BioOne COMPLETE

Avian Navigation

Authors: Wiltschko, Roswitha, and Wiltschko, Wolfgang

Source: The Auk, 126(4) : 717-743

Published By: American Ornithological Society

URL: https://doi.org/10.1525/auk.2009.11009

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

The Auk

An International Journal of Ornithology

Vol. 126 No. 4 October 2009



The Auk 126(4):717–743, 2009.

© The American Ornithologists' Union, 2009.

Printed in USA.

SPECIAL REVIEWS IN ORNITHOLOGY

AVIAN NAVIGATION

ROSWITHA WILTSCHKO[1] AND WOLFGANG WILTSCHKO

Fachbereich Biowissenschaften der Universität Frankfurt, Siesmayerstraße 70, Haus A, D 60054 Frankfurt am Main, Germany

THEIR SUPERB ABILITY to fly allows birds to move faster than any other animals: even small passerines fly at top speeds of up to 40–50 km h^{-1}, pigeons can fly about 60–70 km h^{-1}, and birds like swifts are even faster. The distances birds cover during everyday life are considerably longer than those covered by mammals of similar size. Some marine birds venture out for extended foraging trips over the sea; albatrosses (*Diomedea* spp.), for example, may cover several thousands of kilometers. Displaced carrier or homing pigeons (*Columba livia* f. *domestica*) are famous for homing over hundreds of kilometers from unfamiliar sites, and many wild birds also home over considerable distances (for an overview, see R. Wiltschko 1992). Numerous avian species migrate each year to spend the winter in the tropics or in the summer of the opposite hemisphere, covering thousands of kilometers. Two of the most spectacular examples of large migration routes are those of Sooty Shearwaters (*Puffinus griseus*) from New Zealand, which wander all over the Pacific Ocean up to Kamchatca and Alaska, and Arctic Terns (*Sterna paradisaea*), which breed in the Arctic tundra and winter on the Antarctic coast, flying around the globe every year. The mechanisms of orientation and navigation of birds must be adapted to these tremendous demands.

After a few publications on theoretical considerations about avian navigation and initial preliminary experiments, systematic studies to analyze birds' navigational mechanisms began in the 1950s, when the sun compass was the first orientation mechanism to be identified (Kramer 1950). Our knowledge has increased considerably since then, although a number of open questions remain. Here, we briefly summarize what is known today about birds' navigational mechanisms.

"This combination of innate and learned components makes the navigational system highly flexible…. [It] enables birds to make use of a wide variety of factors the environment has to offer, at the same time ensuring that the learned mechanisms are perfectly adapted to the local situation. This makes avian navigation so powerful and effective."

REFERENCE TO THE GOAL

When flying around in their spacious territories, on extended foraging trips or during migration, birds are usually so far away from their goal that they are beyond any direct sensory contact. Yet they have to reach it speedily and efficiently to minimize time, energy expenditure, and the risk of predation. They face the task of finding the distant goal without the help of any direct cue emerging from it.

Birds solve this problem by establishing contact with their goal through the help of an external reference, in a two-step process first suggested by Kramer (1953, 1957) in his "map-and-compass" model originally designed for homing pigeons. In the first step, equivalent to use of a map, birds determine the compass course to their goal—information that, in human terms, would be something like "in the south" or "in the east." In the second step, they consult a "compass" to locate this course, obtaining information like "this way" or "go there" (Fig. 1). The crucial

[1]E-mail: wiltschko@bio.uni-frankfurt.de

The Auk, Vol. 126, Number 4, pages 717–743. ISSN 0004-8038, electronic ISSN 1938-4254.

© 2009 by The American Ornithologists' Union. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, http://www.ucpressjournals.com/reprintInfo.asp.

DOI: 10.1525/auk.2009.11009

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

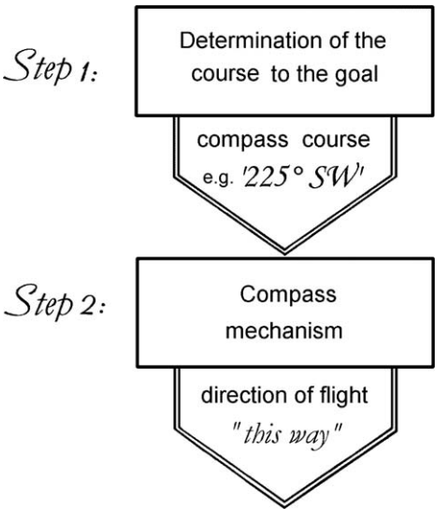


Fig. 1. The map-and-compass model proposed by Kramer (1953, 1957), considering navigation as a two-step process.

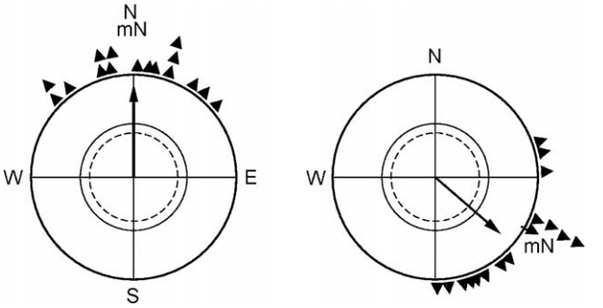


Fig. 2. Demonstrating the use of the magnetic field as a compass. Orientation of European Robins in cages in spring with the magnetic field as the only cue in the geomagnetic field (left) and in an experimental magnetic field of the same intensity and inclination, but with north shifted by 120° to east-southeast (right). Triangles: mean headings of individual birds; arrows: mean vectors in relation to the radius of the circle = 1. Inner circles are the 5% (dotted) and the 1% significance border of the Rayleigh test for statistical significance (data from W. Wiltschko et al. 2001).

idea of this model, that contact with the goal is established by an external reference, is not limited to homing; it can be generalized as a "compass model" to include any task of reaching a distant goal (see R. Wiltschko and Wiltschko 2003). Once the bird is aware of the compass course that leads to the goal, it is able to fly there.

Hence, to understand the navigational system of birds, we must answer two questions. First, how do birds set the course to the goal? And second, what types of compass mechanisms do they use? We will begin here with the second question, because the compass mechanisms the birds employ are much better understood than the mechanisms that provide the compass courses.

Compass Mechanisms

A compass is a mechanism that indicates where directions like north, east, south, and west lie, independent of the location on earth where it is used. There are only two types of natural cues that provide the required information: (1) the geomagnetic field and (2) celestial cues like the sun, the stars, and associated factors. Both have been shown to be used by birds for directional orientation. The magnetic field is always available, but the mechanisms based on celestial cues differ between day and night and are weather dependent in that their use requires a more-or-less clear sky.

The Magnetic Compass of Birds

The magnetic field of the earth is a vector field. The field lines leave the earth at the southern magnetic pole near the geographic South Pole, curve around the globe, and re-enter the earth at the northern magnetic pole near the North Pole. With respect to the horizontal, they are inclined upward in the Southern and downward in the Northern Hemisphere. In most regions, the field lines run roughly north–south, but near the poles there are larger differences between geographic and magnetic north. The total intensity of the geomagnetic field varies between ~60 μT at the poles and ~30 μT near the magnetic equator, where field lines are parallel to the earth's surface (see Skiles 1985).

Birds' ability to use the geomagnetic field for orientation was first demonstrated in the 1960s in migratory birds. During the migration season, these birds show a strong preference for their seasonally appropriate migratory direction, not only in nature but also in captivity. For example, in the Northern Hemisphere, southern directions are preferred in autumn and northern directions in spring. The limited space of a cage allowed the experimenters to easily manipulate the magnetic field around the cage with Helmholtz coils in a controlled way, to expose the birds to various magnetic conditions and record their responses. In the crucial experiments, European Robins (*Erithacus rubecula*) were tested in an experimental magnetic field with intensity and inclination identical to those of the local geomagnetic field, but with magnetic north turned to east-southeast. The birds, following the shift in magnetic north, then preferred southeasterly headings (Fig. 2; e.g., W. Wiltschko 1968). This response clearly showed that they used the magnetic field to orient their migratory behavior.

Functional properties of the avian magnetic compass

Using migratory orientation as a criterion for whether birds could detect a specific magnetic field and what they assumed to be magnetic north, researchers analyzed how the avian magnetic compass works. It was found to differ fundamentally from our technical compass in three ways (for summary, see W. Wiltschko and Wiltschko 2007b): it is an "inclination compass," it spontaneously operates only within a limited functional window, and it is light dependent.

Inclination compass.—Birds from the Northern Hemisphere were tested in spring in a field with magnetic north unchanged but with the inclination turned upward, as it is found in the Southern Hemisphere. In this situation, the birds reversed their headings, now preferring southerly instead of northerly directions. This response indicated that they do not rely on the polarity of the

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

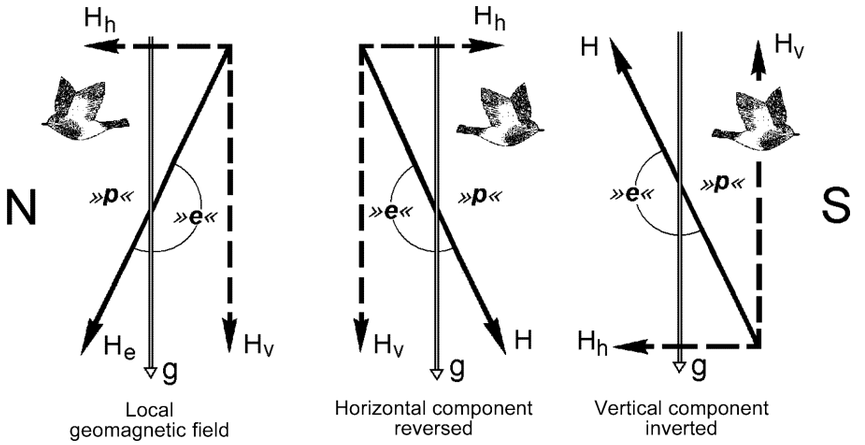


FIG. 3. Schematic view of the geomagnetic field from the west, illustrating the course of the field lines and how the inclination compass of birds works (N = north; S = south; H_e = vector of the earth's magnetic field; H = vector of an experimental magnetic field; H_h and H_v = horizontal and vertical components of the magnetic field, respectively; g = gravity; »p« and »e« are readings of the avian inclination compass. The bird in the figure flies poleward.

magnetic field, which they seem unable to sense. Instead, they respond to the course of the field lines and their inclination (Fig. 3). As a consequence, this type of compass distinguishes not between magnetic north and south (a distinction based on polarity) but between poleward, where the field lines are inclined downward, and equatorward, where they are tilted upward.

Such a compass becomes ambiguous at the magnetic equator, where the field lines run horizontally. In a horizontal magnetic field, birds were indeed found to be disoriented, and this was also true for species that cross the magnetic equator on their annual migrations twice a year (W. Wiltschko 1974, Beason 1989). How birds solve the problem of orientation at the magnetic equator is not entirely clear; switching over to using, for example, celestial cues until the inclination is again above threshold is a possibility. Experiments with Bobolinks (*Dolichonyx oryzivorus*) supported this idea (Beason 1992). For the problem that after crossing the magnetic equator the birds have to continue poleward instead of equatorward, an elegant solution was found: experiencing the horizontal field itself triggers this change in heading (W. Wiltschko and Wiltschko 1992).

Functional window.—When European Robins were kept in a geomagnetic field of 46 μT and tested in fields with varying intensity, a functional window became evident: decreasing or increasing the local intensity about 25–30% caused disorientation. The finding that weaker fields lead to disorientation was not surprising; they could simply have been below threshold. Yet the observation that increasing the intensity also prevented birds from orienting in their migratory direction was unexpected. It offered an *a posteriori* explanation for the failure of many early attempts to demonstrate magnetic-compass orientation: the test fields had been too strong, outside the functional window.

The functional window is not fixed, however, but can be adjusted to different intensities. Birds regain their ability to use their magnetic compass in weaker as well as in stronger fields by staying in the respective fields for a while. Interestingly, this adjustment does not represent a shift or an enlargement of the functional window. European Robins adjusted to weaker or stronger fields retained their ability to orient in the local magnetic field. They could also orient in a field more than 3 times as high after exposure to that field, but they were disoriented in a field with intermediate intensity. It seems that exposure to an intensity outside the normal functional range creates a new functional window at this intensity. Recent experiments indicate that the time required for adjustments to other intensities is not very long: 1 h proved sufficient to allow birds to become oriented at an intensity twice that of the geomagnetic field (W. Wiltschko et al. 2006). For migrants, this flexibility means that their magnetic compass can be optimally adjusted to new intensity values: on their way toward their winter quarters, they reach regions where the intensity of the geomagnetic field is considerably lower than in their breeding range, but the gradually decreasing intensity they encounter en route adjusts their magnetic compass to the new magnetic situations.

Wavelength dependence.—Tests with migratory birds under monochromatic light of different wavelengths indicated that the avian magnetic compass requires short-wavelength light from 360 nm ultraviolet (UV) up to ~565 nm green; under longer wavelengths, the birds were disoriented (Rappl et al. 2000, Muheim et al. 2002; for a summary, see W. Wiltschko and Wiltschko 2007b). The monochromatic lights have to be rather dim, however; above a certain light intensity that decreases from green to UV, migratory birds showed disorientation or axial response that no longer represented normal compass orientation (R. Wiltschko et al. 2007b).

Physical mechanisms underlying the avian magnetic compass

For a long time, the question of how birds are able to sense the direction of the magnetic field remained unanswered. Any hypothesis to explain magnetoreception in birds must take the known characteristics of the avian magnetic compass into account. Such a hypothesis, the "radical-pair model," was forwarded by Ritz et al. (2000). The model suggests that magnetoreception in birds is

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

based on spin-chemical processes in specialized photopigments. Light-induced photon absorption leads to the formation of a pair of radicals with unpaired electrons. These radical pairs may be in the singlet state, with electron spins antiparallel, or in the triplet state, with spins parallel. The amount of each state and their products depends, among other circumstances, on the alignment of the molecule in the external magnetic field and could, therefore, be used to detect the magnetic directions. For this, the birds must be able to compare the amount of singlets or triplets in the various spatial directions, which requires an orderly array of pigments. The authors therefore suggested that the magnetosensitive processes take place in the eyes, forming centrally symmetric patterns on the retina (Ritz et al. 2000).

The radical-pair model accounts for all characteristics of the avian magnetic compass described above (for details, see W. Wiltschko and Wiltschko 2007b). Meanwhile, the prediction that magnetoreception takes place in the eyes is also experimentally confirmed: the magnetic compass was found to be strongly lateralized in favor of the right eye (W. Wiltschko et al. 2002, Rogers et al. 2008).

The radical-pair model predicts that the oscillating magnetic fields in the MHz range would interfere with the singlet–triplet interconversion and, thus, should disrupt the magnetic compass. This was found to be true: oscillating fields caused disorientation in migratory birds (Ritz et al. 2004, Thalau et al. 2005), which indicates that the avian magnetic compass is indeed based on radical-pair processes. Tests in oscillating fields with different frequencies and intensities identified the lifetime and properties of the crucial molecule, which was found to be optimally sensitive for detecting magnetic directions (Ritz et al. 2009). Cryptochrome, suggested by Ritz et al. (2000) and found in the retina of chickens and passerines (Haque et al. 2002, Möller et al. 2004, Mouritsen et al. 2004), has the required properties and is discussed as the receptor molecule.

An alternative model for magnetoreception had suggested receptors based on magnetite, a specific form of Fe_3O_4 (e.g., Yorke 1979, Kirchvink and Gould 1981, Kirschvink and Walker 1985, Shcherbakov and Winklhofer 1999, and others). Small particles of magnetite have been found in the skin of the upper beak of pigeons and passerines (Fleissner et al. 2003, 2007), but temporarily stunning them with a local anesthetic had no effect on migratory orientation, so these particles do not seem to be involved in the avian magnetic compass (e.g., Stapput et al. 2008).

Magnetic-compass orientation in different tasks

When the findings on magnetic-compass orientation in European Robins were first published, they met with considerable skepticism, and many other migratory birds were tested for their ability to use the magnetic field for orientation. A magnetic compass has been found in passerine birds and in a shorebird species, in diurnal, nocturnal, and twilight migrants from Europe, North America, and Australia migrating short, medium, and long distances. It seems to be a very widespread mechanism. Table 1 lists these species (for a list of the respective references, see W. Wiltschko and Wiltschko 2007b).

But the magnetic compass is by no means restricted to migrants. In the early 1970s, Keeton (1971) reported that magnets fixed on their backs would have a disorienting effect on displaced homing pigeons released under overcast skies, which suggested that the birds use the magnetic compass in homing to locate their home course. Young pigeons raised without ever seeing the sun

Table 1. Migratory birds that have been shown to use a magnetic compass.

Taxon	Distribution	Distance	Time of migration
Charadriiformes			
Sanderling (Scolopacidae: *Calidris alba*)	Arctic	Medium to long	Day and night
Passeriformes			
Barn Swallow (Hirundinidae: *Hirundo rustica*)	Holarctic	Long	Day
Dunnock (Prunellidae: *Prunella modularis*)	Europe	Short to medium	Night
Northern Wheatear (Turdidae: *Oenanthe oenanthe*)	Eurasia	Long	Night
Garden Warbler (Sylviidae: *Sylvia borin*) [a,c]	Europe	Long	Night
Whitethroat (Sylviidae: *S. communis*)	Eurasia	Long	Night
Blackcap (Sylviidae: *S. atricapilla*) [a]	Europe	Medium to long	Night
Subalpine Warbler (Sylviidae: *S. cantillans*)	Mediterranean	Medium	Night
Goldcrest (Sylviidae: *Regulus regulus*)	Europe	Short	Day and night
Pied Flycatcher (Muscicapidae: *Ficedula hypoleuca*) [a]	Europe	Long	Night
European Robin (Turdidae: *Erithacus rubecula*) [a,b,c]	Europe	Medium	Night
Common Rosefinch (Fringillidae: *Carpodacus erythrinus*)	Eurasia	Long	Night
Chaffinch (Fringillidae: *Fringilla coelebs*)	Europe	Short	Day
Snow Bunting (Emberizidae: *Plectrophenax nivalis*)	Arctic	Short	Day and night
Indigo Bunting (Emberizidae: *Passerina cyanea*)	North America	Long	Night
Bobolink (Icteridae: *Dolichonyx oryzivorus*) [a]	North America	Long	Night
Red-eyed Vireo (Vireonidae: *Vireo olivaceus*)	North America	Long	Night
Yellow-faced Honeyeater (Meliphagidae: *Lichenostomus chrysops*) [a]	Australia	Medium to long	Day
Silvereye (Zosteropidae: *Zosterops lateralis*) [a,b,c]	Australia	Medium	Twilight

[a] Species in which an inclination compass has been demonstrated.
[b] Species in which lateralization of the magnetic compass has been demonstrated.
[c] Species in which light-dependence of the magnetic compass has been demonstrated.

