under natural condition they do not do so. This became most obvious in tests[33] with blackcaps, *Sylvia atricapilla*, because these birds changed their reaction relative to the e-vector significantly when the natural one was replaced by an artificial one. These findings lead to the question of whether tests with polarizers reflect the natural situation realistically.

The reference system for the migratory direction

To transfer genetically encoded directional information into an actual course, birds need an external reference. To find out what orientation mechanisms serve this function, experiments were performed with hand-raised birds whose experience was carefully controlled and monitored. The results suggested, surprisingly, that here the orientation system is redundant.

Young garden warblers[61] and pied flycatchers[9] were taken from the nest before their eyes had opened and raised in closed rooms so that they never saw the sky. Later, tested in the geomagnetic field in the absence of visual cues, they were able to find their migratory direction (fig. 4). When the ambient magnetic field was altered, the birds changed their behavior accordingly[9], indicating that the magnetic field can serve as the reference system for the genetically encoded directional information.

Another reference system had been proposed by Emlen[26]. He found that young indigo buntings could orient in a planetarium only if they had observed the starry sky between fledging and the onset of migration[24]. He concluded that celestial rotation, i.e. the apparent movement of the stars around the celestial pole, may act as directional reference for the innate migratory direction. When he made young indigo buntings watch a planetarium sky rotating around Betelgeuse in Orion, these birds later sought their southerly migratory direction opposite to Betelgeuse instead of to Polaris[26]. These findings suggested that celestial rotation can serve as a reference system for the migratory direction and calibrate the star compass accordingly.

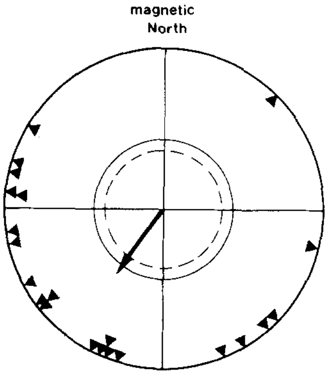


Figure 4. The orientation of young hand-raised garden warblers, raised without ever seeing the sky, in the local geomagnetic field, during the first autumn migratory period[61].

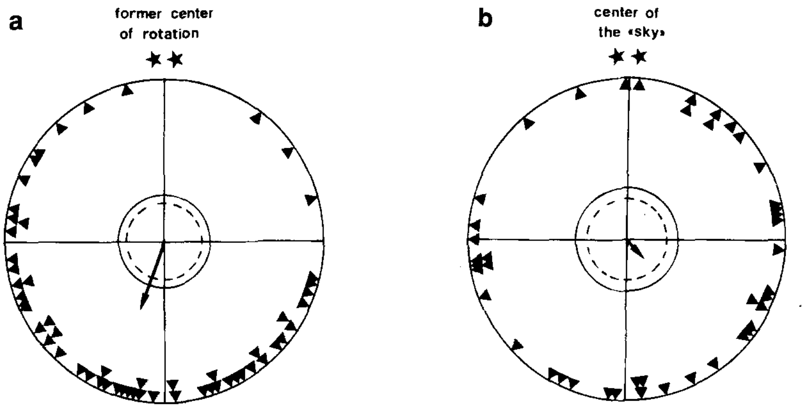


Figure 5. Young garden warblers tested under a stationary artificial 'sky' in the absence of meaningful magnetic information. (a) Birds raised under a similar, yet rotating 'sky'; (b) birds raised under the stationary 'sky'. In this and the following diagrams, stars indicate the presence of natural or artificial stars[66].

Similar experiments were conducted with young garden warblers[66]. A simple artificial 'sky', consisting of 16 light dots and rotating constantly with 1 rotation/day, was presented to the birds instead of the natural sky. When they were later tested under the same, now stationary 'sky' in the absence of meaningful magnetic information, they oriented away from the former center of rotation (fig. 5a). A second group of birds raised under a similar, yet stationary 'sky' and tested under identical conditions, was disoriented (fig. 5b). These findings clearly show that celestial rotation is crucial for calibrating the stars and establishing a star compass; the appearance of the sky itself seems to be totally unimportant[66].

