

# Avian Navigation: A Combination of Innate and Learned Mechanisms

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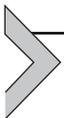
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In the past 50 years, the field of animal navigation has been growing fast. The birds are by far the best studied group, and their orientation mechanisms are better known than that of other vertebrates or invertebrates. In this review, we will summarize our present knowledge on avian navigation, focusing on the mechanisms that allow birds to reach their goal and the factors providing navigational information as far as they are known.



## 1. HISTORICAL ANNOTATIONS

In the first issue of this journal, [Klaus Schmidt-Koenig \(1965\)](#) published a review on *Current Problems in Bird Orientation*, summarizing the research on avian navigation at that time. At this time, the study of bird orientation and navigation was still an early state. Although the first theoretical concepts date back into the late nineteenth century (e.g., [Viguiet, 1882](#); [Exner, 1893](#)) and occasional experiments were performed during the first half of the twentieth century, systematic studies on avian navigation began only after 1950, when two methodological discoveries offered new possibilities in orientation research, namely (1) that migrants tend to head in their migratory direction also in captivity ([Kramer, 1949](#)) and (2) that displaced pigeons, when released, usually vanished in directions close to their home direction ([Matthews, 1951](#); [Kramer & von Saint Paul, 1952](#)).

## 1.1 Methodological Progress

The first discovery allowed entirely new techniques for the analysis of the orientation mechanisms of migrating birds, because it was now possible to change the environmental conditions in a controlled way around the small space of a cage. This opened up the era of cage studies analyzing the migratory orientation of passerine birds. Several types of circular cages for testing migrants were developed. [Kramer \(1949\)](#) had used a cage with a circular perch and recorded the head direction of his test bird by direct observation. [Sauer \(e.g., 1957\)](#), using a similar cage, observed nocturnally migrating birds in a planetarium under various sky conditions. [Fromme \(1961\)](#) constructed an octagonal cage with eight radially positioned perches that recorded the bird's activity automatically, and [Emlen and Emlen \(1966\)](#) built a funnel-shaped cage where the bird hopped up and slipped down the inclined walls, leaving inky footprints that could be evaluated. This last-mentioned type of cage, in various variations, is still used today to record the directional tendencies of migrants. In general, the directional tendencies recorded in cages agree well with the ringing recoveries of the respective species.

The second discovery on the vanishing bearings of pigeons gave a considerable impetus to the study of homing in birds. One can follow pigeons with good binocular about 2.5 km before they are lost from sight. Because these “vanishing bearings” seemed to reflect what pigeons consider their home direction, recording them became an important method in orientation research, not only with pigeons, but also with terns, ducks, and even with small passerines (e.g., [Griffin & Goldsmith, 1955](#); [Bellrose, 1958](#); [Matthews, 1961](#); [Sargent, 1962](#)). [Matthews \(e.g., 1951, 1953a\)](#), [Kramer \(e.g., 1953, 1957\)](#), and his students [Schmidt-Koenig \(e.g., 1958, 1963a\)](#) and [Wallraff \(e.g., 1959\)](#) focused their research on pigeon homing using this new method. Vanishing bearings continued to provide important data in homing studies until about 2000, when GPS-based flight-recorders allowed tracking the entire homing flight of pigeons with great precision ([Steiner et al., 2000](#); [von Hünnerbein et al., 2000](#)).

With directional training, another new method was introduced into orientation research: birds were conditioned to look for a food reward in a specific direction ([Kramer & von Saint Paul, 1950](#)). This method was widely applied in the first years after its discovery to analyze the functional properties of the sun compass. This was problematic, however, as in some cases it proved difficult to train birds to use this mechanism, while it could be easily demonstrated in spontaneous behavior like homing (see [Schmidt-Koenig,](#)

1958). The same is true for the magnetic compass: for a long time it seemed impossible to condition birds to magnetic directions (see Griffin, 1987), whereas the use of the magnetic field could be easily demonstrated in migratory orientation (e.g., Wiltschko, 1968). Hence the focus changed to the spontaneous behaviors, because these behaviors are more reliable than conditioned responses and show the compass mechanisms in their natural context. Conditioning is now mainly used to demonstrate compass orientation in birds that do not show spontaneous directional preferences.

## 1.2 Early Orientation Studies

One finding from the early orientation studies that had a large impact on the field of navigation research was the discovery of the *sun compass* by Kramer (1950). When it became evident that birds can use the sun for locating directions, the first actual orientation mechanism was recognized. During the following years, great efforts were devoted to the analysis of this mechanism. Changing the birds' internal clock became an important experimental tool (e.g., Hoffmann, 1954; Schmidt-Koenig, 1958): a clock-shift causes birds to misjudge the sun's position and, because of this, to select directions that deviate significantly from those of untreated controls. Until today, this is a standard method to demonstrate sun compass use. During the 1950s and 1960s, many studies focusing on the analysis of the sun compass involved directionally trained birds (e.g., Hoffmann, 1954; Schmidt-Koenig, 1963b; von Saint Paul, 1954,1956), but also displaced pigeons with their internal clock shifted were released (e.g., Schmidt-Koenig, 1958, 1961). The observed deflections were found to be correlated with the amount of time shift, and it also became evident that pigeons use only the sun's azimuth while its altitude is ignored.

In pigeon homing, vanishing bearings of birds released in different directions and distances from their loft were recorded and analyzed for spatial and temporal patterns (e.g., Wallraff, 1959; Schmidt-Koenig, 1963a), with the hope that such patterns might provide insights into the nature of the navigational processes. Yet a general pattern that would apply to all lofts was not found; rather, the patterns observed in the various regions differed considerably. At many release sites, however, characteristic behaviors were observed that could be reproduced in subsequent releases. These patterns differed between sites: e.g., at some sites, the pigeons usually departed to the right of their home direction, at others, to the left. These so-called "local effects" (Wallraff, 1959) or "local deviations" (Schmidt-Koenig, 1961), later called *release site biases* (Keeton, 1973) proved very common. Homing

performance, assessed from the speed of the returning birds, also varied between sites. Initial orientation was found to be considerably improved by experience and training (Wallraff, 1959; Schmidt-Koenig, 1963a). An influence of topography was less clear, and the same was true for meteorological conditions, as oriented as well as disoriented flights were observed under overcast conditions (e.g., Hitchcock, 1955; Schmidt-Koenig, 1958).

Schmidt-Koenig's (1965) review thus appeared at a time when, except for the sun compass, no navigation mechanism or factor could yet be named. Looking back, this era appears to be dominated by a strongly generalizing view of navigation. It seemed to be an unspoken assumption that the navigational factors were the same everywhere and more or less innate, although differences between regions had already been reported. Experiments with migrants on establishing a home range (Mauersberger, 1957; Löhrl, 1959) were briefly mentioned, but not interpreted in the sense that the crucial factors for navigation have to be learned, a possibility that was hardly considered. The same applies to the sun compass: the sun's arc strongly depends on geographic latitude and hence must be adapted to the region where the bird lives, but this problem was not yet addressed.



## 2. THEORETICAL BACKGROUND

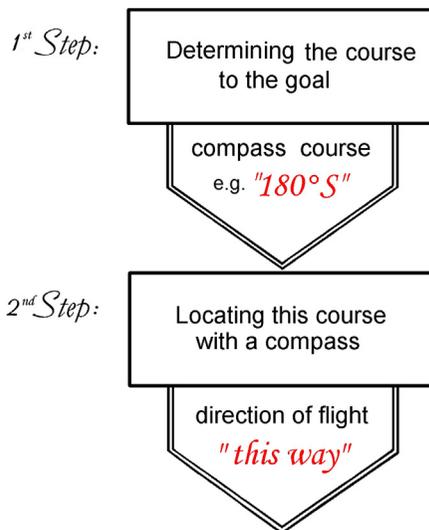
Schmidt-Koenig (1965) devoted the last section of his review to "Recent hypotheses, theories and concepts." Here, among hypotheses like sun navigation (e.g., Matthews, 1953b), star navigation (e.g., Sauer, 1961), and inertial navigation (Barlow, 1964), he also briefly mentioned Kramer's (1953, 1957, 1961) *Map-and-Compass Concept*. Most of these hypotheses, like the older ones by Viguier (1882) and Yeagley (1947), were based on the use of specific navigational factors or mechanisms; the "Map-and-Compass model," in contrast, is an open concept, not focusing on any specific factor. Instead, it describes an important aspect of the general structure of the navigational process, namely, that it includes a compass mechanism.

### 2.1 The "Map-and-Compass" Model

Kramer had first recognized the role of the sun in direction finding when a Starling (*Sturnus vulgaris*) changed its spontaneous directional tendencies accordingly after the position of the sun had been altered by mirrors (Kramer, 1950). Soon it became evident that the sun compass was also

involved in pigeon homing: released with their internal clock shifted, pigeons showed a characteristic deflection from untreated control birds, indicating sun compass orientation (Kramer, 1957; Schmidt-Koenig, 1958). Yet these clock-shift experiments also revealed a general characteristic of avian navigation, since they clearly demonstrated that compass orientation is an integral component of the navigational process. As a consequence, Kramer (1953, 1957, 1961) proposed his “Map-and-Compass” model, which considers avian navigation as a two-step process: in the first step, the “*map*” step, the bird determines its position relative to the goal and derives the home direction as a compass course, like e.g., “ $180^\circ$  south”; in the second step, the *compass step*, the bird locates this course with the help of a compass, converting it into information of the type “go there” or “this way” (see Figure 1).

The “Map-and-Compass” model, which is still the most important theoretical concept in navigation, now allowed researchers to study the mechanisms by which birds determined their home direction and the compass mechanisms separately. It also had a considerable impact on the general way of thinking, even if it took a while until this was generally realized in all its consequences. Griffin (1952) had earlier tried to classify homing according to the assumed complexity of the mechanisms: Type I, *piloting*, meant homing by following familiar landmarks and random search, if those were



**Figure 1** Kramer’s “Map and Compass” model: in the first step, the birds determine the compass course to the goal; in the second step, the birds use a compass to locate this course and convert it into information of the type “this way” or “go there.”

not present; Type II meant *compass orientation*, and Type III was *true navigation*, with the latter negatively defined, as it was emphasized that it did not involve landmarks. This classification proved inadequate, as Keeton (1974) pointed out in his review in this journal: orientation by landmarks, even in the vicinity of home, includes a compass (e.g., Graue, 1963; Alexander & Keeton, 1974; Biro et al., 2007; Armstrong et al., 2013; see the concept of the *Mosaic Map* in Section 4.2.3), and compass orientation is an integrated component of true navigation.

The “Map-and-Compass” model also contradicted the sun navigation hypothesis (Matthews, 1953b), as the sun provides a compass only (Kramer, 1953, 1957), not a mechanism to derive the home course (see Sections 4.2 and 4.3). The same is true for Barlow’s (1964) hypothesis of inertial navigation, because the proposed mechanism does not leave room for a compass.

## 2.2 Expanding the Model

When Kramer first formulated his model, he intended to describe the navigation processes of displaced homing pigeons: the birds determine their home course by yet unknown mechanisms and then use the sun compass to locate this direction. The sun compass, however, can be replaced by other compass mechanisms. Meanwhile, the *magnetic compass*, that is, the birds’ ability to locate directions with the help of the geomagnetic field, was discovered (W. Wiltschko & Merkel, 1966; W. Wiltschko, 1968), and Emlen (1967a) had identified the orienting information from the stars (Sauer, 1957) as a *star compass*.

Kramer did not say anything definite about the mechanisms that pigeons use for determining their home course. Yet Schmidt-Koenig (1965) already recognized that birds can use different strategies, which were later described in more detail by Wallraff (1974) and W. Wiltschko and Wiltschko (1982) (see Section 4). Yet the “Map-and-Compass” model is not restricted to homing. It can be generalized to include all navigation processes with a compass involved (see R. Wiltschko & Wiltschko, 2003). The “map” step need not necessarily be a navigation process; any other process that provides the compass course to a goal will fit the model (see Figure 1). For example, in avian migrants, the compass course for the first migration of juveniles to the yet unknown wintering area is provided by an innate migration program (see Berthold, 1988; Gwinner, 1996), indicating the direction (or a sequence of directions) to the traditional winter quarter of their population. In principle, one can also subsume orientation within the home range under this

model, when birds for example fly a specific compass direction to a familiar drinking place—in this case, the compass course is acquired by experience.

When we summarize our present knowledge of avian navigation in the following sections, we will use Kramer's model as a guideline, starting out by describing the compass mechanisms, since they are already fairly well understood, and afterward discuss the mechanisms that allow birds to determine the direction to their goal, where many questions are still open.



### 3. COMPASS MECHANISMS

A compass is a mechanism that indicates directions independent of the present whereabouts. Birds have three known compass mechanisms:

1. a magnetic compass, based on the geomagnetic field; it is available day and night;
2. a sun compass, where the birds compensate for the sun's apparent movement with the help of their internal clock; it provides directional information during the day and includes features like polarized light, in particular at sunset and sunrise; and
3. a star compass, providing compass orientation during the night.

The two celestial compass mechanisms require at least partly clear skies and cannot be used under solid overcast, whereas the magnetic compass is independent of prevailing meteorological conditions. Magnetic anomalies and magnetic storms strong enough to disrupt the magnetic compass are extremely rare, so that the magnetic compass is practically always available.

We start out with the magnetic compass, because it is the only mechanism that is *innate* in the sense that it is based on direct sensory input.

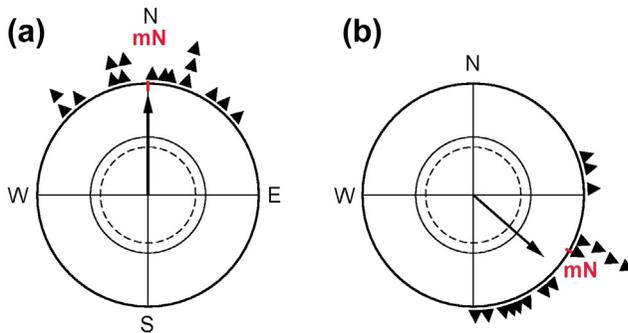
#### 3.1 The Magnetic Compass

The geomagnetic field surrounds the earth. The field lines leave the ground at the southern magnetic pole, pointing upward in the southern hemisphere, curve around until they run parallel to the earth's surface at the magnetic equator, then point downward in the northern hemisphere and reenter the earth at the northern magnetic pole. The intensity of the magnetic field is highest at the poles with about  $65 \mu\text{T}$  (microTesla) and decreases toward the magnetic equator to about  $30 \mu\text{T}$ , with a minimum below  $25 \mu\text{T}$  at the coast of Brazil (for details, see [Skiles, 1985](#)). This general change in intensity is locally modified by magnetic anomalies, but these are mostly rather weak. Aside from these spatial variations, the magnetic field of the earth undergoes

temporal variations on several time scales, with the most dramatic ones being the reversals of polarity that occurred many times in the geological past.

The magnetic compass was first demonstrated in migratory European Robins, *Erithacus rubecula* (Turdidae), whose directional tendencies during migration were recorded in cages. In the local geomagnetic field, the birds preferred their seasonally appropriate migratory direction, southward in autumn and northward in spring. When magnetic North around the test cage was turned to the East or to the West by a set of Helmholtz coils, the birds changed their headings accordingly (Figure 2), showing that the orienting information came from the magnetic field (W. Wiltschko & Merkel, 1966; W. Wiltschko, 1968). In this way, a magnetic compass was also demonstrated in about 20 other migratory species from different continents and with varying distances of migration; they include day migrants, night migrants, and twilight migrants (for a list, see W. Wiltschko & Wiltschko, 2007).

In nonmigratory species, the lack of a reliable directional preference that could be altered by changing magnetic North often presented a problem. In homing pigeons, demonstrating their magnetic compass was based on their tendency to fly off in home direction (Keeton, 1971; Walcott & Green, 1974; Ioalè, 1984): under overcast skies, magnets disrupt their orientation. In other nonmigratory species, directional preferences had to be induced by directional training. For example, young domestic chicks, *Gallus gallus*



**Figure 2** Orientation of the same European Robins during spring migration (a) in the local geomagnetic field and (b) with magnetic North turned by  $120^\circ$  to ESE; here, the birds follow the shift in magnetic North. (Modified from R. Wiltschko & Wiltschko, 2014.) Triangles at the periphery of the circle mark the mean headings of individual birds; the arrow represents the grand mean vector based on these headings drawn proportional to the radius of the circle. The two inner circles indicate the 5% (dotted) and the 1% significance border of the Rayleigh test.

(Phasianidae), and domestic ducklings, *Anas platyrhynchos domestica*, were imprinted on a red table tennis ball and trained to search for this social stimulus in a specific magnetic direction (Freire et al., 2005; Freire & Birch, 2010); Zebra Finches, *Taeniopygia guttata* (Estrildidae) were trained with a food reward (Voss et al., 2007) to demonstrate magnetic compass orientation.

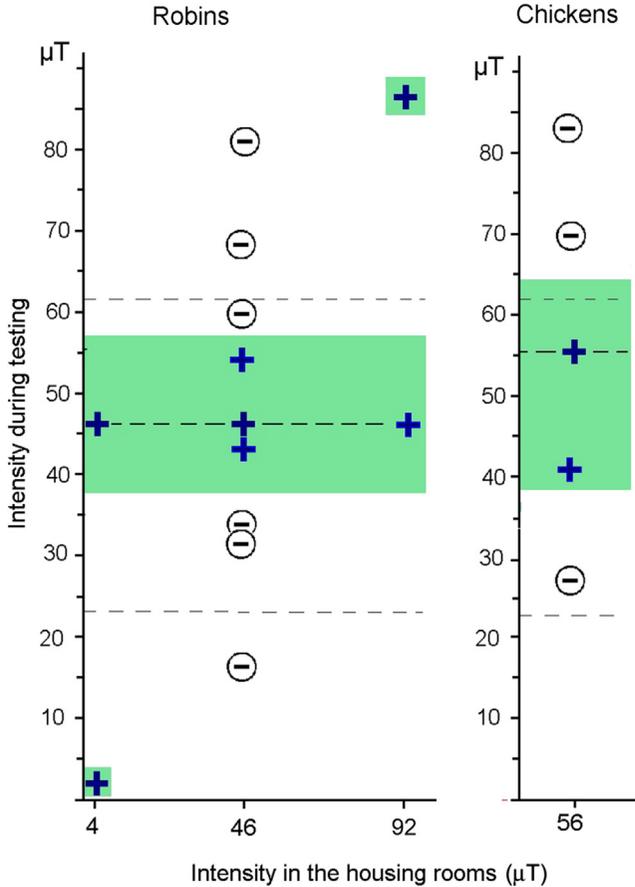
The number of species tested for magnetic compass orientation is so high because researchers initially found it hard to believe that birds should possess a sensory quality that we humans apparently lack (but see Baker, 1981).