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

showed normal orientation, which indicates that a functioning navigational system can develop with the magnetic compass as the only compass (W. Wiltschko et al. 1987b). Experiments by Walcott and Green (1974), who released homing pigeons with small coils that allowed the magnetic field around their heads to be changed, indicated the use of an inclination compass, and experiments with pigeons displaced under monochromatic lights suggested a wavelength dependence similar to that found in European Robins (R. Wiltschko and Wiltschko 1998). Lateralization in favor of the right eye is also suggested (Prior et al. 2004), which points to a mechanism like that found in European Robins.

Recently, magnetic-compass orientation has been demonstrated in two more species of nonmigrants, Domestic Chickens (*Gallus gallus*; Freire et al. 2005) and Zebra Finches (*Taeniopygia guttata*; Voss et al. 2007). Because these birds do not show spontaneous directional preferences, directional tendencies had to be induced by conditioning the birds to look for a reward—a social stimulus in chickens, and a food reward in Zebra Finches—in a specific magnetic direction in an otherwise featureless arena. The birds mastered these tasks, showing that the magnetic compass can also be used in small-scale environments as a component of spatial memory.

The two conditioning studies mentioned above were the first successful ones after numerous earlier attempts to condition birds to magnetic directions had failed (e.g., Griffin 1987). For a detailed discussion of the possible reasons why these two studies succeeded where earlier ones had not, see W. Wiltschko and Wiltschko (2007b).

In chickens, conditioning also was used to analyze the properties of the magnetic compass, and they were found to be in excellent agreement with those described in European Robins. Light-dependence and a functional window were demonstrated; orientation was disrupted by an oscillating magnetic field in the MHz-range, which indicates that it too is based on radical-pair processes, whereas local anesthesia of the putative receptors in the upper beak had no effect (W. Wiltschko et al. 2007). These findings are important for evolutionary considerations: passerines and galliforms belong to different lineages of birds that separated 90 mya, in the beginning of the Late Cretaceous (Ericson et al. 2006). Finding the same type of magnetic compass in these not-closely-related species suggests that it is common to all modern birds and already existed in their ancestors in the Mesozoic.

In summary, a magnetic compass is widespread among birds, and it can be employed to locate courses of different nature in different tasks: the migratory direction, the home direction, directions in a limited space set by the experimenter, and those remembered by the bird. It is a mechanism that birds can call upon whenever they have to locate directions.

The Sun Compass

In contrast to the geomagnetic field, the sun is not a constant cue but moves across the sky in the course of the day. This means that the time of day must be considered if the sun's position is interpreted to derive geographic directions. Sun-compass orientation thus involves the internal clock. Yet the sun's arc is not constant but depends on geographic latitude and also changes with season. This makes the sun compass a rather complex mechanism.

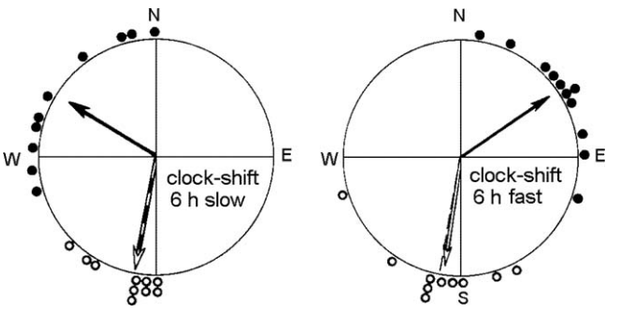


Fig. 4. Demonstrating sun-compass use: homing pigeons are released north of their loft, and the home direction is indicated by a dashed radius. Symbols at the periphery of the circle mark the vanishing bearings of individual birds, and arrows represent the mean vectors. Open symbols represent untreated control birds, and solid symbols birds whose internal clock was shifted 6 h.

The use of the sun for orientation was first demonstrated by Kramer (1950) in his classic mirror experiment. He tested a European Starling (*Sturnus vulgaris*) in a round cage that was placed in the center of a pavilion with six symmetrically positioned windows. When the windows were equipped with large mirrors that deflected the incoming light by ~90°, the bird changed its directional preference accordingly, which indicates that it used the sun for orientation.

Schmidt-Koenig (1958) used a different approach, making use of the fact that the internal clock was involved. He confined pigeons in a light-tight room for at least five days under a photoperiod that was shifted with respect to the natural one, usually by 6 h, to reset their internal clock. When later released, the birds misjudged the time of day and, consequently, the position of the sun. A pigeon whose internal clock was shifted 6 h fast, released at 0600 hours, would interpret the morning sun in the east to be the noon sun in the south and, for example, intending to head south, would head east instead. This would result in a typical counterclockwise deflection, which indicates the use of the sun compass. Setting the internal clock 6 h slow results in a corresponding clockwise deflection (Fig. 4). This is true for experiments in the Northern Hemisphere; in the Southern Hemisphere, where the sun moves from east via north to the west, the induced deflections are the mirror image of those described above (see R. Wiltschko et al. 1998).

Functional properties of the avian sun compass

Clock-shift experiments became an important tool to demonstrate sun-compass orientation and to analyze the functional mode of this mechanism.

Use of the solar azimuth.—The early researchers (e.g., Schmidt-Koenig 1965) observed that birds apparently rely only on the sun's azimuth (i.e., the direction of the sun), ignoring its altitude. In the example described above, the pigeon is released at its subjective noon when it should be expecting the sun to be high. Instead it sees the sun low above the horizon, but nevertheless it treats it as if it were the noon sun and shows the respective deflection. Clock-shift experiments near the Equator indicated that

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

pigeons can still determine the solar azimuth when its distance from the zenith was between 6° and 3° (Schmidt-Koenig 1990).

Different rates of change in the solar azimuth in the course of the day.—After sunrise, the sun quickly gains altitude but makes only slow progress in azimuth; around noon, when the sun is high, the azimuth changes rapidly but the changes in altitude are small. These differences in the solar azimuth's rate of change are relatively small at higher latitudes but become considerable at temperate latitudes and extreme at the Equator, where, at the equinoxes, the sun is in the east all morning and in the west all afternoon. The first indications that birds correctly compensate for the different rates of change in the solar azimuth came from clock-shift experiments near the Equator in Brazil: pigeons whose internal clock was shifted 4 h showed a 180° change when they were released in the afternoon while their internal clock still indicated morning (Ranvaud et al. 1988). Experiments in New Zealand at 37°S also involved 4-h shifts, with one group of pigeons released during the hour after sunrise and the hour before sunset, when the expected deflection was only 38°, and another released between 0900 and 1100 hours, when it was 125°. The two groups differed markedly in the size of deflection from the untreated controls (Fig. 5), which indicates that pigeons are indeed aware of the different rates of change in the solar azimuth (R. Wiltschko et al. 2000).

Polarized light.—The light from the sky is partly polarized, with the maximum polarization, 70%, forming a band at 90° to the position of the sun. Hence, birds could, theoretically at least, use the polarization pattern to determine the sun's position when the sky is partly cloudy. Insects like bees and ants are known to do so (see von Frisch 1965, Wehner 1982), but displaced homing pigeons do not seem to use the pattern of polarized light in this way (Kramer 1952, Chelazzi and Pineschi 1974). Keeton (1969), who had released pigeons whose internal clock was shifted 6 h under a partly cloudy sky, reported that the birds showed the typical deflection as long as the sun was visible to the experimenters.

In migratory birds, however, the polarization pattern appears to play an important role, in particular at sunset, when many night-migrating birds start their nocturnal flight. At this time the pattern is very conspicuous, forming a vertical band at 90° from the sun through the zenith. Observing a clear sky at dusk was found to improve orientation (e.g., Moore 1986, Akesson et al. 2001). The use of polarized light as a sunset cue was first indicated when Able (1982) reported that the orientation of migrants in test cages could be affected by polarization filters that rotated the axis of the e-vector of polarized light: the birds changed their headings accordingly, although the western part of the sky was still the brightest (see Moore 1986, Able 1989). In later experiments comparing the response to natural and artificially polarized light, differences in the birds' response became evident. Night-migrating Blackcaps (*Sylvia atricapilla*) preferred directions parallel to the artificial e-vectors produced by polarization filters, whereas they maintained an angle of ~60° to the natural e-vector, heading into their southwesterly migratory direction (Helbig and Wiltschko 1989). Moore (1986) and Able (1989), whose test species had southerly migratory directions more or less coinciding with the one end of the natural e-vector axis, could not detect this difference.

Use of polarized light, however, was indicated when Blackcaps and European Robins tested at sunset in a compensated magnetic field continued to prefer their migratory direction but became disoriented when the test cage was covered with a depolarizer that eliminated polarization (Fig. 6; Helbig 1990, 1991). Experiments with an Australian diurnal migrant, the Yellow-faced Honeyeater (*Lichenostomus chrysops*), indicated a similar role of polarized light as an orientation cue. These birds remained oriented in a compensated magnetic field as long as the pattern of polarized light was visible; when it was disrupted by depolarizers, they were disoriented, although the sun itself was still visible as the brightest spot in the sky (Munro and Wiltschko 1995).

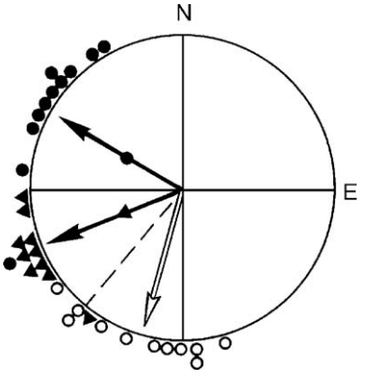


Fig. 5. Demonstration that pigeons consider the different rates of change in the solar azimuth in the course of the day. Pigeons were released at different times of day. The home direction is marked by a dashed radius. Open symbols indicate bearings of untreated control birds, and solid symbols indicate bearings of birds whose internal clock was shifted by 4 h. Triangles mark bearings at a time when the difference in solar azimuth between actual time and the birds' subjective time was ~38°, and dots mark bearings at a time when the respective difference was ~125° (data from R. Wiltschko et al. 1998).

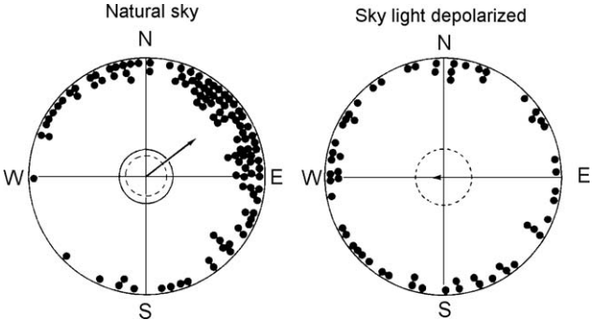


Fig. 6. Demonstration of orientation by polarized light: orientation of European Robins in a distorted magnetic field under the clear evening sky and under depolarizers. Symbols at the periphery of the circle mark headings of birds that were tested alternately in both conditions. Inner circles are the 5% (dotted) and the 1% significance border of the Rayleigh test (modified from Helbig 1991).

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

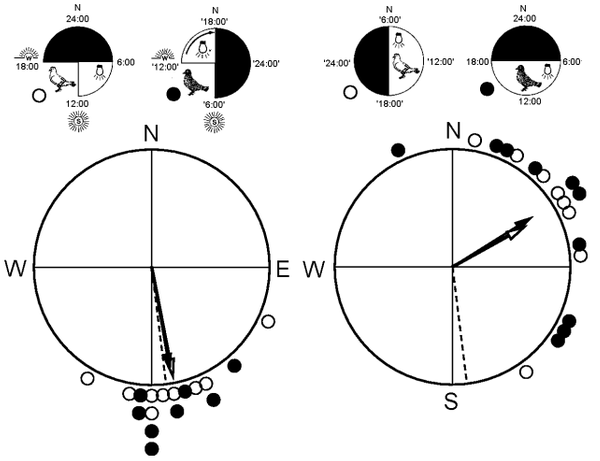


FIG. 7. Demonstration that the sun compass is based on experience. The home direction is indicated by a dashed radius. Left: solid symbols indicate bearings of pigeons that lived in a photoperiod permanently shifted 6 h slow, the home direction is indicated by a dashed radius, and open symbols indicate vanishing bearings of untreated control birds. Right: solid symbols indicate bearings of pigeons formerly kept in a photoperiod permanently shifted 6 h slow whose internal clock had been reset to normal time, and open symbols indicate bearings of control birds whose internal clock was shifted 6 h fast. The diagrams above indicate the light-and-dark phase of the respective group of pigeons (data from W. Wiltschko et al. 1976).

The ontogenetic development of the sun compass

The fact that the sun's arc depends on geographic latitude means that the compensation mechanisms of the sun compass must be finely tuned to the location where the birds live. Considering this, it was no surprise that the sun compass is not innate but is based on experience. This was first demonstrated by a series of experiments with young pigeons that had been raised in a permanent 6-h slow-shifted photoperiod: these birds knew the sun only in the afternoon, which was their subjective morning. During the time when their artificial photoperiod overlapped with the natural one, they were allowed to fly freely in their loft and also received several training flights. When released in critical tests on a sunny afternoon, they oriented just as the control birds that had lived in the natural photoperiod did. To find out whether they really used the sun compass, the experimental group's internal clock was shifted back to the natural day, whereas that of the control birds was shifted 6 h fast (Fig. 7). Released under sunlight, the experimental birds now showed the typical deviation, which indicates use of the sun compass, and their orientation did not differ from that of the fast-shifted controls (W. Wiltschko et al. 1976).

The behavior of the experimental group clearly shows that the pigeons were using a sun compass, albeit a false one adjusted to the experimental situation: for them, the "morning" sun had been in the south, and the sun at midday in the "west"; they did not know about the afternoon sun because they had been confined in their loft. This documents that the sun compass is a mechanism based on experience. Clock-shift experiments in New Zealand showed that the pigeons there, descendents of European pigeons introduced by early settlers, learn a sun compass that compensates for the counterclockwise movement of the sun in the Southern Hemisphere (R. Wiltschko et al. 1998).

Learning the sun compass.—The ontogeny of the sun compass was analyzed in young homing pigeons. These birds leave the nest when they are ~24 days old and start to fly at an age of ~5 weeks, at first only short distances, but soon they begin to fly longer distances and more perseveringly. A series of experiments that shifted the internal clock of young birds of various ages and experience indicated that the sun compass spontaneously develops in the third month of life. There seemed to be a lot of variance, however, although most birds younger than 12 weeks did not show the typical deflection indicating sun-compass orientation, some individuals already showed deflected headings. From the age of 12 weeks onward, young pigeons responded with the typical deflection (R. Wiltschko and Wiltschko 1981). However, early training flights and the associated flying experience advance the development of the sun compass considerably, such that it is already working at the age of 8–9 weeks. Being faced with the necessity to orient apparently initiates the learning processes in young pigeons and can lead to establishment of the sun compass at a younger age.

Young pigeons that had seen the sun only in the afternoon proved unable to use the sun compass in the morning and were disoriented by magnets glued to their backs (R. Wiltschko et al. 1981). When released with their internal clocks shifted 6 h slow in their subjective morning, they oriented homeward like the controls (R. Wiltschko and Wiltschko 1980). Both of these findings indicate that pigeons without sun experience in the morning used their magnetic compass instead. Apparently, birds have to observe large portions of the sun's arc at different times of day to develop a sun compass that works during the entire day.

Magnetic field as reference.—The observation that young pigeons have to observe the sun's arc led to the question of how they register the sun's progress. One possibility was the use of the magnetic compass. To test this hypothesis, young pigeons at the age when they learn the sun compass were exposed to the natural sun for 10 sunny days in an artificial magnetic field with magnetic north turned 120° clockwise to east-southeast. Released away from their loft, they showed a marked clockwise deflection from control birds (Fig. 8), which suggests that they had learned an abnormal sun compass in the experimental magnetic field (R. Wiltschko and Wiltschko 1990). This indicates that the magnetic compass, an innate mechanism, provides the reference system for learning the sun compass.

Old, experienced pigeons exposed to the natural sun in a field with shifted magnetic north did not respond with a deflection, but rather flew in the same direction as the controls—they seemed to have ignored the altered directional relationship between sun and magnetic field (R. Wiltschko and Wiltschko 1990). This difference between young pigeons at the age of learning the sun compass and older pigeons suggests a sensitive period during which young birds pay particular attention to the sun and its directional relationship to the magnetic field. Apparently, the learning processes that establish the sun compass present a defined developmental process, with a special readiness to obtain the relevant information.