In the course of his experiments, Emlen[24] found that indigo buntings were not able to orient by the stars when they could see the sky only after migration had already begun. He suggested that establishing the star compass might represent an imprinting-like learning process which could occur only during a certain sensitive period that ended with the onset of migration. Current experiments indicate that birds indeed have to watch the rotating sky before the onset of migration in order to be able to use the star compass; the directional significance of the stars, however, is not fixed, but subject to later modifications[5,6,16,62,63].

The Savannah sparrow *Passerculus sandwichensis*[12,13] and the pied flycatcher *Ficedula hypoleuca*[9,15] are two more species that have been studied from this point of view. All these experiments indicate that the information on the migratory direction is represented twice; relative to celestial rotation via the stars and relative to the magnetic field. Each of these two systems appears to be sufficient to guarantee orientation in the species-specific migratory direction.

Theoretically, the sunset factors could also serve as a reference system for the migratory direction. Yet they would make a very crude system, as the exact position of sunset varies with geographic latitude and, even more important, with season, the largest changes occurring at the times of equinox, i.e. at times when many birds are on their way. Moore[40] and Katz[35] discussed innate reactions relative to the position of sunset. Experimental evidence, however, does not support this view; in laboratory tests, blackcaps did not use an artificial 'setting sun' as orientation cue[56]. Hand-raised Savannah sparrows, tested outdoors, could not orient at sunset without magnetic information[14], indicating that the directional significance of the sunset factors is not innate, but is derived from other systems.

Interactions during ontogeny

The above-mentioned experiments might suggest that celestial rotation and the magnetic field are two independent reference systems for the genetically encoded migratory direction, existing side by side. This leads to questions about possible interactions between the two systems.

A few studies suggest that during ontogeny, celestial rotation and the stars might affect the later orientation by the magnetic field. When tested in the geomagnetic field without visual cues, hand-raised garden warblers that had grown up outdoors under the natural sky were much more poorly oriented than their conspecifics that had never seen the sun or the stars[65]. In Savannah sparrows and pied flycatchers, however, this phenomenon was not found[13,19]. Yet the respective experiments indicate that a view of the natural sky during early summer might affect the set direction which the birds later selected with the magnetic compass, in a way not yet completely understood.

To investigate whether the magnetic field during ontogeny affected the later orientation by the stars, young garden warblers were raised under a rotating artificial 'sky'. The various groups of birds were placed under the 'sky' in such a way that the center of rotation lay in different directional relationships to the geomagnetic field. When these birds were later tested under a stationary 'sky' in

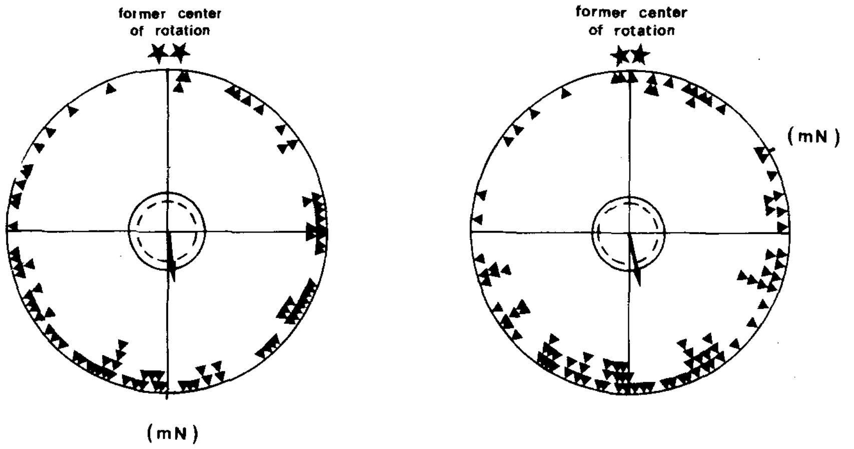


Figure 6. Orientation of young garden warblers under a stationary artificial 'sky', without meaningful magnetic information. The birds had been raised under a rotating sky in the geomagnetic field; the former center of rotation and former magnetic north (mN) are indicated[66].