### 3.1.1 Functional Characteristics of the Avian Magnetic Compass

The same techniques—recording migratory orientation or directional training—were also used to analyze the functional properties of the birds' magnetic compass. The analysis revealed some surprising characteristics, suggesting that the avian magnetic compass is fundamentally different from our technical compass with the spinning magnetic needle.

#### 3.1.1.1 Functional Window

A first characteristic is that the birds' magnetic compass works only in a fairly narrow functional window around the field strength of the ambient magnetic field. Increasing or decreasing magnetic intensity by more than about 25–30% led to disoriented behavior. This was true for robins (W. Wiltschko, 1978) and chickens alike (W. Wiltschko et al., 2007, Figure 3) and is also indicated in Garden Warblers, *Sylvia borin* (W. Wiltschko, 1974). This functional window is not fixed, however, but can adjust to other intensities if the birds stay in these intensities for a certain time. European Robins, caught in a geomagnetic field of 46  $\mu\text{T}$ , could in this way gain orientation ability in a field of 150  $\mu\text{T}$  (W. Wiltschko, 1978). The adjustment to higher fields worked surprisingly fast: after only a 1-h stay, robins were able to orient in a 92  $\mu\text{T}$ , twice as strong as the local geomagnetic field (W. Wiltschko et al., 2006a). Adjusting to lower intensities took longer, yet after about 17 h robins were able to obtain directional information from a field as weak as 4  $\mu\text{T}$ , less than 1/10 of the local intensity (Winklhofer et al., 2013). At the same time, the birds remained oriented in the local geomagnetic field, e.g., when staying at 150  $\mu\text{T}$ , they could still orient at 46  $\mu\text{T}$ . Yet they were disoriented in an intermediate field of 81  $\mu\text{T}$  (W. Wiltschko, 1978). Altogether, it looks as if staying in intensities outside the functional window neither shifted nor enlarged this window, but induced another window at the new intensity.



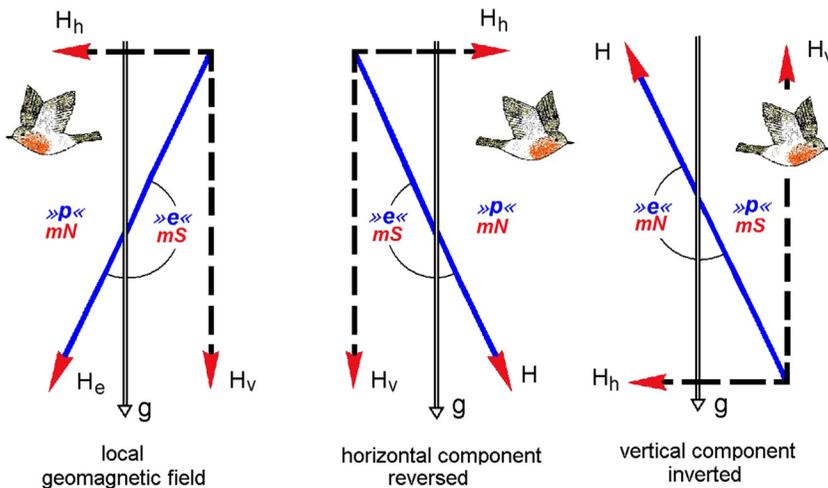
**Figure 3** Functional window of the magnetic compass. (a) Orientation of robins kept in various magnetic intensities. (b) Orientation of chickens. Blue (dark gray in print versions) +, oriented behavior; black encircled –, disoriented behavior. The thicker dashed line marks the local intensity of the capture site of the robins, 46  $\mu\text{T}$ , and the local intensity for the chickens, 56  $\mu\text{T}$ . The green (gray in print versions) zones indicate the estimated functional range of the magnetic compass for birds kept in the intensity indicated at the abscissa; the thin dashed lines enclose the range of intensities found on earth today. After data from *W. Wiltschko, 1978, W. Wiltschko et al., 2006a, and Winklhofer et al., 2013.*

This flexibility of the functional window is important for migratory birds. During autumn migration, migrants reach regions where the intensity is considerably lower than in their breeding grounds. On their flight toward the south, however, they experience gradually decreasing intensities and can thus slowly adjust to the new magnetic situation.

### 3.1.1.2 Inclination Compass

Another unexpected characteristic of the avian magnetic compass is that the polarity of the field does not matter. In the northern hemisphere north of the magnetic equator, the vertical component of the geomagnetic field points downward; when it is inverted to point upward, our technical compass still points northward, but the birds reverse their headings (W. Wiltshcko and Wiltshcko, 1972). This indicates that the magnetic compass of birds is an *inclination compass*, based on the axial course of the field lines and their inclination in space (Figure 4.). As a consequence, it does not distinguish between magnetic North and South, like our polarity-dependent technical compass, but between *poleward*, where the axis of the field lines points to the ground, and *equatorward*, where it points upward.

Towards the magnetic poles, the angle of inclination becomes increasingly steep. Experiments near the northern pole showed that birds could still orient with their magnetic compass at inclination angles deviating slightly



**Figure 4** The inclination compass of birds. Cross-section through the magnetic field as seen from the west.  $H$ , magnetic vector;  $H_e$ , vector of the local geomagnetic field;  $H_h$ ,  $H_v$ , horizontal and vertical components of the magnetic field, with the red (gray in print versions) arrow tips indicating the polarity; the axial course of the field lines is indicated in blue (darker gray in print versions);  $g$ , gravity vector indicating downward. Red (light gray in print versions)  $mN$ ,  $mS$ , *magnetic North and South*, the readings of a polarity compass; blue (dark gray in print versions)  $\gg p \ll$ ,  $\gg e \ll$ , *poleward and equatorward*, the readings of the avian inclination compass. The robins' flying direction indicates where the birds seek their spring migratory direction. After W. Wiltshcko & Wiltshcko, 1972 modified.

less than  $3^\circ$  from the vertical (Åkesson et al., 2001). Later laboratory experiments produced corresponding results (Lefeldt et al., 2015).

The inclination compass was first demonstrated in European Robins, but was subsequently found in a number of other passerine migrants, among them long distance migrants like the Garden Warbler that winters south of the Sahara desert, mostly beyond the magnetic equator. For these species, the inclination compass means that the directional information becomes ambiguous at the magnetic equator: they can still sense the axial course of the field lines, but, since these run horizontally, can no longer distinguish between poleward and equatorward. Beyond the magnetic equator, which lies north of the geographic equator in Africa, they have now to go poleward to continue toward south. When an equator crossing was simulated in the laboratory, the horizontal field was found to act as trigger and caused Garden Warblers to reverse their headings (W. Wiltschko & Wiltschko, 1992), which, in nature, would have made them go south. What happens at the magnetic equator itself is not entirely clear. Experiments with Bobolinks, *Dolichonyx oryzivorus* (Icteridae), simulating a magnetic equator crossing in a planetarium (Beason, 1992), however, suggest that the birds might rely on celestial cues to interpret the two ends of the magnetic axis.

Pigeons also seem to have an inclination compass: released with a small set of coils around their head under overcast conditions, they headed away from home when the coil was polarized “north up” so that the net direction of the resulting field pointed upward (Walcott & Green, 1974; Visalbergi & Alleva, 1979). So far, an inclination compass has been demonstrated in all bird species tested for it; it appears to be common to all birds.

The functional mode as an inclination compass, ignoring the polarity of the magnetic field, means that the avian magnetic compass was not affected by the reversals of polarity occurring in the past.

### 3.1.1.3 Light Dependency

The avian magnetic compass is light-dependent. In total darkness, migratory birds can no longer orient in their migratory direction (e.g., Stapput et al., 2008). For nocturnal migrants, however, this does not seem to cause a problem, since even very low light levels seem sufficient for magnetic compass orientation. In laboratory tests, birds were well oriented in light levels as they occur more than 45 min after sunset. Clear nights ought to be sufficiently light even without the moon, and migrants avoid migrating in really dark conditions like under heavy overcast, the more, since this is often associated with rain.

Tests under narrow-band light of various wavelengths showed that birds require short-wavelength light: they were oriented under UV, blue, turquoise, and green light; while they were disoriented under yellow and red light. The same wavelength-dependency was found in Australian Silvereyes (*Zosterops l. lateralis*), European Robins, and Garden Warblers. It is also indicated in Homing Pigeons and Domestic Chickens that were tested only under one color from the blue–green range, where they could orient, and under red light, where they were disoriented (for review, see [R. Wiltschko et al., 2010](#)).

### **3.1.2 Reception of Directional Information from the Magnetic Field**

The above-mentioned characteristics of the avian magnetic compass implied an unusual reception mechanism. In 2000, Ritz and colleagues proposed a magnetoreception model based on spin-chemical processes, which provides an explanation for the unusual properties of the magnetic compass of birds.

#### **3.1.2.1 The Radical Pair Model**

The model assumes that photon absorption in a photopigment leads to an electron transfer, forming a pair of radicals. Radical pairs occur in singlet and triplet states; the ratio between these two states depends, among other factors, on the alignment of the radical pairs in the external magnetic field. By comparing the singlet or triplet yield in the various spatial directions, birds could derive directional information (for details, see [Ritz et al., 2000](#)). As the site of magnetoreception, [Ritz et al. \(2000\)](#) suggested the eye because of its access to light and its spherical shape.

The triplet yield of the radical pair in an alignment of  $0^\circ$ , i.e., parallel to the magnetic vector, is equal to that in an alignment of  $180^\circ$ , antiparallel, which would explain why the avian magnetic compass does not respond to the polarity of the field. [Ritz et al. \(2000\)](#) proposed that the different ratios of singlet/triplet may cause an activation pattern on the retina that is centrally symmetric to the magnetic vector and hence indicates magnetic directions. As this pattern also depends on magnetic intensity, it can explain the functional window and its flexibility: when birds are suddenly brought into an intensity that differs markedly from the one they are used to, they are faced with a novel pattern that at first leads to confusion. Yet since the pattern retains its central symmetry to the magnetic vector, they manage to interpret it after a while and thus regain their orientation ability.

Testing the radical pair model was based on the disrupting effect of radio frequency fields ([Ritz et al., 2000](#)). The results supported the model: the birds were disoriented, indicating that radio frequency fields indeed

interfered with magnetoreception (Ritz et al., 2004; Thalau et al., 2005; Ritz, 2011; Kavokin et al., 2014). The same disruptive effect of radio frequency fields was also observed in conditioning experiments with Domestic Chickens (W. Wiltschko et al., 2007) and Zebra Finches (Keary et al., 2009). Whether the recently reported disorienting effect of man-made magnetic noise (Engels et al., 2014) is really caused by direct interference with the reception mechanism is still unclear.

### 3.1.2.2 The Probable Receptor Molecule

As receptor molecule, Ritz et al. (2000) had suggested cryptochrome, a blue-light receptor with flavin as chromophore (see Chaves et al., 2011 for details). In immuno-histochemical studies, a type of cryptochrome, cryptochrome 1a, was identified in the UV/violet cone photoreceptors in the retina of chickens and European Robins. Within these cones, it is located at the disk membranes in the outer segment (Nießner et al., 2011). Since the UV/violet cones are distributed all over the retina, they represent all spatial directions, thus fulfilling the requirements of the radical pair model. The absorption spectrum of cryptochrome is reflected by the wavelengths-dependency of bird orientation. Activated cryptochrome 1a was indeed found under all light conditions where birds had shown oriented behavior in their migratory direction (Nießner et al., 2013).

For a more detailed description of the proposed avian reception mechanisms for magnetic directional information, see R. Wiltschko and Wiltschko (2014).

### 3.1.2.3 A Unique Development of Birds?

So far, a magnetic inclination compass has been found in all avian species studied so far, and the same applies to the functional window, although here, only very few species have been tested. The wavelength-dependency also appears to be a common feature of the magnetic compass of all birds. A radical pair mechanism is likewise indicated in the species tested with radio frequency fields added, and cryptochrome 1a, the most probable receptor molecule, is found in European Robins and chickens in the same location, with the activation of cryptochrome 1a in agreement with the orientation of robins. Taken together, the existing evidence so far suggests the same type of magnetic compass in all birds. In particular the agreement between European Robins and Domestic Chickens is instructive, as these two species belong to different lineages of birds that were already separated 95 million years ago (Ericson et al., 2006). This suggests that this type of magnetic

compass was already present in the late Mesozoic in the common ancestors of all modern birds.

The magnetic compass mechanisms of other vertebrates, as far as they have been analyzed, are different in their functional mode (see [R. Wiltschko and Wiltschko, 1995](#)): most of them do not require light, and even the light-dependent magnetic compass of amphibians has a different wavelength-dependency ([Phillips & Borland, 1992](#)). Possibly, the avian magnetic compass is a unique development of the ancestors of birds.

### **3.1.3 Biological Significance of the Magnetic Compass in Birds**

Birds can use their magnetic compass in all situations where a compass is helpful. The fact that the magnetic compass was first discovered in migrants and that still the majority of birds demonstrated to have a magnetic compass are migrants seemed to suggest that it is associated with migratory orientation. However, the main reason for this lies in the fact that the spontaneous urge of migrants to head in their migratory direction during migration season provides an easy, reliable basis for orientation experiments. Since magnetic compass orientation has also been demonstrated in a number of nonmigrants, it is evident that this mechanism is by no means restricted to migratory birds—on the contrary, it seems to be common to all birds.

If the magnetic compass was indeed developed by the common ancestors of modern birds already in the late Mesozoic, it was first used for orientation within the home range; here, the advantage of a good, efficient navigational system pays off every day. It will still be used to orient the daily flights in the area of the birds' home, in particular on overcast days, e.g., to fly to sites with good food sources or to drinking places—in these cases, the birds would remember the respective compass directions. The use of the magnetic compass during such spontaneous flights is not yet experimentally accessible, but the successful conditioning experiments with Domestic Chickens and Zebra Finches in small arenas of 1 m diameter or less show that birds apply their magnetic compass also in small-scale environments.

The magnetic compass is also used to locate courses determined by navigational processes, after experimental displacement, but probably also when birds spontaneously venture out for foraging and exploring. It may also be involved in the processes determining the respective compass course, as it can provide a directional reference for the navigational mechanisms (see [Sections 4.2 and 4.3](#) below). And when some bird species began to migrate and undertake increasingly long flights, they already had a compass

mechanism available which they could use to orient in specific directions. This may have facilitated their transition to a migratory lifestyle.

### 3.2 The Sun Compass

The sun moves across the sky in the course of the day, in the northern hemisphere from the east via south to the west and in the southern hemisphere from the east via north to the west. Using the sun for direction finding means that these movements must be taken into account and compensated for. Yet the progress along the horizon, i.e., the change in sun azimuth, is not linear. After sunrise the sun quickly gains, and before sunset it quickly loses altitude, with little progress in azimuth, while around noon when the sun is high in the sky, the progress in azimuth is large, while the changes in altitude are small. The specific form of the sun's arc strongly depends on geographic latitude and season: at high latitudes, it is fairly flat, at lower latitudes it is much steeper, becoming extreme in the tropics, where the sun is in the east all morning and in the west all afternoon. Associated with the sun is the pattern of polarized light in the sky. At  $90^\circ$  from the sun, there is a maximum band of about 70% polarization that fades to both sides; it changes position as the sun moves. At sunrise and sunset, the band of maximum polarization runs straight up from horizon across zenith and down again.

In addition, due to the movement of the earth around the sun, the sun's arc undergoes marked seasonal changes: between the tropics, the sun culminates in the north or in the south, depending on season; in temperate latitudes, the altitude of sun culmination changes markedly, leading to a shift in sun azimuth at a given time of day: e.g., at  $50^\circ$  N, the difference in sun azimuth at 8:30 in the morning between summer and winter solstice is about  $30^\circ$ . Sunrise and sunset likewise change with season, with the sun at, for example,  $50^\circ$  N in summer setting at about  $305^\circ$  NW and in winter at about  $235^\circ$  SW. The time with the fastest shifts is around the spring and autumn equinox.

This means that the mechanisms compensating for the sun's movement must be adapted to the regions where the bird lives and additionally adjusted to the changes over the course of the year.

#### 3.2.1 *Compensating for the Sun's Movement*

To interpret the sun's position correctly, birds must be aware of the time of the day with the help of their internal clock. Shifting this clock became a common tool to demonstrate the sun compass (see [Section 1.2](#)). Earlier researchers usually assumed an average progress of the sun of  $15^\circ$ /h, expecting a deflection

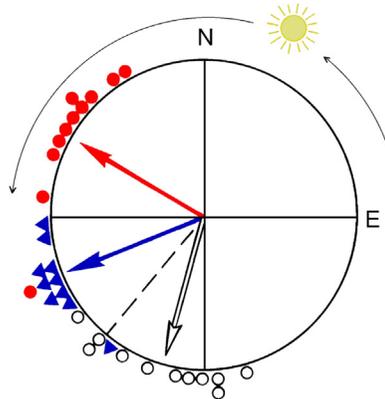
of about  $90^\circ$  for a 6 h clock shift. Yet this is not correct. Especially in summer, the expected shift based on the difference in sun azimuth in 6 h can be considerably larger: e.g., at  $50^\circ$  latitude, depending on the hour of release, it can be up to  $130^\circ$ .

When pigeons are released with their internal clock reset 6 h fast early in the morning when the sun is just rising, they should, according to their internal time, expect the sun high up in the sky. Nevertheless, they treat the sun just above horizon as the sun near noon and depart showing the typical deflection from the mean of untreated controls (e.g., [Schmidt-Koenig, 1958](#); [Keeton, 1979](#); and many others). This means that the sun's altitude is ignored, with the pigeons only relying on sun azimuth. Pigeons are able to read the sun azimuth even when the sun is high up in the sky: experiments in the tropics under a sun culminating in zenith showed that they can use their sun compass even when the sun is only between  $3^\circ$  and  $6^\circ$  from zenith ([Ganzhorn et al., 1989](#)).

It was unclear, however, to what extent the pigeons consider the varying rates of change in sun azimuth in the course of the day. This question was approached in a series of clock-shift experiments near Auckland, New Zealand, where, at  $37^\circ$  S, the differences in the rate of change in sun azimuth in the southern summer are considerable: within the first hour after sunrise and the last hour before sunset, the sun's progresses less than  $10^\circ$ , while in the hour around noon, its progress is more than  $40^\circ$ . Birds were released with their clock shifted 4 h fast at the times when the expected deflection of such a shift based on the differences in sun azimuth was minimum and when it was maximum. The observed size of the deflections of the two groups from the controls differed significantly ([Figure 5](#); [R. Wiltschko et al., 2000](#)). Obviously, pigeons were aware of the different rates of change in sun azimuth and compensated for them accordingly—their sun compass appears to operate with a realistic representation of the true sun's arc in their home region and the respective season.