Adjustment to seasonal changes.—The sun compass, once learned, must remain flexible, because the changes of the sun's arc in the course of the year make a continuous gradual adjustment

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

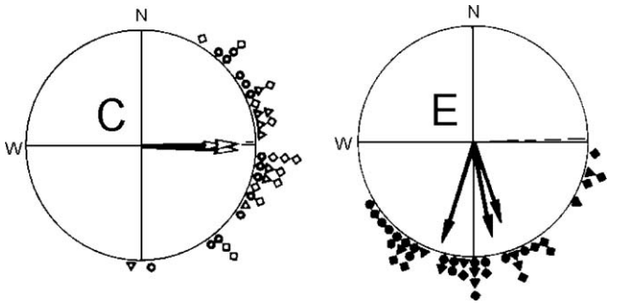


Fig. 8. The magnetic field serves as reference for the sun compass. Vanishing bearings of three releases of young pigeons are indicated by differently shaped symbols. The home direction is indicated by a dashed radius. Left: bearings of control birds (C) that had observed the sun in the natural geomagnetic field. Right: bearings of experimental birds (E) that had observed the sun for >10 sunny days in a magnetic field with north shifted by 120° to east-southeast (data from R. Wiltschko and Wiltschko 1990).

necessary. How the birds cope with this problem has not been analyzed. A series of experiments with adult pigeons that were subjected to a 6-h slow shift and lived in this artificial photoperiod for three months, being allowed to fly freely during the overlap time between the natural and their subjective day, showed that these birds altered their sun compass, adjusting it to the experimental situation (W. Wiltschko et al. 1984). The sun compass thus remains flexible, and adjusting it to the seasonal changes of the sun's arc should not pose a problem. Analogizing to the processes that establish the sun compass, one might assume that the magnetic field serves as a directional reference for these adjustments.

The experiments analyzing the development of the sun compass were all performed with homing pigeons, with nothing known about the development of the sun compass in other avian species. We can only speculate that it occurs in a similar way, but data are not available.

Use of the sun compass in various orientation tasks

Most studies on sun-compass orientation involved displaced homing pigeons. Sun-compass use was also demonstrated in displaced Mallards (*Anas platyrhynchos*; Matthews 1963) and feral pigeons (Edrich and Keeton 1977). Another behavior in which the sun compass plays an important role is caching and recovery of seeds. Tested in an aviary ~5 m in diameter, three species of American jays—Western Scrub-Jay (*Aphelocoma californica*), Pinyon Jay (*Gymnorhinus cyanocephalus*), and Clark's Nutcracker (*Nucifraga columbiana*)—shifted their searching behavior in the predicted way when their internal clock was shifted by 6 h (W. Wiltschko and Balda 1989, W. Wiltschko et al. 1999). This implies that they remembered their caches in terms equivalent to "in the northern sector of the aviary." In a similar task involving searching for seed hidden by the experimenter, sun-compass use was demonstrated in Black-capped Chickadees (*Poecile atricapillus*; Duff et al. 1998). Thus, in these species, the sun compass is used as a component of spatial memory. Early conditioning experiments also suggested sun-compass orientation in Western Meadowlarks (*Sturnella neglecta*; von Saint Paul 1956) and White-throated Sparrows (*Zonotrichia albicollis*; Able and Dillon 1977). This diversity of species from the various phylogenetic lineages suggests that the sun compass is rather widespread among birds, and probably common to all.

Interestingly, however, there is no convincing evidence for sun-compass use in the orientation of diurnal migrants during migration. It is true that the sun compass was first described by Kramer (1950) in the European Starling, a day-migrating species, but the individual he tested did not head in its migratory direction, preferring instead a direction of unclear nature. Clock-shift experiments with Yellow-faced Honeyeaters, another diurnal migrant, did not produce the predicted deflection, but led to a behavior that could be interpreted as phototaxis (Munro and Wiltschko 1993). It seems as if the sun compass, although a very prominent mechanism in homing and tasks within the home region, does not play a similarly important role in the orientation of diurnal migrants. The reasons may lie in the dependence of the sun's arc on geographic position: as migrants move toward lower latitudes, they would have to continuously adjust their compensation mechanisms to the sun's changing arc. Migrants with a strong east–west component in their migratory direction would have to continuously compensate for the gradual time shift as they cross meridians. This could make sun-compass use during the day problematic for extended migration flights of hundreds or thousands of kilometers. For tasks within the birds' home region, on the other hand, it seems well suited, in that it can be finely tuned to the local arc of the sun.

This does not mean, however, that diurnal migrants do not possess a sun compass. It is to be expected that they establish this mechanism and use it when they are not on migration. They probably have two types of sun compass—one in the breeding area and another in the wintering area, both adjusted to the respective local conditions. Long-distance migrants crossing the Equator, such as Barn Swallows (*Hirundo rustica*) or Bank Swallows (*Riparia riparia*), would have two very different sun-compass mechanisms: one compensating for the sun's clockwise movement in the Northern Hemisphere and another compensating for its counterclockwise movement in the Southern Hemisphere.

The Star Compass

Birds using the stellar sky to indicate directions also are faced with the problem that the stars change their position. In the Northern Hemisphere, the circumpolar stars rotate counterclockwise about the polar star Polaris, which marks the northern celestial pole. In the Southern Hemisphere, the circumpolar stars rotate clockwise around the southern celestial pole. These stars near the poles are visible all night, and their number depends on geographic latitude. Stars near the celestial equator rise in the east, wander across the sky, and set in the west. Furthermore, because of a difference in lengths between the solar and the celestial day, the sky changes its appearance with season so that some constellations are characteristic of the summer and others of the winter sky.

Star orientation was first discussed by Sauer (e.g., 1957), who assumed that night-migrating birds have innate knowledge of the stars and might use them for true navigation. Emlen (1967a) showed that migrants indeed use the stars: Indigo Buntings (*Passerina cyanea*) reversed their headings when the northern stars were projected to the southern side of a planetarium. By

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

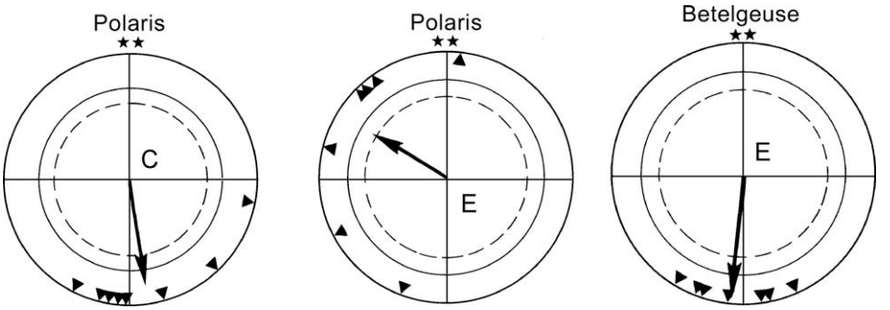


Fig. 9. Celestial rotation serves as directional reference for the star compass. Young Indigo Buntings were hand-raised under a rotating planetarium sky and later tested under the same, now stationary, sky. Left: orientation of control birds (C) for which the planetarium sky had rotated around Polaris, simulating the natural situation. Middle and left: orientation of experimental birds (E) for which the planetarium sky had rotated around Betelgeuse in *Orion*, plotted with respect to Polaris (middle) and with respect to Betelgeuse (right). The inner circles are the 5% (dotted) and the 1% significance border of the Rayleigh test (data from Emlen 1970).

manipulating the circannual cycle of his birds, he could test individuals in spring migratory condition and in autumn migratory condition side by side under the same stars, and he found that both groups preferred their seasonally appropriate migratory direction (Emlen 1969a). This clearly showed that the directions chosen under stars depended solely on the physiological condition of the birds and not on the appearance of the sky. This finding proved the assumption of stellar navigation incorrect, pointing to the use of stars as a compass only.

Functional properties of the star compass

Experiments by Potapov (1966), who shifted the internal clock of nocturnal migrants, and Emlen (1967b), who presented birds with a planetarium sky that was advanced by 3, 6, or 12 h with respect to the natural sky, clearly showed that the internal clock is not involved in star orientation. This means that night-migrating birds do not use single, prominent stars and compensate for their movement. Instead, they have a very efficient way to overcome any problems arising from the movement of the stars: they derive directional information from the pattern of constellations with respect to each other and to the celestial pole. Nocturnal migrants are assumed to proceed in a manner similar to that of young children who are told to find north at night: seek out Ursa Major, prolong the line connecting the two hind stars by ~5 times, and by this find the polar star that indicates the north direction. This procedure is independent from the current position of Ursa Major and can be used at any time of year.

Little is known about the specific stars or constellations on which birds rely for directional orientation. Some observations seemed to suggest that the circumpolar region is of particular importance (Emlen 1967b), but the few data show a lot of variance. Yet because the star compass is learned (see below), it seems possible that different birds focus on different constellations, developing their own individual version of a star compass.

Cues underlying the star compass

The assumption that night-migrating birds have innate knowledge of the stars also proved incorrect. Emlen, having found that hand-raised birds could orient under stars only if they had had a chance to observe the natural sky before autumn migration (Emlen 1969b), identified celestial rotation as the mechanism underlying the star compass. He hand-raised two groups of young Indigo Buntings in the planetarium; for one group, it was rotating around Polaris, simulating the natural situation; for the other, it rotated around Betelgeuse, a star in the constellation Orion. When both groups were later tested under the same planetarium sky, now stationary, the first group looked for their southern migratory direction by heading away from Polaris, whereas the other headed away from Betelgeuse (Fig. 9; Emlen 1970).

Later experiments with Garden Warblers (*Sylvia borin*) showed that celestial rotation enables birds to use a completely artificial star pattern consisting of only 16 little light dots for compass orientation. Birds that had observed these "stars" rotating during the premigratory period could later orient under these now stationary stars, whereas birds in a second group that had been hand-raised under the same, albeit stationary, star pattern were disoriented (W. Wiltschko et al. 1987a). These findings suggest that birds do not have any innate knowledge about the composition of the natural sky but that celestial rotation can give directional significance to any star pattern.

The experiments mentioned above were performed with hand-raised birds and involved exposure to celestial rotation during the premigratory period. The processes they reflect are significant in relation not only to the star compass, but also to the processes that provide the birds with the migratory direction as a compass course. We will come back to these below.

The magnetic field is also used as a reference system for calibrating the star compass. Birds were able to use an artificial, simple star pattern for orientation after they had observed it together with a magnetic field like the geomagnetic field (W. Wiltschko and Wiltschko 1976).

Use of the star compass

Star-compass orientation has been demonstrated mostly in night-migrating passerines with the help of migratory behavior. Planetarium experiments similar to those with Indigo Buntings described above showed that European Robins and Bobolinks have a star compass (Lutsyuk and Nazarchuk 1971, Beason 1987).

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Outdoor experiments that showed continuing orientation in the migratory direction under stars in the absence of meaningful magnetic information also indicated a star compass in European Robins, and in Garden Warblers and Pied Flycatchers (*Ficedula hypoleuca*) (W. Wiltschko and Wiltschko 1975a, b; Bingman 1984). Matthews (1963) observed that displaced Mallards, released at night, preferred northwesterly directions as long as the stars were visible but showed random orientation under overcast skies, which suggests the presence of a star compass in this species.

Other birds in other behavioral contexts have not yet been studied with regard to stellar orientation. It would be very interesting to learn how nocturnally active groups of birds, like owls, nighthawks, pootoos, and frogmouths, orient and whether or not they are able to derive directional information from the starry sky.

Interrelations between the Compass Mechanisms

With the magnetic compass and the celestial compass mechanisms, birds have two different sources of directional information available. This raises the question of how they rate and rank the respective mechanisms. Normally, magnetic and celestial information will agree and point out the same directions. Setting them in conflict, however, will reveal the birds' preferences, indicating a hierarchy of cues.

Interrelations between sun compass and magnetic compass

We already mentioned the ontogenetic relationship between sun compass and magnetic compass in homing pigeons, with the magnetic field providing the reference system for linking sun position and internal clock with geographic direction. When the sun-compass mechanisms have been established, however, the sun compass could, in principle, independently provide directional information. In the clock-shift experiments described above, manipulation of the internal clock caused pigeons to misinterpret the sun's position. This led to the typical deflection from the mean of untreated control birds, although the magnetic compass could have told the birds the correct direction—this appeared to suggest that information from the sun compass dominates that from the magnetic field. The magnetic compass seemed to become a back-up system for overcast days.

However, the first researchers doing clock-shift experiments had noticed already that the deflection induced by a 6-h shift of the internal clock was often smaller than predicted by the difference in solar azimuth between the actual time of day and the pigeons' subjective time (e.g., Schmidt-Koenig 1961). A detailed analysis of numerous clock-shift experiments with pigeons revealed a dependence on age and experience (Fig. 10): young pigeons with little experience, at the age when they had just spontaneously established the sun compass, more or less showed the expected deviation (see also Neuss and Wallraff 1988). As the birds became older and more experienced, the deflection decreased to only a little more than 50% (R. Wiltschko et al. 1994). This suggested that the older, more experienced pigeons also used other directional information.

A potential source of such information was the geomagnetic field. To test this hypothesis, experienced clock-shifted pigeons were released with a magnet that temporarily disrupted their magnetic compass. These birds showed significantly larger deflections than clock-shifted, otherwise untreated birds, with the deflection

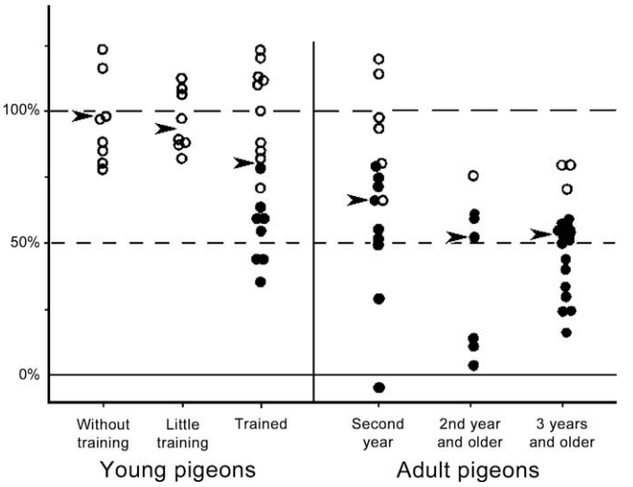


Fig. 10. Size of the deflection induced by a 6-h shift of the internal clock as a function of age and experience. The deflection expected on the basis of the difference in solar azimuth between the actual time of day and the birds' subjective time of day was set to 100%. Open symbols indicate observed deflections not different than expected, and solid symbols indicate deflections that are statistically significantly smaller than expected. Arrowheads mark the medians (data from R. Wiltschko et al. 1994).

mostly reaching the expected size (R. Wiltschko and Wiltschko 2001). Obviously, old, experienced pigeons use the sun compass and magnetic compass together, flying a compromise between the directions the two systems indicate.

When young pigeons have just established their sun compass, they seem to favor this mechanism, but why should the magnetic compass gain importance again as pigeons grow older and more experienced? One can only speculate about possible reasons. Older pigeons, in contrast to young ones, have already experienced the seasonal changes of the sun's arc and the necessity to adjust their compensation mechanism. For this adjustment, they probably used the magnetic compass as a directional reference, and this experience may have made them more ready to include the constant information from the magnetic compass in their navigational processes.

Another point is that clock-shifted pigeons, although they show the typical deflection in initial orientation, nevertheless return home, albeit with a certain delay. For example, from distances ≤40 km, many birds with their internal clock shifted 6 h fast usually reached their loft on the day of release—that is, before a new sunset and sunrise could shift the internal clock back to normal. This excludes sun-compass use. It seems likely that the pigeons, when recognizing that their sun compass leads them astray, temporarily abandon it and rely on their magnetic compass instead.

Interrelations between polarized light and magnetic compass in migrants

For night-migrating birds that start their migration flight around sunset, celestial cues at this time of day, like the view of the setting sun and the pattern of polarized light running through the zenith, were found to improve orientation (e.g., Moore 1986).

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

When subsequent experiments showed that the birds changed their headings accordingly when the e-vector was rotated with the help of polarization filters, although the geomagnetic field was unchanged, the polarization pattern was considered the most important cue, dominating over magnetic cues (e.g., Moore 1986, Able 1989). However, the findings of Helbig and Wiltschko (1989) showed that the response of migrants to artificially polarized light differed from that to the natural e-vector and raised the question of whether experiments with polarization filters reflected the relationship between polarized light and magnetic information realistically. In the natural sky, the maximum polarization is ~70% in a band 90° from the position of the sun, with the degree of polarization decreasing on both sides, whereas polarization filters polarize the light by 100% over the entire sky, at the same time cutting off part of the UV light, thus giving the sky an unnatural appearance. Also, the interaction between natural and artificial polarization may lead to an inhomogeneity of the distribution of light, which, in turn, could affect the birds' behavior (see Helbig 1991).

Cage studies.—Tests with migrants at the time of sunset under the natural sky in an experimentally altered magnetic field produced different results. Birds tested only once under these conditions showed inconsistent responses: several species seemed to ignore the shift in magnetic north and continued in their normal migratory direction; others responded bimodally, headed into an intermediate direction, or were altogether disorientated; and still others followed the shift in magnetic north and changed their headings accordingly (e.g., Sandberg et al. 1988, 1991; Åkesson 1993, 1994; Sandberg and Moore 1996; Sandberg and Pettersson 1996; Sandberg et al. 2000). By contrast, birds that were repeatedly tested in this situation generally followed the change in magnetic north. Some species, like Dunnock (*Prunella modularis*; Bingman and Wiltschko 1988), Snow Bunting (*Plectrophenax nivalis*; Sandberg and Pettersson 1996), Red-eyed Vireo (*Vireo olivaceus*), and Northern Waterthrush (*Seiurus noveboracensis*; Sandberg et al. 2000), responded immediately to the shift in magnetic north. Australian Silvereyes (*Zosterops lateralis*, a twilight migrant) responded immediately to a counterclockwise shift (Fig. 11, upper diagrams) but only with some delay to a clockwise one (R. Wiltschko et al. 1999). These findings indicate that, at least in these species, the magnetic field dominates over the polarization pattern at sunset. The delayed response of one group of Silvereyes implies that some of the other species also may have responded to the shift in magnetic north in the end but were not tested long enough for this to become evident. Apparently, some birds strongly rely on the sunset cues and need some time to become aware of the shift in magnetic north, whereas others check the magnetic field more frequently.

