



# Animal navigation: how animals use environmental factors to find their way

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**Abstract** Animals use the geomagnetic field and astronomical cues to obtain compass information. The magnetic compass is not a uniform mechanism, as several functional modes have been described in different animal groups. The Sun compass requires the internal clock to interpret the position of the Sun. For star compass orientation, night-migrating birds seem to use the star pattern as a whole, without involving the internal clock. Both the astronomical compass mechanisms are based on learning processes to adapt them to the geographic latitude where the animals live and, in long-living animals, to compensate for the seasonal changes. Several mechanisms are used to determine the compass course to a goal. Using information collected during the outward journey is mostly done by path integration: recording the direction with a compass and integrating its twists and turns. Migratory animals have innate programs to guide them to their still unknown goal. Highly mobile animals with large ranges develop a so-called navigational ‘map’, a mental representation of the spatial distribution of navigational factors within their home region and their migration route. The nature of the factors involved is not yet entirely clear; magnetic intensity and inclination are the ones best supported so far.

## 1 Introduction

Many animals perform extended migrations. Most famous are the annual migrations of millions of birds that, in autumn, leave regions with adverse winter conditions to overwinter in more favorable parts of the Earth. The record holder in distance is the Arctic tern, *Sterna paradisaea*, a sea bird breeding in the Arctic regions that spends the winters at the edge of the Antarctic Continent, thus staying in eternal summer, avoiding coldness and darkness. But many other birds migrate as well, covering several thousand kilometers every year; among them are, e.g., water birds, raptors, swifts and small songbirds such as swallows, warbler and others. They spend the summer in the northern temperate zones and move to lower latitudes, some of them crossing the equator for wintering. Whales cover long distances between their Arctic or Antarctic feeding grounds and areas with warmer water where they give birth to their calves. But also terrestrial mammals, like many hoofed animals, perform long distance migrations to follow the annual change in vegetation, e.g., the caribou in northern Canada or zebras, gnus and antelopes in eastern Africa. Some animals migrate between nesting and feeding grounds, e.g., marine turtles. Many fishes migrate; some of them, like eels and salmon, only at the beginning and end of their life. Even some insects

migrate: the monarch butterfly, *Danaus plexipus*, is a prominent example.

Most of these migrations involve specific routes and defined end points. Eels and salmon, as well as marine turtles are known to leave their feeding sites after years to return to the places where they were born to lay their eggs. Banded birds were found to return to the same breeding site year after year, and many of them seem to spend the non-breeding season in the same wintering grounds every year.

Birds are also known to return after passive displacement from unfamiliar sites. Homing pigeons, *Columba livia domestica*, bred from the Mediterranean rock dove, were domesticated and used to transport messages already since antiquity. But other bird species, too, were found to be able to compensate for displacements; that is, they can directly head toward a specific goal. The same appears to be true for numerous other animals, with the distances involved correlated with the size of their home range.

Yet, the ability to navigate is not only required for extended migrations and displacements like those mentioned above, but also during their everyday movements within their home range animals profit greatly from good orientation, because it is advantageous to optimize routes—this saves energy and helps to avoid predation.

To answer the question what factors animals use to navigate, it is important to understand how they proceed when they want to reach a specific goal. Birds are by far the best-studied group—homing pigeons are

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available *ad libitum* and can be easily used for orientation experiments. When they are released at a distant site, they leave this site heading in directions close to the home direction. With migratory birds, their innate tendency to seasonally move in their migratory directions provides a reliable, solid baseline for cage experiments. Hence much of our present knowledge on animal navigation comes from studies with birds, but many of the processes and procedures identified in birds seem to have parallels in other animals.

## 2 The “Map-and-Compass” model

Systematic research on animal navigation began in the second half of the twentieth century, when Gustav Kramer [1] and Karl von Frisch [2] in 1950 reported that birds and bees can use the Sun for orientation. The *Sun compass*, thus, was the first orientation mechanism described (see below). In the course of his experiments with homing pigeons, Kramer recognized that avian navigation is a two-step process and proposed his *Map-and-Compass model* (e.g., [3]): When birds intend to return home from a distant site, they first determine the compass course leading to the goal and then use a compass to look up this direction and follow it home. Thus the first step of navigation, the *Map step* means applying mechanisms for determining the present position and put it in directional relation to the goal, and the second step, the *Compass step*, means applying mechanisms which allow to locate specific directions.

The Map-and-Compass model was first developed to describe the homing process of pigeons after displacement, with the Sun compass for the compass step, while the mechanisms by which the pigeons determine their home course could not yet be identified. This model, however, can be expanded to characterize avian navigation in general. In the beginning, young birds use information obtained during the outward journey, and for the first migration to the still unknown wintering area, the map step is replaced by a genetic program that makes birds move into an innate direction for a certain time. Experienced birds, however, are then able to truly navigate, using local site-specific information, within and beyond their home region as well as during migration (for review, see, e.g., [4]). Little is known about the navigation procedures of other animals, but we tend to assume that in many cases they might proceed in a similar way when they have to reach a specific goal. However, in some cases under certain conditions, they might use more direct mechanisms.

When Kramer [3] proclaimed the Map-and-Compass model, the Sun compass was the only navigational mechanism yet known. Research during the last decades increased our knowledge on the factors and mechanisms of animal navigation considerably, even if many questions are still open. In particular, the compass mechanisms have fairly well been analyzed in many animals.

## 3 Compass mechanisms

How do animals proceed when they have to locate directions? In principle, they use the same factors that we humans, too, use, namely the geomagnetic field and astronomical cues. Three compass mechanisms have been identified in animals, namely a magnetic compass, a Sun compass for directional orientation during the day and a star compass for orientation at night

### 3.1 The magnetic compass

We humans need a technical device—a compass where a magnetic needle aligns itself with the course of the field lines—to locate the direction of the geomagnetic field. Many animals, in contrast, can sense the direction of the magnetic field directly.

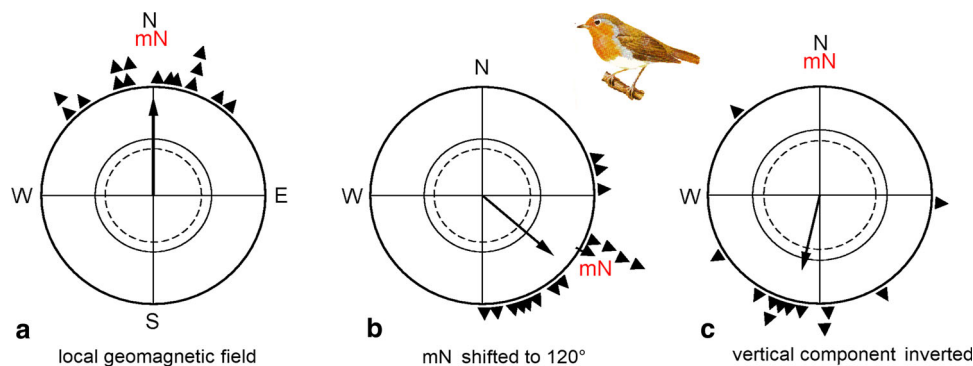
#### 3.1.1 The distribution of a magnetic compass among animals

A sense for magnetic directions was first discovered in migratory birds: During the migratory season, these birds show a spontaneous tendency to prefer their migratory direction also in suitable cages, and when the north of the ambient magnetic field was shifted by a coil system, European robins (*Erithacus rubecula*, Turdidae) changed their preferred direction accordingly (Fig. 1a, b) [5]. These findings initially met with considerable skepticism because it was a novel, unexpected sensory ability alien to man. Meanwhile, however, a magnetic compass has been demonstrated in more than 20 bird species, including other migrants and also in non-migrants, e.g., homing pigeons [6] and even domestic chicken (*Gallus gallus domesticus*) [7]. It was also found in animals of other groups, first in cave salamanders [8], but soon also in all groups of vertebrates—in fish such as stingrays [9], salmon [10,11], eels [12,13] and others, in frogs (e.g., [14]), alligators [15], marine turtles [16] and mammals like rodents [17] and bats [18]. Findings in humans have been controversially discussed (see [19]).