### **3.2.2 Establishing the Sun Compass**

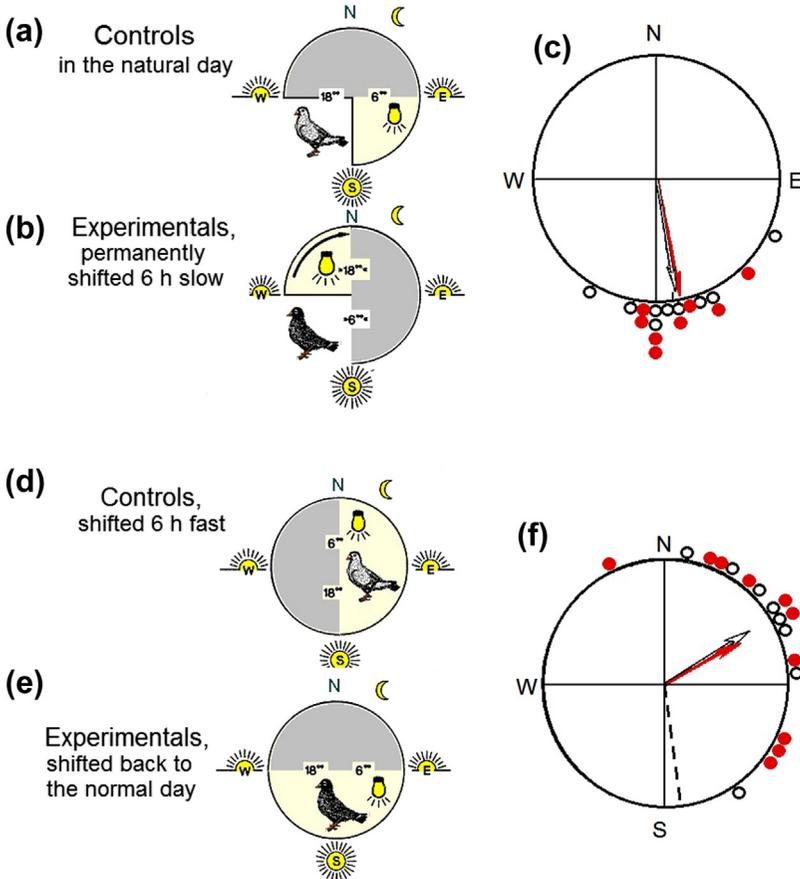
This close adjustment of the compensation mechanisms to the regional sun's arc is based on experience. This became evident when young pigeons were raised in a permanently 6 h slow-shifted artificial day. In the afternoon, when the natural and their artificial day overlapped, the experimental birds were set free for exercise flights around their loft and for training flights away from home, together with the control birds that were running on natural time. When the sun went down, the birds were separated and the



**Figure 5** A 4 h fast clock shift with homing pigeons in New Zealand, indicating that the birds are aware of the different rates of change in sun azimuth in the course of the day. The sun and the outer half-circle indicate the counterclockwise movement of the sun in New Zealand; the dashed radius indicates the home direction  $219^\circ$ . Open circles, vanishing bearings of untreated control birds; solid blue (dark gray in print versions) triangles, bearings of clock-shifted pigeons released within the first hour after sunrise or the last hour before their subjective sunset when the azimuth difference for 4 h was minimum; solid red (gray in print versions) circles, bearings of clock-shifted pigeons released in midmorning when the azimuth difference for a 4 h shift is maximum. The arrows represent the mean vectors of the respective sets of bearings drawn proportional to the radius of the circle which is equal to one. After R. Wiltschko et al., 2000.

permanently shifted experimental spent the rest of their day under artificial light in their loft (Figure 6(a) and (b)). In critical tests during the overlap time, both groups were well homeward oriented (Figure 6(c)). To find out whether the experimental birds indeed used the sun as a compass, their internal clock was reset (Figure 6(e)): although their internal clock now ran on natural time, the experimental birds showed a counterclockwise deflection (Figure 6(f); W. Wiltschko et al., 1976). This clearly showed that they used a sun compass, albeit a false one adjusted to the experimental situation: they had learned that the sun in their “morning” was in the south and at their “noon” in the west.

The sun compass being a learned mechanism proved advantageous for Homing Pigeons, the descendants of the Mediterranean Rock Dove, *Columba livia*, when European settlers introduced them into the southern hemisphere where the sun culminates in the north instead of in the south as in their original home region: without any problems, they could establish a sun compass adjusted to their new home (see R. Wiltschko et al., 2000).



**Figure 6** Orientation of young pigeons raised in a permanent 6 h slow shifted photoperiod, indicating that the sun compass is learned. Photoperiodic conditions of the control birds (a) and the permanently shifted experimental birds (b), both groups had access to the outside during the overlap time: (c) released under the afternoon sun, both groups oriented alike in homeward direction. (d) 6 h fast shift of the control birds and (e) shift back to the natural photoperiod of the experimental birds: (f) the control birds showed the typical deflection from the untreated controls; the experimental birds were deflected although they now lived in the natural day. Open symbols, bearings of birds from the control group; red (gray in print versions) solid, bearings of birds from the experimental group. The arrows represent the respective mean vectors drawn proportional to the radius of the circle. The home direction  $172^\circ$  is indicated by a dashed radius. Data from *W. Wiltschko et al., 1976*.

### 3.2.2.1 Development of the Sun Compass

In a series of experiments, the time and the circumstances of the learning processes were analyzed. Keeton (1971) already observed that the orientation of very young, inexperienced homing pigeons under sunny conditions could be disrupted by applying magnets to their backs, indicating that their sun compass was not yet fully developed to guarantee orientation. The learning processes establishing the sun compass normally appear to take place about the end of the third month after hatching, with some variability between individuals. At the age of 8–10 weeks, young pigeons did not yet respond to clock-shifting, whereas when they were about 12 weeks old, they showed the typical deflection. Early training flights were found to advance the establishment of the sun compass: after 10 short flights, pigeons as young as 8–10 weeks already responded to clock shifting with vanishing bearings deflected in the typical way (R. Wiltschko & Wiltschko, 1981). During the training flights, the young birds had been faced with the necessity to orient, and this, in turn, appears to have accelerated the development of a functioning sun compass.

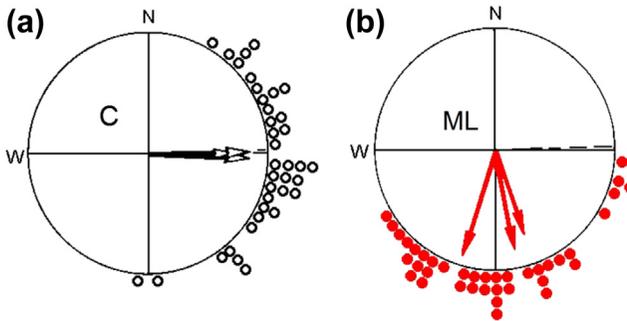
For establishing a sun compass working during the entire day, pigeons have to observe large portions of the sun's arc; knowing the sun's arc only half the day proved not sufficient. This is suggested by the observation that young pigeons that had experienced the sun only in the afternoon did not respond to clock-shifting in their subjective morning (R. Wiltschko & Wiltschko, 1980), but appeared to use the magnetic compass instead, as indicated by the disorienting effect of magnets (R. Wiltschko et al., 1981).

This necessity to observe the sun during most parts of the day ensures that the birds can form a mental representation of the sun's arc that is reflecting the local conditions so that the mechanisms compensating for the sun's movement are closely tuned to the situation in their home region.

### 3.2.2.2 The Reference for the Sun's Movement

Birds have to accurately measure the sun's progress in order to establish adequate compensation mechanisms. This raises the question about the reference system for the sun's movement. Here, the magnetic compass, indicating directions by direct sensory input, appears to provide the reference against which the sun's progress is calibrated.

This is indicated by experiments with young pigeons that were raised in a small loft around which magnetic North was deflected by Helmholtz coils so that they observed the sun in an altered directional relationship to the



**Figure 7** Orientation of young pigeons indicating that the magnetic field acts as a reference system for learning the sun curve. The birds were released on sunny days (three releases pooled): (a) the control birds were homeward oriented, (b) the experimental birds that had spent 10 sunny days in an aviary where they could observe the sun in a magnetic field shifted  $120^\circ$  to east-southeast showed a significant deflection in the expected direction. Symbols as in Figure 6; the home direction  $89^\circ$  is indicated by a dashed radius. Data from R. Wiltschko & Wiltschko, 1990.

magnetic field. They were allowed out of this loft for exercise or training flights only under solid overcast. When released under sun, they departed in directions that were significantly shifted in the expected direction compared to the controls (W. Wiltschko et al., 1983). The same was true for young pigeons that were confined in such a loft for 10 sunny days during the phase of sun compass learning at the end of their third month of life. When afterward released in sunny weather, they also showed a corresponding deflection in the direction in which magnetic North had been shifted (Figure 7; R. Wiltschko & Wiltschko, 1990).

These findings indicate the close relationship between the two compass mechanisms: the sun compass is a mechanism derived from the magnetic compass by learning processes. After it is established, however, the sun compass becomes an independent mechanism. Adult pigeons can orient when they have to rely on their sun compass alone because their magnetic compass has been disrupted by magnets (e.g., Keeton, 1971; R. Wiltschko et al., 1981).

### 3.2.2.3 Flexibility of the Sun Compass

The experiments with young pigeons described above show that observing the sun in an altered directional relationship to the magnetic field caused them to deviate markedly from the control birds in their first subsequent release (see Figure 7). The very same treatment, however, had no effect on the behavior of adult pigeons (R. Wiltschko & Wiltschko, 1990). This suggests a *sensitive*

*period* during the third month of life, during which the young pigeons pay great attention to the sun and closely observe its movements. The respective learning processes appear to be different from those of, for example, normal associative learning; they seem to be preprogrammed, involving underlying innate components. This ensures that the sun compass is ready at the time when wild Rock Doves begin to move independently from their parents.

The compensation mechanisms must be shaped by experience to be adjusted to the local situation; yet once established, they are not fixed, but remain flexible to keep the sun compass adjusted to changes in the sun's arc. The young pigeons raised under a permanent slow shift (see above) adjusted to the natural day after the end of the study, and in later clock-shift experiments, they showed the typical deflection (W. Wiltschko et al., 1976). When experienced birds that had already developed a functioning sun compass were later subjected to a permanent 6 h slow shift, they also adjusted their sun compass to the experimental situation: after a few training flights, their vanishing bearings did not differ from that of untreated controls any longer, and when their internal clock was reset to natural time, their response indicated that they had recalibrated their sun compass (W. Wiltschko et al., 1984).

The same mechanisms adjusting the pigeons' sun compass to these drastic experimental changes in the directional relationship between sun and magnetic field may also ensure the adjustment of the compensation mechanisms to seasonal changes. This has not been explicitly studied yet, but these changes would introduce an error into the sun compass that can hardly be tolerated, in particular in the tropics. The finding that pigeons are aware of the different rates of change in sun azimuth (R. Wiltschko et al., 2000) is in agreement with this assumption. Hence we expect the sun compass to be always closely tuned to the temporal and local situation with the pigeons' home region.

### **3.2.3 The Biological Significance of the Sun Compass in Birds**

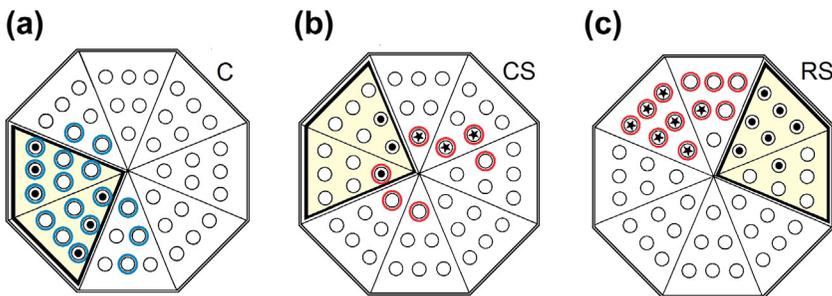
The abovementioned studies analyzing the sun compass were mostly performed with Homing Pigeons, using their reliable tendency to fly home after displacement, comparing the bearings of clock-shifted and untreated birds. In the same way, sun compass orientation was also demonstrated in displaced wild Mallards, *Anas platyrhynchos* (Matthews, 1963).

#### **3.2.3.1 Sun Compass Orientation in Passerine Birds**

Demonstrating the sun compass in passerine species required different techniques. In three species of American jays, a spontaneous behavior, namely

their caching and recovering of seeds could be utilized: the birds were allowed to cache their seeds in cups in one quadrant of an aviary; when they were released in the aviary 5 days later with their internal clock shifted 6 h and all cups open, they searched in the adjacent quadrant, showing the typical deflection indicating sun compass use—obviously, the jays had memorized the direction of the quadrant where they had cached their seeds, in the example in Figure 8(b), “in the west-northwestern quadrant of the aviary” (Figure 8; W. Wiltschko & Balda, 1989; W. Wiltschko et al., 1999). For other passerines, like Starlings (e.g., Hoffmann, 1954), several species of nocturnal migrants (von Saint Paul, 1954, 1956; Able and Dillon, 1977), and Black-capped Chickadees, *Parus atricapillus* (Duff et al., 1998), evidence for sun compass orientation was obtained by conditioning experiments. The ontogeny of the sun compass has not yet been studied in birds other than pigeons, but it is expected to take place in a similar way.

Altogether, the number of avian species where the sun compass has been demonstrated is much smaller than the number of species in which the magnetic compass has been demonstrated, due to the fact that researchers readily accepted the sun compass because it intuitively made sense. Soon it was more or less generally assumed that all birds have a sun compass, which is probably true.



**Figure 8** Recovery of seeds by a Scub Jays, *Aphelocoma coerulescens* (Corvidae), indicating an involvement of the sun compass. The bird was allowed to cache seeds in the sand-filled cups in one sector of the octagonal aviary and 5 days later was released for recovery with all cups open. (a) Control test, C; no manipulation between caching and recovery; (b) 6 h slow shift, CS; (c) RS, re-shift to the normal day, corresponding to a 6 h fast shift. The sectors open for the caches are surrounded by dark lines and shaded light yellow (light gray in print versions); the original caches are marked by black dots, the “shifted caches,” that is, the cups corresponding to the original caches under the assumption of sun compass use are marked by black stars. Cups where the bird probed during recovery are in blue (dark gray in print versions) circles in the control test and in red (gray in print versions) circles in the tests after clock-shifting. After W. Wiltschko & Balda, 1989.

### 3.2.3.2 Sun Compass Use in the Home Region

The sun compass is a well-adapted mechanism for orientation within the home range and the home region. The directional training experiments mentioned above suggest that it is also used within small-scale environments; the caching experiments with jays (see [Figure 8](#)) showed that in these species, it is an integrated component of spatial memory. The experiments with displaced homing pigeons and ducks demonstrate its use in more extended flights within the home region. We can safely assume that birds use it also to orient their spontaneous flight, even if this has escaped experimental analysis so far.

### 3.2.3.3 Sun Compass and Sun-Related Cues during Migration

The sun compass does not seem to play a large role in bird migration, however. Although some early authors (e.g., [Bellrose, 1972](#)) seemed to assume that the sun compass was the major mechanism used by day-migrating birds, there is little convincing evidence to support this. [Kramer \(1950\)](#) described the sun compass first based on his mirror experiment with a Starling that did not prefer its natural migratory direction. Later clock-shift experiments with Starlings produced ambiguous results ([W. Wiltschko & Wiltschko, 1985](#)). Yellow-faced Honeyeaters, *Lichenostemos chrysops* (Meliphagidae), an Australian day migrant, did not show the expected deflection when their internal clock was shifted ([Munro & Wiltschko, 1993](#)), although the pattern of polarized light allowed orientation in the absence of magnetic and solar information ([Munro & Wiltschko, 1995](#)). A European day migrant, the Tree Pipits, *Anthus trivialis* (Motacillidae), tested under clear sky at sunset, followed a shift in magnetic North, evidently ignoring the setting sun ([Åkesson et al., 2006](#)).

Considering the spatial and temporal changes in the sun's arc, it may not be so surprising that the sun compass appears to be only of minor importance during migration: heading south in autumn and north in spring, migratory birds would have to constantly adjust the compensation mechanisms to the changes in latitude, whereas heading east or west would require a permanent readjustment of the internal clock to the changes in longitude—for extended migratory flights, the sun compass does not seem to be the optimal mechanism.

This does not mean, however, that these birds do not use the sun compass during the breeding season when moving around in their home range, as indicated by the successful conditioning experiments with migrants (e.g., [von Saint Paul, 1954, 1956](#); [Able & Dillon, 1977](#)). After reaching their

wintering area, they probably establish a new sun compass, one that is adapted to the respective local situation. For long distance migrants wintering in the southern hemisphere, like the Swift *Apus apus*, this means that they would have two very different compensation mechanisms: one compensating for a clockwise movement of the sun in their European breeding area and one compensating for a counterclockwise movement in their South African winter quarters.

While the sun does not appear to be a major factor in the orientation of day migrants during migration, there is evidence suggesting that sun-related cues like the sunset point and polarization pattern at dusk may play a role in the orientation of nocturnal migrants when they start their migration flights around sunset. Birds seemed to be better oriented when they had access to the natural sunset factors (Moore, 1978; Katz, 1985); shifting their view of the setting sun with mirrors led to a corresponding shift (Moore, 1982), and clock-shift experiments suggest that the response to the setting sun is part of the sun compass (Able & Cherry, 1986; Helbig, 1991a). Other experiments showed that nocturnal migrants also responded strongly to patterns of polarized light. In most cases, however, the polarized light was artificially produced by polarizers placed over the test cages, and birds showed a strong tendency to align parallel to the axis of polarization (e.g., Able, 1982, 1989; Moore & Philipps, 1988), a response that was different from their response to the natural pattern of polarization (Helbig & Wiltschko, 1989). Hence it cannot be excluded that the artificial polarization pattern—100% polarized over the entire sky—in some cases elicits unnatural responses that are artifacts.

However, in magnetic fields that did not provide directional information, natural polarized light could be used as an orientation cue: at dusk, night-migrating birds with access to the natural sky headed in their migratory direction, whereas under depolarizers, the same birds were disoriented (Helbig, 1991a).

### 3.3 The Star Compass

The stars form a complex pattern in the sky which moves around the celestial pole in the course of the day: the circumpolar stars close to the pole perform a full visible rotation, those closer to the celestial equator rise and set. Because the earth is moving around the sun, the sidereal day, i.e. the time until a given star is seen in the same position as before, is about 4 min shorter than the solar day. As a consequence, the stellar sky slowly shifts in the course of the seasons—the winter sky is different from the

summer sky. Birds using the stars for orientation have to cope with these changes.

Many of the experiments on the star compass were performed in planetariums where the stellar sky could be manipulated at will; in this way, “skies” of different times, different locations, and different combinations of stars could be presented to the birds. The stellar orientation, first described by Sauer (e.g., 1957) was later identified as a *star compass*. Reversing the planetarium sky caused Indigo Buntings, *Passerina cyanea* (Emberizidae) to reverse their headings (Emlen, 1967a,b). Similar experiments with other nocturnal migrants produced similar results (e.g., Katz & Michelsons, 1978), emphasizing the role of stars as orientation cues. This was supported by outdoor experiments where birds at night headed in their migratory direction in the absence of magnetic information using the stars alone (e.g., W. Wiltschko & Wiltschko, 1975a,b; Bingman, 1984, 1987). However, in some cases, birds were reported to be disoriented when they had to rely on the stars (e.g., Moore, 1978; Pakhomov & Chernetsow, 2014), but this need not necessarily mean that they have no star compass; it also could be a response to the particular experimental situation.