After being tested several times in the shifted magnetic field, Dunnocks and Silvereyes were tested in a partly compensated magnetic field where they had to rely on celestial cues alone. They continued in the same direction they had preferred in the shifted field (Fig. 11, center diagrams). Obviously, for them, celestial cues had obtained a new directional significance: they had recalibrated the pattern of polarized light according to the experimental magnetic field (Bingman 1987, R. Wiltschko et al. 1999). Their magnetic compass course remained unchanged (Fig. 11, lower diagrams; R. Wiltschko et al. 1999).

There is also an example to the contrary: Savannah Sparrows (*Passerculus sandwichensis*) were exposed for several days to the natural sky in a magnetic field with shifted north. Tested later in the geomagnetic field without celestial cues, they changed their magnetic course according to the cue-conflict situation (Able and Able 1995). Unfortunately, these birds had not been tested in the cue-conflict situation itself, so their response to the presence of the conflicting cues is unknown.

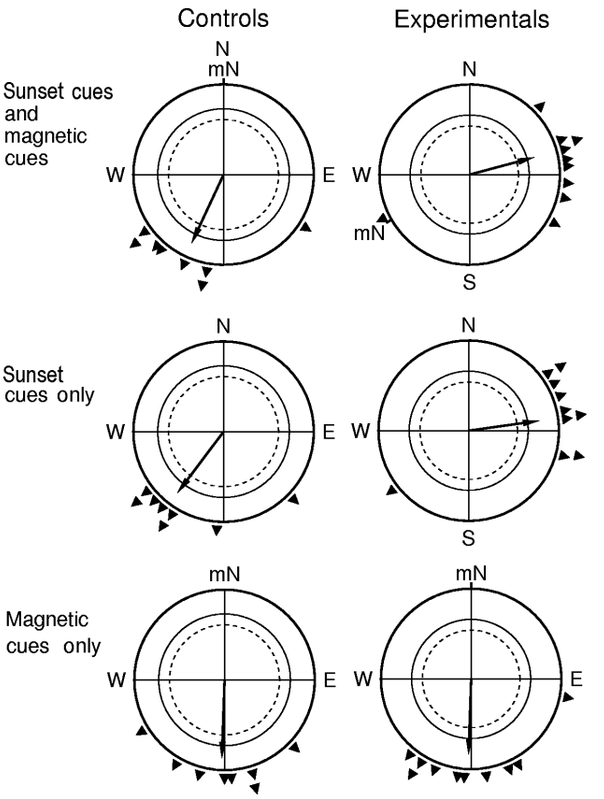


FIG. 11. Recalibration of polarized light cues at sunset. Two groups of Australian Silvereyes were first tested with regard to the natural sky at sunset—the control groups in the local geomagnetic field, and the experimental group in a field with magnetic north shifted to 240° east-southeast (upper diagrams). They were subsequently tested under the natural sky in a compensated magnetic field (middle diagrams) and in the local geomagnetic field without a view of the sky (lower diagrams). The inner circles are the 5% (dotted) and the 1% significance border of the Rayleigh test (data from R. Wiltschko et al. 1999).

The discussion on the possible role of polarized light was recently revived by a review in which Muheim et al. (2006a) proposed that the magnetic compass is regularly calibrated by the pattern of polarized light at sunrise and sunset. The authors argued that in this way birds could ensure that their migratory direction corresponds to an absolute geographic direction and is not affected by, for example, changing magnetic declination (= difference between magnetic north and true north). The findings that indicated recalibration of sunset cues by the magnetic field were dismissed: Muheim et al. (2006a) stated that in these cases, the birds had not been able to see the pattern of polarization down to the horizon, claiming that the area just above the horizon was

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

crucial for the calibration processes. Data on Savannah Sparrows that seemed to support this view were subsequently published (Muheim et al. 2006b). These findings, however, are difficult to interpret. One point is that polarizers had been used to alter the pattern of polarization in a very unnatural way (see above). Another is that control tests documenting orientation in migratory direction were not reported, so that it is unclear whether the behavior reflects migratory orientation at all. When these experiments were repeated with Australian Silvereyes, exposing the birds to the natural pattern of polarization down to the horizon in a shifted magnetic field, the findings of Muheim et al. (2006b) could not be replicated: as before, there was no indication that exposure to conflicting cues at dusk had affected the magnetic compass course (R. Wiltschko et al. 2008). These data contradict the assumption of a regular calibration of the magnetic compass by polarized light; they also do not support a special role of the polarization pattern just above the horizon.

Release studies.—Sandberg et al. (2000), who had recorded the orientation of four species of birds in a cue-conflict situation at dusk, later released their birds and recorded the directions in which they took off. Red-eyed Vireos and Northern Waterthrushes that had followed the altered magnetic north direction in the cage departed in directions that suggested recalibration of celestial cues by the shifted magnetic field. The two other species, Indigo Bunting and Gray Catbird (*Dumetella carolinensis*), which did not seem to respond to the shift in magnetic north in the cage, also responded to the shift as if they had recalibrated celestial cues when they were set free (Sandberg et al. 2000). Another study, involving Gray-cheeked Thrush (*Catharus minimus*) and Swainson's Thrush (*C. ustulatus*), also exposed birds at dusk to the natural sky in a magnetic field with north shifted, but unfortunately without recording their orientation during exposure (Cochran et al. 2004). These birds were then released and tracked with the help of transmitters during the night. Their routes deviated from controls, a finding that was interpreted as reflecting recalibration of the magnetic compass by sunset cues. However, it is unclear to what extent these birds really used their magnetic compass; it also seems possible that they used celestial cues, overcompensating for a false previous recalibration (for a detailed discussion, see R. Wiltschko et al. 2008).

Interrelations between stars and magnetic compass

Experiments analyzing interactions between directional information from the stars and the magnetic field in night-migrating birds were performed in a similar way as those on the interactions between polarized light and the magnetic field: migrants were exposed to a planetarium sky with the northern stars projected to the south in the geomagnetic field or to the natural starry sky in an altered magnetic field. The classic planetarium experiments with Indigo Buntings (Emlen 1967a, b) had demonstrated the use of the stars and, because the magnetic field had not been compensated, indicated the stars to be the dominant cues. Later planetarium experiments (Beason 1989) revealed individual differences between the birds' responses to a cue-conflict situation in the planetarium: ~60% of the Bobolinks did not respond with a directional change when the northern stars were projected to the south; the others followed the stars at first, but within two to six days they reversed their headings back to magnetic north. Outdoor tests with European warblers in the genus *Sylvia* and European Robins showed that the warblers responded immediately to the shift in magnetic north by changing their headings accordingly, whereas the European Robins responded only with delay, after they had experienced the cue-conflict for at least two nights (W. Wiltschko and Wiltschko 1975a, b; Bingman 1987).

In subsequent experiments in partly compensated magnetic fields, Garden Warblers and European Robins continued into the altered directions by stars alone, which indicates that they had recalibrated the celestial cues by the experimental magnetic field (W. Wiltschko and Wiltschko 1975a, b; Bingman 1987). European Robins could locate their migratory direction with the help of a simple artificial sky consisting of only 16 dots of light, provided that they had first experienced this sky together with a magnetic field of suitable intensity (W. Wiltschko and Wiltschko 1976). Thus, the star compass and magnetic compass are also linked by calibration processes.

An integrated system indicating direction

The magnetic compass is the only one based on direct sensory perception: the receptors in the eye indicate the axis of the field lines directly. Celestial cues are perceived by the visual system, but the birds additionally require experience-based knowledge to derive directions. The manifold interactions described above show that the magnetic compass, sun compass, and star compass should not be considered independent mechanisms, but integrated components of one complex system providing directional information. The ontogenetic relationship between sun compass and magnetic compass and results of the cue-conflict experiments reveal a great flexibility of the celestial mechanisms and, at the same time, the birds' efforts to keep in agreement the various mechanisms indicating directions: pigeons that were transferred to a permanently shifted day recalibrated their sun compass, and migratory birds recalibrated their star compass and adjusted the directional significance of the sunset cues.

We must be aware of the possibility that not all bird species rate and rank the various cues in the same way. In particular, we can expect differences between migrants, because migration has developed many times independently in the various lineages of birds (Helbig 2003). Additionally, the mechanisms may have been adapted to specific conditions encountered on migration routes. Hence, species-specific differences among migrants would not be surprising. At the same time, the ranking of directional cues may vary with the phase of migration and with geographic latitude (for a detailed discussion, see R. Wiltschko et al. 2008). Yet all birds aim to bring the various compass mechanisms into harmony so that all directional cues agree and provide the same information.

Setting the Course to the Goal

To use a compass mechanism, the birds must first be aware of the compass course to the goal. How birds obtain this information depends on the spatial task they have to solve; there are fundamental differences between the mechanisms that provide the course for flights within the home range and in homing and those that set the course for the first migration.

Within their more-or-less extended home ranges, birds can be assumed to know the courses to important resources by

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

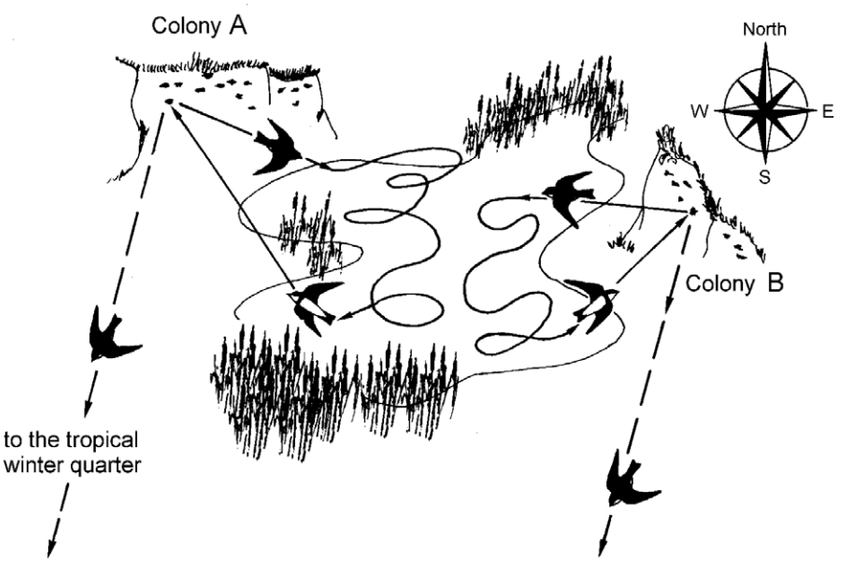


Fig. 12. Illustration of the compass model, showing different types of courses that birds can locate using a compass. Bank Swallows leave their colonies to go foraging, flying remembered courses. When returning to their colony, they fly courses determined by navigational processes. In autumn, they fly an innate course toward their tropical winter quarters (modified from R. Wiltschko and Wiltschko 1995).

experience. A bird may remember, for example, that a suitable water hole is to the south of its nest, and Bank Swallows may know from exploring that a lake with good conditions for hunting insects is to the east (Fig. 12). Here, aside from compass mechanisms, familiar landmarks are involved (see below). Homing, on the other hand, involves returning to a home area from greater distances—the birds are away from their goal, and often in unfamiliar territory. This means, however, that they have left home before, either voluntarily on their own wings or because they were experimentally displaced. Hence, homing is always the return to a familiar place, and there are gradual transitions between navigation within the home range and homing.

By contrast, migration means a flight toward an unknown goal, at least for first-time migrants. The young migrants have to reach a distant area thousands of kilometers away, where they have never been before. Banding recoveries and visual observation show that the population-specific winter quarters are more-or-less extended (but not unlimited) areas, which the young birds have to find at the end of their first migration. Their second and all later migrations are different, insofar as the goal is now familiar. We will begin with discussing the mechanisms that determine the home course, because homing is a task every bird has to face, whereas setting the course for migration concerns only the migratory species.

Determining the Home Course

When exploring a foreign city starting from a hotel, there are two options for finding the way back: either one pays close attention to the route and reverses it to return, or one asks the porter for a map of the city, later identifies one's position on that map, and uses the map to return. This example demonstrates the two principal possibilities that birds have for obtaining information for homing (Schmidt-Koenig 1970): (1) route reversal—relying on information collected during the outward journey, and (2) bicoordinate navigation—relying on local information obtained at the starting point of the homeward flight, in experiments, at the release site. These are fundamentally different strategies, but both can indicate the home direction as a compass course. In the following, we will discuss both strategies, together with some others that have been suggested but that do not conform to the compass model.

Route reversal

The idea that birds may gather the information for their homing flight during the outward journey was first forwarded in the 19th century, when Darwin (1873) and Exner (1883), for example, suggested "inertial navigation" as a possible mechanism. This hypothesis was again suggested by Barlow (1964), who assumed that displaced birds were able to precisely record all twists, turns, and accelerations during the transport, integrate them, and directly derive their home direction from this information. The home direction, consequently, would be represented with respect to the bird's own body, which means that the bird would have to continuously keep track of its own movements and integrate the new ones with the previous ones. This mechanism would require an unrealistic accuracy in recording movements and accelerations, given that all errors would add up, thus rendering the navigational answer rather inaccurate. Attempts to prevent pigeons from recording the accelerations during the outward journey had no effect (e.g., Wallraff 1965). Also, because inertial navigation would not give the home direction as a compass course, this hypothesis is at variance with, for example, the results of the clock-shift experiments that clearly demonstrated the general use of a compass mechanism.

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Another way of using route-based information would be to integrate the route along a reference system, a strategy that can be characterized as "route reversal with the help of an external reference." This would provide the home direction as a compass course, and it would be far more precise, because errors would tend to even out. On spontaneous flights, birds would sum up and integrate the net direction of their route, reversing this direction to obtain the home direction. The question is whether birds can do this also when passively displaced. This seems to be the case, as indicated by experiments with Graylag Geese (*Anser anser*), Bar-headed Geese (*A. indicus*), and Barnacle Geese (*Branta leucopsis*) in which young goslings that had been imprinted on humans were brought to a place on a curvaceous route with extended detours. They started out heading directly home, regardless of whether they had walked the route following their human "mother" or had been transported in a cart (von Saint Paul 1982). The observation that they disregarded sections of the route where the cart had been covered, starting in a wrong direction, shows that they were indeed using information obtained during the outward journey.

On their spontaneous flights, birds have the sun compass and the magnetic compass available; during experimental displacement, the conditions usually allow only the use of the magnetic compass. To test the hypothesis that the magnetic compass provides the directional reference for route reversal, young pigeons were transported to the release site in a distorted magnetic field, which prevented them from obtaining meaningful directional information during the outward journey. When released, they departed randomly, whereas the normally transported control birds were homeward oriented (Fig. 13). Another control group was transported to the release site under normal conditions but after arrival was exposed to the distorted magnetic field for a time span equivalent to that required to reach the site. This group also departed homeward oriented, which shows that being transported in the distorted magnetic field, and not staying in the distorted field *per se,* had caused the disorientation (R. Wiltschko and Wiltschko 1978). Transporting young birds in a normal magnetic field, but under conditions that interfere with magnetoreception, like total darkness or long-wavelength light (see above), had the same disorienting effect (W. Wiltschko and Wiltschko 1981, R. Wiltschko and Wiltschko 1998). These findings clearly show that pigeons need a working magnetic compass to determine their home course by route reversal. They support the hypothesis that birds indeed record the net direction of the outward journey, integrating detours if necessary, with the magnetic field providing the external reference.

However, route reversal can be demonstrated in this way only in very young, inexperienced pigeons. When pigeons grow older and more experienced, for example when they are >12 weeks old or have participated in training flights (or both), depriving them of magnetic directional information during the outward journey loses its effect and no longer leads to disorientation (R. Wiltschko and Wiltschko 1985, Jorge et al. 2006). This suggests a change in navigational strategy. Apparently, pigeons rely exclusively on route-based information only during a short, transient phase in their early life.

The "map" system

The alternative strategy is to derive the home course from local information obtained at the starting point of the homing flight. Birds are famous for returning home after displacement to distant sites; what kind of information can they use at locations they have never visited before? Any model explaining their navigational abilities should also provide an explanation for the following common observations on the behavior of pigeons after release: (1) The navigational process does not require a long time or extensive flying around; frequently, bearings taken after 1 min already show a strong convergence in the direction in which the birds finally depart. (2) The vanishing bearings are mostly oriented in directions that are close to the true home direction, but seldom coincide with it. This led to the concept of the navigational "map" or "grid map."

The concept of the grid map.—Kramer (1953, 1957) had referred to the "map" without specifying any particular mechanism. Wallraff (1974) detailed the concept for bicoordinate navigation, suggesting a "grid map" of gradients, that is, factors whose values change continuously in space. The basic assumption is that there are (at least) two gradients that intersect at an angle that is not very acute. The birds know the scalar values of the gradients at their home site, and they are familiar with the directions of these

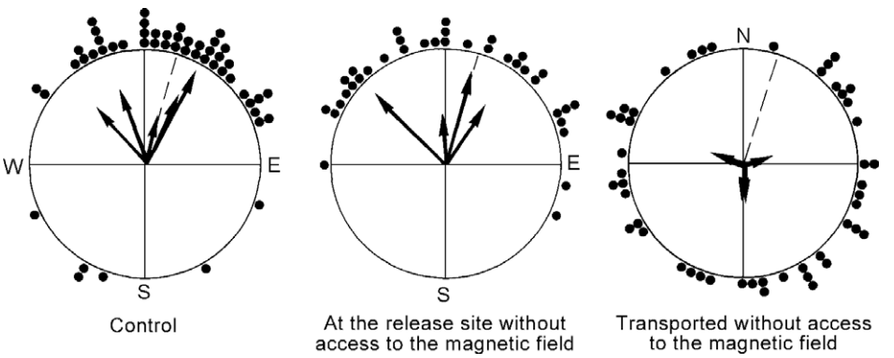


Fig. 13. Young, inexperienced pigeons determine their home course by route reversal with the magnetic field as reference. The home direction is indicated by a dashed radius. Symbols at the periphery of the circle mark the vanishing bearings of individual birds, and arrows represent the mean vectors of the four releases (data from R. Wiltschko and Wiltschko 1978, 1985).