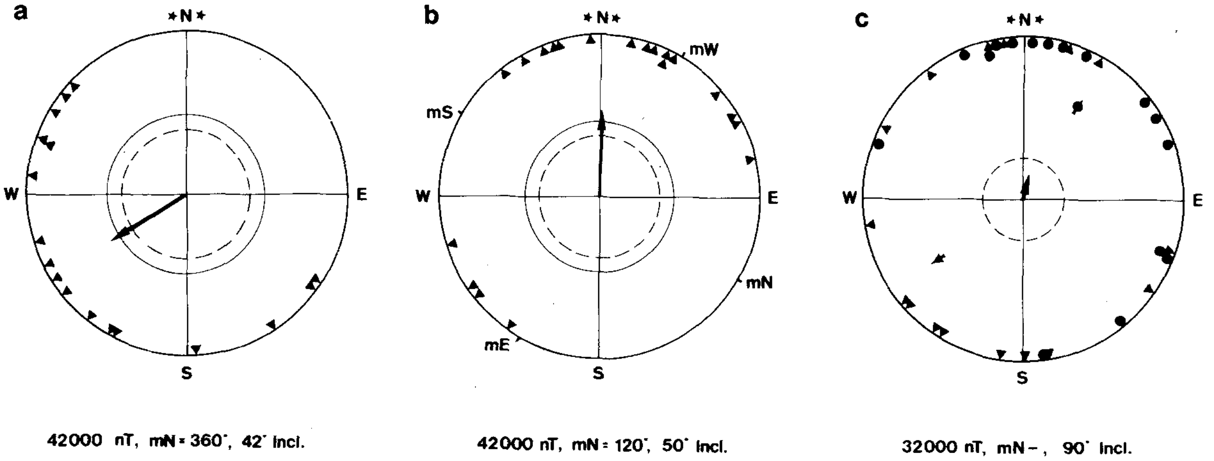
the absence of meaningful magnetic information, all the birds sought their migratory direction away from the former center of rotation, regardless of what its position with respect to magnetic north had been (fig. 6); an effect of the former magnetic field could not be demonstrated[66].

Thus, during ontogeny, celestial rotation and the stars may affect the later orientation by the magnetic compass, whereas the inital calibration of the star compass appears to be independent of the direction of the ambient magnetic field.

The interaction of the sunset factors with the other cues during ontogeny is less well studied. Alerstam and Högstedt[4] reported data which appear to suggest that sunset factors can be calibrated by the magnetic field in an imprinting-like process during the nestling stage. A more extensive study by Able and Able (in press) with Savannah sparrows also indicated that a sunset factor, namely the polarization pattern, acquired its directional significance from the geomagnetic field. In these tests, however, the learning processes took place after fledging. The setting sun itself was found to be of little importance.

Interaction of magnetic field and stars during autumn migration

During migration the relationship between the various cues changes considerably. The star compass is no longer controlled by celestial rotation. This is documented by experiments in which the stars and the magnetic field gave conflicting information[62]: when warblers of the genus *Sylvia* were tested under the clear night sky in an artificial magnetic field the north of which had been turned by 120° to ESE, the birds followed magnetic information (fig. 7a,b); they changed their preferred direction along with the change of magnetic north, although they could see the natural stars.



42000 nT, mN = 360°, 42° Incl.

42000 nT, mN = 120°, 50° Incl.

32000 nT, mN –, 90° Incl.

Figure 7. Orientation of garden warblers tested under the clear natural sky (a) in the local geomagnetic field, (b) in an experimental field with magnetic north = 120° ESE, and (c) without meaningful magnetic information[62]. In fig. 7c, triangles mark the bearings of birds that had been previously tested in the local geomagnetic field, and solid circles mark bearings of birds that had been previously tested in the experimental magnetic field. The small arrows indicate the respective means of the two subsamples.

Further tests with these birds in a reduced magnetic field that no longer allowed magnetic orientation indicated that the birds even re-calibrated their star compass according to the experimental magnetic field[62]; the birds that had been tested in the altered magnetic field maintained their preferred direction now by the stars alone, without further magnetic information (fig. 7c).