A magnetic compass was also demonstrated in sea slugs (Nudibranchia) [20], in crustaceans like spiny lobsters [21], sandhoppers (Amphipoda) (e.g., [22]) and others, and also in insects such as termites [23], beetles [24], moths [25] and butterflies (e.g., [26]), honeybees [27] and ants [28,29]. A magnetic compass thus appears to be widespread and may even be a general characteristic of mobile animals.

#### 3.1.2 Different functional modes

The magnetic compass in animals is not a uniform mechanism, however. It has been analyzed in detail only in very few species so far, but there are at least two fundamentally different functional modes and some modifications. The mechanisms in birds are the ones best known so far and, here, the magnetic compass functions very differently from our technical compass.



**Fig. 1** Orientation behavior of European robins during spring migration in round cages under dim narrow-band 565 nm green light, demonstrating compass orientation by the geomagnetic field. Headings **a** in the local geomagnetic field (46 nT,  $mN = 360^\circ$ ,  $66^\circ$  inclination); **b** with the horizontal component (magnetic north) shifted to  $120^\circ$  ESE; **c** with the vertical component inverted. –  $mN$ , magnetic north. The

triangles at the periphery of the circles indicate the mean headings of individual birds, the arrows represent the grand mean vector in the respective test condition in relation to the radius of the circle = 1. The two inner circles mark the 5% (dotted) and the 1% significance border of the Rayleigh test (see [213] for details) (data from [214])

Birds are not sensitive to the polarity of the magnetic field (see Fig. 1a, c); instead, they sense the axial course of the field lines and distinguish between their two ends by the inclination [30]. This means that for birds, the magnetic compass does not indicate *magnetic north and south*, as our technical compass does, but *poleward*, where the field lines point downward and *equatorward*, where they point upward. This type of compass, an *inclination compass*, becomes ambiguous at the magnetic equator and requires long-distance migrants to ‘reverse’ their heading from *equatorward* to *poleward* when they cross the equator to continue heading southward. – The inclination compass was first analyzed in European robins, but was also found in all other bird species tested for it so far. It is remarkably accurate; it was shown to still work at an inclination of  $87^\circ$ , i.e., only  $3^\circ$  from the vertical [31, 32] and at  $5^\circ$ , close to the horizontal [33].

The avian magnetic compass proved to be light dependent, requiring short-wavelength light from UV to about 565 nm green (see Fig. 1); under red light, birds are disoriented [34–36]. It spontaneously functions only in magnetic intensities with which the birds are familiar; decreasing or increasing the ambient intensity about 25% leads to disorientation [37, 38]. However, birds can adjust to intensities outside this functional window when they are exposed to other intensities for a while: Robins caught and kept in a field of  $46 \mu\text{T}$  thus became able to orient at intensities as low as 5 nT [39] and as high as 150 nT, but could not orient at the intermediate intensity of 81 nT [37]. This ability allows migrating birds to cope with the decreasing intensities that they encounter when reaching lower latitudes.

These characteristics of their magnetic compass indicate that birds have a specific way to perceive magnetic directions. In the 1980s, Schulten and Windemuth [40] suggested the *radical pair model*, which was later detailed by Ritz and colleagues. It assumes the avian magnetic compass to be based on radical pair

processes, with the direction of the ambient magnetic field changing the ratio singlet/triplet of the radical pair (for details, see [41]). This effect does not depend on the polarity of the magnetic field and thus results in an *inclination compass* as found in birds. As site of magnetoreception, the authors suggested the eyes, because of their spherical shape, and there are receptor cells aligned in all spatial directions. Hence the different ratio of singlet/triplet would result in an activation pattern on the retina that is centrally symmetric to the course of the field lines (see [41] for details). Changes in intensity would modify the activation pattern, which appears to confuse the birds at first, but since the pattern retains its central symmetry to the field lines, birds can learn to interpret the altered pattern.

As receptor molecule providing the radical pairs, Ritz and colleagues suggested cryptochrome, a protein with FAD (flavin adenine dinucleotide) as chromophore [41], because it is the only known photo pigment in animals that forms radical pairs. Several types of cryptochromes were indeed found in the retina of birds (see, e.g., [42]). In particular Cry1a, located in the outer segment of the V/UV receptor cells of robins, chickens and zebra finches (*Taeniopygia guttata*, Estrildidae) seems highly suitable for magnetoreception. These cells are distributed all across the retina [43, 44] and thus could produce the assumed activation pattern. Cry1a is activated at all wavelengths where birds were found to be oriented [45]. Later studies indicate that the crucial radical pair is formed during re-oxidation ([46]; for review, see [42]).

Amphibians and marine turtles were also shown to have an *inclination compass*, i.e., a compass that is not sensitive to the polarity of the magnetic field. Their compass mechanisms, however, were found to differ from that of birds in their light dependency. While birds are still oriented under 565 nm green light, the wavelength range of normal orientation in the newt *Nothophthalmus* (Salamandridae) appears to end at about 450

nm blue [47]. Marine turtles, in contrast, could use their inclination compass also in total darkness [48]. Only little is known about the magnetic compass of other vertebrates. A few fishes and mammals have been studied: salmon [49], subterranean rodents [50], and bats [51] were found to respond to the polarity of the magnetic field—they have a *polarity compass*. Details of their reception mechanisms have not yet been analyzed; permanent magnetic material like *magnetite* (a specific form of iron oxide,  $\text{Fe(II)Fe(III)}_2\text{O}_4$ ) has been discussed.

Even less is known about the functional mode of the magnetic compass of arthropods. Among crustaceans, only the compass mechanism of spiny lobsters has been analyzed; they were found to have a *polarity compass* [52]. The two species of insects tested so far, the flour beetle *Tenebrio* [53] and the monarch butterfly [54], in contrast, have an *inclination compass*.

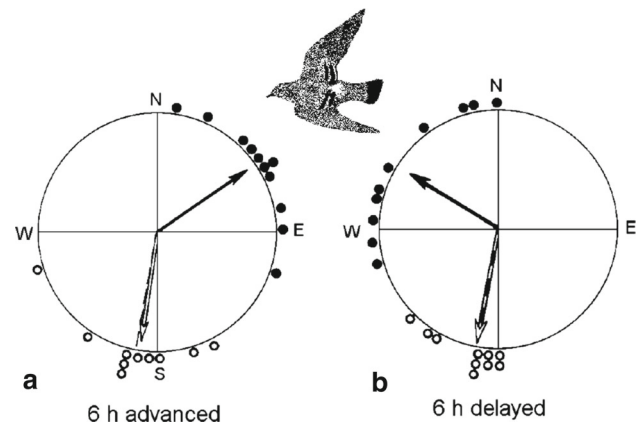
The different functional modes of the magnetic compass suggest independent evolutionary developments. The magnetic compass is an important orientation mechanism with the great advantage of being always available, independent of the time of the day and the weather conditions. Magnetic disturbances, such as magnetic storms and local anomalies, are rarely strong enough to interfere with it.

### 3.2 The Sun compass

The Sun is widely used for direction finding during the day. The first indications of the Sun as an orienting cue were already reported in the beginning of the twentieth century, when Santschi [55] could re-direct ants by reflecting the Sun with a mirror. In 1950, the Sun compass was discovered independently in animals as different as birds [1], and in honeybees [2]. This initiated a systematic search for Sun compass orientation in the animal kingdom. Soon a Sun compass was found in various crustaceans (summarized by [56]), various insect groups like ants and bees, beetles and others, spiders (summarized by [57,58]), butterflies like the Monarch [59], and marine snails [60]. Among vertebrates, it was found in several species of fishes (e.g., [61]; for review see [62]), in reptilian species such as lizards [63], snakes [64,65], turtles [66,67] and alligators [68]. Yet in amphibians (e.g., [69]) and mammals, where rodent species were tested (e.g., [70]), the data were less clear. It has to be considered, however, that amphibians mostly avoid being exposed to clear sunlight, and rodents are mostly nocturnally active.