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

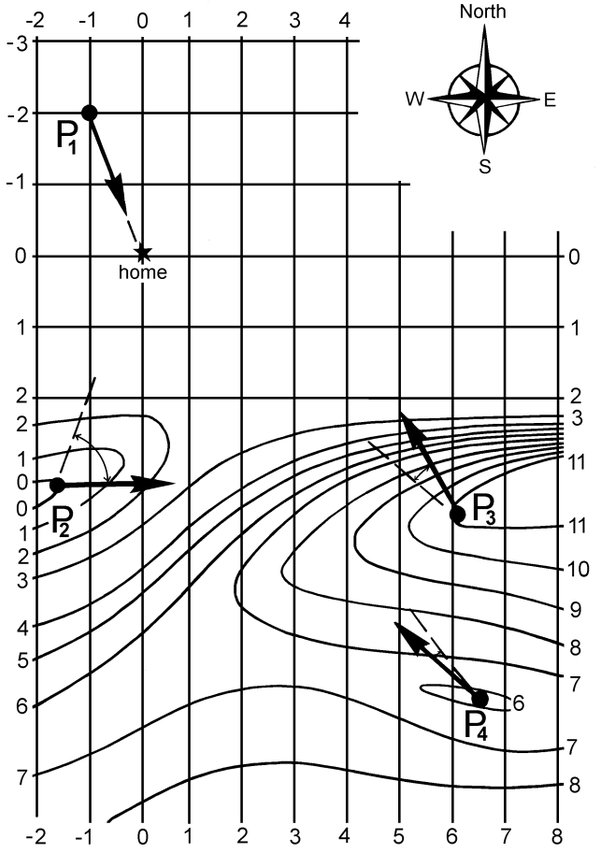


FIG. 14. Model illustrating how geophysical gradients are used for navigation. The intensity of two gradients is given in relation to the home values. Around P_1, the gradients are regular, and the birds determine their home course correctly. At P_2, P_3, and P_4, one of the gradients has an irregular distribution, leading to deviations from the true home course, so-called "release-site bias."

gradients. The directionally oriented mental representation of the distribution of these gradients forms the grid map. At distant sites, birds compare the local scalar gradient values with those remembered from home and interpret the differences with the help of their map to derive their home direction as a compass course. In the example given in Figure 14, the birds know that gradient A increases toward the north, whereas gradient B increases toward the east. A bird at point P_1 realizes that the values of both gradients are lower than the home values and that the difference in A is relatively larger than the one in B; hence, it has to fly a little north of northeast to reach home.

The model also explains the ability of birds to navigate at unfamiliar sites, because gradients can be extrapolated beyond the range of direct experience. Being familiar with the direction in which the gradients increase and decrease from direct experience within its home range, a bird can assume that the gradients will maintain this course at greater distances beyond this range. In the example in Figure 14, if a bird, knowing that gradient A increases toward the north, encounters values of A that are greater than any it has experienced before, it can conclude that it is farther north than ever before and, hence, has to fly south to return.

Another important aspect of the model is the assumption that birds compare scalar values. The local scalar value of a gradient can be detected at the site, whereas it would be impossible to detect, for example, the local gradient direction without scanning a more-or-less extended area. This explains why the navigational process is fairly fast, not requiring extensive flying around. Experiments with pigeons released from cages have shown that they already have some idea about their departure direction before they take off into the air (e.g., Chelazzi and Pardi 1972, Mazzotto et al. 1999). Pigeons fly around at the release site, but most of this maneuvering is in the direction in which they will later depart.

Release-site bias.—At many sites, pigeons depart in directions that are significantly different from the true home direction. The observed deviations vary widely; they are mostly in the range of about 20–30°, but at some sites may reach sizes of >90°. At any specific site, they show a certain variance, but in general they are remarkably constant over time: at some places, pigeons always deviate to the right of the home direction, at others to the left (for examples, see R. Wiltschko 1992). When their internal clock is shifted, the birds show the typical deflection, not from the home direction, but from the direction of untreated control birds that depart in the local bias direction (e.g., Schmidt-Koenig 1960).

The early researchers named this phenomenon *Ortsmißweisung* or *Ortseffekt* (Schmidt-Koenig 1958, Wallraff 1959), which translates as "local misdirection," emphasizing the local character of its manifestation. Keeton (1973) was the first to systematically analyze this phenomenon, at a site where his pigeons showed a marked bias of >70° (Fig. 15, left), and he called it "release-site bias." He observed it in experienced and inexperienced pigeons alike, and in both those that were familiar with the site and those that were not. It also was independent of cloud cover—that is, whether the birds were using their sun compass or magnetic compass. By shifting their internal clock, he could make the pigeons depart in their home direction, but their homing was delayed, as is normal for clock-shifted birds. The latter two findings indicate that the phenomenon of release-site bias is

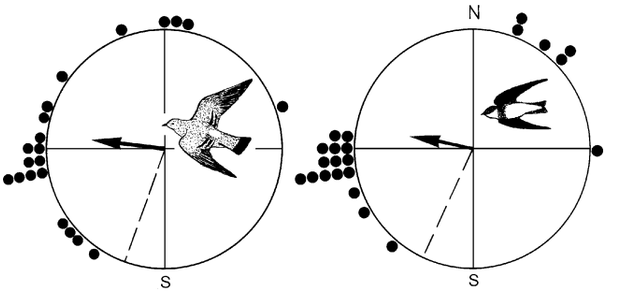


FIG. 15. Homing pigeons and Bank Swallows use the same factors for navigation. At a site ~140 km to the north, homing pigeons and Bank Swallows from a colony in the vicinity of the loft showed the same westerly release-site bias, which suggests navigation by the same factors. The home direction is indicated by a dashed radius (data from Keeton 1973).

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

independent of the compass mechanisms used; rather, it seems to be associated with the map step of navigation. Hence, Keeton (1973) hypothesized that release-site biases are attributable to local irregularities in the distribution of the map factors: "the birds are probably reading the map cues correctly, but the map itself is twisted" (Keeton 1973:14).

The concept of the grid map also includes an explanation for this phenomenon. The distribution of natural factors is never completely regular; irregularities in the course of gradients are to be expected. The points P_2, P_3, and P_4 in Figure 14 (lower part) show how such irregularities can cause birds to misjudge their position, leading to a course that deviates from the true home course. At those sites, the respective course is subjectively correct for the birds. According to this interpretation of release-site bias, the occurrence of these deviations from the true home direction indicates the use of the navigational map. Release-site bias mainly affects the initial orientation; as soon as birds leave the area of irregularities in the map factors, they can correct their error. Release-site bias may lead to some detours, but it does not reduce homing success.

Keeton (1973) made another important discovery. When he released Bank Swallows from a colony near his loft at the site where his pigeons had shown the marked bias to the right, he found that these birds, too, showed a similar bias (Fig. 15, right). This indicates that release-site bias is not restricted to pigeon homing but is a general phenomenon in avian navigation. Both pigeons and Bank Swallows seem to make use of the same type of navigational factors and respond to them in the same way, and this probably applies to other species as well.

Possible navigational factors.—This leads to the question of the nature of the gradients involved. The observation that the effect of shifting the birds' internal clock depends only on the amount of time shift, but not on the distance and direction of the release site, clearly shows that the factors used to determine the home course do not vary with the time of day. This excludes celestial cues as possible navigation cues and points to geophysical factors.

The nature of the factors used by pigeons and other birds as components of their grid map is still unclear; it is one of the great remaining enigmas in avian navigation. Several factors have been considered over the years. The first, discussed as early as the 19th century, is the intensity or inclination (or both) of the geomagnetic field (Viguier 1882; also see Phillips 1996). Experimental evidence supports an involvement of magnetic navigational factors (e.g., Walcott 1978, Kiepenheuer 1982), but they are certainly not the only factors used. Several authors suggested the use of olfactory information in navigation, claiming that the birds could derive their home course from characteristic odors of the landscape (for a review, see, e.g., Papi 1986, 1991). It is true that in some regions, depriving pigeons of olfactory input and olfactory manipulation had large effects on their behavior, but these effects have been controversially interpreted. The role of odor as a navigational factor is not supported by meteorological studies, which argue against the existence of suitable odor gradients (e.g., Becker and van Raden 1986, Waldvogel 1987). Unspecific or activational effects cannot be excluded, a recent study (Jorge et al. 2009) having supported an activational effect.

Other factors considered potential navigation cues are gravity, although studies at gravity anomalies did not produce conclusive evidence (Lednor and Walcott 1984), and infrasound—that is, low-frequency sound produced by wave action, wind over mountains, and so on, which pigeons are able to hear (see Hagstrum 2000). To detect the direction of infrasound, however, birds would have to rely on Doppler effects, which would require flying; hence, this factor could not be used before birds are in the air. The changing view of distant mountains or other landscape features has also been discussed as a navigational factor (e.g., Baker 1984).

Factors like the geomagnetic field and the gravity field form worldwide gradients. Infrasound, odors, and landscape features may form extensive regional gradients. Other gradients of regional or local range that are potentially suitable for navigation may also be used by birds and be included in their map. Rather than relying on one factor alone, they seem to have a variety of factors available and probably include all factors that provide suitable information in their map. This means that the navigational factors used need not be identical in all parts of the world. There may be regional differences in the availiability and suitability of potential navigational cues, and birds may opportunistically develop their map according to the situation in their home region. The multifactorial nature of the map makes analyzing its components—and, in particular, isolating the contribution of any single factor—most difficult, and the results obtained in one region are not necessarily transferable to another (W. Wiltschko et al. 1987c).

We will not go into details on the nature of map factors here, because this would necessarily be highly speculative. Interested readers are referred to the studies on the various potential cues mentioned above.

The mosaic map.—Close to home, the differences in the scalar values of the navigational factors from the home values presumably become so small that the birds can no longer detect them, and they must turn to another navigational mechanism. Clock-shift experiments revealed that the map-and-compass model of navigation also applies in the vicinity of the loft: the typical deviation induced by shifting the internal clock was observed between 1 and 1.5 km from the loft (e.g., Graue 1963, Keeton 1974), which indicates that pigeons determine their home course as a compass course also in the area where familiarity with the terrain and landmarks can be inferred.

These findings led to the concept of the "mosaic map" of landmarks, which proposes that birds remember the position of prominent landmarks in their home area with respect to each other and to their home. For example, birds are assumed to store in their memory information like "a big oak tree is 2 km to the north." This type of information results in a "map" that consists not of a few continuous factors like gradients, but of numerous separate entities such as landmarks, forming a mosaic-like, directionally oriented representation of the lay of the land around home (Graue 1963, Wallraff 1974). It means that the birds using this mosaic map for navigation will also obtain their home direction as a compass course. Only the view of the loft itself could occasionally override the use of the sun compass (Graue 1963, Keeton 1974).

Navigation by the mosaic map largely escapes experimental analysis. It is indirectly indicated by the already mentioned observation that shifting the internal clock has an effect also in the vicinity of the loft and by experiments with pigeons deprived of object vision. When released away from home, birds wearing frosted lenses departed with oriented bearings, and many of them returned to the vicinity of their loft, but few reached the loft itself

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

(Schmidt-Koenig and Schlichte 1972, Benvenuti and Fiaschi 1983). Birds tracked in Upstate New York approached the loft up to about 1 or 2 km (Schmidt-Koenig and Walcott 1978); in Germany and Italy, some pigeons even managed to reach their loft, but their numbers were much lower than those of the control birds with intact vision (Schlichte 1973, Benvenuti and Fiaschi 1983). These findings suggest that visual landmarks have a role during the last phase of homing, for pinpointing the loft itself.

The size of the mosaic map is difficult to estimate; observations suggest a radius between 5 and 10 km (Michener and Walcott 1967, Braithwaite 1993). However, it must be expected that its size is highly variable, depending on the lay of the land, the occurrence of suitable landmarks, and the steepness of the local gradients. The mosaic map and the grid map supplement each other, and they must be expected to partly overlap so that pigeons always have map information available.

Use of landmarks alone?—An alternative hypothesis proposes that pigeons in familiar areas follow sequences of familiar landmarks alone, without a compass, a strategy that is at variance with the compass model. This idea was first proposed by Griffin (e.g., 1944) as "type I orientation," before the sun compass had been discovered, and later became known as "piloting." But after the experiments with frosted lenses described above, which demonstrated homing without use of landmarks (e.g., Schlichte 1973, Benvenuti and Fiaschi 1983), it was no longer a focus of attention. With the development of flight recorders based on global positioning systems (GPS), it became possible to record the tracks of returning pigeons with great accuracy. The routes of birds repeatedly released from the same sites, mostly up to ~10 km from a loft in England, were found to become stereotypic after about 10–12 flights, and this stereotypy was attributed to navigation by following sequences of familiar landmarks that led the way home (e.g., Biro et al. 2004, Meade at al. 2005). Yet at other lofts, such route stereotypies were not observed (R. Wiltschko et al. 2007a).

Shifting birds' internal clock is a simple way to test for the use of a compass. The typical deflection in clock-shifted birds is observed at familiar and unfamiliar sites alike (R. Wiltschko et al. 1994). Even pigeons that had homed >50 times from the same location 40 km from their loft were deflected when their internal clock was shifted, choosing departure directions different from their usual ones (Füller et al. 1983). These birds must have been extremely familiar with the release site, yet in the critical test, they seemed to disregard familiar landmarks, with their departure bearings clearly documenting that they still determined their home direction as a compass course. In corresponding experiments closer to home, where the birds can be assumed to rely on landmarks, pigeons that flew stereotypic routes responded to shifting their internal clock with some deviations in the expected direction (Biro et al. 2007). Although these deviations were mostly not very pronounced, they indicated that the sun compass is still involved along very familiar routes near home. Familiarity with the route, however, seems to help birds realize their error very quickly and initiate corrections. In view of these findings, navigation by familiar landmarks alone, without a compass, seems doubtful.

A change in strategy during development of the navigational system

As already pointed out, during a short, transient phase in early life, route reversal is the only navigational strategy of young, inexperienced pigeons. Depriving older pigeons of outward-journey information no longer has a disorienting effect, which indicates that they can base their navigational processes on map information alone. The reason for this change in navigational strategy becomes clear when the preconditions, the advantages and disadvantages of the use of route-based versus site-based information, are considered.

Route reversal requires a functioning magnetic compass and mechanisms to record and integrate accelerations. Birds' magnetic compass is innate in the sense that it is based on a direct sensory input, and integrating the route is probably likewise based on a spontaneous ability. Hence, inexperienced young birds can be expected to possess the necessary abilities for recording the net directions of the outward journey. Any specific knowledge about the local conditions is not needed. Use of the map system, by contrast, requires detailed knowledge of the regional distribution of the gradients, in particular of the directions in which they increase and decrease, and of the positions of suitable prominent landmarks within the home area. Such knowledge cannot be innate; it has to be acquired by experience. Young birds must perform extended learning processes to obtain the necessary knowledge for establishing their map system. This means, however, that when young, inexperienced birds begin to fly, their maps are not yet developed. Consequently, they must rely on mechanisms that do not require any specific preknowledge and, hence, use route reversal as their first navigational strategy.

Later, when they have obtained the necessary knowledge and have established their map system to a working stage, they are no longer restricted to route reversal. They begin to rely on site-specific information, which they interpret with the help of their maps. In general, the use of this map information is advantageous, because any mechanism based on information obtained during the outward journey alone is susceptible to errors. Highly accurate recording and processing of this information is necessary, because errors cannot be corrected with route-based information alone and will lead to later mistakes in determining the home course. This may not have serious consequences as long as birds fly only short distances from home; as soon as they begin to venture farther away, however, it may become critical. Using site-specific information allows birds to determine their home course anew as often as they feel necessary, which enables them to correct any errors. Irregularities in the distribution of the map factors may cause certain detours, but they do not reduce the chances of reaching home. This increased safety should strongly stimulate birds to rely on map information.

It is unclear whether and to what extent information collected during the outward journey continues to play a role. Experienced adult pigeons are hardly affected when deprived of outward-journey information (R. Wiltschko and Wiltschko 1985), but this does not necessarily mean that they do not use it when available. Where great irregularities in the distribution of gradients lead to large biases, including route-specific information could help birds minimize these biases and avoid extended detours (see R. Wiltschko and Wiltschko 2000).

Details of the learning processes necessary to establish the map are not known, because they escape experimental analysis. It is to be assumed that they normally take place during spontaneous flights, starting in the third month of a pigeon's life at

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

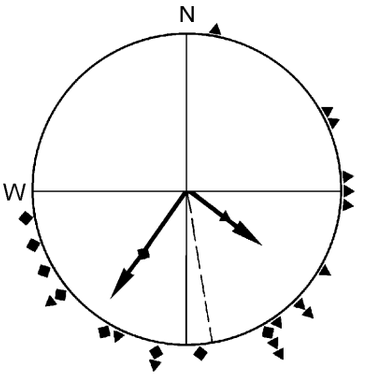


Fig. 16. Effect of one spontaneous flight on the orientation of young homing pigeons at a site 65 km from the loft. The home direction is marked by a dashed radius. Triangles indicate vanishing bearings of birds that stayed out of sight of the loft for >1 h on the day before the release, and diamonds indicate bearings of birds that remained at the loft. The two arrows represent the respective mean vectors.

approximately the same time when the sun compass is established. When pigeons are about three months old, depriving them of outward-journey information ceases to have an effect (R. Wiltschko and Wiltschko 1985); at the same time, they begin to show release-site biases (see W. Wiltschko and Wiltschko 1982). Both these observations indicate map use. Young pigeons are eager to fly, and they often stay out of sight of their loft for a considerable time. With the help of their magnetic compass and, later, their sun compass, they can record the direction in which they are leaving their loft and look for prominent landmarks in this direction and, on more extended flights, record how the geophysical gradients change. This information is then stored in their map system, forming the basis for their later interpretation of the map factors. Figure 16 shows the effect of one spontaneous flight lasting >1 h on the way pigeons interpreted the local factors at a site 65 km away. The maps continue to be supplemented and updated later in life (Grüter and Wiltschko 1990), but experiences during the first months must be expected to form the framework.