### 3.3.1 Analyzing the Star Compass

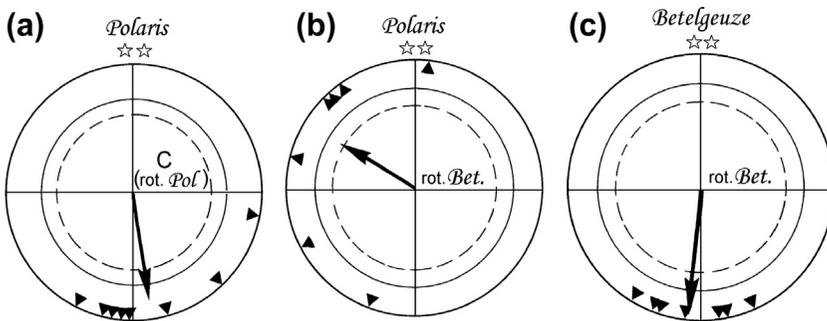
Altering the latitude setting of the planetarium did not affect the orientation of the birds; the rotation of the sky in the course of the night also did not affect the birds’ orientation (Emlen, 1967b). When the annual cycle of some birds was advanced and that of others delayed so that both groups could be tested together under the same planetarium sky, the birds in spring migration mode headed northward, those in autumn migration mode headed southward (Emlen, 1969a). These observations clearly showed that the direction of headings is not dictated by the stellar sky, but that the stars represent a true compass in the sense that they provide directional information that the birds used to locate the appropriate direction.

Shifting the birds’ internal clock likewise did not affect the orientation of birds at night under the natural stars (Matthews, 1963) or under the planetarium sky (Emlen, 1967b). This excluded a mechanism similar to that of the sun compass and spoke against the birds using individual stars for guidance. Instead it suggested that birds derived directions from the constant directional relationship between stars, possibly in a similar way as boy and girl scouts do when they find north by prolonging the hind axis of *Ursa major*. Attempts to identify crucial configurations by blocking certain constellations

revealed considerable individual variance. The northern stars within  $35^\circ$  of the rotation center seemed to be of particular importance, but the data did not allow a final conclusion (Emlen, 1967b).

### 3.3.2 Establishing the Star Compass

Like the sun compass, the star compass is a learned mechanism. Young Indigo Buntings could orient by the stars only if they had observed the natural sky before autumn migration (Emlen, 1969b). *Celestial rotation* was identified as the crucial factor. Emlen (1970) hand-raised two groups of birds under the planetarium sky; the control group was reared under the normal sky, rotating around *Polaris*, the polar star; the experimental group was reared under a sky that rotated around *Betelgeuze* in the constellation Orion. Tested during the autumn migration under the now stationary planetarium sky, the control birds headed in their seasonally appropriate southerly migratory direction away from *Polaris*, whereas the experimental group headed away from *Betelgeuze* (Figure 9). This clearly demonstrated the important role of celestial rotation and the center of rotation in setting up the star compass.



**Figure 9** Planetarium experiments showing the role of celestial rotation in establishing the star compass. Two groups of Indigo Buntings were hand-raised and exposed to a natural looking planetarium sky, the control group with *Polaris* the center of rotation (rot. Pol.), simulating the natural situation, the experimental group with *Betelgeuze* in the constellation *Orion* as center of rotation (rot. Bet.). During autumn migration, both groups were tested under the same, now stationary planetarium sky at various times during the night. (a) The control group preferred their natural southerly migratory direction; the experimental groups oriented (b) toward northwest with respect to *Polaris*, but in their natural southern migratory direction with respect to *Betelgeuze*. Symbols at the periphery of the circle mark the mean headings of individual birds; the arrows represent the grand mean vector based on these headings, drawn proportional to the radius of the circle. The two inner circles indicate the 5% (dashed) and 1% significance border of the Rayleigh test. Data from Emlen (1970).

The crucial role of celestial rotation during the development of the star compass was also confirmed by experiments with Garden Warblers that were hand-raised under a rotating artificial “sky” consisting of only 16 light dots. Later during the autumn migration season, when these birds were tested under the same, now stationary “sky” in the absence of magnetic information, they oriented away from the former center of rotation, whereas a second group that had been hand-raised under a similar, but stationary sky was disoriented (W. Wiltschko et al., 1987a; see also Able & Able, 1990a; Michalik et al., 2014). Obviously, birds have no innate concept of the complex pattern of the natural sky: any pattern of small light dots can successfully substitute for the natural stars as long as the birds can observe the respective pattern rotating with one revolution per day.

During migration, however, the sky changes: in autumn, as the birds move south, the celestial pole with the polar star gets lower and approaches the horizon, becoming harder to see. New stars appear in the southern sky. These have to be integrated into the birds’ mental representation of stars. Here, the magnetic compass appears to provide an important reference system (e.g., W. Wiltschko & Wiltschko, 1975a; see Section 3.4.2.1 below).

### **3.3.3 Biological Significance of the Star Compass**

So far, the star compass has only been demonstrated in a few species of passerine birds that migrate at night. Since the majority of birds are primarily day-active, the star compass could be a special mechanism developed by the night-migrants to orient during their extended nocturnal flights. Primarily night-active birds, like owls or nightjars, have not yet been studied, so that it is unknown whether they, too, use the stars as a compass for orientation in their home range.

## **3.4 Interaction between Compass Mechanisms**

In general, birds appear to have more than one compass mechanism, and this raises the question about the ranking and relative importance of the information provided by the different mechanisms. This question has been addressed in the so-called “cue-conflict experiments,” testing birds in situations where the various compass mechanisms give conflicting information.

### **3.4.1 Interactions between Celestial and Magnetic Cues during Daytime**

Almost all our knowledge about the interactions between sun compass and magnetic compass comes from experiments with Homing Pigeons.

Since the magnetic compass serves as a reference system for establishing the sun compass and probably also for adjusting it to seasonal changes (see [Section 3.2.2.2](#)), the two mechanisms are connected, but once established, the sun compass becomes an independent mechanisms of its own. The deflection observed in clock-shift experiments appears to indicate a dominant role of the sun compass, since birds are deflected, although their intact magnetic compass could have told them the correct direction. The size of the deflection, however, is often smaller than predicted by the difference in sun azimuth between the time of release and the pigeons' subjective time (see [Schmidt-Koenig, 1958](#)). An analysis of a large number of clock-shift experiments revealed changes over time: in young pigeons that had just established the sun compass, the observed deflection is of the predicted size, but as the birds get older and more experienced, the relative size of the deflection decreases down to about 50–60% of expected amount in old experienced birds ([R. Wiltschko et al., 1994](#)), indicating the involvement of another cue.

When experienced clock-shifted pigeons were released with magnets attached to their back, disrupting their magnetic compass, the deflections increased up to the expected size ([R. Wiltschko & Wiltschko, 2001](#)), which appeared to suggest that older pigeons flew a compromise between the heading indicated by the sun compass and by the magnetic compass. This rather surprising finding means that as pigeons grow older, the sun compass loses part of its dominance, and sun compass and magnetic compass appear to be used together. Older birds have experienced and probably corrected for the seasonal changes of the sun's arc, but whether this is the reason for their not relying on the sun compass alone is unclear. The above-mentioned experiments were performed in Germany; in Italy, clock-shifted pigeon showed deflections of the expected size right away, and magnets did not increase the size of the deflection ([Ioalè et al., 2006](#)).

Clock-shifted pigeons return to their loft, usually with considerable delay, but over shorter distances, many of them home on the day of release, that is, before the natural day and night cycle could have reset their internal clock. Some birds with their internal clock advanced, return even before their subjective day ends. This means that they must have realized their error. Tracks of clock-shifted birds revealed a great amount of individual variation in where and when they corrected their course. They do not seem to abandon the sun compass altogether, however, but merely downgrade it: their longer routes tend to deviate to the expected side until the loft is reached ([Gagliardo et al., 2009a](#); [Schiffner et al., 2014](#)). At the time

when their subjective day ended, clock-shifted pigeons usually made a stop and later restarted homeward oriented; pigeons carrying small magnets, however, left the place where they had stopped in random directions (Gagliardo et al., 2009a). The magnetic compass appears to take over when pigeons realize that their sun compass is amiss.

The two studies with day migrants have already been mentioned (Section 3.2.3.3); the findings suggest that the magnetic compass is the dominant mechanisms used by day migrants, with the sun compass playing only a minor role.

### **3.4.2 Interactions between Celestial and Magnetic Cues in Night-Migrating Birds**

A large number of cue-conflict experiments were performed with nocturnal migrants, in particular at the time of sunset when these birds normally start their nocturnal flights. Theoretically, in such tests, birds seem to have several options: follow the celestial cues, follow the magnetic field, or chose a compromise.

#### **3.4.2.1 First Cue-Conflict Experiments**

The first of these experiments have already been described: reversing the planetarium sky (Emlen, 1967a), shifting the sunset point with mirrors (Moore, 1982), or shifting the birds' internal clock (Able & Cherry, 1986) were actually cue-conflict experiments, because the tests took place in the local magnetic field. These studies seemed to suggest a dominance of celestial cues. In other cue-conflict experiments, in particular with night-migrants at the time of sunset, birds were tested in cages with magnetic North shifted under the natural sky. At the first glimpse, the results look somewhat confusing, as all kinds of responses were observed, yet upon closer inspection, a certain pattern becomes evident.

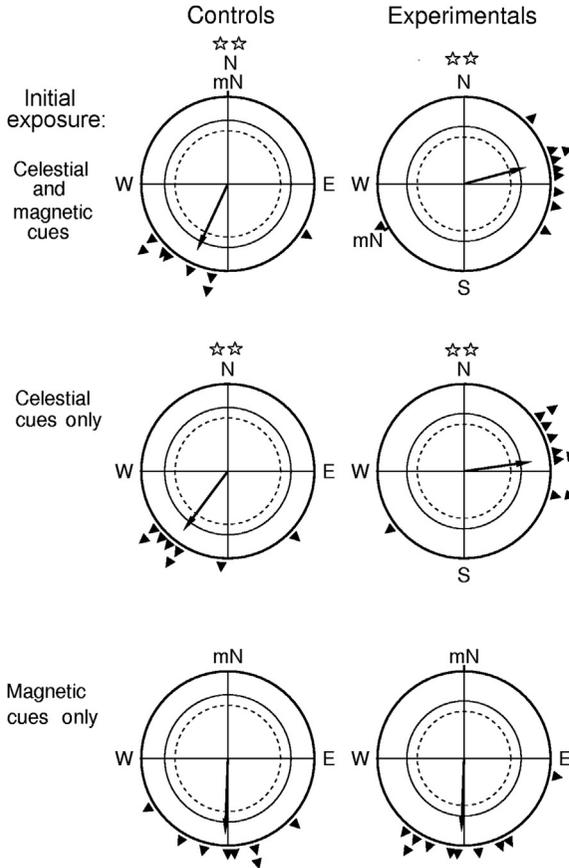
In a number of experiments where birds were tested only once under conflicting cues, most birds seemed to follow the sunset cues (e.g., Sandberg et al., 1988a,b, 1991; Åkesson, 1993, 1994; Sandberg & Pettersson, 1996; Åkesson et al., 2006). Others seemed to compromise between celestial and magnetic cues—they showed a deflection, but this was markedly smaller than the shift in magnetic North (Åkesson, 1994; Sandberg & Moore, 1996). Two species followed the shifted magnetic field (Sandberg et al., 2000), whereas in other cases, the cue conflict led to bimodal or random orientation. Birds that were *repeatedly* tested in the same cue-conflict situation, however, finally followed the magnetic field in all cases; here, the magnetic

cues proved dominant. Yet there were differences between species: birds like three species of *Sylvia*-warblers and *Prunella modularis*, Dunnock, responded immediately to the shift in magnetic North (W. Wiltschko & Wiltschko, 1975a; Bingman & Wiltschko, 1988), whereas European Robins responded only with a delay, following the shift in magnetic North only in the third or fourth test (W. Wiltschko & Wiltschko, 1975b; Bingman, 1987). In Australian Silvereyes, a species migrating at dusk and dawn, the response depended on the direction in which magnetic North was shifted: they responded to a counterclockwise shift of magnetic North immediately (see Figure 10, upper diagrams), but to a clockwise shift with some delay (W. Wiltschko et al., 1998).

The birds' behavior in the repeated tests in the cue-conflict situation raised the question about possible aftereffects on celestial as well as magnetic cues. Garden Warblers and European Robins recalibrated the celestial cues, in this case the stars: in a vertical magnetic field not providing directional information, they now oriented by stars alone in the direction in which the shifted magnetic field had directed them (W. Wiltschko & Wiltschko, 1975a,b). Dunnocks (Bingman & Wiltschko, 1988) and Silvereyes (W. Wiltschko et al., 1998) recalibrated the sunset cues (Figure 10, center diagrams). In Silvereyes, this recalibration was only effective at dusk, the time of day when the birds had experienced the cue conflict; their response to the respective cues at dawn remained unaffected (R. Wiltschko et al., 2001). Sandberg et al. (2000) combined cage studies with release experiments: while only two species of their test birds followed the shift in magnetic North in the cages, all four species responded to this shift when released and the altered magnetic information was no longer available—they obviously had recalibrated the celestial cues.

Aftereffects on the magnetic cues were tested only in two species, and here, the results diverge: Savannah Sparrows, *Passerculus sandwichensis* (Emberizidae), appeared to have recalibrated their magnetic compass (Able & Able, 1995; but see Section 4.4.1.3), whereas in Silvereyes, the magnetic compass appeared unchanged (Figure 10, lower diagrams) (R. Wiltschko et al., 1999).

Taken together, the findings reported here generally support a long-term dominance of the magnetic compass, but this does not necessarily become obvious at once, as birds may respond to the shift in magnetic North with delay. Evidently, some birds consult their magnetic compass more frequently than others. So it seems possible that the birds tested only once and whose behavior indicated a dominance of the sunset cues would have



**Figure 10** Magnetic and sunset cues in experimental conflict: tests with Australian Silvereyes at the time of sunset and aftereffects on celestial and magnetic cues: *Upper diagrams*: tested under the natural sky at dusk: the control birds, tested in the local geomagnetic field, preferred their natural southern migratory direction, but in a magnetic field with north turned by  $120^\circ$  counterclockwise to  $240^\circ$  WSW, the experimental birds responded to the shift in magnetic North, preferring east-northeasterly directions; *central diagrams*: the same birds tested later under the natural sky without magnetic information—they preferred the direction that they had preferred earlier in the magnetic fields, demonstrating that the experimental birds had recalibrated the sunset cues; *lower diagrams*: tested later in the geomagnetic field without celestial cues, both groups preferred their natural migratory direction, indicating that their course with respect to the geomagnetic field remained unaffected. Symbols as in Figure 9. Data from *W. Wiltschko et al., 1998, R. Wiltschko et al., 1999.*

eventually responded to the shift in magnetic North, if they had they been tested more often—many of these studies involved European Robins, a species that was found to respond with delay. In the long run, birds seem to recalibrate the celestial cues, with some birds doing this faster than others.

This ability of birds to calibrate celestial cues, in particular the stars, by the magnetic field during migration appears very helpful for long-distance migrants. When moving south in autumn, the center of celestial rotation becomes increasingly lower and harder to see, while new stars become visible at the southern horizon and gain altitude as the birds progress. These stars have to be calibrated and integrated in the star compass, and here, the magnetic field provides a reliable reference system. For a more detailed discussion of the earlier cue-conflict experiments with a detailed list of species and experimental conditions, see [R. Wiltschko & Wiltschko \(1999\)](#).

#### 3.4.2.2 Calibrating the Magnetic Compass by Polarized Light?

While the cue-conflict experiments up to the year 2000 indicated a long-term dominance of the magnetic compass, a tracking study in 2004 seemed to suggest a recalibration of the magnetic compass by sunset cues. Yet this recalibration was effective only for one night; birds that could be followed a second night again headed into their normal northerly migratory direction ([Cochran et al., 2004](#)). This caused the authors to propose a daily calibration of the magnetic compass by sunset factors. Shortly thereafter, [Muheim et al. \(2006a\)](#) published a review where they reinterpreted the earlier cue-conflict experiments, claiming a dominant role of sunset cues, in particular the band of polarized light, for calibration of the magnetic compass during migration. It was argued that the mean between sunrise and sunset indicates geographic North, and that this may be helpful especially in regions with fast changing magnetic declination (difference between magnetic and geographic North). In view of the earlier studies that had indicated a dominance of magnetic cues, the area just above the horizon was pointed out to be of particular importance for recalibration, and in most of the previous experiments, it had indeed been hidden to the birds. This is a remarkable hypothesis, as it seems rather odd that a mechanism relying on a temporally constant factor with certain spatial variations—the magnetic compass—should be calibrated by a highly variable factor—the sunset cues—which show a considerable shift with geographic latitude as the birds move south and the fastest temporal shifts at equinox, i.e., at the times of bird migration.

[Muheim et al. \(2006b\)](#) presented data with Savannah Sparrows that were first tested indoors with the magnetic field as the only cue, then exposed

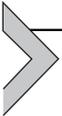
them to artificially polarized light oriented perpendicular to the natural band of polarization at either sunrise *or* sunset and then tested them indoors again. Both groups were randomly oriented, but their individual headings were found to lie roughly 90° on either side of their previous headings, which the authors interpreted as in agreement with their hypothesis.

The publications by Cochran et al. (2004) and Muheim et al. (2006a,b) called forth a new series of cue–conflict experiments, this time allowing birds to see the sky down to the horizon. In a cage study, Silvereyes that were well oriented in closed rooms were exposed to the natural sky at sunset *and* sunrise in a magnetic field turned by 90° to the west and thereafter again tested indoors. Their headings by the magnetic compass were unchanged, and the differences in the headings before and after exposure averaged 0° (R. Wiltschko et al., 2008). In similar cage tests, Pied Flycatchers, *Ficedula hypoleuca* (Muscicapidae), showed considerable scatter, but a marked shift caused by the treatment could not be observed (Gaggini et al., 2010). The results of a study with several species of diurnal and nocturnal migrants that were exposed to the conflicting cues at sunset *and* sunrise also spoke against a recalibration by polarized light (Åkesson et al., 2015). In a telemetry study, Song Thrushes, *Turdus philomelos*, could be followed at least 15 km; birds that had been exposed to the natural sky in a 120° shifted magnetic field nevertheless headed in their seasonally appropriate migratory direction like the untreated controls (Chernetsov et al., 2011). In a similar telemetry study, Wheatears, *Oenanthe oenanthe* (Muscicapidae), were exposed to the same artificial pattern of polarization that was originally used by Muheim et al. (2006b); yet there was likewise no difference in the departure directions of the treated birds and controls (Schmaljohann et al., 2013). These studies thus could not replicate the findings of Cochran et al. (2004) and Muheim et al. (2006b). A recent study with Pied Flycatchers, combining cage tests and telemetry data, found a clear effect on the directional choices only in the cages where the birds oriented along the former axis of the polarization; the subsequent tracks of released birds, however, seemed unaffected (Giunchi et al., 2015). Yet, Muheim et al. (2009), repeating their 2006b study with White-throated Sparrows, *Zonotrichia albicollis* (Emberizidae), got similar results to their previous study.