#### 3.2.1 Functional mode and ontogeny of Sun compass orientation

To derive directional information from the Sun, the animals must know the Sun's arc and consider the time of the day. This does not pose a problem, because animals are endowed with an internal clock. Their endogenous circadian rhythm is synchronized with the natural day by sunrise and sunset, (see, e.g., [71]). With this sense



**Fig. 2** Clock-shift experiments with displaced homing pigeons, demonstrating the use of the Sun compass. **a** Fast shift: internal clock is 6 h advanced; **b** slow shift: internal clock is 6 h delayed. The dashed line marks the home direction  $192^\circ$ , the symbols at the periphery of the circle give the vanishing bearings of individual birds: open, controls living in the natural day, solid: experimental birds with their internal clock shifted. The arrows indicate the mean vectors (see [213])

for the time of the day, they interpret the Sun's position. The customary demonstration of Sun compass use is based on this phenomenon. In the so-called *clock-shift* experiments, the internal clock of the test animals is shifted, mostly for 6 h, by subjecting them to an artificial photoperiod that, e.g., starts 6 h before sunrise and ends 6 h before sunset. After about 5 days, the internal clock is adjusted to the new, artificial photoperiod. When the animals are then exposed to the Sun, they misjudge its position and orient in a direction that deviates markedly from that of untreated controls—in the Northern Hemisphere, a forward shift results in a counterclockwise, and a backward shift in a clockwise deviation (Fig. 2). Such *clock-shift* experiments were first conducted by Schmidt Koenig [71] with homing pigeons, but soon this method has been widely applied, e.g., also in connection with directional training (see e.g., [72])

When animals are tested in a *clock-shift* experiment, the altitude of the Sun is markedly different from what they should expect according to their subjective time, e.g., 6 h forward-shifted pigeons tested at 6:00 in the morning should expect the Sun high up in the sky because this is their subjective noon; instead it is low above the horizon. They seem to ignore this discrepancy, however, which indicates that for the Sun compass of birds, only the Sun's azimuth is important, whereas its altitude is ignored. Schmidt-Koenig therefore describe the Sun compass of pigeons as a *Sun-azimuth compass* ([72]; see also, e.g., [73] for ants). The same seems to apply to many other animals; for fishes, however, the Sun's altitude seemed to be also involved in the orientation process (see e.g., [74]).

Yet the Sun's azimuth does not change uniformly in the course of the day; just after sunrise and just before sunset, when the Sun rapidly gains or loses altitude, its increase is rather slow, below the average of  $15^\circ$  per hour, whereas around noon, when the Sun is high up in the sky, it moves much faster. This raised the question whether the animals are aware of this and compensate for the changes in azimuth correctly. This was first demonstrated in the desert ant *Cataglyphis* (Formicidae): These ants are aware of the different rates of change in the course of the day [73] and interpret the Sun's azimuth accordingly. The same appears to apply to honeybees [75, 76]. Fishes, too, consider the different rates of change in Sun's azimuth largely correctly [77], and this is also true for birds [78].

The Sun's arc, however, and with it the rate of changes in azimuth, depends on the geographic latitude and season. This means that for precise Sun compass orientation, the animals' compensation mechanisms must be based on the true Sun's arc of their home region and the correct time of the year. This is accomplished by learning processes: ants and bees observe the sky before they begin the foraging phase of their life. These learning processes are rather fast, taking only a few days, and seem to be supported by innate components (see e.g., [79] for details)—ants that had experienced the Sun only early in the morning could interpret its position in the afternoon correctly [80]. This is probably required because of the rather short life span of these social insects, which also makes an adaptation to the seasonal changes largely unnecessary. Ants that have overwintered, however, must learn the Sun compass in spring anew [81], which may also apply to overwintering bees.

In birds, the ontogeny of the Sun compass has been studied only in homing pigeons. Here, it is likewise learned [82], with the learning processes taking considerably longer and requiring observation of the Sun's arc during large portions of the day. Birds that had experienced the Sun only in the afternoon could not use their Sun compass in the morning [83]. Learning the Sun compass normally begins when the pigeons are about 12 weeks old, but it can be advanced by early flying experience [84]. The magnetic compass serves as reference against which the movement of the Sun is observed [85]. We tend to assume that the respective processes are similar in all bird species. How the avian Sun compass is adjusted to the seasonal changes has not yet been analyzed; it is to be expected, however, that the processes are similar to those of its first establishment. Little is known about the establishment of the Sun compass in other animals. Experiments with fishes that never saw the natural Sun suggested that their Sun compass may be in large parts innate (see [85]).

The Sun compass is the most important orientation mechanism within the animals' home range and over shorter distances, where animals follow their Sun compass in spite of contradicting information from their magnetic compass. During long-range migrations, however, animals would have to additionally cope with the changes of the Sun's arc with geographic latitude

or, when they migrate east/west, with the resulting shift in local time. Interestingly, while a Sun compass was demonstrated in numerous fish species (see e.g., [60, 61], experiments involving migration with species like salmon and eels failed to produce unequivocal evidence for Sun compass orientation [87, 88]. With birds, the Sun compass is likewise demonstrated in displacements and conditioning (see e.g., [89] for summary), but day migrating birds during migration did not respond to clock shifting as expected (e.g., [90]). The findings suggested that they paid attention to the Sun, but that the Sun compass does not serve as major compass system for orienting the migration flight.

### 3.2.2 The role of polarized light

The Sun is accompanied by a particular pattern of polarization in the sky light, with the polarization reaching a maximum  $90^\circ$  from the Sun. It gradually changes as the Sun moves. In contrast to us, many animals can see this polarization pattern in the sky and use it for orientation, so that for them, the Sun compass is actually a 'skylight' compass (see e.g., [91]). The pattern of polarization is also visible below the water surface (see e.g., [92]) so that polarized light is also a potential orientation cue for aquatic animals living near the surface. Responses to polarized light have indeed been observed in crustaceans such as *Daphnia* (e.g., [93]) and decapods [94].

The use of polarized light for orientation was first discovered in honeybees and ants [95, 96] and in the following years was also found in many other insect species. In insects, where the upper parts of the eyes are specialized to detect the polarization of light (for reviews, see e.g., [57, 97]; for details about the insects' polarization vision, see e.g., [98]). Experiments with desert ants of the genus *Cataglyphis* showed that these ants are familiar with the polarization pattern and its changes in the course of the day; they use it for compass orientation [80]. They need not see the entire sky, but a small portion is sufficient. Dung beetles have even been reported to be able to use the polarized moonlight for nocturnal orientation [99].

Many vertebrates, too, are sensitive to polarized light. This is indicated in fishes (e.g., [100]), amphibians [101], reptiles (e.g., [102, 103]) and, among mammals, bats [104]. Birds are also able to perceive polarized light [105] and with them the effect of polarized light on orientation behavior has been studied in some detail. The pattern of polarized light at sunset was shown to play some role in the orientation of a night-migrating American songbird [106] that starts migration flight at about that time. Several authors began to test the relative importance of polarized light compared to other cues, with some studies appearing to indicate a dominance of polarized light [107–109]. Several of these studies are not unproblematic, however, because they involved polarizers, which polarize the entire skylight almost 100%, and this unnatural pattern appears to alter the normal behavior. Birds were observed to orient

roughly parallel to the axis of polarization, which was significantly different from their response to the natural polarization pattern [110]. A dominant role of polarization could not be generally confirmed (e.g., [111, 112] a.o.).