The Direction of Migration

During migration birds leave their home area and temporarily move to another one often hundreds or thousands of kilometers away. In higher and temperate latitudes, migration allows birds to escape the seasonal changes in climate; in the tropics, migration may be a response to dry and wet seasons that allows birds to seek out optimal foraging conditions. The navigational problems are similar in both cases: young migrants must reach a distant population-specific area and, in species in which individuals migrate alone, find this goal on their own.

The innate migration program

A large-scale displacement program involving >10,000 European Starlings of Baltic origin transported from The Netherlands to Switzerland during autumn migration indicated that young first-time migrants do not have knowledge of their goal but have knowledge of the population-specific migratory direction leading them there: displaced perpendicular to their normal migration route, they continued in the same direction on a new route parallel to the traditional one (Perdeck 1958). A recent study with White-crowned Sparrows (*Zonotrichia leucophyrys gambelii*) displaced across North America and radiotracked after release confirmed these findings (Thorup et al. 2007). Further analyses revealed a migration program that provides the young birds with information that under normal circumstances enables them to reach their winter quarters (e.g., Gwinner 1968, Berthold 1988). This program encodes the wintering area with respect to the breeding ground in "polar coordinates," namely as distance and direction of migration. Being innate, genetically transmitted from one generation to the next, it reflects the past experience of generations of migrating ancestors and must be expected to be optimally adapted by evolution to the population's needs.

Young birds of species that migrate in family groups also have genetically transmitted knowledge of their population-specific migratory direction available, as an experiment by Schüz (1949, 1950) indicated. Eggs of White Storks (*Ciconia ciconia*) from East Prussia with a southeasterly migratory direction were displaced to Essen, West Germany, to be raised in the local population, which migrated southwest. At the beginning of migration, the young White Storks were color coded, and half of them were held back in captivity. Those that remained free joined their foster parents on the southwesterly route (Schüz 1950). The others were set free after all the local White Storks had left the area; they were observed heading southeast (Schüz 1949). These observations clearly show that even young birds that migrate in groups led by adults possess innate information of their migratory direction, but that this innate information can be overridden by the social tendency to join groups of conspecifics.

Two reference systems.—The innate migratory direction must be encoded with respect to an external reference to be converted into an actual compass course. This occurs mainly during the premigratory period, so that the migratory direction is available when migration starts. So far, two systems have been shown to serve as references: celestial rotation and the geomagnetic field.

Emlen (1970) was the first to recognize the importance of celestial rotation for establishing the migratory direction: young Indigo Buntings, hand-raised under a rotating planetarium sky, were later tested under the same, now stationary planetarium sky. They oriented away from the former center of rotation, regardless of which star pattern had been the former center (Fig. 9). The same was later found to be true of hand-raised Garden Warblers exposed to an artificial sky of only 16 dots of light: young birds that had observed this simple sky rotating during the premigratory period later oriented away from the former center of rotation, whereas birds that knew the same sky only as stationary were disoriented when tested in a compensated magnetic field (Fig. 17; W. Wiltschko et al. 1987a). The sunset cues alone, however, do not seem to indicate the migratory direction to young migrants (Bingman 1983), which is not surprising, given that the cues associated with sunset undergo the same seasonal and latitudinal changes as the sun itself.

The geomagnetic field is the other factor that can act as a reference for the genetic information on migratory direction. Hand-raised birds from several species of passerines that had been totally deprived of celestial information and were tested with the

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

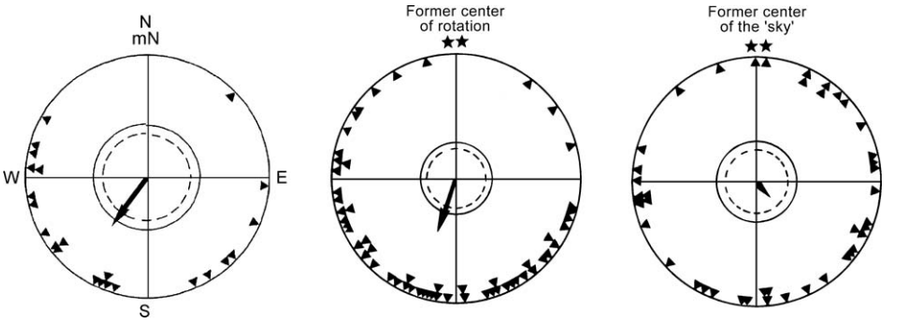


FIG. 17. The geomagnetic field and celestial rotation serve as reference systems for the innate migratory direction in Garden Warblers. Left: headings of birds that had been hand-raised without a view of celestial cues, tested during autumn migration in the local geomagnetic field. Center: birds that had been hand-raised under an artificial sky that made one revolution per day, tested during autumn migration under the same, now stationary, sky. Right: birds hand-raised under a stationary artificial sky and later tested under the same stationary sky. Inner circles are the 5% (dotted) and the 1% significance border of the Rayleigh test (data from W. Wiltschko and Gwinner 1974; W. Wiltschko et al. 1987b).

magnetic field as the only cue preferred their natural migratory direction, which indicates that the migratory direction is encoded as a magnetic-compass course (e.g., Gwinner and Wiltschko 1978, Bingman 1981, Beck and Wiltschko 1982, Able and Able 1990b, Shumakov 1990, Bletz et al. 1996; Fig. 17, and see Fig. 18, left).

The innate directional information is not necessarily restricted to one course alone. Some species reach their wintering area not on a straight route but change their course during migration. For example, Garden Warblers and Pied Flycatchers from Central Europe fly first to the Iberian Peninsula on a southwesterly course, then continue on more southerly to southeasterly courses to reach their wintering areas south of the Sahara Desert, in this way avoiding a large sea crossing and the very harsh conditions in the central Sahara. A similar non-straight route is known from Yellow-faced Honeyeaters in Australia that follow the Great Dividing Range to stay in ecologically favorable habitats. In those species, the various legs of the route have been found to be coded as sequences of directions in relation to the geomagnetic field (e.g., Gwinner and Wiltschko 1978, Beck and Wiltschko 1988, Munro et al. 1993). Whether the later migratory directions are also encoded with respect to celestial rotation is unclear.

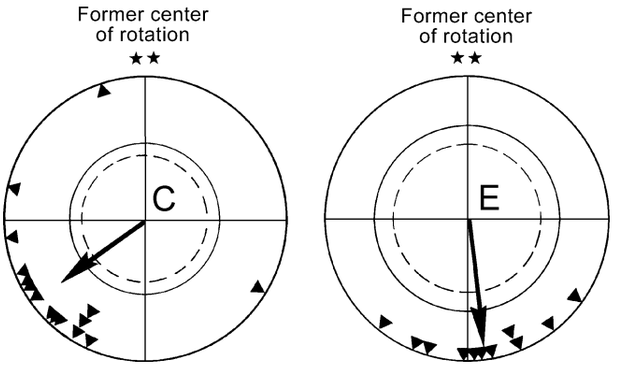


Fig. 18. Garden Warblers combine celestial rotation and information from the geomagnetic field to obtain their population-specific migratory direction. Mean headings of birds tested under a stationary artificial sky in a compensated magnetic field are shown. Left: birds that had experienced the artificial sky rotating together with the local geomagnetic field showed the population-specific southwesterly course with respect to the former center of rotation. Right: birds that had experienced the same rotating sky in a compensated magnetic field oriented away from the former center of rotation. Inner circles are the 5% (dotted) and the 1% significance border of the Rayleigh test (data from Weindler et al. 1996).

It must be mentioned that in Garden Warblers the change in direction seems to be controlled by the endogenous time program of migration alone (Gwinner and Wiltschko 1978), whereas in Pied Flycatchers it appears to require some external stimulus, because in the latter the second leg of migration was oriented only if the birds were exposed to the magnetic conditions found in the region where the change in direction occurs (Beck and Wiltschko 1988).

Interactions between the celestial rotation and the magnetic field.—The observation that two factors can act as reference for the migratory direction raises the question of a hierarchy between them and possible interactions. Experiments that set the two cues in conflict during the premigratory period revealed the dominance of celestial rotation. Young Savannah Sparrows were hand-raised under the natural night sky, the natural daytime sky, and an artificial sky that made one revolution per day; at the same time, they were exposed to a magnetic field with north turned 90°. These birds changed their magnetic compass course and headed in the magnetic direction that had been opposite to the center of celestial rotation (Able and Able 1990a, b, 1993). The same effect was observed in Pied Flycatchers (Bingman 1984, Prinz and Wiltschko 1992). This means that the birds chose information from celestial rotation over that from the magnetic field and adjusted their magnetic course accordingly.

At higher latitudes, where magnetic inclination becomes rather steep, birds seem to require additional information from celestial rotation to later achieve unimodal orientation with their magnetic compass alone. This is the case for the northern populations of Blackcaps (Shumakov and Zelenova 1988) and Pied Flycatchers (Weindler et al. 1995), whereas the southern population of

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

these species can realize their population-specific compass course by magnetic information alone (Beck and Wiltschko 1988, Bletz et al. 1996). Here, celestial rotation and the geomagnetic field work together to convert the innate information into an actual course.

Studies with Garden Warblers using a simple artificial sky making one rotation per day revealed another interesting interaction of celestial rotation and the magnetic field. During the first part of migration, Central European Garden Warblers head ~225° southwest, and young birds that had been exposed to the rotating sky in the local geomagnetic field during the premigratory period later preferred their population-specific southwesterly course under the now stationary stars alone. Birds that had been exposed to the rotating sky in a compensated magnetic field, however, headed south—they headed away from the former center of rotation, but without showing the typical deviation to the west that characterized their population-specific migratory direction (Fig. 18; Weindler et al. 1996). This suggests that the information on their migratory course consists of two components, namely a reference direction away from the center of rotation, corresponding to geographic south, which is controlled by celestial rotation, and the deviation from this reference, which seems to be encoded only with respect to the magnetic field. To combine these two components for their natural migration course, the birds must observe rotating stars together with the geomagnetic field—then they can locate this direction later also with the help of stars. Thus, celestial cues alone do not seem sufficient for establishing the population-specific southwesterly migration course of Garden Warblers; additional information from the magnetic field is needed.

The direction of celestial rotation also proved important: birds that had observed an artificial sky rotating in the reverse direction in the geomagnetic field later headed southward, apparently unable to combine the magnetically encoded information with the reference given by celestial rotation (Weindler et al. 1997).

Why use two reference systems?—The conversion of the genetically coded information into an actual migratory direction as described above involves complex interactions between celestial rotation and the magnetic field. One wonders why this is so, because one reference system would appear to be sufficient. It is true that Garden Warblers can find their migratory direction with the help of the magnetic field alone (e.g., Gwinner and Wiltschko 1978; see Fig. 17), but under natural conditions, young birds would be able to regularly observe the rotating sky. Celestial rotation always indicates geographic north, whereas magnetic north changes with time because of secular variation (see Skiles 1985). In particular, at higher magnetic latitudes close to the magnetic poles, there may be considerable variability in magnetic declination in time and space. Including celestial rotation in the innate information could ensure that the migration course becomes largely independent of the changing magnetic conditions.

We can only speculate why the deviation from south is encoded only with respect to the magnetic field. Maybe the magnetic field is more suitable to encode a deviation because it can be perceived directly, whereas a longer observation period is necessary to recognize the center of celestial rotation. On the other hand, the migratory direction of most birds has a component that leads them closer to the Equator; this component, indicated by celestial rotation, is constant in time. Yet the population-specific routes may deviate considerably from this reference direction, in response to the ecological conditions en route. It must remain flexible and be modified when these conditions change, thus ensuring that birds take optimal routes to reach their winter quarters. This means that the respective component of the migratory direction is subject to constant modifications by selection. Adapting the migratory direction to these changes in the environment may be easier when only one reference system is involved.

We must keep in mind that our knowledge of the respective processes is still very limited. Only a few species have been analyzed with regard to the development of their migratory direction, and we cannot expect that the way in which the migratory direction is genetically encoded is identical in all migrating species. As we pointed out above, migration developed independently many times in the various lineages of birds (Helbig 2003), and so perhaps did the mechanisms that encode the course of migration. Thus, differences between species would not be surprising. Some species may have found particular solutions for the problem of choosing optimal routes, as Alerstam and Gudmundson (1999) suggested in the case of migrating waders in the High Arctic.

Distance of migration.—The distance of migration is encoded by a time program within the circannual cycle, producing the required amount of migratory activity for a number of days so that the total amount of migratory activity is adapted to the length of the migration route. This was demonstrated by experiments with hand-raised birds of several species in the genera *Phylloscopus* and *Sylvia* and in Blackcaps from different populations (Gwinner 1968, Berthold 1973, Berthold and Querner 1981). The mean total amount of *Zugunruhe* (nightly activity in these nocturnal migrants) was closely related to the mean distance of migration. The finding that the amount of *Zugunruhe* in crossbreeds between populations with different distances of migration was intermediate between the parent populations indicates that it is an inherited property (Berthold and Querner 1981). At the end of migration, when birds have reached their wintering region, the migration program becomes more flexible, allowing birds to stop migration when they have reached a suitable habitat or go on until they have found one.

Migration to a familiar goal

The migration back to the breeding ground and all later migrations differ from the first one in that they no longer involve finding an unknown region, but lead the birds back to an area where they have been before. This means that the birds are familiar with the local navigational factors of their goal area and also, because of their experience during the first migration, with the navigational factors of the route.

The large-scale displacements already mentioned (Perdeck 1958, Thorup et al. 2007) clearly showed that displaced adult migrants also head directly toward their traditional wintering areas from locations off the normal migration route. Adult European Starlings displaced from The Netherlands to Switzerland changed their course from west-southwest to northwest and headed toward northern France and southern England, where this Baltic population normally wintered (Perdeck 1958), and the tracks of displaced adult White-crowned Sparrows in the study by Thorup et al. (2007) were directed toward the winter quarters of that population. The young European Starlings that had wintered south of their normal wintering range headed toward their Baltic region of origin on their return migration (Perdeck 1983). This means that migrants on later

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

migrations can use mechanisms of true navigation. Experiments with hand-raised migrants showed that innate information on the direction of migration continues to be available (Helbig 1992); yet experience-based mechanisms seem to dominate in determining the course to the now familiar goal area.

What specific type of navigational factors migrants use is not known; we can assume, however, that they are similar to the ones pigeons and other birds use for homing. Considering the distances to be covered, a preference for large-scale, possibly worldwide gradients is to be expected en route, whereas regional and local factors may also play a role when the birds have reached the region of their goal. It is also conceivable that during the extended flights between breeding and wintering areas, navigation normally plays only a minor role—birds may fly their innate course during most of their migratory journey, switching to navigation only when approaching the home area to pinpoint last year's breeding or wintering site.

A System Combining Innate and Learned Components

As we have shown above, homing and migration follow a common scheme: the direction to the goal is first determined as a compass course, then located with a compass. Both steps include innate and experience-based components.

The environment is variable; mechanisms that are innate must be based on the factors that are reliably available in a stable, predictable form. The geomagnetic field is one of them, with its field lines running north–south in lower and temperate latitudes, becoming more variable only in the regions around the magnetic poles. The birds can sense the field lines directly, which endows them with an innate magnetic compass. This enables them to distinguish magnetic directions, probably in a manner similar to our ability to distinguish up from down using our sense of gravity, and forms a suitable backbone for their navigational system.

Among celestial cues, celestial rotation is the only factor that can give directional information by itself, but to obtain this information, birds have to observe the rotating sky for a certain period. By contrast, the celestial cues normally used for direction finding—sun, stars, and polarized light—vary with time of day, season, and geographic latitude. Thus, the birds must be capable of interpreting them adequately, which is ensured by learning processes; similar learning processes probably adjust them to seasonal changes when necessary. Being established through learning processes guarantees that the mechanisms based on celestial cues are always perfectly tuned to the situation in the birds' home region.

The same is true of the mechanisms that determine the compass course in homing: young birds initially rely on route reversal, a strategy based on innate abilities, and this strategy ensures homing while they acquire the knowledge needed for establishing their maps. This, in turn, enables them to switch to site-specific information. Figure 19 summarizes the mechanisms employed in

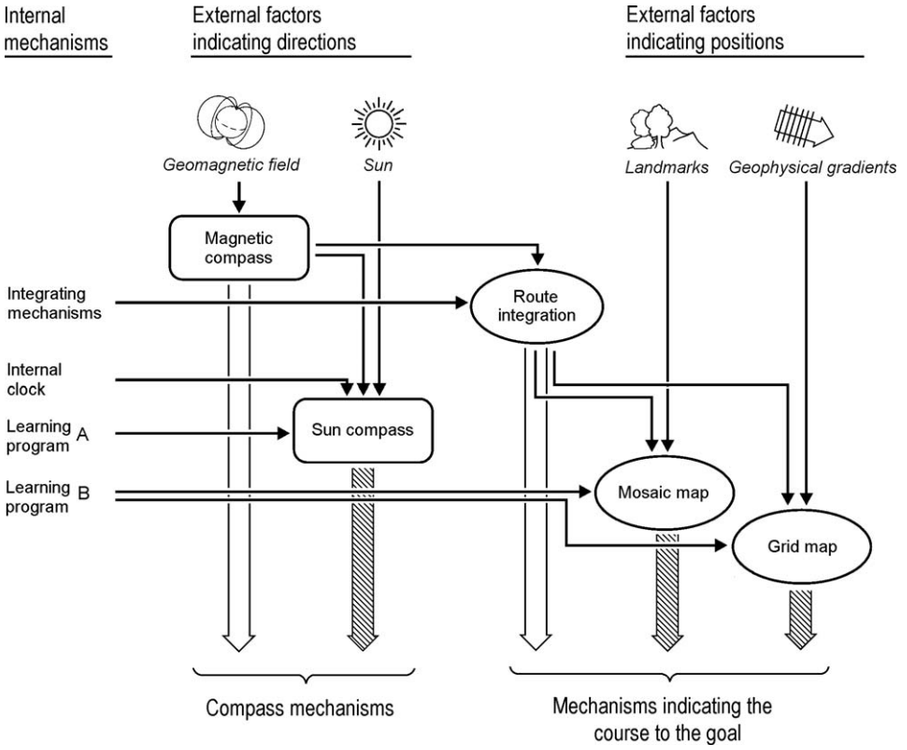


Fig. 19. Model of the ontogenetic development of the avian navigational system combining innate and learned components. Open arrows indicate mechanisms based solely on innate components, and hatched arrows indicate mechanisms based on experience (modified from R. Wiltschko and Wiltschko 2003).