The new cue–conflict experiments, although in the majority contradicting the hypothesis of a recalibration of magnetic cues by polarized light, raise the question about the reasons for the occasionally observed differences; for a discussion of possible explanations, see R. Wiltschko et al. (2008) and Liu and Chernetsov (2012).

### 3.4.3 *An Integrated Compass System*

The avian mechanisms of directional orientation are redundant in the sense that birds are able to use two different types of cues—magnetic and celestial ones—for locating directions. The cue-conflict experiments described above, however, suggest that maybe the magnetic compass and the celestial compass mechanisms should not be considered as independent, but rather as different components of an integrated system for locating directions. It is striking that birds, when experiencing a situation with conflicting cues, try to solve the arising contradictions by recalibrating the one set of cues by the other, and in the majority of cases, the celestial cues by the magnetic field. This recalibration process ends the conflict so that all directional information is in harmony again, and birds can derive their direction of flight from all available directing cues.



## 4. MECHANISMS SETTING THE COURSE TO THE GOAL

This section is devoted to the first step of the navigation process, namely how birds determine the compass course to their goal. This part of the navigational process is more difficult to study, and our knowledge on the mechanisms setting the course is not as detailed as that on the compass mechanisms; in some cases it is based in indirect evidence. A general concept of how birds may proceed meets the agreement of most researchers, even if a number of questions are still waiting to be answered. Two scenarios must be distinguished, namely (1) the return to a familiar site and (2) the first migration of juvenile migrants to their still unknown winter quarter.

Before discussing the mechanism of determining the course to the goal, we will describe some behavioral observations that must be taken into account in considerations on navigational processes.

### 4.1 Observations in Displacement Experiments

The most common case is that birds want to return to a familiar goal, which, in the case of displaced pigeons, is their home loft, or in the case of displaced wild birds, either their nest or, outside the breeding season, their home territory.

#### 4.1.1 *Return Distances*

Birds are able to return over remarkable distances. Pigeons are known since antiquity to home over hundreds of kilometers from distant, unfamiliar sites. The same is true for displaced wild birds, like swifts, swallows, and some small passerines; seabirds have been found to return even over thousands

of kilometers from sites where they have never been before (for review with a list of references, see [R. Wiltschko, 1992](#)).

From their second migration onward, migrants are also able to navigate toward their wintering area or breeding site over large distances. A very important experiment with migrants was performed already in the 1950s, namely a mass displacement of Starlings ([Perdeck, 1958](#)). Thousands of transmigrants of presumably Baltic origin were caught in the Netherlands and displaced perpendicular to their normal migration route to Switzerland. The subsequent ringing recoveries showed a dichotomy of behavior between adult and juvenile migrants: while the young birds on their first migration continued in their southwesterly migratory direction, reaching new wintering grounds in Southwestern France and Northern Spain, the adult Starlings changed course and headed northward toward their traditional wintering area in Northern France and Southern England. In a subsequent experiment, juvenile Starlings on their way back in spring were displaced from the Netherlands to Switzerland; the majority of these birds was found heading toward their breeding grounds, which several of them reached ([Perdeck, 1974, 1983](#)). This clearly documents the general navigation ability of migratory birds.

This ability may not to be unlimited, however. When [Perdeck \(1967\)](#) later displaced Starlings to Barcelona, Spain, only a few adult birds reached their traditional wintering area. For the young birds, this displacement seemed too far, and the vast majority established a new migration route parallel to their normal one, heading to southern France and northern Italy in spring. In a large-scale displacement experiment, North American White-crowned Sparrows, *Zonotrichia leucophrys* (Emberizidae), were displaced from Washington State to New Jersey, released, and their initial departure paths were radio-tracked. The findings are in agreement with the original [Perdeck \(1958\)](#) experiment: the juveniles continued in their migratory direction heading southward, whereas the adult birds changed course, now heading west-southwest toward their traditional wintering area ([Thorup et al., 2007](#)). Here, the adult birds apparently could compensate a displacement of 3700 km across the North American continent. Older displacement experiments with Laysan Albatrosses, *Diomedea immutabilis*, ([Kenyon and Rice 1958](#)) implied that these birds could return world-wide when released at sea.

#### **4.1.2 Navigation Only to a Familiar Goal**

In the experiments described above, the young first-time migrants did not compensate for the displacement, which is also supported by a corresponding

cage study (Mouritsen and Larsen, 1998). Obviously, birds can navigate only to a *familiar goal*, that is, to an area where they have been before and where they “know the coordinates.” Perdeck’s (1958) findings were often interpreted as showing that young birds still lacked the ability to navigate. This is a misunderstanding, however. Young pigeons at the age of 3 months can clearly navigate to their loft, and it is to be assumed that juvenile migrants can also navigate within their home region before they leave, and they seem to be able to navigate back to their migration route when displaced backward (Thorup et al., 2011). This means that the young birds failed to compensate for the displacement not because of a lack of *ability* to navigate, but because of a lack of *information* about the still unknown goal. Ringing recoveries of the following breeding seasons showed that the displaced juvenile Starlings headed toward the region where they were born and had roamed around prior to migration, and several managed to reach it (Perdeck, 1983).

The necessity to fly around in an area to be able to return there was also demonstrated by Löhrl (1959): nestlings of Collared Flycatchers, *Ficedula albicollis* (Muscicapidae), were hand-raised in an aviary at site A. The first group of these birds was displaced 90 km and released at site B about 2–4 weeks before the onset of migration; another group of birds was also set free at site B, but only after migration had already begun. In the following spring, after they had completed a full round of migration, almost 20% of the male birds that had been released earlier and thus had a chance to explore the area, returned to site B, whereas none of the late group could be found again, neither at A nor at B (see also similar experiments by Mauersberger, 1957; Sokolov et al., 1984).

#### 4.1.3 Behavior at the Release Site

Another observation is also important for considerations on the navigational processes: when released, pigeons do not need to fly around extensively to determine their future vanishing direction. They usually fly around a bit, but mostly already more or less in the direction in which they will later vanish from sight. This is also documented by bearings taken after 1 min (e.g., Wallraff, 1959 and others). Cage experiments even showed that pigeons leave the cage already in the sector of their future vanishing directions (e.g., Kowalski, 1994; Mazzotto et al., 1999). Obviously, birds are aware—at least roughly—of what they take to be their home direction *before* they start to fly.

Flying about at the release site thus does not seem necessary for determining the home course. The seemingly erratic flights might be helpful,

however; they have been interpreted as flight preparations, such as scanning the local situation, checking the wind, looking out for birds of prey or for conspecifics (see [Schiffner et al., 2013](#)).

## 4.2 Navigation by Site-Specific Information with the Help of the “Map”

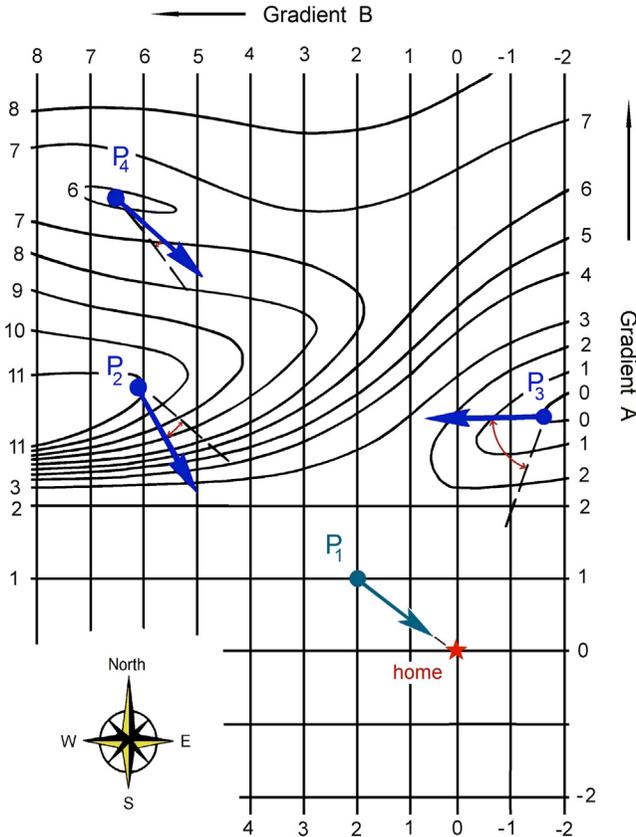
To determine the compass course to a familiar goal, birds can in principle use two fundamentally different strategies that were already considered in the nineteenth century, namely (1) rely on local information obtained at the starting point of their return trip, i.e., in experiments: at the release site ([Viguiet, 1882](#)) and (2) rely on information collected *en route* during the outward journey, i.e. in experiments during displacement ([Exner, 1893](#)).

We will begin by describing the first strategy, which involves bicoordinate navigation ([Schmidt-Koenig, 1965](#); [Wallraff, 1974](#)), where birds determine their position with respect to home with the help of site-specific information, using the local scalar values of environmental gradients. They interpret these values with the help of their navigational “map,” a mental representation of the spatial distribution of these gradients. This concept of navigating has been inspired by the grid system of maps; the principles of this strategy are described in detail by [Wallraff \(1974\)](#), taking the known observations on pigeon homing into account.

### 4.2.1 The Navigational “Map”

The model of bi-coordinate navigation assumes that birds make use of at least two, probably more environmental gradients for navigation. These gradients are geophysical or otherwise bound to the earth; celestial gradients can be excluded because clock-shifting affects only the sun compass, but not the “map” step of navigation, as would be the case if celestial gradients were involved ([Keeton, 1974](#); [Wallraff, 1974](#)).

The birds are assumed to record the local scalar values of these gradients at the release site and derive their home course from the differences between these values and remembered home values. The differences are interpreted with the help of the navigational or grid “map,” a directionally oriented, mental representation of the spatial distribution of the navigational factors, that is, of the overall direction and steepness of the gradients. [Figure 11](#) illustrates this point: the birds know that gradient A is increasing to the north and gradient B to the west. At site  $P_1$ , the scalar differences are +1 in gradient A and +2 in gradient B; from this, the bird concludes that it is in the northwest of home and hence has to fly southeastward.



**Figure 11** The concept of the navigational “grid map”: there are two gradients, gradient A increasing to the north, and gradient B increasing to the west. The home site is indicated by a red (light gray in print versions) star; black lines represent the isolines of differences to the home values. *Lower part*: regular course of the gradients; at site  $P_1$  the birds vanish *homeward oriented*. *Upper part*: irregularities in the course of the gradients; leading to *release site biases* at sites  $P_2$ ,  $P_3$ , and  $P_4$ .

By assuming the use of environmental gradients, the model provides a plausible explanation for the birds’ ability to navigate at distant, unfamiliar sites: gradients can be extrapolated beyond the range of direct experience. If, in the example given above, a bird encounters values of gradient A that are higher than all those it ever experienced, it knows that it is farther north than ever before and has to fly south to return home. At the same time, the assumption that navigation is based on the local scalar values explains how birds can determine their home direction without flying around. The specific local gradient direction is of no importance. Following

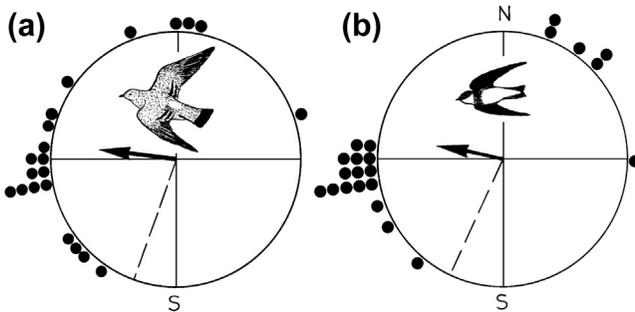
the gradients until the home value has been reached has been considered as an alternative procedure, but this could pose considerable problems. Natural environmental gradient cannot be expected to be always completely regularly distributed, and birds could get “caught” in local highs or lows (see point P<sub>4</sub> in [Figure 11](#), upper part). By comparing scalar values, birds can always determine a course.

The mental representation of the distribution of the navigational factors constitutes a cognitive map in the sense that it does not only allow birds to return home, but to move around freely and head to different goals. It is difficult to conduct experiments with more than one target site, and that is why there are only two such studies ([Baldaccini et al., 1976](#); [Blaser et al., 2013a](#)). They clearly show that pigeons can head to more than one goal and choose according to their motivation: hungry birds flew to a food loft, while well-fed birds headed to their home loft ([Blaser et al., 2013a](#)). When having the choice between their old loft and their new one, pigeons headed towards the loft that was closer ([Baldaccini et al., 1976](#)) - this observation implies that the “map” allows birds to estimate and compare distances.

#### **4.2.2 Release Site Biases**

The courses the birds take when they depart need not necessarily be identical with the true home direction. Vanishing bearings somewhat different from the true home direction are a common phenomenon in pigeon studies (see [Wallraff, 1959](#); [Schmidt-Koenig, 1961](#); [Windsor, 1975](#); and many others).

[Keeton \(1973\)](#) analyzed the orientation of his pigeons at the Castor Hill release site in Upstate New York, about 143 km north—northeast of his loft, in some detail: the birds generally flew westward, deviating up to 90° clockwise from the home direction of 200° ([Figure 12\(a\)](#)). This behavior was largely independent of previous experience and independent of cloud cover. Pigeons from other lofts in the region behaved in a similar way. When the birds were clock-shifted so that the deflection aimed them in home direction, they departed in that direction without hesitation, indicating that it was not any local feature that prevented them from flying there. Hence [Keeton \(1973\)](#) concluded that the regularly observed deviation from the home direction was caused by the local distribution of the “map” factors used to determine the home course: “...the map itself is twisted” ([Keeton, 1973](#), p. 14 verb.). He coined the term “release site bias” for this phenomenon and attributed it to regional irregularities in the distribution of the



**Figure 12** Vanishing bearings of pigeons (a) and Bank Swallows from a colony near the loft (b) released at Castor Hill, a site with a large “release site bias,” suggesting that both species use the same type of navigational factor. Symbols as in [Figure 6](#). Data from [Keeton, 1973](#).

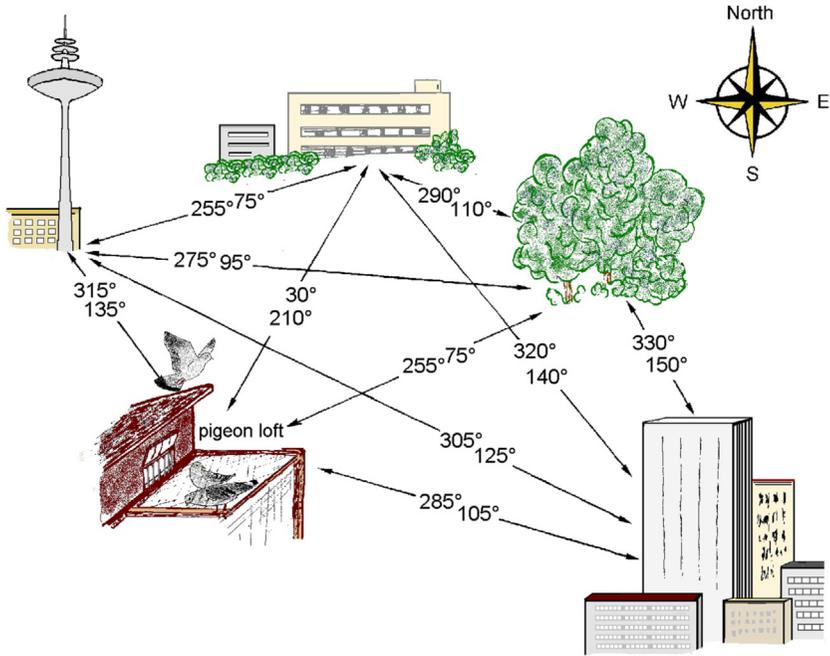
navigational factors. Pigeons repeatedly released from a site where they initially had shown a large bias, slowly adjusted their initial course so that it approached the home course, yet without reaching it ([Kowalski & Wiltschko, 1987](#)). Obviously, birds can learn to cope with local irregularities of the “map” factors, at least to some extent.

In the Castor Hill study, [Keeton \(1973\)](#) also released Bank Swallows, *Riparia riparia* (Hirudinidae), from a colony near his loft at that site. These birds also departed westward, showing a very similar bias ([Figure 12\(b\)](#)). This implies that the two species of birds used the same kind of navigational factors.

The idea that irregularities of the navigational factors can cause the birds to misjudge their position and hence to make certain mistakes in determining their home course is in agreement with the current navigational concept (see  $P_2$  and  $P_3$  in [Figure 11](#)). Release site biases are thus an indicator for the use of local factors; the behavior of pigeons—larger or smaller deviations to the right or to the left of the home direction—is typical for each site. This means, in turn, that these biases reflect the regional distribution of the navigational factors around the respective loft, with the different patterns indicating rather different distributions. For examples from different regions, see [Wallraff \(1959\)](#), [Schmidt-Koenig \(1963a\)](#), [Windsor \(1975\)](#), and [Grüter et al. \(1982\)](#) (see also [Mora & Walker, 2009](#)).

#### 4.2.3 The Mosaic “Map”

The use of gradients enables birds to navigate at distant sites; when approaching home, however, the difference to the home values becomes



**Figure 13** The concept of the “mosaic map”: the birds remember the directional relationship of prominent landmarks with respect to the loft and to each other. *Redrawn from W. Wiltschko & Wiltschko, 1982.*

increasingly smaller until it is so small that it can no longer be detected. Here the birds must switch to other cues. The obvious options are landmarks, but already Graue (1963) realized that pigeons do not orient by landmarks alone—they do not appear to follow sequences of landmarks. Even at sites less than 2 km from the loft, where pigeons certainly are expected to be very familiar with the local landmarks, they respond to clock shifting with a deflection, indicating that compass orientation is also involved in navigation processes in the vicinity of home, sometimes even in view of the loft (see Keeton, 1974; Biro et al., 2007; Armstrong et al., 2013).

These observations led to the concept of the “mosaic map” of landmarks (see Wallraff, 1974). It is thought to be a directionally oriented mental representation of the distribution of prominent landmarks in the home area, stored together with the directions from these landmarks to home or other prominent spots, as illustrated in Figure 13. These landmarks need not only be visual; other local features like magnetic anomalies, infrasound sources etc. (see Section 4.2.5) may also be included. A bird finding itself near a specific landmark knows what compass course it has to pursue to reach home.