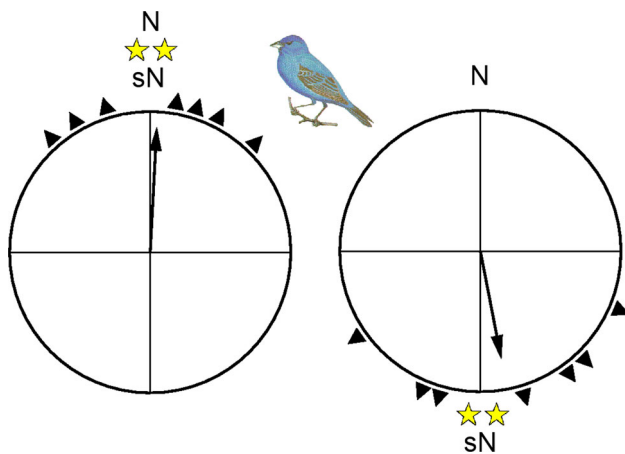
Yet migratory birds can use the natural polarization pattern for orientation. A twilight migrant stayed oriented when other orienting cues like the geomagnetic field had been removed (e.g., [113]), and this is also applicable for a day migrant. In a compensated magnetic field, the birds were still oriented as long as the natural skylight was visible, even when the Sun itself was obscured [114].

A crucial role of polarized light is also that it can mediate celestial rotation to migratory birds, which is an important factor for transforming the genetically coded information on the migratory direction into an actual direction (see below). This effect was only observed in birds that had full view of the natural sky, whereas birds that had observed the sky through depolarizers could not do so, even if they had been able to see the Sun and its movement [115].

The Sun compass, i.e., the skylight compass, is the dominant mechanism in the compass orientation of many animals: They prefer to use it when it is available.

### 3.3 The star compass

Using the stars for orientation has been described so far only for nocturnally migrating birds; they can use the stars as a compass. This was first demonstrated in planetarium experiments. Reversing the planetarium sky caused birds to reverse their headings (Fig. 3) [116, 117].



**Fig. 3** Planetarium experiments with indigo buntings, *Passerina cyanea*, demonstrating the star compass. The orientation of the same birds **a** under the normal planetarium sky with the northern stars projected toward north, **b** under a reversed planetarium sky with the northern stars projected toward south. (data from [11], Appendix 8). The triangles at the periphery of the circles mark the mean headings of the individual birds: the arrows represent the mean vectors (see [213])

A star compass is also indicated by outdoor experiments, where birds at night headed in their migratory direction with the stars as only available cue (e.g., [118–120]).

The stars move in the course of the night, but an analysis of the star compass showed that the internal clock was not involved [121]. This excluded mechanisms similar to that of the Sun compass (see above) and spoke against the use of individual stars, suggesting that birds might derive directions from the pattern as a whole or parts of the pattern. Experiments blocking certain constellations revealed a considerable individual variance. In general, the circumpolar stars within  $35^\circ$  of the center of rotation center seemed to be important, yet the results did not allow a final conclusion [121].

The star compass is also a learned mechanism. Young migrants could use the stars as a compass only if they had observed the sky rotating before they start autumn migration. In an experiment, two groups of hand-raised birds were exposed to a rotating planetarium sky, with the control group under the normal sky, rotating around the polar star *Polaris*, while the test group was exposed under a sky rotating around *Betelgeuze* in Orion. Later, during autumn migration, both groups were tested under the now stationary planetarium. The control group preferred the normal southerly migratory direction, heading away from *Polaris*, whereas the test group headed away from *Betelgeuze* [122]. Birds do not seem to have an innate concept about what the sky looks like. The complex natural sky could be replaced by a simple pattern of only 16 light dots—as long as the birds had observed this pattern rotating with 1 rotation per day, they later could use it to orient in their migratory direction relative to the center of rotation [123, 124]. *Celestial rotation* was thus identified as the crucial factor for establishing the migratory direction with respect to the stars.

The view of the sky changes gradually. The stars rise 4 min earlier each day, so that the sky in autumn looks different from that in spring. At the same time, the sky changes its appearance with geographic latitude. During autumn migration, as the bird moves south, the northern stars slowly lose altitude and approach the horizon, while new stars appear at the southern horizon. Birds have to integrate these new stars into their star compass. Experiments under the natural sky with altered magnetic fields indicate that the magnetic compass provides the reference system which gives directional meaning to the new stars during migration (e.g., [118, 119], a.o.).

So far, a star compass has been demonstrated only in a few species of songbirds that migrate at night. Since the majority of birds are primarily day active, the star compass could be a special mechanism developed by the nocturnal migrants to orient their extended flights. It is unknown whether generally night-active birds, like, e.g., nightjars or owls, also use the stars as a compass as such birds have not yet been studied.

## 4 The course to the goal

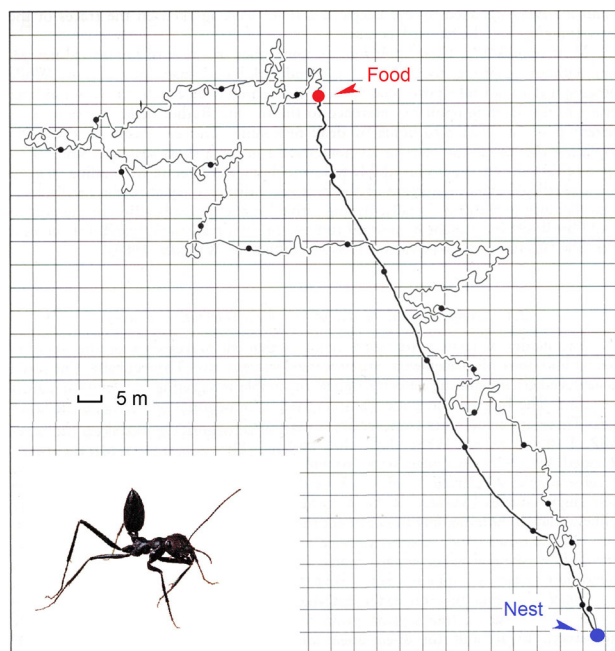
The mechanisms of determining the course to the goal, that is, the direction that is to be pursued to reach the goal, are less well known than the compass mechanisms, although there has been considerable progress during the last decades. Again, birds, in particular homing pigeons, are the best studied group, but also marine turtles and the desert ant *Cataglyphis* have been studied in detail.

For most animals, a frequent task is to orient within their home range, i.e., to return to a resting place, their burrow, their nest, etc. In this case, for the first step of the navigational process, the animals have the option to use various informations collected during the outward journey. Animals that cover larger distances, e.g., birds, can also establish a learned system based on remembering the spatial distribution of several environmental factors, the so-called navigational ‘map’. Another task is to reach a yet unknown goal in migration—for this animals have to rely on innate programs.

### 4.1 The use of information obtained during the outward journey

When returning to a specific place, such as a burrow or a nest, animals can theoretically rely on landmarks, following the sequence of landmarks they observed during the outward journey in reverse order. Many animals have been shown to respond to landmarks, in particular in the vicinity of their nest (e.g., [125, 126] a.o.). However, it is difficult to demonstrate that this strategy is used during natural movements, and clear evidence is not available. If the outward journey has not been on a straight route, following a sequence of landmarks backwards has the disadvantage that the return paths is not the most direct, but shows the same windings and detours.