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

homing and their ontogenetic relationship. Based entirely on experience, the grid map and mosaic map realistically represent the distribution of navigational factor in the birds' home region—they are perfectly adjusted to the area where the birds live.

The same principle is found in the navigational processes of migration: an innate program enables the young birds to reach their still unknown winter quarters on their first migration flight, using the geomagnetic field and celestial rotation as directional references. At the same time, when they move toward their wintering area guided by this program, they have the opportunity to familiarize themselves with the distribution of the navigational factors en route and in their wintering area. Therefore, they can make use of this knowledge and head directly to their goal area by means of true navigation during later migrations.

This combination of innate and learned components makes the navigational system highly flexible. The innate components allow navigation before the experience-based ones are established and provide the opportunity to acquire the necessary experience. This enables birds to make use of a wide variety of factors the environment has to offer, at the same time ensuring that the learned mechanisms are perfectly adapted to the local situation. This makes avian navigation so powerful and effective.

Literature Cited

Able, K. P. 1982. Skylight polarization patterns at dusk influence migratory orientation in birds. Nature 299:550–551.

Able, K. P. 1989. Skylight polarization patterns and the orientation of migratory birds. Journal of Experimental Biology 141:241–256.

Able, K. P., and M. A. Able. 1990a. Calibration of the magnetic compass of a migratory bird by celestial rotation. Nature 347:378–380.

Able, K. P., and M. A. Able. 1990b. Ontogeny of migratory orientation in the Savannah Sparrow, *Passerculus sandwichensis*: Calibration of the magnetic compass. Animal Behaviour 39:905–913.

Able, K. P., and M. A. Able. 1993. Daytime calibration of magnetic orientation in a migratory bird requires a view of skylight polarization. Nature 364:523–525.

Able, K. P., and M. A. Able. 1995. Interactions in the flexible orientation system of a migratory bird. Nature 375:230–232.

Able, K. P., and P. M. Dillon. 1977. Sun compass orientation in a nocturnal migrant, the White-throated Sparrow. Condor 79:393–395.

Åkesson, S. 1993. Effect of geomagnetic field on orientation of the Marsh Warbler, *Acrocephalus palustris*, in Sweden and Kenya. Animal Behaviour 46:1157–1167.

Åkesson, S. 1994. Comparative orientation experiments with different species of passerine long-distance migrants: Effect of magnetic field manipulation. Animal Behaviour 48:1379–1393.

Åkesson, S., J. Morin, R. Muheim, and U. Ottosson. 2001. Avian orientation at steep angles of inclination: Experiments with migratory White-crowned Sparrows at the magnetic North Pole. Proceedings of the Royal Society of London, Series B 268:1907–1913.

Alerstam, T., and G. A. Gudmundsson. 1999. Bird orientation at high latitudes: Flight routes between Siberia and North America across the Arctic Ocean. Proceedings of the Royal Society of London, Series B 266:2499–2505.

Baker, R. R. 1984. Bird Navigation: The Solution of a Mystery? Hodder and Stoughton, London.

Barlow, J. S. 1964. Inertial navigation as a basis for animal navigation. Journal of Theoretical Biology 6:76–117.

Beason, R. C. 1987. Interaction of visual and non-visual cues during migratory orientation by the Bobolink (*Dolichonyx oryzivorus*). Journal für Ornithologie 128:317–324.

Beason, R. C. 1989. Use of an inclination compass during migratory orientation by the Bobolink (*Dolichonyx oryzivorus*). Ethology 81:291–299.

Beason, R. C. 1992. You can get there from here: Responses to simulated magnetic equator crossing by the Bobolink (*Dolichonyx oryzivorus*). Ethology 91:75–80.

Beck, W., and W. Wiltschko. 1982. The magnetic field as reference system for the genetically encoded migratory direction in Pied Flycatchers (*Ficedula hypoleuca* Pallas). Zeitschrift für Tierpsychologie 60:41–46.

Beck, W., and W. Wiltschko. 1988. Magnetic factors control the migratory direction of Pied Flycatchers (*Ficedula hypoleuca* Pallas). Pages 1955–1962 *in* Acta XIX Congressus Internationalis Ornithologici (H. Ouellet, Ed.). National Museum of Natural Sciences, University of Ottawa Press, Ottawa.

Becker, J., and H. van Raden. 1986. Meteorologische Gesichtspunkte zur olfaktorischen Navigationshypothese. Journal für Ornithologie 127:1–8.

Benvenuti, S., and V. Fiaschi. 1983. Pigeon homing: Combined effect of olfactory deprivation and visual impairment. Comparative Biochemistry and Physiology A 76:719–723.

Berthold, P. 1973. Relationships between migratory restlessness and migration distance in six *Sylvia* species. Ibis 115:594–599.

Berthold, P. 1988. The control of migration in European warblers. Pages 215–249 *in* Acta XIX Congressus Internationalis Ornithologici (H. Ouellet, Ed.). National Museum of Natural Sciences, University of Ottawa Press, Ottawa.

Berthold, P., and U. Querner. 1981. Genetic basis of migratory behavior in European warblers. Science 212:77–79.

Bingman, V. P. 1981. Savannah Sparrows have a magnetic compass. Animal Behaviour 29:962–963.

Bingman, V. P. 1983. Magnetic field orientation of migratory naive Savannah Sparrows with different first summer experience. Behaviour 87:43–53.

Bingman, V. P. 1984. Night sky orientation of migratory Pied Flycatchers raised in different magnetic fields. Behavioral Ecology and Sociobiology 15:77–80.

Bingman, V. P. 1987. Earth's magnetism and the nocturnal orientation of migratory European Robins. Auk 104:523–525.

Bingman, V. P., and W. Wiltschko. 1988. Orientation of Dunnocks (*Prunella modularis*) at sunset. Ethology 77:1–9.

Biro, D., R. Freeman, J. Meade, S. Roberts, and T. Guilford. 2007. Pigeons combine compass and landmark guidance in familiar route navigation. Proceedings of the National Academy of Sciences USA 104:7471–7476.

Biro, D., J. Meade, and T. Guilford. 2004. Familiar route loyalty implies visual pilotage in the homing pigeon. Proceedings of the National Academy of Sciences USA 101:17440–17443.

Bletz, H., P. Weindler, R. Wiltschko, W. Wiltschko, and P. Berthold. 1996. The magnetic field as reference for the innate migratory direction in Blackcaps, *Sylvia atricapilla*. Naturwissenschaften 83:430–432.

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Braithwaite, V. A. 1993. When does previewing the landscape affect pigeon homing? Ethology 95:141–151.

Chelazzi, G., and L. Pardi. 1972. Experiments on the homing behaviour of caged pigeons. Monitore Zoologico Italiano (N.S.) 6:11–18.

Chelazzi, G., and F. Pineschi. 1974. Evidence for a sun compass in city pigeons (*Columba livia*). Monitore Zoologico Italiano (N.S.) 8:215–220.

Cochran, W. W., H. Mouritsen, and M. Wikelski. 2004. Migrating songbirds recalibrate their magnetic compass daily from twilight cues. Science 304:405–408.

Darwin, C. 1873. Origin of certain instincts. Nature 7:417–418.

Duff, S. J., L. A. Brownlie, D. F. Sherry, and M. Sangster. 1998. Sun compass and landmark orientation by Black-capped Chickadees (*Parus atricapillus*). Journal of Experimental Psychology: Animal Behavior Processes 24:243–253.

Edrich, W., and W. T. Keeton. 1977. A comparison of homing behavior in feral and homing pigeons. Zeitschrift für Tierpsychologie 44:389–401.

Emlen, S. T. 1967a. Migratory orientation in the Indigo Bunting, *Passerina cyanea*. Part I: Evidence for use of celestial cues. Auk 84:309–342.

Emlen, S. T. 1967b. Migratory orientation in the Indigo Bunting, *Passerina cyanea*. Part II: Mechanism of celestial orientation. Auk 84:463–489.

Emlen, S. T. 1969a. Bird migration: Influence of physiological state upon celestial orientation. Science 165:716–718.

Emlen, S. T. 1969b. The development of migratory orientation in young Indigo Buntings. Living Bird 1969:113–124.

Emlen, S. T. 1970. Celestial rotation: Its importance in the development of migratory orientation. Science 170:1198–1201.

Ericson, P. G. P., C. L. Anderson, T. Britton, A. Elzanowski, U. S. Johansson, M. Källersjö, J. I. Ohlson, T. J. Parsons, D. Zuccon, and G. Mayr. 2006. Diversification of Neoaves: Integration of molecular sequence data and fossils. Biological Letters 2:543–547.

Exner, S. 1883. Negative Versuchsergebnisse über das Orientierungsvermögen der Brieftauben. Sitzungsberichte der Akademie der Wissenschaften Wien, Mathematisch-Naturwissenschaftliche Klasse III 102:318–331.

Fleissner, G., E. Holtkamp-Rötzler, M. Hanzlik, M. Winklhofer, G. Fleissner, N. Petersen, and W. Wiltschko. 2003. Ultrastructural analysis of a putative magnetoreceptor in the beak of homing pigeons. Journal of Comparative Neurology 458:350–360.

Fleissner, G., B. Stahl, P. Thalau, G. Falkenberg, and G. Fleissner. 2007. A novel concept of Fe-mineral-based magnetoreception: Histological and physicochemical data from the upper beak of homing pigeons. Naturwissenschaften 94:631–642.

Freire, R., U. H. Munro, L. J. Rogers, R. Wiltschko, and W. Wiltschko. 2005. Chickens orient using a magnetic compass. Current Biology 15:R620–R621.

Füller, E., U. Kowalski, and R. Wiltschko. 1983. Orientation of homing pigeons: Compass orientation vs piloting by familiar landmarks. Journal of Comparative Physiology 153:55–58.

Graue, L. C. 1963. The effect of phase shifts in the day–night cycle on pigeon homing at distances of less than one mile. Ohio Journal of Science 63:214–217.

Griffin, D. R. 1944. The sensory basis of bird navigation. Quarterly Review of Biology 19:15–31.

Griffin, D. R. 1987. Foreword to papers on magnetic sensitivity in birds. Animal Learning & Behavior 15:108–109.

Grüter, M., and R. Wiltschko. 1990. Pigeon homing: The effect of local experience on initial orientation and homing success. Ethology 84:239–255.

Gwinner, E. 1968. Circannuale Periodik als Grundlage des jahreszeitlichen Funktionswandels bei Zugvögeln. Untersuchungen am Fitis (*Phylloscopus trochilus*) und am Waldlaubsänger (*P. sibilatrix*). Journal für Ornithologie 109:70–95.

Gwinner, E., and W. Wiltschko. 1978. Endogenously controlled changes in migratory direction of the Garden Warbler, *Sylvia borin*. Journal of Comparative Physiology 125:267–273.

Hagstrum, J. T. 2000. Infrasound and the avian navigational map. Journal of Experimental Biology 203:1103–1111.

Haque, R., S. S. Chaurasia, J. H. Wessel III, and P. M. Iuvone. 2002. Dual regulation of cryptochrome 1 mRNA expression in chicken retina by light and circadian oscillators. NeuroReport 13:2247–2251.

Helbig, A. J. 1990. Depolarization of natural skylight disrupts orientation of an avian nocturnal migrant. Experientia 46:755–758.

Helbig, A. J. 1991. Dusk orientation of migratory European Robins, *Erithacus rubecula*: The role of sun-related directional information. Animal Behaviour 41:313–322.

Helbig, A. J. 1992. Ontogenetic stability of inherited migratory directions in a nocturnal bird migrant: Comparison between the first and second year of life. Ethology Ecology & Evolution 4:375–388.

Helbig, A. J. 2003. Evolution of bird migration: A phylogenetic and biogeographic perspective. Pages 3–20 *in* Avian Migration (P. Berthold, E. Gwinner, and E. Sonnenschein, Eds.). Springer-Verlag, Berlin.

Helbig, A. J., and W. Wiltschko. 1989. The skylight polarization patterns at dusk affect the orientation behavior of Blackcaps, *Sylvia atricapilla*. Naturwissenschaften 76:227–229.

Jorge, P. E., A. E. Marques, and J. B. Phillips. 2009. Activational rather than navigational effects of odors on homing of young pigeons. Current Biology 19:650–654.

Jorge, P. [E.], L. Vicente, and W. Wiltschko. 2006. What strategies do homing pigeons use during ontogeny? Behaviour 143:105–122.

Keeton, W. T. 1969. Orientation by pigeons: Is the sun necessary? Science 165:922–928.

Keeton, W. T. 1971. Magnets interfere with pigeon homing. Proceedings of the National Academy of Sciences USA 68:102–106.

Keeton, W. T. 1973. Release-site bias as a possible guide to the "map" component in pigeon homing. Journal of Comparative Physiology 86:1–16.

Keeton, W. T. 1974. The orientational and navigational basis of homing in birds. Advances in the Study of Behavior 5:47–132.

Kiepenheuer, J. 1982. The effect of magnetic anomalies on the homing behaviour of pigeons. Pages 120–128 *in* Avian Navigation (F. Papi and H. G. Wallraff, Eds.). Springer-Verlag, Berlin.

Kirschvink, J. L., and J. L. Gould. 1981. Biogenetic magnetite as a basis for magnetic field detection in animals. BioSystems 13:181–201.

Kirschvink, J. L., and M. M. Walker. 1985. Particle-size considerations for magnetite-based magnetoreceptors. Pages 243–256 *in* Magnetite Biomineralization and Magnetoreception in Organisms

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

(J. L. Kirschvink, D. S. Jones, and B. J. MacFadden, Eds.). Plenum Press, New York.

Kramer, G. 1950. Weitere Analyse der Faktoren, welche die Zugaktivität des gekäfigten Vogels orientieren. Naturwissenschaften 37:377–378.

Kramer, G. 1952. Experiments on bird orientation. Ibis 94:265–285.

Kramer, G. 1953. Wird die Sonnenhöhe bei der Heimfindeorientierung verwertet? Journal für Ornithologie 94:201–219.

Kramer, G. 1957. Experiments on bird orientation and their interpretation. Ibis 99:196–227.

Lednor, A. J., and C. Walcott. 1984. The orientation of pigeons at gravity anomalies. Journal of Experimental Biology 111:259–263.

Lutsyuk, B. C., and G. K. Nazarchuk. 1971. Mögliche Orientierung von Vögeln nach dem Erdmagnetfeld [in Russian]. Vestnik Zoologica 5:35–39.

Matthews, G. V. T. 1963. The astronomical bases of 'nonsense' orientation. Pages 415–429 *in* Proceedings XIII International Ornithological Congress (C. G. Sibley, Ed.). Blackwell Scientific, Oxford, United Kingdom.

Mazzotto, M., L. Nacci, and A. Gagliardo. 1999. Homeward orientation of pigeons confined in a circular arena. Behavioural Processes 46:217–225.

Meade, J., D. Biro, and T. Guilford. 2005. Homing pigeons develop local route stereotypy. Proceedings of the Royal Society of London, Series B 272:17–23.

Michener, M. C., and C. Walcott. 1967. Homing of single pigeons—Analysis of tracks. Journal of Experimental Biology 47:99–131.

Möller, A., S. Sagasser, W. Wiltschko, and B. Schierwater. 2004. Retinal cryptochrome in a migratory passerine bird: A possible transducer for the avian magnetic compass. Naturwissenschaften 91:585–588.

Moore, F. R. 1986. Sunrise, skylight polarization, and the early morning orientation of night-migrating warblers. Condor 88:493–498.

Mouritsen, H., U. Janssen-Bienhold, M. Liedvogel, G. Feenders, J. Stalleicken, P. Dirks, and R. Weiler. 2004. Cryptochromes and neuronal-activity markers colocalize in the retina of migratory birds during magnetic orientation. Proceedings of the National Academy of Sciences USA 101:14294–14299.

Muheim, R., J. Bäckman, and S. Åkesson. 2002. Magnetic compass orientation in European Robins is dependent on both wavelength and intensity of light. Journal of Experimental Biology 205:3845–3856.

Muheim, R., F. R. Moore, and J. B. Phillips. 2006a. Calibration of magnetic and celestial compass cues in migratory birds—A review of cue-conflict experiments. Journal of Experimental Biology 209:2–17.

Muheim, R., J. B. Phillips, and S. Åkesson. 2006b. Polarized light cues underlie compass calibration in migratory songbirds. Science 313:837–839.

Munro, U., and R. Wiltschko. 1993. Clock-shift experiments with migratory Yellow-faced Honeyeaters, *Lichenostomus chrysops* (Meliphagidae), an Australian day-migrating bird. Journal of Experimental Biology 181:233–244.