Tests in the reverse situation in a planetarium – natural magnetic field, altered sky – yielded similar results in the bobolink, *Dolichonyx orycivorus*[5]. Thus, during migration, magnetic information proved dominant, and the magnetic compass controlled the directional significance of the stars.

The experiments described above had been conducted using wild birds caught during migration, i.e. birds that had grown up under natural conditions and had already migrated some distance. Experiments with hand-raised garden warblers yielded different results[46]. When tested under an artificial 'sky' and in the natural geomagnetic field, which gave conflicting information, the birds followed the stars, apparently ignoring magnetic information. Here, in hand-raised birds, the star compass continued to be the dominant system, and it was unaffected by the ambient magnetic field. Earlier experiments by Emlen[26] had suggested a similar situation in hand-raised indigo buntings.

At first glance, this difference in behavior between wild-caught and hand-raised birds seems rather surprising. Yet it might reflect an important aspect of the interaction between the two systems. Celestial rotation and the stars seem to be most important during ontogeny and the start of migration when the migratory direction is first established. As the birds move south, the familiar stars of the home region descend and finally disappear below the northern horizon, while new configurations appear; the sky undergoes a slow, but continuous change. Also, the stars are frequently hidden by clouds. The wild birds had experienced all this already before they were tested, while the hand-raised birds had always been offered the same, unchanging sky that was never obscured. Possibly, the unavoidable experience associated with migration had led to the shift in the control of the star compass from celestial rotation during ontogeny to the magnetic field during migration, because the magnetic field, which is rather regular at lower latitudes, provides a good reference for calibrating new stars.

Another function of the stars during migration must be mentioned; they obviously help nocturnal migrants to keep a straight course. Radar ornithologists reported oriented movements under solidly overcast skies and even between clouds[10,29], yet an analysis of the tracks revealed that they were more scattered and less linear than those recorded under a clear sky[55]. This seems to indicate that optical sky marks play an important role in maintaining flight direction.

This is also reflected in the outcome of cage studies with captive birds. Many authors[22,25,50] found that their test birds showed much more scatter in the absence of visual cues, and from that they concluded that stars were essential for orientation. An analysis of the behavior of birds tested with and without stellar cues[58] showed, however, that under stars the birds' activity was significantly more