Another strategy would be to record the direction of an outward journey with a compass and reverse this direction to head home. If the outward journey was not straight, but consisted of frequent changes in direction, the animal must consider the various compass directions and the respective distances of the parts of path and integrated them, to obtain the net direction of the outward journey. This strategy—*path integration* [127]—has been observed in desert ants: Leaving their nest, they start to search around for food, with winding paths covering a certain area—after having found a food item, however, they carry it back to their nest on the direct route (Fig. 4) [127]. Experiments have shown that the ants use their skylight compass, integrating all the twists and turns of the outward journey (for details, see [128]). They also have a rather precise idea of the distance to home—after covering that distance, they start to systematically search around [129]. Path integration may be combined with landmark memories to guide ants and bees back to their nest (see e.g., [130–132], which is a very effective, safe strategy. Little is

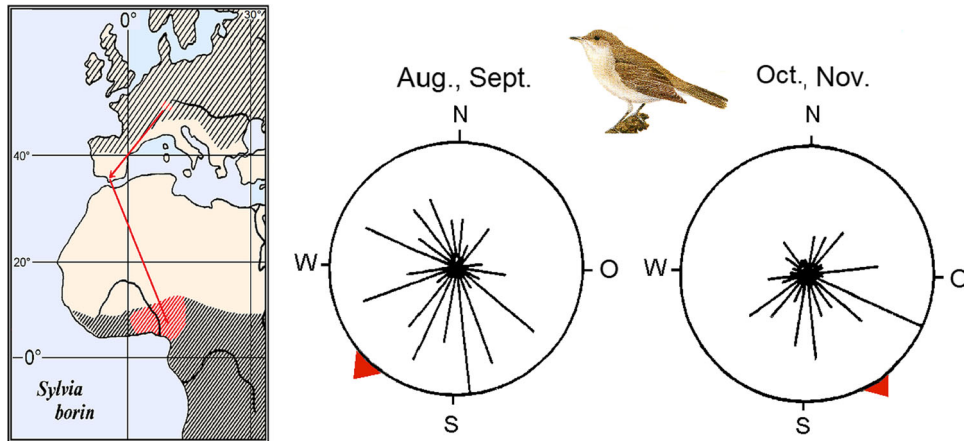


**Fig. 4** Outward paths and return path of a foraging desert ant *Cataglyphis*, illustrating path integration. The outward path (thin line) is characterized by searching around; after the ant found a food item, it returns on a more direct route (thicker line). The small circles indicate the position every 1 min. The outward path is 592.1 m long and took 18.8 min, the return path is 140.5 m long and took 6.5 min (after [215], modified)

known about other animals, but it may be assumed that many make use of this strategy.

Experiments with young, inexperienced homing pigeons indicate that for determining the heading home, they also rely on information obtained during the outward journey. The first spontaneous flights escape analysis, but young birds can apply path integration also when passively transported, using their magnetic compass to record the direction of the outward journey. Displacing them in a distorted magnetic field caused disorientation, while staying in the same distorted field after arrival at the release site had no effect [133]—having access to magnetic compass information during displacement proved crucial. This effect could only be observed in young, inexperienced birds, however; experienced pigeons apparently change their navigational strategy and do not need this type of outward journey information any longer [134]. Yet to what extent they may additionally use it when available is unclear.

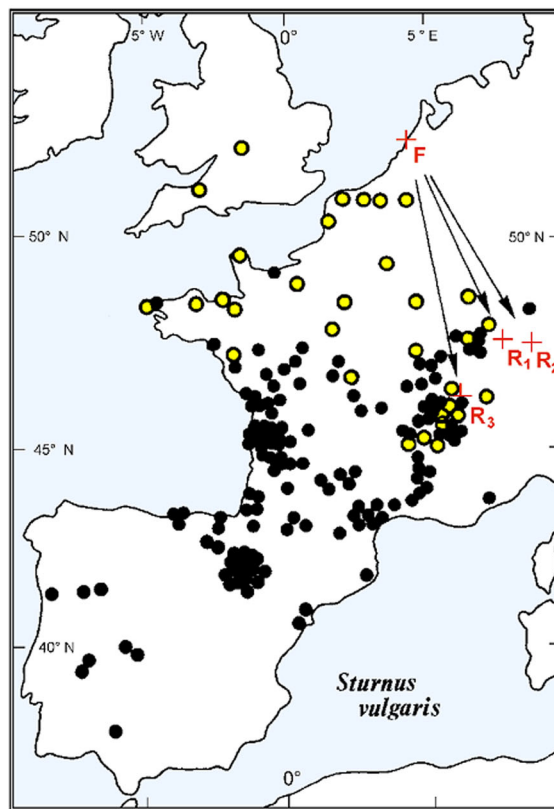
Relying on route information and path integration is an efficient strategy over short distances, as it does not require any previous knowledge. Yet over longer distances, it has the disadvantage that small mistakes may accumulate, and there is no way to correct these mistakes relying on outward journey information alone.



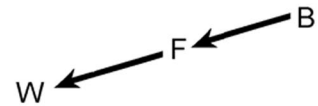
**Fig. 5** The innate migration program of garden warblers, *Sylvia borin*. (Left): birds from southern Germany migrate via the Iberian Peninsula to their African wintering areas (marked red). (Right): the headings of hand-raised birds

tested during their first autumn migration, showing the shift in direction from SW during August and September to SE in October and November (from [137], modified)

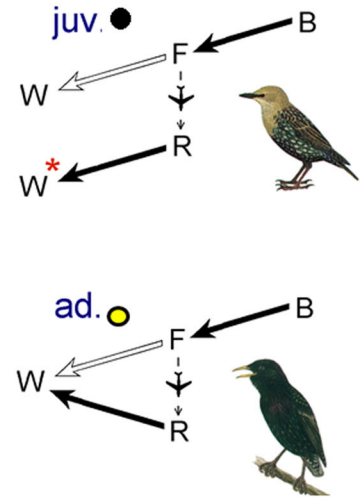
**Fig. 6** Displacement experiment with starlings, *Sturnus vulgaris*, migrating from the Baltic area to winter in Northern France and Southern England. The birds were caught as trans migrants in Holland and displaced by airplane to Switzerland. (Left) The original data [138]; (right) Scheme showing the different behavior of juvenile (black dots) and adult (yellow dots) migrants



normal migration:



after displacement to Switzerland:



**4.2 Migration: reaching a still unknown goal by innate programs**

Many animals start migrating immediately after they are born. With mammals like caribous or gnus and zebras, but also with whales, the young ones stay with their mothers and follow them to the regions where they have to go—here, parental guidance leads them along traditional routes. This may also apply to some bird species that migrate as families in flocks. Other young animals, however, have to start migrating alone, and

they are endowed with innate programs that guide their movements.

In migratory birds, the innate program consists of directions and distances to the wintering area of their species/population. The direction is genetically encoded with respect to the magnetic compass and celestial rotation: Birds hand-raised without ever seeing the sky, tested during autumn migration in cages in the geomagnetic field headed into their migratory direction ([e.g., [135, 136] a.o.); they even change direction if their migration route is not straight (Fig. 5)



[137]). Birds hand-raised under a rotating planetarium sky or an artificial “sky” with an arbitrary pattern of little light dots headed away from the center of rotation [122,124]. When migratory birds were caught during migration and displaced several 100 km perpendicularly to their migration route, young birds migrating for the first time continued in their migratory direction, ending up in a different region (Fig. 6)—not knowing their goal yet, they could not yet navigate toward it. Adult birds that had already stayed in the wintering area the year before, in contrast, compensated for the displacement (see below); they changed course and headed directly toward their winter quarters ([138,139] a.o.).

Newly hatched marine turtle spontaneously move from the beach into the ocean, guided by visual cues, heading toward the brightest part of the sky. After having reached the water, they start swimming into the incoming waves, probably detecting their direction by their orbital movements, and later maintain this direction by their magnetic compass. Hatchling loggerheads, *Caretta caretta* (Cheloniidae) from Florida then enter the Atlantic gyre where they stay the next years (see [140] for details). Innate directional responses to certain combinations of magnetic intensity and inclination ensure that they stay inside favorable marine areas ([141] a.o.).