Munro, U., and R. Wiltschko. 1995. The role of skylight polarization in the orientation of a day-migrating bird species. Journal of Comparative Physiology A 177:357–362.

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

Neuss, M., and H. G. Wallraff. 1988. Orientation of displaced homing pigeons with shifted circadian clocks: Prediction vs observation. Naturwissenschaften 75:363–365.

Papi, F. 1986. Pigeon navigation: Solved problems and open questions. Monitore Zoologico Italiano (N.S.) 20:471–517.

Papi, F. 1991. Olfactory navigation. Pages 52–85 *in* Orientation in Birds (P. Berthold, Ed.). Birkhäuser, Basel, Switzerland.

Perdeck, A. C. 1958. Two types of orientation in migrating *Sturnus vulgaris* and *Fringilla coelebs* as revealed by displacement experiments. Ardea 46:1–37.

Perdeck, A. C. 1983. An experiment of the orientation of juvenile starlings during spring migration: An addendum. Ardea 71:255.

Phillips, J. B. 1996. Magnetic navigation. Journal of Theoretical Biology 180:309–319.

Potapov, R. L. 1966. Navigation ability of certain passerines. Doklady Akademii. Nauk SSSR 171:226–228.

Prinz, K., and W. Wiltschko. 1992. Migratory orientation of Pied Flycatchers: Interaction of stellar and magnetic information during ontogeny. Animal Behaviour 44:539–545.

Prior, H., R. Wiltschko, K. Stapput, O. Güntürkün, and W. Wiltschko. 2004. Visual lateralization and homing in pigeons. Behavioural Brain Research 154:301–310.

Ranvaud, R., K. Schmidt-Koenig, J. Kiepenheuer, O. C. Gasparotto, and L. R. G. Britto. 1988. Compass mechanisms of homing pigeons at the magnetic equator. Pages 297–304 *in* Acta XIX Congressus Internationalis Ornithologici (H. Ouellet, Ed.). National Museum of Natural Sciences, University of Ottawa Press, Ottawa.

Rappl, R., R. Wiltschko, P. Weindler, P. Berthold, and W. Wiltschko. 2000. Orientation behavior of Garden Warblers (*Sylvia borin*) under monochromatic light of various wavelengths. Auk 117:256–260.

Ritz, T., S. Adem, and K. Schulten. 2000. A model for photoreceptor-based magnetoreception in birds. Biophysical Journal 78:707–718.

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

Ritz, T., R. Wiltschko, P. J. Hore, C. T. Rodgers, K. Stapput, P. Thalau, C. R. Timmel, and W. Wiltschko. 2009. Magnetic compass of birds is based on a molecule with optimal directional sensitivity. Biophysical Journal 96:3451–3457.

Rogers, L. J., U. Munro, R. Freire, R. Wiltschko, and W. Wiltschko. 2008. Lateralized response of chicks to magnetic cues. Behavioural Brain Research 186:66–71.

Sandberg, R., J. Bäckman, F. R. Moore, and M. Lõhmus. 2000. Magnetic information calibrates celestial cues during migration. Animal Behaviour 60:453–462.

Sandberg, R., and F. R. Moore. 1996. Migratory orientation of Red-eyed Vireos, *Vireo olivaceus*, in relation to energetic condition and ecological context. Behavioral Ecology and Sociobiology 39:1–10.

Sandberg, R., U. Ottosson, and J. Pettersson. 1991. Magnetic orientation of migratory wheatears (*Oenanthe oenanthe*)

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

in Sweden and Greenland. Journal of Experimental Biolology 155:51–64.

Sandberg, R., and J. Pettersson. 1996. Magnetic orientation of Snow Buntings (*Plectrophenax nivaIis*), a species breeding in the High Arctic: Passage migration through temperate-zone areas. Journal of Experimental Biology 199:1899–1905.

Sandberg, R., J. Pettersson, and T. Alerstam. 1988. Shifted magnetic fields lead to deflected and axial orientation of migrating robins, *Erithacus rubecuIa*, at sunset. Animal Behaviour 36 : 877–887.

Sauer, F. 1957. Die Sternorientierung nächtlich ziehender Grasmücken, *Sylvia atricapilla*, *borin* und *curruca*. Zeitschrift für Tierpsychologie 14:29–70.

Schlichte, H. J. 1973. Untersuchungen über die Bedeutung optischer Parameter für das Heimkehrverhalten der Brieftauben. Zeitschrift für Tierpsychologie 32:257–280.

Schmidt-Koenig, K. 1958. Der Einflug experimentell veränderter Zeitschätzung auf das Heimfindevermögen bei Brieftauben. Naturwissenschaften 45:47.

Schmidt-Koenig, K. 1960. The sun azimuth compass: One factor in the orientation of homing pigeons. Science 131:826–828.

Schmidt-Koenig, K. 1961. Die Sonne als Kompaβ im Heim-Orientierungssystem der Brieftauben. Zeitschrift für Tierpsychologie 18:221–244.

Schmidt-Koenig, K. 1965. Current problems in bird orientation. Advances in the Study of Behavior 1:217–276.

Schmidt-Koenig, K. 1970. Ein Versuch, theoretisch mögliche Navigationsverfahren von Vögeln zu klassifizieren und relevante sinnesphysiologische Probleme zu umreiβen. Verhandlungen der Deutschen Zoologischen Gesellschaft 64:243–244.

Schmidt-Koenig, K. 1990. The sun compass. Experientia 46:336–342.

Schmidt-Koenig, K., and H. J. Schlichte. 1972. Homing in pigeons with impaired vision. Proceedings of the National Academy of Sciences USA 69:2446–2447.

Schmidt-Koenig, K., and C. Walcott. 1978. Tracks of pigeons homing with frosted lenses. Animal Behaviour 26:480–486.

Schüz, E. 1949. Die Spät-Auflassung ostpreussischer Jungstörche in Westdeutschland 1933. Vogelwarte 15:63–78.

Schüz, E. 1950. Früh-Auflassung ostpreussischer Jungstörche in West-Deutschland durch die Vogelwarte Rossitten 1933–1936. Bonner Zoologische Beiträge 1:239–253.

Shcherbakov, V. P., and M. Winklhofer. 1999. The osmotic magnetometer: A new model for magnetite-based magnetoreceptors in animals. European Biophysics Journal 28:380–392.

Shumakov, M. E. 1990. The development or orientation capabilities of young night migrants under natural and experimental conditions. Baltic Birds 5, vol. 2:146–149.

Shumakov, M. E., and N. P. Zelenova. 1988. Ontogenesis of nonvisual orientation of Blackcaps (*Sylvia atricapilla*). Pages 255–257 *in* Abstracts of the XII Eastern Baltic Ornithological Conference, Vilnius.

Skiles, D. D. 1985. The geomagnetic field: Its nature, history, and biological relevance. Pages 43–102 *in* Magnetite Biomineralization and Magnetoreception in Organisms (J. L. Kirschvink, D. S. Jones, and B. J. MacFadden, Eds.). Plenum Press, New York.

Stapput, K., P. Thalau, R. Wiltschko, and W. Wiltschko. 2008. Orientation of birds in total darkness. Current Biology 18:602–606.

Thalau, P., T. Ritz, K. Stapput, R. Wiltschko, and W. Wiltschko. 2005. Magnetic compass orientation of migratory birds in the presence of a 1.315 MHz oscillating field. Naturwissenschaften 92:86–90.

Thorup, K., I.-A. Bisson, M. S. Bowlin, R. A. Holland, J. C. Wingfield, M. Ramenofsky, and M. Wikelski. 2007. Evidence for a navigational map stretching across the continental U.S. in a migratory songbird. Proceedings of the National Academy of Sciences USA 104:18115–18119.

Viguier, C. 1882. Le sens de l'orientation et ses organs chez les animaux et chez l'homme. Revue Philosophique de la France et de l'Etranger 14:1–36.

von Frisch, K. 1965. Tanzsprache und Orientierung der Bienen. Springer-Verlag, Berlin.

von Saint-Paul, U. 1956. Compass directional training of Western Meadowlarks (*Sturnella negIecta*). Auk 73:203–210.

von Saint Paul, U. 1982. Do geese use path integration for walking home? Pages 298–307 *in* Avian Navigation (F. Papi and H. G. Wallraff, Eds.). Springer-Verlag, Berlin.

Voss, J., N. Keary, and H.-J. Bischof. 2007. The use of the geomagnetic field for short distance orientation in Zebra Finches. NeuroReport 18:1053–1057.

Walcott, C. 1978. Anomalies in the earth's magnetic field increase the scatter of pigeons' vanishing bearings. Pages 143–151 *in* Animal Migration, Navigation and Homing (K. Schmidt-Koenig and W. T. Keeton, Eds.). Springer-Verlag, Berlin.

Walcott, C., and R. P. Green. 1974. Orientation of homing pigeons altered by a change in the direction of an applied magnetic field. Science 184:180–182.

Waldvogel, J. A. 1987. Olfactory navigation in homing pigeons: Are the current models atmospherically realistic? Auk 104:369–379.

Wallraff, H. G. 1959. Örtlich und zeitlich bedingte Variabilität des Heimkehrverhaltens von Briegtauben. Zeitschrift für Tierpsychologie 16:513–544.

Wallraff, H. G. 1965. Über das Heimfindevermögen von Brieftauben mit durchtrennten Bogengängen. Zeitschrift für Vergleichende Physiologie 50:313–330.

Wallraff, H. G. 1974. Das Navigationssystem der Vögel. Ein theoretischer Beitrag zur Analyse ungeklärter Orientierungsleistungen. Oldenbourg, Munich, Germany.

Wehner, R. 1982. Himmelsnavigation bei Insekten. Naturforschende Gesellschaft, Zürich, Switzerland.

Weindler, P., M. Baumetz, and W. Wiltschko. 1997. The direction of celestial rotation influences the development of stellar orientation in young Garden Warblers (*Sylvia borin*). Journal of Experimental Biology 200:2107–2113.

Weindler, P., W. Beck, V. Liepa, and W. Wiltschko. 1995. Development of migratory orientation in Pied Flycatchers in different magnetic inclinations. Animal Behaviour 49:227–234.

Weindler, P., R. Wiltschko, and W. Wiltschko. 1996. Magnetic information affects the stellar orientation of young bird migrants. Nature 383:158–160.

Wiltschko, R. 1992. Das Verhalten verfrachteter Vögel. Vogelwarte 36:249–310.

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Wiltschko, R., C. Haugh, M. Walker, and W. Wiltschko. 1998. Pigeon homing: Sun compass use in the Southern Hemisphere. Behavioral Ecology and Sociobiology 43:297–300.

Wiltschko, R., R. Kumpfmüller, R. Muth, and W. Wiltschko. 1994. Pigeon homing: The effect of a clock-shift is often smaller than predicted. Behavioral Ecology and Sociobiology 35:63–73.

Wiltschko, R., U. Munro, H. Ford, and W. Wiltschko. 1999. After-effects of exposure to conflicting celestial and magnetic cues at sunset in migratory Silvereyes *Zosterops l. lateralis*. Journal of Avian Biology 30:56–62.

Wiltschko, R., U. Munro, H. Ford, and W. Wiltschko. 2008. Contradictory results on the role of polarized light in compass calibration in migratory songbirds. Journal of Ornithology 149:607–614.

Wiltschko, R., D. Nohr, and W. Wiltschko. 1981. Pigeons with a deficient sun compass use the magnetic compass. Science 214:343–345.

Wiltschko, R., I. Schiffner, and B. Siegmund. 2007a. Homing flights of pigeons over familiar terrain. Animal Behaviour 74:1229–1240.

Wiltschko, R., K. Stapput, H.-J. Bischof, and W. Wiltschko. 2007b. Light-dependent magnetoreception in birds: Increasing intensity of monochromatic light changes the nature of response. Frontiers in Zoology 4:5.

Wiltschko, R., M. Walker, and W. Wiltschko. 2000. Sun-compass orientation in homing pigeons: Compensation for different rates of change in azimuth? Journal of Experimental Biology 203:889–894.

Wiltschko, R., and W. Wiltschko. 1978. Evidence for the use of magnetic outward-journey information in homing pigeons. Naturwissenschaften 65:112.

Wiltschko, R., and W. Wiltschko. 1980. The process of learning sun compass orientation in young homing pigeons. Naturwissenschaften 67:512–514.

Wiltschko, R., and W. Wiltschko. 1981. The development of sun compass orientation in young homing pigeons. Behavioral Ecology and Sociobiology 9:135–141.

Wiltschko, R., and W. Wiltschko. 1985. Pigeon homing: Change in navigational strategy during ontogeny. Animal Behaviour 33:583–590.

Wiltschko, R., and W. Wiltschko. 1990. Zur Entwicklung der Sonnenkompaβorientierung bei jungen Brieftauben. Journal für Ornithologie 131:1–19.

Wiltschko, R., and W. Wiltschko. 1995. Magnetic Orientation in Animals. Springer-Verlag, Berlin.

Wiltschko, R., and W. Wiltschko. 1998. Pigeon homing: Effect of various wavelengths of light during displacement. Naturwissenschaften 85:164–167.

Wiltschko, R., and W. Wiltschko. 2000. A strategy for beginners! Reply to Wallraff (2000). Animal Behaviour 60:F37–F43.

Wiltschko, R., and W. Wiltschko. 2001. Clock-shift experiments with homing pigeons: A compromise between solar and magnetic information? Behavioral Ecology Sociobiology 49: 393–400.

Wiltschko, R., and W. Wiltschko. 2003. Avian navigation: From historical to modern concepts. Animal Behaviour 65:257–272.

Wiltschko, W. 1968. Über den Einfluβ statischer Magnetfelder auf die Zugorientierung der Rotkehlchen (*Erithacus rubecula*). Zeitschrift für Tierpsychologie 25:536–558.

Wiltschko, W. 1974. Der Magnetkompaβ der Gartengrasmücke (*Sylvia borin*). Journal für Ornithologie 115:1–7.

Wiltschko, W., and R. P. Balda. 1989. Sun compass orientation in seed-caching scrub jays (*Aphelocoma coerulescens*). Journal of Comparative Physiology A 164:717–721.

Wiltschko, W., R. P. Balda, M. Jahnel, and R. Wiltschko. 1999. Sun compass orientation in seed-caching corvids: Its role in spatial memory. Animal Cognition 2:215–221.

Wiltschko, W., P. Daum, A. Fergenbauer-Kimmel, and R. Wiltschko. 1987a. The development of the star compass in Garden Warblers, *Sylvia borin*. Ethology 74:285–292.

Wiltschko, W., R. Freire, U. Munro, T. Ritz, L. Rogers, P. Thalau, and R. Wiltschko. 2007. The magnetic compass of Domestic Chickens, *Gallus gallus*. Journal of Experimental Biology 210:2300–2310.

Wiltschko, W., M. Gesson, and R. Wiltschko. 2001. Magnetic compass orientation of European Robins under 565 nm green light. Naturwissenschaften 88:387–390.

Wiltschko, W., and E. Gwinner. 1974. Evidence for an innate magnetic compass in Garden Warblers. Naturwissenschaften 61:406.

Wiltschko, W., K. Stapput, P. Thalau, and R. Wiltschko. 2006. Avian magnetic compass: Fast adjustment to intensities outside the normal functional window. Naturwissenschaften 93:300–304.

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

Wiltschko, W., and R. Wiltschko. 1975a. The interaction of stars and magnetic field in the orientation system of night migrating birds. I. Autumn experiments with European Warblers (Gen. *Sylvia*). Zeitschrift für Tierpsychologie 37:337–355.

Wiltschko, W., and R. Wiltschko. 1975b. The interaction of stars and magnetic field in the orientation system of night migrating birds. II. Spring experiments with European Robins (*Erithacus rubecula*). Zeitschrift für Tierpsychologie 39:265–282.

Wiltschko, W., and R. Wiltschko. 1976. Interrelation of magnetic compass and star orientation on night-migrating birds. Journal of Comparative Physiology A 109:91–99.

Wiltschko, W., and R. Wiltschko. 1981. Disorientation of inexperienced young pigeons after transportation in total darkness. Nature 291:433–434.

Wiltschko, W., and R. Wiltschko. 1982. The role of outward journey information in the orientation of homing pigeons. Pages 239–252 *in* Avian Navigation (F. Papi and H. G. Wallraff, Eds.). Springer-Verlag, Berlin.

Wiltschko, W., and R. Wiltschko. 1992. Migratory orientation: Magnetic compass orientation of Garden Warblers (*Sylvia borin*) after a simulated crossing of the magnetic equator. Ethology 91:70–74.

Wiltschko, W., and R. Wiltschko. 2007a. Conditioning to magnetic directions. NeuroReport 18:949–950.

Wiltschko, W., and R. Wiltschko. 2007b. Magnetoreception in birds: Two receptors for two different tasks. Journal of Ornithology 148 (Supplement 1):61–76.

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Wiltschko, W., R. Wiltschko, and W. T. Keeton. 1976. Effects of a "permanent" clock-shift on the orientation of young homing pigeons. Behavioral Ecology and Sociobiology 1:229–243.

Wiltschko, W., R. Wiltschko, and W. T. Keeton. 1984. The effect of a "permanent" clock-shift on the orientation of experienced homing pigeons. Behavioral Ecology and Sociobiology 15:263–272.

Wiltschko, W., R. Wiltschko, W. T. Keeton, and A. I. Brown. 1987b. Pigeon homing: The orientation of young birds that had been prevented from seeing the sun. Ethology 76:27–32.

Wiltschko, W., R. Wiltschko, and C. Walcott. 1987c. Pigeon homing: Different effects of olfactory deprivation in different countries. Behavioral Ecology and Sociobiology 21:333–342.

Yorke, E. D. 1979. A possible magnetic transducer in birds. Journal of Theoretical Biology 77:101–105.

Received 22 June 2009, accepted 11 July 2009.

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use