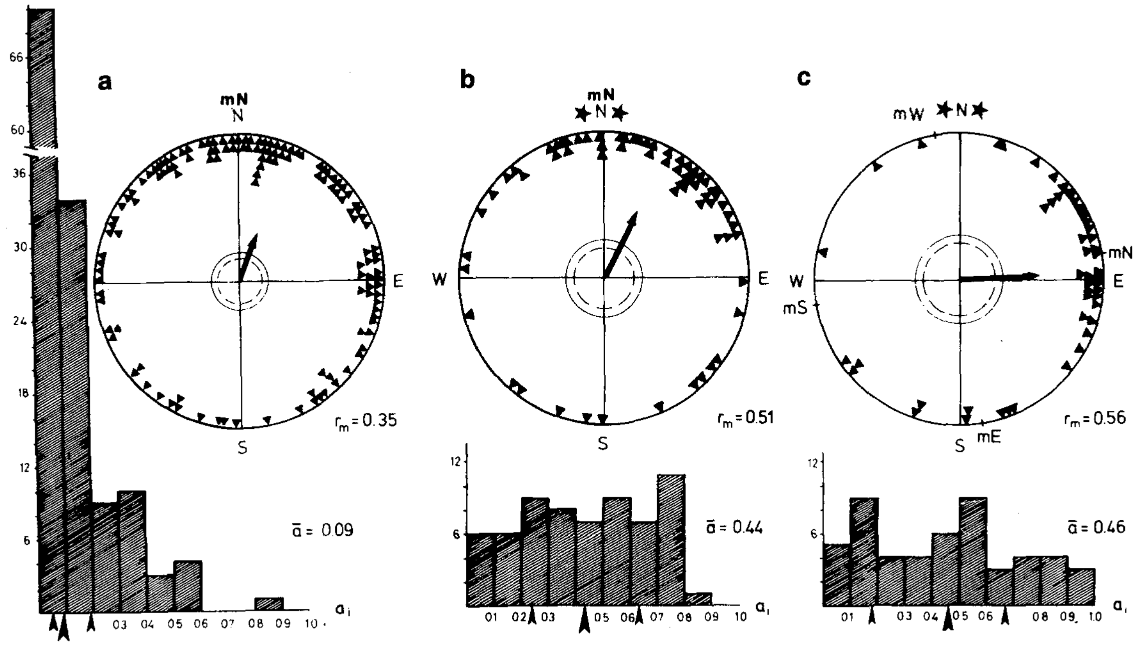


Figure 8. Orientation behavior of European robins in the local geomagnetic field (a) in the absence of visual cues, (b) under natural stars, (c) under artificial stars[58]. Symbols in the circular diagrams as in fig. 2, r_m = vector length representing the accuracy of directional selections. Below: Frequency distribution of a_i representing the concentration of activity in the selected direction. The medians and the 1st and 3rd quartile are marked with arrows; (a) gives the medians numerically.

concentrated, while the distribution of the means was not affected (comp. fig. 8). Obviously, the presence of stars does not allow a more accurate establishment of the migratory direction, but it facilitates maintaining the selected direction in the cage, which is reflected by a higher concentration of activity in that direction.

The role of sunset factors during autumn migration

The role of the orientation cues associated with sunset, and their possible interaction with other cues, appear to be much less uniform. All authors[17, 35, 37, 39, 40, 56] agree that the availability of the sunset cues generally improves orientation; for some species, they seem to be even more important than the stars. But whether they provide directional information or whether they simply act as a prominent visual mark that helps to confirm orientation is not completely clear. Clock-shift experiments with 3 h slow-shifted birds resulted in random behavior[3]. When the e-vector axis was rotated with the help of polarizers, the birds followed the e-vector axis and oriented parallel to it[2]. The data of Helbig and Wiltschko[33], however, suggest that such an artificial e-vector might be more attractive to the birds than the natural one and evoke a general change in reaction towards it.

While these findings point to a great importance of sunset factors, other data indicate only a minor role. Sandberg[48], testing European robins under polarizers, reported that the birds ignored the pattern of polarization. In many cases, however, the directions preferred by his test birds appear to be a compromise between the appropriate migratory direction and phototaxis towards the setting sun. Altering magnetic north resulted in changes in behavior that are difficult to interpret; frequently, the orientation became bimodal[49], which might reflect the axial character of the e-vector as a cue. Also, in the outdoor experiments mentioned before, the warblers followed the change in magnetic north, although they had been able to see the natural band of polarization at sunset[62].

Spring migration

Spring migration leads the birds back to their breeding area. The experiments by Löhrl[36] and Sokolov[54] indicate that birds already select their future breeding site in autumn before leaving for migration; thus in spring the birds head for an area where they have already spent some time and that is familiar to them.

Theoretically, the same mechanisms as those present in autumn, with reversed directions, would allow the birds a successful return. Laboratory experiments with hand-raised birds that were kept over the winter showed that these birds became migratorily active again and headed toward northerly directions[7, 14, 31], demonstrating that some innate information on their spring migratory direction is available to the birds. Whether this is just a reversal of the autumn directions or an independent set of directional information is still an open question – the fact that at least some species take different routes in autumn and in spring may be taken to suggest the latter.

Experimental evidence indicates that the orientation mechanisms used in spring are the same as in autumn; the magnetic field can serve as a reference also for the spring migratory direction[31], and recent experiments under the artificial sky suggest that the same might be true for the learned star compass[46]. When the stellar sky and the magnetic field yield conflicting information in spring, wild-caught European robins oriented according to magnetic north and recalibrated their star compass accordingly[16, 63], as the warblers and the bobolinks had done in autumn. The positive effect of stars on the concentration of activity during the tests (represented by a_i in fig. 8) was also observed in spring[58], while the accuracy of directional selection (represented by r_m in fig. 8) was not affected by the presence of stars.