Fishes like Pacific salmon and eels migrate only twice during their life—from their birthplace to the region where they spend most of their life and later back to their birth place; they also follow innate programs for their migration. Sockeye Salmon, *Oncorhynchus nerka* (Salmonidae), leave their hatching site in little streams and creeks, responding to currents and heading in specific directions by magnetic and celestial cues, first to reach a nursery lake and later to migrate downstream toward the ocean (for details, see [142]). These innate programs are specifically adapted to the stream systems where they live [143]. When in the ocean, specific magnetic conditions elicit swimming in particular directions to make them stay in their normal habitat [144]. Eels, born in the ocean, migrate to spend most of their life in fresh water. European eels, *Anguilla anguilla*, born in the Sargasso Sea, follow the current of the Gulf stream, but this passive transportation is supported by active swimming, presumably in directions indicated by their magnetic compass. When in brackish water, they enter an estuary and move upstream, swimming actively against the current for various distances into fresh water [145].

Marine turtles as well as salmon and eels return to their birthplace to lay their own eggs. They imprint on their hatching site and store the respective conditions in their memory. Marine turtles probably rely on the local magnetic conditions [146], whereas salmon imprint on the odors of their natal creeks [147].

### 4.3 True navigation: use of local, site-specific information: the ‘Map’

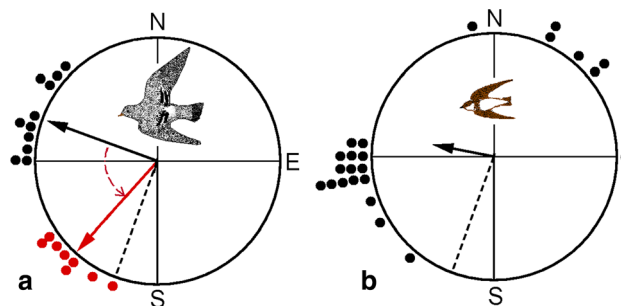
Many animals return after passive displacement over various distances; they are capable of true navigation

in the sense that they can head towards a specific goal from unfamiliar sites. The mechanisms they use are largely unknown; they have been analyzed to some extent only in birds, in particular in homing pigeons.

In the middle of the last century, navigation by astronomical factors was suggested for birds: Matthews forwarded the *Sun navigation hypothesis* [148], and Sauer interpreted his planetarium results with migrants as indicating true navigation by stellar cues [149]. The clock-shift experiments (see above), however, clearly show that shifting the internal clock affects the compass only, while the bird determined their location and the home course correctly (e.g., [72], see above). The planetarium experiments by Emlen ([116], see above) identified the birds’ use of stars as compass orientation. This indicates that the factors birds use for true navigation are not astronomical, but geophysical in nature.

#### 4.3.1 The concept of the navigational ‘map’

Pigeons return when displaced to unfamiliar distant sites from the area of their direct experience they usually leave these sites heading into directions not far from their home direction—this indicates that they can interpret the local factors more or less correctly, even if they have never been there before. It suggests that these factors have the nature of *gradients*—birds familiarize themselves with the course of these gradients in their home area and can extrapolate this knowledge when they are at an unfamiliar site. They compare the local values of the gradients with the remembered values from home. If a pigeon has experienced that, e.g., factor A increases toward north and at a given site it encounters values of A that are larger than within its home range, it knows that it is farther north and consequently has to head south to return. Wallraff [150] described this model in detail, assuming that the birds’



**Fig. 7** Vanishing bearings of **a** pigeons and **b** bank swallows from a colony near the loft, released at a site 143 km away; the home direction  $200^\circ$  is indicated by a dashed radius. Both species showed a marked clockwise deviation from the home direction, indicating that they used the same navigational factors and interpreted them in a similar way. In **a**, the black dots mark bearings of untreated control birds and the red dots those of pigeons whose internal clock was 5 h advanced. The clock-shifted pigeons, although vanishing closer to the home direction, returned much later, and more got lost (data from [150])

navigation is based on at least two, possibly more gradients that enable birds to determine their position relative to home, and from this derive the home course.

The birds' headings often deviate somewhat from the true home direction, with these deviations being characteristic for a given site—the so-called *release site biases* (Fig. 7). These deviations are attributed to local irregularities in the distribution of the navigational factors [151]; they are normally not very large and do not prevent birds from returning—obviously, the initial error is later corrected.

The 'map' is a learned system, based on experience. Young birds acquire the respective knowledge during spontaneous flights in their home range. When homing pigeons are regularly released at the loft, in about their third months of life, they start to venture further away from their loft, often staying out of sight for more than an hour. It is to be assumed that during these flights they are aware of their flight directions by a compass and observe how the potential navigational factors change with distance in the various directions, thus establishing their navigational 'map', a *directionally oriented mental representation* of the spatial distribution of the navigational factors in their home region. This applies to migratory and sedentary birds alike. Young migrants roam around in their home region before their start migration—e.g., young bank swallows, *Riparia riparia* (Hirundinidae) from a colony at the southeastern English coast were found to move all over England, several as far north as Scotland, before they left for fall migration [152]. A study with hand-raised migrants showed that only birds that had had the chance to fly around at the release site for some time could return to that region next spring; birds that had been released after the onset of migration and left right away did not come back [153].

While all birds probably establish a 'map' of their home region, migrating birds also experience the distribution of 'map' factors during their first migration, establishing a 'map' of their migration route. This is documented by the observation that from their second migration onward, migrants are able to compensate for displacements—they abandon their traditional migratory direction and head directly toward their goal—their breeding ground or wintering area (see Fig. 6) (e.g., [138, 139]). Tracking displaced migrants showed that in species with long migration routes, some birds also headed to intermediate feeding areas and from there join the traditional migration route for the rest of the journey [154].

#### 4.3.2 The nature of the factors included in the navigational 'map'

The nature of the factors used for true navigation is still a largely open question. A number of factors have been suggested, among them some with global gradients like magnetic factors (see [155] a.o.) or gravity [156], but also factors of more regional importance like infrasound [157] and odors (see e.g., [158, 159]). Most of these con-

siderations involve the navigation of birds (see [160] for review).

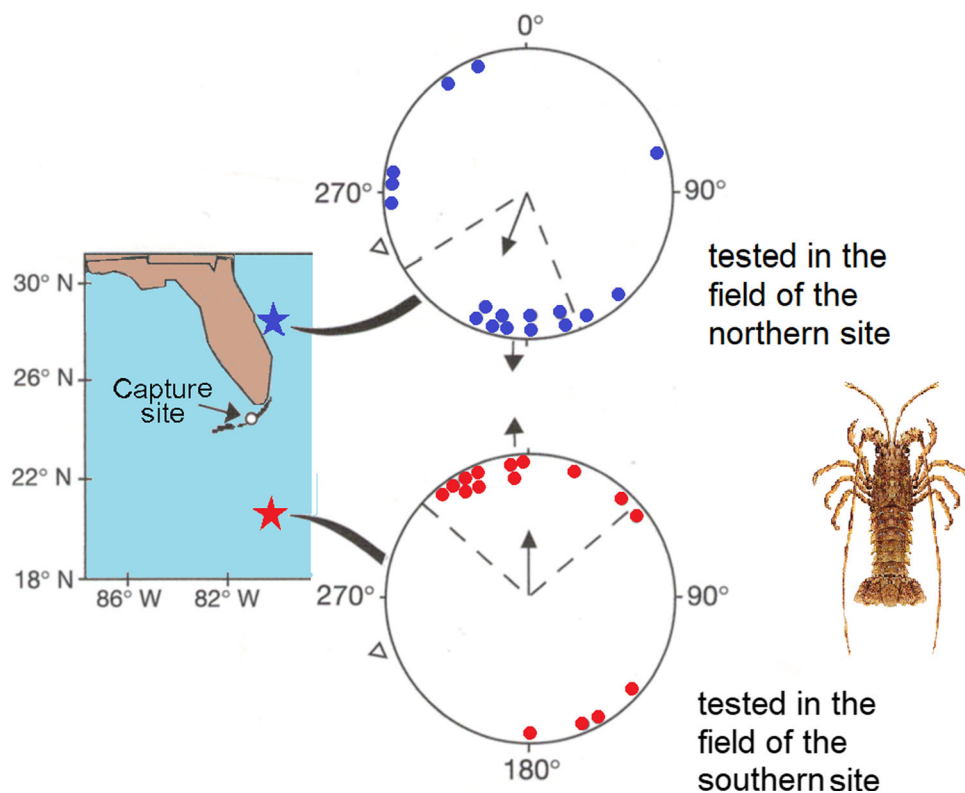
*Magnetic factors:* Magnetic factors are the ones that are best supported by experimental evidence so far. They involve total intensity and inclination, both forming global gradients running roughly north/south from pole to pole. In many parts of the Earth, the angle between the two gradient directions is sufficiently large to form a bi-coordinate 'map' [161]. Magnetic declination was also considered as a navigational factor [162], but later experiments did not support such a role [163, 164].