In this respect, the mosaic map of landmarks is equivalent to the navigational or grid map: it indicates the home direction as a compass course. But instead of two, three, or more continuous factors like gradients whose scalar values characterize a site, it consists of numerous single entities.

The size of the mosaic map is unclear; observation by Michener and Walcott (1967) and Braithwaite (1993) suggests an extension between 5 and 10 km. It probably varies considerably between regions, depending on the local situation. On the one hand, an extended, detailed mosaic map means a heavy memory load, on the other hand, it must be ensured that there is no gap between the grid map and the mosaic map—on the contrary, we must expect that both types of “map” overlap. Earlier experiments with pigeons deprived of object vision by frosted lenses indicated that these birds could approach the loft in Lincoln, Massachusetts, up to about 1 km (Schmidt-Koenig & Walcott, 1978), while in Frankfurt, Germany, they came closer, with some birds even entering the loft (Schlichte, 1973)—here, the nonvisual navigational factors seem to ensure orientation up to the loft. A recent mathematical analysis of pigeon tracks recorded around the Frankfurt loft allowed a rough estimate of the number of factors involved in the navigational process; this analysis indicated the use of an additional type of cues as the pigeons approached home, which was interpreted as an additional use of landmarks and the mosaic map besides environmental gradients (Schiffner et al., 2011a).

#### **4.2.4 Establishing the “Maps”**

Both the navigational map and the mosaic map of landmarks must be a realistic representation of the situation in the birds’ home region and hence have to be learned, probably in a process of preprogrammed learning, thus ensuring the proper development of an efficient navigational system. Birds normally acquire the necessary knowledge while flying around when they are young.

##### **4.2.4.1 “Map”-Learning in Young Homing Pigeons**

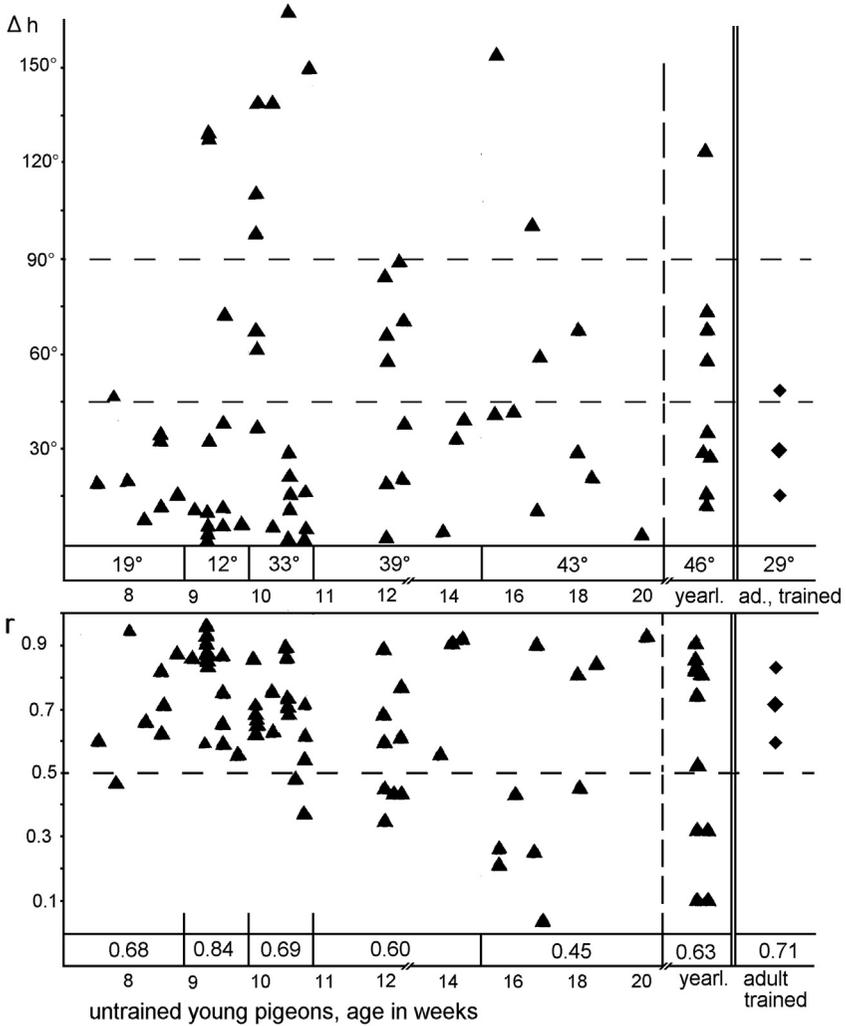
Pigeons start to fly when they are about 5–6 weeks old; at an age of about 8–10 weeks, they begin to venture farther away from their loft. As they get older, they sometimes undertake extended flights, staying out of sight for more than an hour. The experiences obtained during these spontaneous flights shape their navigational system. By chance we once observed the effect of one such extended flight at a distant site: when released the next day about 70 km north of their loft, the young pigeons showed marked

biases, with the birds that had ventured away orienting significantly different from those that had stayed home (see [R. Wiltschko & Wiltschko, 2009](#)). Apparently, an experience during that flight had caused the young birds to interpret the local map factors at the distant site in a different way.

The time course for the development of the navigational “map” was documented in a study with groups of young pigeons of different ages released for the first time away from home ([Figure 14](#)). When the birds were younger than 9 weeks, their vectors were rather long and the deviation from home was fairly small. As the birds grew older, their behavior became more variable: small and large deviations from home were observed—some groups of young pigeons began to show release site biases. This indicates the beginning of the use of the navigational “map” (see above), but the young birds, probably because of their limited knowledge of the distribution of the “map” factors, misinterpreted them at some sites; yet, as the fairly long vector indicates, all birds make similar mistakes. Later, however, the individual variability increases, as indicated by shorter vectors, and such variability is still observed in untrained yearling birds ([W. Wiltschko & Wiltschko, 1982](#)).

The spontaneous flights usually escape observation. [Gagliardo et al. \(2007\)](#) equipped three untrained pigeons with a GPS-logger for one day to record their spontaneous flights; they found that they mostly stayed within 400 m of their loft, one bird ventured 800 m away. Yet it is unclear how representative these data are. When young, little trained pigeons were released at distances of 3.2–13.5 km and their homing flights recorded, they showed considerably more scatter than adult birds; the efficiency of their tracks was significantly lower, with individual birds flying up to 10 times the direct distance ([Schiffner et al., 2011b](#)). On the first glimpse, this may look like poor orientation, but it can also be interpreted as exploration: being away from home, the young pigeons took the chance to look around and explore the area. Some of the observed behaviors could act as safeguards against getting lost: (1) the tracks were restricted to the northern or southern semicircle, depending on where the home direction lay; (2) hardly any bird ventured farther from the release site than the direct distance between the release site and home, and (3) after flying some distance, some pigeons returned to the release point and went off in another direction—the release site appeared to be an anchor point around which they organized their exploratory flights ([Schiffner et al., 2011b](#)).

When pigeons grow older and more experienced, their orientation improves. It is generally observed that experienced birds, that is pigeons that have completed some trainings program, are better homeward oriented with



**Figure 14** Orientation of inexperienced pigeons at various ages. *Upper diagram:*  $\Delta h$ , angular deviation from the home direction; the dashed lines mark the 45° and 90° deviation. *Lower diagram:*  $r$ , lengths of the mean vectors; the dashed line marks 0.5. The median value for the respective age group in weeks is indicated by the numbers above the abscissa. Corresponding data for adult, experienced pigeons are given at the right edge for comparison; here the median and the quartile 1 and 3 are indicated. Redrawn from *W. Wiltschko & Wiltschko, 1982*.

less scattered vanishing bearings. Normally, pigeons from scientific lofts are subjected to training programs in order to familiarize them with the local lay of the land and the distribution of the navigational factors in their home region and to obtain a group of birds with homogeneous experience, which leads to longer vectors closer to home. The observation that extensive local experience reduced an initially large release site bias (Kowalski & Wiltschko, 1987) was already mentioned. The same applies to distant sites, where knowing part of the route already appears to cause better initial orientation and shorter homing times than observed in pigeons that had the same amount of flying experience, but were completely unfamiliar with the region (Grüter & Wiltschko, 1990). Having homed from the distant site once before improved the homing times even further, while similar homing experience from other directions had no effect (Grüter & Wiltschko, 1990). These findings suggest that pigeons are continually updating their navigational “map” in regions that are new to them. The “map” thus becomes an increasingly realistic, more detailed representation of the distribution of the navigational factors.

#### 4.2.4.2 Establishing “Maps” in Migrants

The findings described above were all obtained with Homing Pigeons, but we can assume that map learning occurs in other birds in a similar way. After becoming independent, young birds show postfledging dispersal, where they roam around, and by doing this, experience the course of the potential navigation factors, can check their suitability and thus establish a map of their home region. This is indicated by Löhrl’s (1959) and Sokolov’s et al. (1984) observation that young migrants can return to an area only if they have had time to fly around there. A large-scale project with Bank Swallows in Britain (Mead and Harrison, 1979) revealed a marked exploratory phase after fledging, with young birds from a colony at the English South Coast going north all across England, with some birds reaching Scotland, before they headed south toward their African winter quarters.

During their migration flights, birds also acquire knowledge of the navigational factors *en route* so that in later migrations, they do not have to rely on innate information alone (see Section 4.4), but can use navigational processes to reach their wintering area or breeding area (see Perdeck, 1958, 1983; Thorup et al., 2007). The development of tracking devices now allows the routes taken by migrants to be recorded. These studies have revealed a wide variety of *en route* behavior: while some individuals seem to follow very similar routes year after year, others seem to choose different

routes (see e.g., [Berthold et al., 2004](#); [Alerstam et al., 2006](#); [Thorup & Holland, 2009](#)).

The majority of migrants return to the same breeding site year after year, and many of them spend their winter in the same area (see [Sokolov, 1997](#); for review). Here, large-scale navigational abilities appear advantageous, because a site that allowed successful breeding or wintering the year before is likely to allow it again—hence returning there seems a smaller risk than trying out an entirely new site. For these birds, migration means navigation between time-tested sites. Atlantic Puffins, *Fratercula arctica* (Alcidae), on the other hand, do not seem to have a fixed population-specific wintering region; individual birds choose different areas to spend their winter, but tend to return to these areas in the following years ([Guilford et al., 2011](#)).

#### 4.2.5 The Navigational Factors

The nature of the navigation factors used by pigeons and other birds in their navigational or grid “map” is still a largely open question. Global environmental gradients, such as magnetic intensity ([Viguiet, 1882](#); [Walcott, 1978](#); [Dennis et al., 2007](#); [R. Wiltschko et al., 2010b](#)) and gravity ([Lednor & Walcott, 1984](#); [Dornfeld, 1991](#); [Blaser et al., 2013b, 2014](#)) have been suggested, but also odors (see e.g., [Papi, 1986](#); [Wallraff, 2004](#)) and infrasound ([Quine, 1982](#); [Hagstrum, 2000](#)) and even the view of landscape features as they change with distance ([Baker, 1984](#)).

A possible role of gravity is unclear. First experiments in a gravitational anomaly were negative in the sense that the pigeons’ behavior was unaffected ([Lednor & Walcott, 1984](#)), but [Dornfeld \(1991\)](#) reported that gravity anomalies had some effect, occasionally leading to poorer initial orientation. Recently, [Blaser et al. \(2013b, 2014\)](#) proposed a “gravity vector hypothesis” with gravity as a navigational factor, which, however, would require extremely precise measurements with unrealistic storage conditions and is hardly compatible with the “Map-and Compass” concept. When the authors observed increased scatter, disoriented behavior and losses in and near gravity anomalies, they attributed this to the altered gravity conditions.

Infrasound was considered as a navigational factor after it became known that pigeons could hear these very low frequencies ([Quine, 1982](#)). [Hagstrum \(2000\)](#) elaborated a model that showed how infrasonic cues could be used for navigation and interpreted the different behavior at three sites in Upstate New York as caused by the prevailing infrasound conditions ([Hagstrum, 2013](#)); yet for using this factor, birds would have to fly to take advantage of the Doppler effect. This does not necessarily exclude the use of infrasound,

however; the information could be included later, when the birds are flying, to support the navigation processes.

Most studies testing the role of environmental cues were devoted to odors and the magnetic field, however.

#### 4.2.5.1 Olfactory Navigation

In 1971, Papi and colleagues reported that pigeons deprived of their sense of smell showed poorer initial orientation, were slower in homing and many of them failed to return. The authors concluded that odors played a role as navigational factors: borne by the wind, they would reach the pigeons from different directions which would then be associated with the respective odor. This 1971 paper was the first of a huge number of papers documenting the effect of anosmia and trying to affect the pigeons' behavior by various olfactory manipulations, like depriving them of natural odors, deflecting the wind entering the pigeons' home aviary and other manipulations at the loft, offering artificial odors at the loft and at the release site, displacing pigeons to site A, then transporting them without access to natural odors to site B which lay opposite of A, and releasing them there anosmic, and others. Most of these experiments were performed in Italy by Papi and his group and by Wallraff, who also performed similar experiments in southern Germany. Here is no room to describe the enormous number of different experiments and their outcome that has been interpreted to support a role of odor as navigational cues; they are reviewed briefly by [Gagliardo \(2013\)](#) and in some detail by [Papi \(1986\)](#) and [Wallraff \(2004\)](#). Anosmia has a similar disrupting effect on adult migrants, as the birds no longer compensated a displacement and fell back on their migratory direction ([Holland et al., 2009](#)).

The olfactory navigation hypothesis, although fervently propagated by its protagonists, was met with considerable skepticism. Experiments in other regions produced results that did not necessarily support olfactory navigation. For example, after joint experiments in Upstate New York, the Italian and the American researcher could not agree on the interpretation of the data and wrote separate discussions ([Papi et al., 1978](#)). A comparative study ([W. Wiltschko et al., 1987b](#)) using the same technique of making pigeons anosmic showed that the effect in Italy was significantly larger than in the USA or Germany. But also the physical background of the olfactory hypothesis was questioned: meteorologists and other researchers denied the existence of suitable odors that were sufficiently stable in distribution to provide a solid basis for navigation ([Becker & van Raden, 1986](#); [Waldvogel, 1987, 1989](#); [Ganzhorn & Paffrath, 1995](#)).

In 2009, Jorge and colleagues published data showing that pigeons were also well oriented when they smelled artificial odors instead of the natural ones. They suggested that odors did not carry navigational information, but instead had an activational effect on navigation processes (Jorge et al., 2009). A second study (Jorge et al., 2010) supported this interpretation. However, a recent tracking study in Italy seemed to speak again for a role of natural odors as navigational cues (Gagliardo et al., 2011). This controversy has not yet been resolved, so that the true role of odors must remain open (see also Phillips & Jorge, 2014).

#### 4.2.5.2 Magnetic “Map” Factors

The magnetic field appears to provide more than a compass for birds. In theoretical considerations, magnetic parameters other than the vector quality used for the compass were often discussed as possible components of the “map,” because they represent environmental factors with worldwide gradients mostly running north–south (see Skiles, 1985). Viguier (1882) already proposed a grid map based on total intensity and inclination, and in the late 1990s, Walker (1998) suggested another navigation model based solely on magnetic parameters. In a meta-analysis, Mora and Walker (2009) tried to interpret published data on the regional distribution of release site biases around several lofts in view of the local gradient direction (see also Dennis et al., 2007).

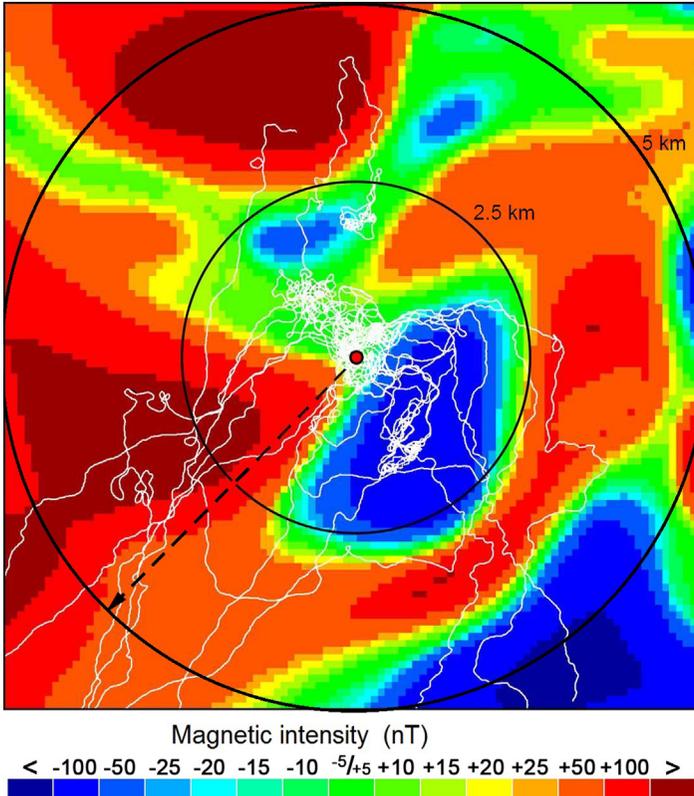
Responses to changes in the geomagnetic field also suggest an involvement of magnetic factors in avian navigation. Keeton et al. (1974) reported that the normal daily fluctuations of the geomagnetic field influenced the vanishing bearings of pigeons, leading to a small shift (see also Kowalski et al., 1988). A recent tracking study showed that these fluctuations affect the steadiness of the entire flight until the birds reach home (Schiffner & Wiltschko, 2011). More evidence supporting a role of magnetic parameters as navigational cues arises from the behavior of pigeons in magnetic anomalies. Walcott (1978) reported disorientation within a strong magnetic anomaly in the Northeast USA, a finding that was later confirmed in anomalies in Germany (Kiepenheuer, 1982; R. Wiltschko et al., 2009), where the pigeons also took much more time to vanish from sight.

This raises the question about which parameter of the magnetic field is crucial—declination, inclination, or total intensity. The first two need a reference direction, which for declination is geographic North and for inclination the horizontal plane or the vertical direction. Their use appears not

very likely, because they change rather slowly so that using differences in these variables would require measuring two directions with a precision that does not seem possible for birds. Total intensity does not require a reference, and the response of pigeons to fluctuations of the geomagnetic field indicates that they may sense differences in intensity in the range of 10–20 nT. In Germany, the magnetic intensity on average increases with 2.5 nT/km (Blum, 1996), in the Northeastern USA with 3.4 nT/km (Lednor, 1982); the magnetic intensity gradient might thus be a suitable navigational factor.