The role of the sunset factors is relatively well studied in spring, yet here, too, the data do not form a completely homogeneous picture. As in autumn, the view of the setting sun and the pattern of polarization generally improved orientation[27, 39, 40]. Clock-shift experiments with 3-h fast-shifted birds[3, 32] suggested that the sunset situation was interpreted as part of the sun compass. Moore[41, 42] reported that Savannah sparrows could be induced to change their direction, also during the night, by reflecting the setting sun with mirrors. Later tests[45] with yellow-rumped warblers, *Dendroica coronata*, indicated that the pattern of polarization, which had been mostly eliminated in the first test, was the more important factor; the bird used the setting sun itself only when an e-vector was not available.

Other studies using polarizers also emphasized the important role of the band of polarization at sunset[1, 2] and at sunrise[43], which seemed to dominate over all other cues. Yet dunnocks, *Prunella modularis*, when tested outdoors in an altered magnetic field at sunset, oriented according to magnetic north and even seemed to recalibrate the pattern of polarization accordingly[18]. In the case of the European robin, Sandberg's birds did not react to the e-vector at all[48], while Helbig's changed their orientation with the e-vector and oriented parallel to it[32]; here, general differences in experimental design might have affected the outcome.

A complex system

Figure 9 shows the interrelations of stars, magnetic field and the sunset factors discussed so far, with the situation during spring migration being very similar to that in autumn.

The star compass, calibrated by celestial rotation, and the magnetic compass represent two mechanisms, each of which alone enables young birds to find their migratory direction. But under normal circumstances, both are in-

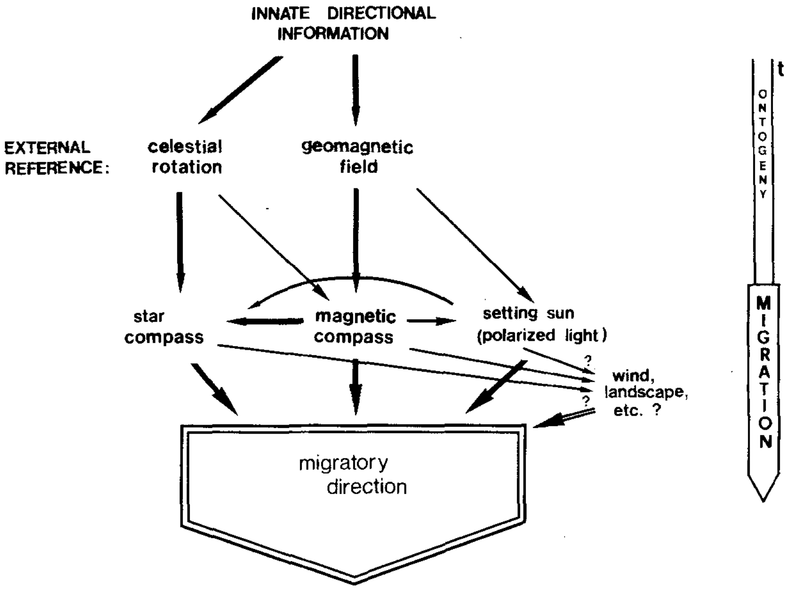


Figure 9. Interactions of stars, magnetic field and sunset factors in migratory orientation[64].

tegral parts of one complex system. Celestial rotation and stars appear to play the most important role during ontogeny and in establishing the first migratory direction, while the magnetic field appears to be of increasing importance during migration when new stars have to be calibrated.

The factors associated with sunset, like the view of the setting sun itself, horizon glow and the characteristic pattern of polarized light, are secondary cues of great importance. They acquire their directional significance during ontogeny, presumably from the magnetic field. Their role during migration appears to vary and it is still open whether some differences found by various authors are due to different methods and/or by species-specific differences in the behavior of the test birds, which might reflect specific adaptations to the species' normal migration. Landscape features or constant winds may also be calibrated, and temporarily help birds to find and maintain their course. Altogether, we may assume that migratory birds can utilize a variety of environmental factors which become secondary sources of directional information. Thus the orientation system is stabilized and becomes less susceptible to any kind of disturbance.