The first indications for the use of magnetic factors came in the late 1970s from the observation that pigeons released in a strong magnetic anomaly seemed disoriented and departed in random directions [165]; similar findings were reported from magnetic anomalies in other regions [166–168]. The use of magnetic factors is also supported by the observation that pigeons treated with a brief, strong magnetic pulse to interfere with the receptor system for magnetic intensity (see below) showed significant deviations from untreated controls at some sites more than 80 km away [169]. In caged migrants, the pulse caused a significant shift in direction that lasted about 3 days, followed by ca. 1 week of disorientation before the birds resumed their normal migratory headings [170]. Treatment with such a pulse had a similar effect on free-flying migrants, but only on experienced birds; young migrants on their first migration (which is still controlled by the innate migration program) remained unaffected [171].

The best evidence for the use of a magnetic 'map', however, comes from magnetically simulated displacements. The first such experiment was performed with the spiny lobster, *Panulirus argus* (Decapoda), at the Florida Keys. When displaced, lobsters tested in arenas, showed directional tendencies to compensate for the displacement, heading toward the capture site. Tested at the capture site in a magnetic field as it occurs north of that site, they headed southward, whereas lobsters tested in a field as found south of that site headed northward (Fig. 8), i.e., in directions that would have brought them back from the respective sites to capture site [172]. Similar results were obtained with green sea turtles, *Chelonia mydas*, at the Florida coast, tested in the magnetic fields found ca. 340 km north and south of the capture site ([173]; see also [174]: They, too, compensate for the simulated displacements.

Corresponding experiments with caged migrating birds likewise showed that displacements can be simulated by testing birds in a magnetic field of a distant site. Reed warblers, *Acrocephalus scirpaceus* (Muscicapidae) caught during spring migration at the Kurish Spit near the Baltic Sea showed northwesterly headings toward their breeding area in Southern Finland; tested in the magnetic field of a site about 1000 km eastward, they changed this direction, now preferring northwesterly headings [175], just as they had had done when really displaced to that site [176]. That is, birds, too, compensated for the virtual displacement simulated by magnetic intensity and inclination (see also [165]).

**Fig. 8** Spiny lobsters, captured at the Florida Keys, tested at the capture site in the geomagnetic field of a site in the north and a site in the south. The lobsters behaved as if they had been displaced and preferred directions that would have brought them back from the simulated sites to the capture site (data from [171], modified)



A magnetic ‘map’ or the involvement of magnetic components in the ‘map’ are also proposed for other animals, among them amphibians [177]—the observations that animals as different as spiny lobsters, marine turtles and birds compensate for magnetically simulated displacements suggests that a magnetic ‘map’ may be widespread among animals.

Little is known about the sensory basis of magnetic ‘maps’. While the perception of magnetic directions in birds is based on radical pair processes and is associated with the visual system (see above), the effect of the magnetic pulse (see above) indicates that sensing the magnetic ‘map’ involves magnetite [178], with the duration of the pulse effect—about 10 days [170]—suggesting superparamagnetic particles (see [179]). The respective information is transmitted to the brain by the trigeminal system (see [180, 181] for details). Without intact trigeminal nerve, birds could not compensate for virtual displacements [182]. How magnetic ‘map’ information is obtained by other animals remains largely unknown.

**Gravity:** It was considered as a possible navigational factor when the disorientation of displaced homing pigeons in magnetic anomalies was observed [155], because magnetic anomalies often coincide with gravity anomalies. Yet releasing pigeons in a gravity anomaly in America spoke against this possibility [183]. Recently, however, an effect of raising pigeons in different gravities anomalies in Southeastern Europe was reported [184], and tracking the flight of pigeons across gravity

anomalies showed increased scatter up to disorientation, together with greater losses, which was interpreted as indicating navigation by use of gravity [156]. A possible role of gravity in avian navigation is still open.

**Infrasound:** Natural infrasound (frequencies below 20 Hz) arises from wind over mountains, waves on the shore, etc.; they are transported over long distances in the atmosphere and in the ground with little attenuation. Pigeons were shown to be able to hear them [185], hence they were considered as a potential navigational cue [186, 187].

Hagstrum [188] analyzed large data sets of the late W.T. Keeton and found a correlation between predictions concerning atmospheric infrasound and the initial orientation of pigeons toward home. Another analysis comparing the orientation of pigeons deprived of hearing with that of untreated controls produced mixed results [189]. Altogether, the validity of the *acoustic navigation model* proposed by Hagstrum [188] is unclear, the more so since it is hardly compatible with the Map-and-Compass model (see [160] for discussion).

**Odors:** The role of odors in avian navigation has been most controversially discussed so far. In the beginning of the 1970s, Papi and colleagues in Italy reported that pigeons deprived of olfaction were reluctant to take off, departed randomly, and many got lost [190]. The authors concluded that odors are essential navigational cues and forwarded the *olfactory navigation hypothesis*. It assumes that birds associate airborne chemical substances with the respective wind direction, thus forming

an olfactory ‘map’, which was believed to provide the most important, it not the only navigational information for birds. Numerous further experiments testing the role of olfaction in pigeon homing in various ways were conducted in the following years (for review, see [159,160,191]).

Replicating the experiments with anosmic pigeons (i.e., pigeons deprived of smelling) in the USA and Germany produced different results; however (e.g., [192,193]), further experiments indicated that the conditions of raising and training the birds were of crucial importance [194] for the pigeons’ response to olfactory deprivation. Experiments with migrating birds also showed that birds deprived of olfaction were unable to compensate for displacements and fell back on their innate migratory direction [195,196].

An odd aspect of the olfactory findings was that olfactory deprivation had an effect only at sites that were unfamiliar to the birds. The protagonists of the olfactory hypothesis claimed that at familiar sites, birds followed sequences of familiar landmarks (e.g., [197], see [160]). In critical tests at a familiar site, however, anosmic pigeons deprived of object vision by frosted lenses departed homeward oriented [198], indicating that they used non-olfactory, non-visual cues to determine their home direction. Anosmic pigeons released at familiar sites also responded to shifting their internal clock with departing in the expected, deflected direction with respect to untreated controls (see above) [199], showing that they did not follow sequences of landmarks, but they determined their home direction as a compass course.

In 2009, Jorge and colleagues replaced natural odors by artificial odors and got similar results as in the olfactory studies [200,201]. The authors suggested that instead of providing navigational information, odors had an activation effect, a hypothesis which was supported by electrophysiological data [202]. This, together with the findings at familiar sites, suggests that odors may play an activating role when pigeons have to integrate new local data into their ‘map’ at an unfamiliar site (see [203] for a discussion). The controversy on the role of odors in bird orientation is still not finally resolved.

Salmons, however, orient by odors solved in the water when returning to their natal creeks. They have been imprinted on the chemical situation of the stream in which they were born [147]. After spending a number of years in the ocean, they begin to return to their parental creek to spawn. When reaching the estuary of their natal river system, they swim upstream, following the imprinted odors until they reach their natal creek (see [204] for an overview). Here, however, odors are not used as part of a ‘map’, but as a direct cue which the fishes follow when heading upstream against the current.