Electrophysiological recordings (Beason & Semm, 1987; Semm & Beason, 1990) revealed responses to small changes in magnetic intensity in the ophthalmic nerve and the trigeminal ganglion (see also Heyers et al., 2010). The location of the corresponding receptors is somewhat controversial: Fleissner et al. (2003) described very small structures of superparamagnetic magnetite, a magnetic form of  $\text{Fe}_3\text{O}_4$ , in nerve endings in the skin of the upper beak of pigeons. These findings were confirmed by Tian et al. (2007), whereas Treiber et al. (2012) failed to find them. Local anesthesia of the upper beak affected the orientation of the pigeons released within the strong Vogelsberg anomaly: while untreated controls flew around erratically for a long time and vanished randomly, apparently confused by the strong, irregular changes in magnetic intensity they experienced in the anomaly (see Figure 15), the treated birds that probably did not experience these changes vanished in an oriented way within normal timespans (R. Wilschko et al., 2009)—preventing them from sensing the unusual magnetic situation seemed to allow them faster decisions on the direction to depart. Together, these findings suggest that pigeons routinely check the magnetic intensity, but are able to navigate without magnetic information when it is not available or not providing meaningful information. A tracking study within the Vogelsberg anomaly supports this view (Schiffner et al., 2011c): untreated pigeons flew around for a considerable time and finally crossed the 2.5 km radius in random directions; when they reached the 5 km radius, however, they had converged into the homeward quadrant, although they were still clearly within the anomaly. Obviously, the irregular, rapid changes in intensity they experienced while flying around finally convinced the birds that the magnetic field was not helpful at this site, and they gave it up in favor of other cues.

An experimental treatment, namely applying a short, strong magnetic pulse designed to affect the magnetization of magnetite particles, also influenced the pigeons' orientation at distant sites: treated birds deviated from the



**Figure 15** Tracks of pigeons released within the Vogelsberg anomaly. The magnetic conditions within a  $5 \times 5$  km area around the release point are shown, with different colors indicating the differences in total intensity to the release point, see scale, but note that the scale is not linear. The release point is marked by a red (gray in print versions) circle; the two outer circles indicate the 2.5 km and the 5 km radius around the release point; the dashed arrow gives the home direction,  $225^\circ$ . From [Schiffner et al., 2011b](#); modified. Please note that this figure is colored in the PDF.

mean of control birds, with the side of the deviation depending on the direction with respect to the head in which the pulse had been applied ([Beason et al., 1997](#)). This also suggests an involvement of magnetite-based receptors in recording local navigational information.

For migratory birds that cover much greater distances than pigeons, magnetic intensity could also be a helpful cue indicating, for example, how far they still have to fly to reach their goal. Evidence that migratory birds use the magnetic field other than as a compass comes from experiments testing birds in different magnetic conditions and from pulse experiments similar

to the ones described above for pigeons. In cage studies, magnetic fields as they occur beyond the goal area caused disorientation (e.g. Henshaw et al., 2010), but during autumn migration only in adult migrants; juveniles on their first migration that had not been in the wintering area before were unaffected (Deutschlander et al., 2012). A pulse caused a change in heading, with the specific effect depending on how the pulse was applied (Beason et al., 1995). The changed course was located with the magnetic inclination compass, which appeared unaffected (W. Wiltschko et al., 2006b). Young migrants that were caught shortly after fledging and had not yet flown about were unaffected by the pulse treatment (Munro et al., 1997). This effect of the pulse on the orientation of adult, but not juvenile migrants is supported by corresponding results of a tracking study (Holland & Helm, 2013), indicating that it was indeed a magnetic component of the “map” that was affected. For details on these and further experiments on the magnetic “map” in migrants, see R. Wiltschko and Wiltschko (2013).

#### 4.2.5.3 Landmarks as Navigational Factors?

A role of landmarks as navigational cues at familiar sites has often been discussed. In the vicinity of home, within the range of the “mosaic map,” the use of landmarks is undisputed, but at more distant sites, there is no convincing evidence to support this view. When pigeons were deprived of landmark view by frosted lenses, this did not affect their initial orientation and homing flight until they reached the area around their loft (e.g., Schmidt-Koenig & Walcott, 1978; Benvenuti & Fiaschi, 1983), with some pigeons even reaching the loft (Schlichte, 1973). This clearly shows that landmarks do not have a marked effect on the navigational process. The skyline of the city, visible as a conspicuous landmark from most release sites within the 40 km radius of the Frankfurt loft, obviously does not act as a “sign post” leading pigeons to their loft: although the skyline was visible from the release sites, pigeons showed biases (e.g., Grüter et al., 1982) and responded to a shift of their internal clock with the typical deviation (see R. Wiltschko et al., 1994, for examples).

Some authors (e.g., Gagliardo et al., 2005; but see R. Wiltschko et al., 2005a; Mora et al., 2012) claimed that the deviation caused by clock shifting is smaller at familiar sites and attributed this to an effect of landmarks, but this is a rather speculative interpretation. In a more extended study of more releases with pigeons that were familiar as well as those that were unfamiliar with the sites released alternately, a difference in the size of the deflection was not observed (R. Wiltschko et al., 2005b). Also, in an earlier study,

pigeons that had been released more than 60 times from a site 40 km from the loft and thus must be considered extremely familiar with this site and the surrounding landmarks responded to clock-shifting with the predicted deflection: instead of flying toward a conspicuous castle in home direction, they took off to the side across a very different-looking gentle hill covered with fruit trees (Füller et al., 1983). This speaks against a role of landmarks as important navigational cues outside the immediate home area.

Claiming orientation by landmarks has always been an attractive idea, because it is a strategy we humans would apply. But it may be a rather anthropocentric approach, not considering the different sensory world of birds. On the one hand, birds can perceive factors we cannot sense and make use of them; on the other hand, the visual system of birds, with the eyes placed on the sides of the head, is rather differently organized (e.g., Martin, 2014). Birds have much wider visual fields, with the binocular field often rather small, and a strong myopia in the lower frontal visual field so that they can see their food on the ground focused, but not the landmarks in front-below when flying (Hodos & Erichsen, 1990). Important for birds is the information on the optic flow-field from which they can extract, e.g., direction and travel time to contact a target for landing, rather than focusing on individual landmarks (for a review on the avian visual system, see Martin, 2014).

#### **4.2.6 A Multifactorial “Map”**

The protagonists of olfactory navigation tended to favor odors as sole “map” factors, with different odors representing the various “map” cues. The two models proposing navigation solely by magnetic cues have been mentioned, they favor different components of the geomagnetic field as navigational cues. The experiments with the birds in the strong anomaly (R. Wiltschko et al., 2009; Schiffner et al., 2011b), however, clearly showed that birds can sense magnetic intensity, but also that they can navigate without magnetic cues, at least in certain regions (see also, e.g., Gagliardo et al., 2009b). Studies with displaced Albatrosses also suggest that birds do not necessarily need magnetic cues: they returned over large distances, although their magneto-reception system was severely hindered by free-moving strong magnets attached to their heads (e.g., Bonadonna et al., 2003; Mouritsen et al., 2003). The gradient “map” for long distance navigation appears to be a multifactorial system, redundant to some extent (see Walcott, 2005; R. Wiltschko & Wiltschko, 2009).

The “map” being a learned system implies that the factors used for navigation need not be the same all over the world. Differences in the

availability and distribution of potential navigational factors between the various regions must be expected, and pigeons will probably select the factors that prove most suitable in their home region. It seems possible that regional cues of only limited range are also involved, if they prove helpful. Differences in the availability and use of cues in different regions are indicated: for example, while pigeons could reorient rather fast in the Vogelsberg anomaly, indicating the presence of usable alternative, nonmagnetic cues (Schiffner et al., 2011c), birds released in a strong magnetic anomaly in the Northeast USA continued to head in random directions for a considerable distance (Walcott, 1978), probably, because no suitable alternatives were available. Evidence for different navigational cue and strategies used in different regions are discussed by W. Wiltschko et al. (1987a), Walcott (1992, 2005) and Schiffner et al. (2013). Pigeons appear to include in their navigational system all suitable factors available in their home region. How they rate and rank the various factors, and to which ones they give priority probably depends on their individual experience during “map” learning (see Section 4.2.4), so that some individual interpretations are to be expected. The same probably applies to migrants.

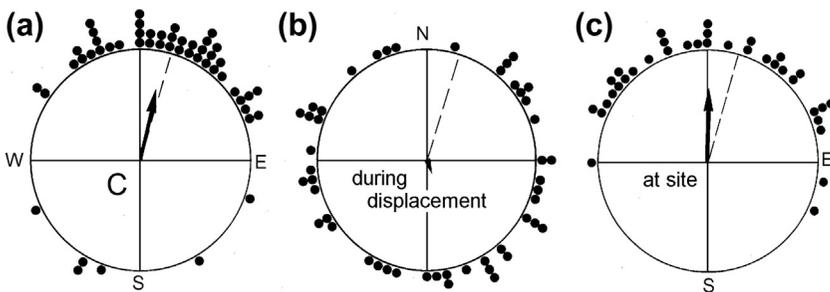
### 4.3 Navigation by Information Obtained during the Outward Journey

The alternative to using site-specific information is relying on information obtained during the outward journey. This seems a simpler strategy, because in contrast to bi-coordinate navigation, it does not require any preknowledge—all the required information is obtained on the way out. Inertial navigation was the first suggestion of this type; but over longer distances, a procedure like the one proposed by Barlow (1964) would become rather inaccurate, because the inevitable small mistakes would continue to add, and the bird would have to remember its home course with respect to its own position and continuously update it as it moves. Another strategy was suggested by the behavior for foraging ants that search around with winding paths, but when they find a prey item, return to their nest on a straight route. They record the direction of the outward journey with their sky compass, integrating twists and turns to obtain the net course of the outward journey; reversing this direction results in the course leading home (see e.g., Wehner et al., 1996). This procedure of collecting route information with a compass as directional reference is a much safer procedure, since the compass stabilizes the directional input, and unavoidable mistakes tend to even out.

### 4.3.1 The Navigational Strategy of Very Young, Inexperienced Birds

Such a strategy—route integration with a compass as reference—is indicated for very young, inexperienced pigeons. They can be assumed to proceed this way on their first flights around their loft, but they seem to apply this procedure also during passive displacement: they seem to record the net direction of the outward journey with help of their magnetic compass, integrating the twists and turns of the journey to obtain a direct course; by reversing this course, they obtain the home direction. This strategy is indicated by the observation that displacement without meaningful magnetic information—either by transport in a distorted magnetic field or in total darkness which interferes with magnetoreception (see Section 3.1.1.3)—leads to disorientation (Figure 16; R. Wiltschko & Wiltschko, 1985). Staying in a distorted magnetic field or in total darkness after arrival at the release site for the same time did not affect their orientation, suggesting that magnetic compass information during the displacement was crucial (R. Wiltschko & Wiltschko, 1978, 1985). Jorge and colleagues (Jorge & Vicente, 2006; Jorge et al., 2008) also observed an increase in scatter up to random in very young pigeons transported in total darkness, which can be attributed to the loss of magnetic compass information.

This kind of navigation would give the home course, perhaps with some scatter, but without pronounced release site biases as they are typical for using “map” information. It appears to be the strategy used initially by very young, inexperienced pigeons, before their “map” is ready to be used. The initial orientation of inexperienced pigeons, reflecting development of the



**Figure 16** Young, inexperienced pigeon use information obtained during the outward journey, with the magnetic field as reference. (a) control birds transported normally; (b) pigeon that were transported to the release site without access to meaningful magnetic information; (c) pigeons kept without access to meaningful magnetic information after arrival at the release site. The home direction,  $16^\circ$ , is indicated by a dashed radius, symbols as in Figure 6. Data from W. Wiltschko & Wiltschko, 1982.

navigational system, is shown in [Figure 14](#) in [Section 4.2.4](#) ([W. Wiltschko & Wiltschko, 1982](#)): pigeons younger than 9 weeks showed small deviation from home and fairly long vectors as one would expect from birds navigating by route reversal. As the young birds grew older, release site biases were observed in an increasing number of groups, indicating the beginning of the use of the navigational “map.” The variability is considerable, though, with some groups of pigeons apparently changing to site-specific information much earlier than others (see [R. Wiltschko & Wiltschko, 1985](#)).

### **4.3.2 The Biological Significance of Route Reversal**

Route reversal thus is a strategy for beginners before the “maps” are fully developed (see also [R. Wiltschko & Wiltschko, 2000](#)). Indeed, it appears to be involved when young pigeons are collecting information for “map” learning: the direction from home is to be combined with the position of landmarks for the mosaic “map” and with changes in the gradient values for the “grid map.” When the “maps” become functional, however, pigeons seem to rely preferably on local information. The reason for this change in strategy is greater safety. Using route-based information has the crucial disadvantage that it allows no course corrections—any initial mistake in the home course is carried on. This may become problematic when birds are farther away from home: for example, when returning from 8 km, they can cope probably with an initial mistake that makes them pass their home by 500 m, but the same initial mistake would lead them 5 km past their home when returning from 80 km. Using “map” information, in contrast, may cause initial biases, but the birds can redetermine their home course as often as they feel necessary and correct previous mistakes. Over the long run, the change to site-specific information is the safer strategy.

Whether older experienced birds give up route-based information altogether or continue to use it along with “map” information is unknown. A second order analysis of samples of experienced pigeons showed that transporting them to the release site without access to meaningful magnetic compass information had no significant effect ([R. Wiltschko & Wiltschko, 1985](#)). These findings only show that experienced pigeons can navigate without route-based information, but whether they use it in parallel with “map” information when available is unclear.

## **4.4 Innate Instructions Setting the Course**

Young migrants starting on their first migration face a very different problem: they have to reach a goal that is still unknown to them, their

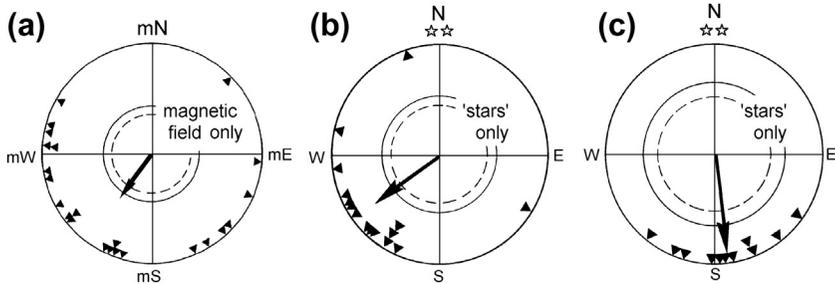
population-specific wintering area. They are endowed with innate instructions that guide them to their distant goal, indicating the direction and distance of migration, with the latter given by the amount and the duration of migratory restlessness (e.g., [Berthold, 1988](#); [Gwinner, 1996](#)). Both the amount of migratory restlessness and the directions are genetically coded; in crossbreeding experiments, birds of the same species belonging to populations with different migration patterns had offspring with intermediate behavior, thus indicating that migratory restlessness as well as the directional preferences are inherited from the parent birds in an intermediate mode ([Berthold & Querner, 1981](#); [Helbig, 1991b](#)).

Modeling migration routes based on innate directions and comparing the results with ringing recoveries for young first-time migrants showed good agreement ([Mouritsen, 1998](#)), supporting the idea that the innate migration program controls the first journey to the wintering area. Modern tracking studies recording the routes of juvenile migrants from the same home area during their first migration (e.g., [Hake et al., 2003](#); [Åkesson et al., 2012](#); and others) are likewise generally in agreement with this idea, even if some birds show rather individual behavior (see e.g. [Gschweng et al., 2008](#)).

In order to obtain the course to the goal, the innate information on the direction has to be transformed into an actual direction of flight. As the migratory direction must be ready at the start of migration, the respective processes must take place during the premigratory period.

#### **4.4.1 Reference Systems for the Migratory Direction**

The magnetic field and celestial rotation are discussed as reference systems for the innate information on the migratory direction, and both are supported by experimental evidence. The sunset factors which have also been considered as important, do not seem to be involved as an independent cue: Savannah Sparrows could orient at sunset only if magnetic information was available ([Bingman, 1983a](#)), although exposing birds of this species during the premigration period to artificially polarized light affected their later orientation ([Able & Able, 1990b](#)). In social species that migrate in flocks, social interactions with experienced conspecifics also seem to play an important role in establishing the course of migration (e.g., [Chernetsov et al., 2004](#)). This is particularly important for birds that depend on specific ecological conditions, like water bodies or swamps, for resting and refueling. Here, migrating traditions emerge and are passed on to the next generation.



**Figure 17** Orientation during autumn migration of hand-raised Garden Warblers with different experiences during the premigratory period. (a) Birds raised indoors with the geomagnetic field as their only cue prefer their natural southwesterly migratory direction, indicating that it is innate with respect to the magnetic field; (b) birds raised under a rotating artificial “sky” in the geomagnetic field, tested under the same, now stationary artificial “sky” in the absence of magnetic information prefer their migratory direction with the help of the artificial “stars”; (c) birds raised under the rotating artificial “sky” in the absence of magnetic information, tested under the now stationary sky without magnetic information head away from the former center of rotation—their “southerly” headings point out that celestial rotation alone induces only a tendency away from its center, without the population-specific deviation from south. The triangles at the periphery of the circle indicate the directional choices, the arrows represent the mean vector drawn proportional to the radius of the circle, and the two inner circles are the 5% (dashed) and the 1% significance border of the Rayleigh test. *Data from Gwinner & Wiltschko, 1978; Weindler et al., 1996.*

#### 4.4.1.1 The Magnetic Field as Reference

The role of the magnetic field in transforming the innate information into an actual direction is documented by the orientation of young migrants that were hand-raised without any view of the sky, with the magnetic field as their only cue: in autumn, these birds oriented in their migratory direction. This applies to Garden Warblers (Figure 17(a); W. Wiltschko & Gwinner, 1974), Savannah Sparrows (e.g., Bingman, 1983a; Able & Able, 1990b), Pied Flycatcher (Beck & Wiltschko, 1982, 1988), Scarlet Grosbeak, *Carpodacus erythrinus* (Fringillidae) (Shumakov, 1990), and Blackcaps (Bletz et al., 1996).

In Pied Flycatchers, an odd phenomenon was described: birds hand-raised in Germany oriented unimodally in their migratory direction, whereas birds hand-raised in Latvia showed axial orientation, preferring their migratory direction and the reverse direction. Only after exposure to a planetarium sky with simulated natural rotation and celestial north in magnetic North did the birds show a unimodal preference for their migratory direction (Weindler et al., 1995). The authors discussed the steeper inclination in Latvia—73° compared to 66° in Germany—as a possible reason for this difference.