During spring migration, however, and all later migrations, the situation is even more complex. The large-scale displacement experiments with starlings mentioned in the beginning[47] clearly show that the return migration to the breeding sites, and later migrations, are more than simply flying in innate directions. The young birds that had spent their winter south of their traditional winter range, because of the displacement, returned to their normal breeding area. Displaced adult starlings that had already spent at least one winter in the traditional winter quarter were able to compensate for the displacement right away; they changed their course and flew towards their normal wintering grounds. Thus, when migratory birds are familiar with their goal area, they are able to head towards it directly.

This means that the birds must be able to determine the course leading to their goal area, which obviously requires mechanisms of true navigation. These mechanisms may be similar to the ones homing pigeons use when released away from their home; the nature, range etc. of these mechanisms are still largely unknown inspite of intensive research. The displacement experiments indicate that they are dominant over any innate directions, yet the true interactions of the two different mechanisms are still open. Under natural circumstances, their information will not diverge, and it is well possible that migrants fly by innate directions during most of their journey, especially when very long distances have to be covered. After reaching the region of their goal, however, they have to switch over to navigational mechanisms in order to find the specific site where they bred or wintered the year before.

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Olfactory navigation in birds

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Summary. Many bird species rely on an osmotactic mechanism to find food sources even at a considerable distance. Pigeons also rely on local odours for homeward orientation, and they integrate those perceived during passive transportation with those at the release site. It is possible to design experiments in which birds are given false olfactory information, and predictions about the effects of this can be made and tested. Pigeons build up their olfactory map by associating wind-borne odours with the directions from which they come; this was shown by experiments which aimed at preventing, limiting or altering this association. Some objections have been made to this conclusion; namely that even anosmic pigeons are sometimes homeward oriented, that they may be demotivated in flying or disturbed in their general behaviour, and that olfactory cues may be only one component of pigeon's navigational repertoire. The most recent experiments, however, confirm that pigeons derive directional information from atmospheric odours. The lack of any knowledge about the chemical nature and distribution of the odorants which allow pigeons to navigate hinders progress in this area of research.

Key words. Bird olfaction; orientation; navigation; homing pigeon.

Introduction

Until the 1950s, observations on bird behaviour in response to olfactory stimuli yielded conflicting results. Many zoologists considered the olfactory ability of birds to be very low and the question sometimes arose whether their olfactory apparatus had a different function from that of sensing odours. The opinion that birds have no olfactory ability was widely held in the 1940s, when an authoritative paper[120] reported the results of a series of physiological and behavioural tests performed on several species, which were found by the author to be insensitive to odours. More recently, however, a re-evaluation of the olfactory ability and the role of olfaction in a bird's life has been prompted by anatomical, physiological and behavioural evidence[10].

Anatomical studies have shown that the relative size of the olfactory bulbs, as measured by the ratio between the olfactory bulb diameter and that of the cerebral hemisphere, expressed as a percentage, varies between 3% and 37%[9]; this is an indication of differences in the importance of olfactory perception in different species. Electrophysiological recordings from the olfactory membrane, nerves, bulbs or associated single units showed clear responses to odorants according to intensity and quality of stimuli[62,85,93,127]. Spontaneous visceral responses to odours, including respiration and heart rate changes, which can be strengthened by pairing the stimulus with an electric shock, have been successfully used to test olfactory sensitivity[84,98,121,123].

A rather long series of both classical and operant conditioning experiments indicating that birds are poor at associating odours with other stimuli[22,120] lent support to the idea that traditional conditioning methods were quite ineffective in demonstrating the sensitivity of birds to odours. A conditioned suppression method – although it was time-consuming – was eventually set up and successfully used[34,86,87,91]. More recently, however, simple conditioning methods were also reported to yield positive results[28,41,46].

The olfactory sensitivity threshold was determined for a few species by using a small number of compounds, whose odour probably has little, if any, biological relevance for the birds tested[88,89,91,98]. Many values lie between 10^{-5} and 10^{-7} M, and they are seldom as low as 10^{-9}. However, the threshold for certain substances of biological relevance might be much lower. In fact, even species with poorly developed olfactory bulbs may be specialized for sensing some compounds, whereas a large olfactory membrane tends to indicate a high capacity for discrimination between odours[2].