#### 4.4.1.2 Celestial Rotation as Reference

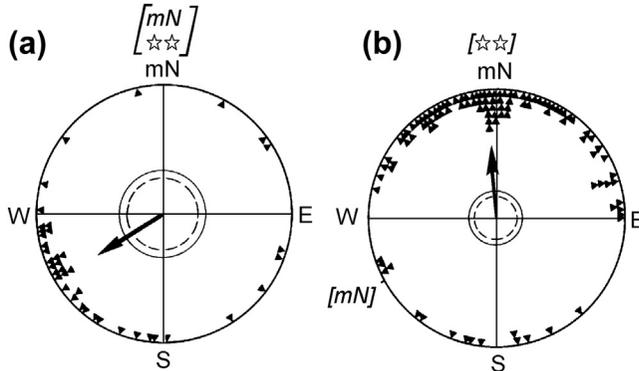
When describing the development of the star compass (Section 3.3.2), we already mentioned the important role of celestial rotation. The experiments reported there actually show how the innate migratory direction is transformed into a direction with respect to the stars, probably in a process of pre-programmed learning. Emlen (1970) demonstrated the importance of celestial rotation in a rather natural-looking planetarium (see Figure 9 in Section 3.3.2); W. Wiltschko et al. (1987a), using a simple artificial “sky” with just 16 light dots, demonstrated that rotation alone was the crucial factors, while the visual appearance of the “sky” proved irrelevant (see also Able & Able, 1990a). The young birds seem to need between 1 and 3 weeks of observing “celestial rotation” to learn a star compass (Michalik et al., 2014).

In these studies, the birds also had access to the local geomagnetic field during the exposure to celestial cues. An experimental group of young Garden Warblers was exposed to a rotating artificial “sky” in the absence of magnetic information, while the control group experienced the rotating sky in the local geomagnetic field. When these birds were later tested under the same, now stationary “sky” without magnetic information, the experimental birds headed away from the former center of rotation—in “southerly” directions; the control birds, in contrast, preferred the population-specific southwesterly course (Figure 17(b) and (c); Weindler et al., 1996). These results suggest that celestial rotation alone indicated only a direction away from its center, whereas the deviation from that direction, in the case of the Garden Warblers about  $45^\circ$  to the right, was coded solely with respect to the magnetic field. In this kind of experiments, the direction of celestial rotation proved important: an artificial “sky” rotating in the reverse direction could induce stellar orientation away from its former center, but could not combine this with the magnetic information leading to the southwesterly course (Weindler et al., 1997).

#### 4.4.1.3 Cue-Conflict Situations during the Premigratory Period

The findings mentioned above indicate interrelations between magnetic and celestial cues. In nature both types of cues indicate the same direction, but experimentally, these cues can be set into conflict to assess their relative importance.

A series of such experiments were performed with Savannah Sparrows, exposing the birds in a magnetic field with north deflected by  $90^\circ$  to various sky conditions, namely to the natural sky all day (Bingman, 1983b; Able & Able, 1990c), to the natural sky by night only, during daytime only (Able &



**Figure 18** Orientation during autumn migration of hand-raised Pied Flycatchers, raised under the natural sky and tested with the geomagnetic field as their only cue. (a) Birds raised in the geomagnetic field orient in their migratory direction; (b) birds raised in a magnetic field with north shifted by  $120^\circ$  to west-southwest orient in the magnetic direction that had been their migratory direction during the premigratory exposure, indicating that celestial rotation dominates over the information coded with respect to the geomagnetic field. The stars and “mN” in bracket indicate where stellar north and magnetic North, respectively, had been during the premigratory period; other symbols as in Figure 17. Data from Prinz & Wiltschko, 1992.

Able, 1990c, 1993), or to an artificial “sky” (Able & Able, 1990a). The results all agree in showing that in the case of conflict between celestial rotation and the magnetic field, *celestial rotation* is the *dominant* cue: tested later during autumn migration with the magnetic field as the only cue, the birds did not prefer their normal migratory direction, but headed in that magnetic direction that had corresponded to their migratory direction with respect to the center of rotation during their experimental exposure. When changing the magnetic heading with the daytime sky, the pattern of polarization proved crucial (Able & Able, 1993).

A similar study with hand-raised Central European Pied Flycatchers exposed to the natural sky in the local and deflected magnetic fields during their first summer produced corresponding results: when the magnetic field was shifted to  $240^\circ$  WSW, the birds changed their magnetic heading from southwest by the respective amount (Figure 18). This means, the birds did not simply head in the magnetic direction that had been in geographic South during the exposure time, but also showed the clockwise deviation that characterizes their normal southwesterly migratory direction. When magnetic North was shifted to  $120^\circ$  ESE, however, the birds were disoriented (Prinz & Wiltschko, 1992). In an earlier study, young Pied Flycatchers had preferred the same direction with respect to the stars in the absence

of magnetic information in spite of having been exposed to different relationships between the natural sky and the magnetic field (Bingman, 1984).

Only two species have been studied so far, but the results agree in suggesting a dominant role of celestial rotation during the time when the migratory direction is established. Both species have been shown to develop their migratory direction without celestial cues by the magnetic field alone (Beck & Wiltschko, 1988; Able & Able, 1990b), but celestial rotation can override the innate course with respect to the geomagnetic field.

#### 4.4.1.4 Interactions between Celestial Rotation and the Magnetic Field Forming the Migratory Course

The findings described in this section so far indicate complex interactions between celestial and magnetic cues during the premigratory period when the transformation of the innate directional information into the actual migratory direction takes place: celestial rotation seems to dominate, but the magnetic field appears to be required for the manifestation of the deviation from true south found in many birds. We can only speculate about the possible reasons.

The center of celestial rotation is geographic North. Celestial rotation and the magnetic field both serve as reference for the migratory direction; the dominance of celestial rotation ensures that the migratory direction is always a specific geographic direction, also in areas and times where the magnetic field may pose problems, like at high latitudes, in regions with large and fast changing magnetic declination and during the period of magnetic reversals. Yet why deviations from the true southerly course seem to be coded only with respect to the magnetic field is not clear. Maybe the magnetic field represents an easier reference for the deviating angle because the birds can sense magnetic directions directly. This is the part of the migratory direction that is probably modified most frequently because of changing ecological conditions along the migration route, and here, coding it with respect to the magnetic field alone may represent a simpler solution.

The interactions described above seem to apply for the situation in the premigratory period and maybe also to the beginning of migration, when the migratory direction is established. As the birds move southward (or northward in the southern hemisphere) in autumn, they are continuously faced with new stars appearing at the southern (or northern) horizon that must be integrated into the star compass. The magnetic field, on the other hand, becomes more stable and less variable in the temperate and lower latitudes, thus providing a good reference system for calibrating the celestial cues. So,

as the birds move on along their migration route, it appears to gain dominance as indicated by the various cue-conflict experiment described in [Section 3.4.2](#).

A very different way of obtaining the course of migration was proposed by [Alerstam et al. \(2001\)](#) for shorebirds breeding in the high Arctic tundra: these birds are suggested to follow their sun compass without adjusting the internal clock to local time, which would lead to routes that are similar to orthodromes, i.e. the shortest routes between two points on a sphere.

#### **4.4.2 Routes Adapted to Specific Ecological Conditions**

The routes derived from the innate instructions on the migratory directions need not necessarily be straight and simple. As already suggested by observations and ringing recoveries (e.g., [Zink & Bairlein, 1995](#)), and recently shown by the tracks of migratory birds equipped with devices like GPS recorders, transmitters (e.g., [Egevang et al., 2010](#)), or geolocators<sup>1</sup> (e.g., [Bairlein et al., 2012](#); see [Section 6](#)), many birds choose routes that avoid large ecological barriers, like high mountain ranges, extended sea crossings, or deserts. In these cases, the innate information generating the migration route must be considerably more complex.

An example of a directional change in the migration route is the autumn migration of Garden Warblers from Central Europe that avoid crossing the Alps and the Mediterranean Sea. These birds start out on a southwesterly course and continue in this direction, until they reach the southern border of the Iberian Peninsula; here, they switch to a more southerly or southeasterly course, heading for their winter quarters south of the Sahara. Hand-raised Garden Warblers showed the respective directional preferences when tested indoors in cages in Germany: at the end of September, when their free-flying conspecifics reach southern Spain and Portugal, they also changed course and now headed south-southeastward ([Gwinner & Wiltschko, 1978](#)). Here, the change in direction was endogenously controlled, embedded in the time program that controls the temporal course of migration. The same seems to apply to the Austrian population of Black-caps that circumvent the Mediterranean in the East ([Helbig, 1991b](#)) and to Yellow-faced Honeyeaters that follow the Dividing Range, an Australian

<sup>1</sup> Geolocators are small tracking devices equipped with a precise clock and a recorder for light intensity. The duration of the light period indicates geographic latitude; while the onset and end of the light period indicates longitude. Although this method is not very accurate and does not work around equinox when the day length is everywhere 12 h, it has proved sufficient to document long migrations and extended foraging routes.

mountain range changing direction from northeast to northwest at the latitude of Brisbane—these birds also performed the change at the right time when tested indoors without access to local factors (Munro et al., 1993).

Central European Pied Flycatchers also fly on a southwesterly course around the Mediterranean and change to a south-southeasterly heading after having reached the southern coast of Iberia. Hand-raised birds tested near their nesting site in Germany in the local geomagnetic field first preferred southwesterly directions until mid-October, when their free-flying conspecifics crossed the Mediterranean; after about that date, their orientation deteriorated to random. For a second group, the magnetic field they would encounter during their journey was roughly simulated in four steps so that they experienced the field of Northern Africa in mid-October; these birds now changed course and continued with a southeasterly heading. A third group was exposed to the magnetic field of Northern Africa right from the beginning of the tests; these birds did not show oriented behavior in any phase of the tests (Beck & Wiltshcko, 1988). Apparently, in this case, the endogenous time program and a local factor—a magnetic field with specific properties—must be combined in the right way to induce the shift in direction; the North African field presented ahead of time at the beginning of migration disrupted the orientation altogether.

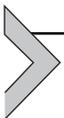
Such an interaction of the endogenous time program with local factors acting as a “sign post” is also supported by corresponding experiments with western Siberian Pied Flycatchers (Chernetsov et al., 2008): young birds tested in their natal region in Siberia were found to head due west in August till mid-September; a group displaced about 4000 km west to Rybatchy on the Curish Spit and tested there was disoriented in September, whereas they showed south-southwesterly headings in October. Here, too, a time program apparently needed to be combined with local factors to control the migratory direction. Chernetsov et al. (2008) discussed that the respective migration program could lead the western Siberian population of Pied Flycatchers on a due westerly course until they reach Europe, where they turn south to head toward their western African wintering area, thus avoiding the deserts of western central Asia.

There are only a few cases where we have some insight into the control of more complex migration routes. There are many other birds with complex routes where one would suspect interactions between the endogenous migration program and “sign posts”—magnetic conditions or other external cues—so that together they lead the birds along ecologically optimal routes to their wintering areas. Others make use of specific wind pattern to save

energy. For example, radar observations showed that many shorebirds, but also other birds, even small passerines like the Blackpoll Warbler, *Dendroica striata* (Emberizidae), move from the northeastern coast of North America to the Caribbean Islands and the north coast of South America by crossing the open western North Atlantic Ocean in a more than 3000 km nonstop flight of up to 80 h. They take advantage of a weather pattern regularly occurring in the region: they seem to wait for the passage of a cold front moving southeast into the Atlantic, and then depart behind the front with strong tail winds. When the front becomes stationary, the birds penetrate it, still heading southeast, until they reach the northeast trade winds, where their flight path change to southwest, again supported by tailwinds (Williams et al., 1977, 1978). The migration program underlying this unusual route must be adapted the specific regional weather conditions.

Wheatears breeding in Alaska were tracked with geolocators and found to migrate across the Asian continent and Arabia to reach their East African wintering grounds (Bairlein et al., 2012). Another example for complex routes are European Rollers, *Coracias garrulus*, from Southern France: they started due south, turned to an easterly course after crossing the Sahara and turned south again after the Gulf of Guinea (Emmenegger et al., 2014). Now, with the modern lightweight tracking devices becoming increasingly smaller and more powerful (see e.g., Wikelski et al., 2007; Bridge et al., 2011), more of such complex, ecologically adapted routes will become known, indicating highly complex migration programs.

Some species, like Garden Warblers or some populations of Pied Flycatchers that make a detour in autumn fly straight routes in spring. Information on the spring route seems to be also genetically coded, as experiments with hand-raised Garden Warblers indicated (Gwinner & Wiltschko, 1980). Under natural condition, however, this innate information in spring can be supplemented by navigational processes based on the information collected during the preceding summer and autumn migrations.



## 5. A DIRECTIONALLY ORIENTED VIEW OF SPACE

During the last 50 years, our knowledge of the avian navigational system increased considerably. A number of mechanisms aside from the sun compass have become known, and the navigational system, with its various components, has been recognized as multifactorial and rather complex. While the researchers in the 1960s and 1970s searched for the *one* factor

used by birds to navigate, the findings of the last decades indicate that such a search must be in vain: the system has a certain redundancy, and the learned components are based on the birds' experience and are thus adapted to the respective local conditions, which appear to differ between regions. This means, however, that findings from one region cannot necessarily be transferred to another region—regional differences and particularities are to be expected (see [W. Wiltschko et al., 1987b](#); [Walcott, 1992](#); [Schiffner & Wiltschko, 2014](#)). This certainly makes the analysis of the navigational system of birds not easier.

It must be kept in mind, though, that only a few avian species have been well studied so far, with many aspects being learned from experiments with Homing Pigeons. This raises the question to what extent can these findings be generalized.

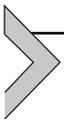
The principle structure of the navigational system is that young birds are endowed with innate mechanisms that require no previous knowledge: the magnetic compass and, based on this, the ability to integrate the route. These mechanisms can guarantee navigation in the vicinity of home and give the birds a chance to gain experience and acquire the knowledge necessary to establish the more complex, learned mechanism. Birds can be assumed to be opportunistic and make use of all available factors that prove helpful. Once the “grid map” is established and birds can obtain navigational information from local factors whenever they decide to head home, they appear to preferentially use this kind of information, which is continuously updated later in life (see [Grüter & Wiltschko, 1990](#)).

Migratory birds must be expected to proceed in a similar way to establish maps of their home region. For their first migration journey to the still unknown goal, they have to rely on the innate migration program to reach their wintering ground, but during this flight, they can acquire information on the distribution of suitable gradients to include them in their navigational “map,” which becomes larger and can span areas like the entire North American continent (see [Thorup et al., 2007](#)). On later migrations, this information can replace the innate instructions, enabling the birds to reach the same breeding area and the same winter quarters year after year. Innate information on the migratory direction is still available in later years ([Helbig, 1992](#)), but, as the large-scale displacement experiments with migrants ([Perdeck, 1958](#); [Thorup et al., 2007](#)) clearly show, navigational processes dominate over the innate information.

The procedure of using innate mechanisms to establish complex learned mechanisms ensures that these are perfectly adapted to the region

where the birds need them and thus guarantee efficient orientation and navigation. We tend to assume that this general structure of the navigational system is similar in all birds. Only a few experiments allow a direct comparison between different species, in particular between Homing Pigeons, free-flying wild birds, and cage studies, but here, the free-flying wild birds seemed to respond like pigeons or in cage studies to the respective treatments (e.g., [Holland et al., 2009](#); [Holland & Helm, 2013](#)). Birds living in the same region apparently use the same navigational factors, as [Keeton's \(1973\)](#) study with Homing Pigeons and Bank Swallows (see [Figure 12](#)) indicates. Although some individual and regional differences must be expected, there is no evidence so far that would indicate principle differences among bird species.

Compass orientation appears to be the backbone of the system by providing the directional reference. Route reversal uses a compass as reference, and the course of the first migration is given as a compass course. A compass is a component of spatial memory, the mosaic map is a directionally oriented mental representation of the distribution of landmarks near home, and the “grid map” is one of the directions and steepness of the environmental gradients used. This suggests that birds generally have a directionally oriented view of space—compass directions appear to be an intrinsic part of their “world,” which would be very helpful for animals with a flying lifestyle that move over longer distances with comparatively high speed.



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## 6. OUTLOOK

The coming years can be expected to increase our knowledge on avian navigation. Research is probably going to develop especially in two fields, the analysis of the tracks that are now becoming available in increasing numbers, and a detailed analysis of the navigational factors, the underlying physical processes and the identification of the parts of the brain where the respective information is being processed.

Near the turn of the century, methodological innovations opened up new possibilities: the development of efficient tracking methods enables researchers to record the routes taken by birds in considerable detail. Radio-tracking over shorter distances has been possible over several decades, but it was first restricted to larger birds that could carry the equipment, until the devices became continuously smaller. Nowadays, large migratory birds and seabirds can be equipped with powerful transmitters and tracked

via satellites (e.g., [Berthold et al., 2004](#), a.m.o.). With other tracking methods, the data are stored in loggers, and the bird has to be recaptured for downloading. GPS-based tracking devices allow recording the position of a bird with great precision and temporal resolution; they are mostly used in studies on pigeon homing (e.g., [Gagliardo et al., 2009a](#); [Schiffner et al., 2011a,b,c](#)), whereas small passerine birds are usually tracked with geolocators (e.g., [Bairlein et al., 2012](#)). New types of equipment are being developed, with the aim of being able to record the routes and the whereabouts of even small birds over a long time (e.g., [Wikelski et al., 2007](#); [Bridge et al., 2011](#)).

The tracks reveal a wealth of information on the behavior of migrants, foraging seabirds, and homing birds. They show the precise wintering areas of specific populations, the routes taken to reach them, and, most important, allow an interpretation of these routes in view of the ecological conditions and much more. At the same time, they document a wide variety of individual behavior. It will take a considerable time before this large amount of detailed information will be adequately evaluated, and it will probably cause us to modify some of our ideas on the migration and behavior of numerous bird species. However, there is a *caveat*: tracks only tell us where a bird was at a given time, but they do not tell us why and by what means it was navigating. This is a matter of interpretation, and here one has to be cautious and must remain conscious of this. Some interpretations are highly speculative, but are later treated as established facts. Where navigational cues and mechanisms are concerned, we must maybe not expect too much from tracking data: pigeons have been tracked since more than 10 years now, but the tracks so far mainly confirmed former findings, without giving fundamentally new insights in the navigational system itself.

The other development is characterized by combining navigational with neurobiological studies and methods. The physical processes underlying the sensing of putative navigational factors like, for example, the magnetic field, gravity, and infrasound, are not yet precisely known. The areas in the brain, where navigational information is processed, are in most cases not yet identified. This applies even to a long-established mechanism like the sun compass: the position of the sun is perceived through the eyes, and the mechanisms of the internal clock are largely known, but where they are combined to produce a sun compass bearing is still unclear. The same is true for most other navigational mechanisms, where the analysis of the crucial brain structures is still at the beginning, with a potential important role of the hippocampus suggested. Here, we may expect considerable progress in the years to come.

The navigational mechanisms of other animals are by far less well known than those of birds. A sun compass and a magnetic compass appear to be rather widespread among the various animal groups, in vertebrates as well as in invertebrates, and the navigational strategy of route reversal with a compass as directional reference has been described for such different animals as social hymenoptera (e.g., Wehner et al., 1996) and rodents (e.g., Kimchi et al., 2004). Yet there are still many questions open, and the navigational mechanisms of other animals are still largely unknown. Recently, some research interest has been focusing on the analysis of the navigation of marine turtles and mammals; so that we can hope for more information on the navigational system of these and perhaps also other animals in the near future.

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