### 4.3.3 Navigation near home: the ‘Mosaic Map’

In the vicinity of home, there is an area where birds are no longer able to distinguish the local values of the navigational factors from the home values. Here, they turn to landmarks. A study where the routes of pigeons deprived of object vision by frosted lenses were recorded showed that these birds managed to approach the loft in Upstate New York about 0.5–5 km [205], while in Germany many birds with frosted lenses ended up closer to the loft, within 100 m, some of them even managing to reach the loft itself [206]. Landmarks thus appear to be important in the immediate vicinity and the final approach to the loft.

Yet even here near their loft, pigeons do not seem to follow sequences of landmarks, but still determine their home course as a compass course. This is indicated by clock-shift experiments within 1.6 km from the loft, where the birds showed deviations from the untreated controls indicating sun compass use [207,208]. This led to the concept of the *Mosaic Map*, which assumes that birds memorize the directional relationship and distance of landmarks near their home, thus forming a ‘map’ analogue to the navigational ‘map’, but consisting of the representation of numerous individual marks instead of gradients (see [150,209]).

## 4.4 A flexible system based on innate and learned components

Young, inexperienced birds first rely on innate mechanisms like route reversal and path integration on the basis of compass orientation; inexperienced migrants are guided by innate migration programs. This gives them a chance to learn and memorize the spatial distribution of potential navigational factors, i.e., to establish a ‘map’ of their home region and their migration route. The ‘map’, in contrast to route-based information, allows birds to re-determine the course to the goal whenever they feel it necessary—this increases the certainty of reaching the goal.

We must assume that young birds include in their ‘map’ all suitable factors that can be used for navigation—the ‘map’ is multifactorial (see e.g., [209,210]) and probably includes more factors than just the ones mentioned above, e.g., the view of landscape feature as they change with distance [211] and others. The ‘map’ appears to be largely redundant: When released within a strong magnetic anomaly, pigeons deprived of magnetic ‘map’ information by local anesthesia of their upper beak left in an oriented way—not being able to sense the anomalous magnetic field they were not confused and obviously turned to non-magnetic cues for navigation right away [212].

Being based on experience, the ‘map’ is perfectly adapted to the situation within the home region and along the migration route and allows birds to directly head to familiar goals. However, the available navigational factors may differ in various regions, and so we cannot expect the ‘map’ to be identical everywhere.

There may be differences in the preferred cues, and findings obtained in one region thus cannot simply be generalized to another without testing.

The above considerations are based on navigational experiments with birds—to what extent they also apply to other animals covering greater distances remains to be determined.

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## References

- G. Kramer, *Naturwissenschaften* **37**, 377 (1950)
- K.V. Frisch, *Experientia* **6**, 210 (1950)
- G. Kramer, *Ibis* **101**, 196 (1959)
- R. Wiltschko, W. Wiltschko, *Adv. Study Behav.* **47**, 229 (2015)
- W. Wiltschko, *W. Z. Tierpsychol.* **25**, 536 (1968)
- W.T. Keeton, *Proc. Natl. Acad. Sci. USA* **68**, 102 (1971)
- R. Freire, U.H. Munro, L.J. Rogers, R. Wiltschko, W. Wiltschko, *Curr. Biol.* **15**, R620 (2005)
- J.B. Phillips, *J. Comp. Physiol.* **121**, 273 (1977)
- A.J. Kalmijn, in *Sensory Biology of Sharks, Skates, and Rays* edited by F.S. Hodson, R.F. Matthewson (Office Naval Res., Arlington, VA 1978), p. 307
- T.P. Quinn, *J. Comp. Physiol.* **137**, 243 (1980)
- P.B. Taylor, *J. Fish. Biol.* **28**, 607 (1986)
- J. Karlsson, *Helgol. Meeresunters.* **39**, 71 (1985)
- J.J. Souza, J.J. Puluhowich, R.J. Guerra, *Comp. Biochem. Physiol.* **90A**, 57 (1988)
- T. Leucht, *J. Exp. Biol.* **148**, 325 (1990)
- G.H. Rodda, *J. Comp. Physiol. A* **154**, 549 (1984)
- K.J. Lohmann, *J. Exp. Biol.* **155**, 37 (1991)
- H. Burda, S. Marhold, T. Westenberger, R. Wiltschko, W. Wiltschko, *Experientia* **46**, 528 (1990)
- R.A. Holland, K. Thorup, M.J. Vonhof, W.W. Cochran, *Nature* **444**, 702 (2006)
- R.R. Baker, *Anim. Behav.* **35**, 691 (1987)
- K.J. Lohmann, A.O.D. Willows, *Encyclopedia of Neuroscience* (Birkhäuser, Boston, 1987), p. 331. (Suppl. 1)
- K.J. Lohmann, *Mar. Behav. Physiol.* **12**, 1 (1985)
- L. Pardi, A. Ercolini, F. Ferrara, F. Scapini, *Atti Accad. Lincei Rend. Sci. Fis. Mat. Nat.* **75**, 312 (1985)
- M. Rickli, R.H. Leuthold, *Ethology* **77**, 209 (1988)
- M.C. Arendse, J.C.M. Vrins, *Neth. J. Zool* **25**, 407 (1975)
- R.R. Baker, J.G. Mather, *Anim. Behav.* **30**, 343 (1982)
- J.A. Etheredge, S.M. Perez, O.R. Taylor, R. Jander, *Proc. Natl. Acad. Sci. USA* **96**, 13845 (1999)
- D. DeJong, *J. Comp. Physiol.* **147**, 493 (1982)
- R. Jander, U. Jander, *Ethology* **104**, 743 (1988)
- P.N. Fleischmann, B. Grob, V.I. Müller, R. Wehner, W. Rössler, *W. Curr. Biol.* **28**, 1440 (2018)
- W. Wiltschko, R. Wiltschko, *Science* **176**, 62 (1972)
- S. Åkesson, J. Morin, R. Muheim, U. Ottoson, U. Pole, *Proc. R. Soc. Lond. B* **268**, 19097–1913 (2001)
- N. Lefeldt, D. Dreyer, N.-L. Scheider, F. Steenken, H. Mouritsen, *J. Exp. Biol.* **218**, 206 (2015)
- S. Schwarze, F. Steenken, N. Thiele, D. Kolbykov, N. Lefeldt, D. Dreyer, N.-S. Schneider, H. Mouritsen, *Sci. Rep.* **6**, 33805 (2016)
- W. Wiltschko, R. Wiltschko, *Nature* **364**, 525 (1993)
- W. Wiltschko, R. Wiltschko, *J. Comp. Physiol. A* **177**, 363 (1995)
- R. Muheim, J. Bäckman, S. Åkesson, *J. Exp. Biol.* **205**, 3845 (2002)
- W. Wiltschko, in *Animal Migration, Navigation, and Homing* edited by K. Schmidt-Koenig, W.T. Keeton (Springer, Berlin, 1978), p. 302
- W. Wiltschko, R. Freire, U. Munro, T. Ritz, L. Rogers, P. Thalau, R. Wiltschko, *J. Exp. Biol.* **210**, 2300 (2007)
- M. Winklhofer, E. Dylida, P. Thalau, W. Wiltschko, R. Wiltschko, *Proc. R. Soc. Lond. B* **280**, 20130850 (2013)
- K. Schulten, A. Windemuth in *Biophysical Effects of Steady Magnetic Fields* edited by G. Maret, N. Boccarda, J. Kiepenheuer (Springer, Berlin, 1986) p. 99
- T. Ritz, S. Adem, K. Schulten, *Biophys. J.* **78**, 797 (2000)
- R. Wiltschko, W. Wiltschko, *Front. Physiol.* **12**, 667000 (2021)
- C. Nießner, S. Denzau, J.C. Gross, L. Peichl, H.-J. Bischof, G. Fleissner, W. Wiltschko, R. Wiltschko, *PLoS One* **6**, e20091 (2011)
- A. Pinzon-Rodriguez, R. Muheim, *Sci. Rep.* **11**, 12683 (2021)
- C. Nießner, S. Denzau, K. Stapput, M. Ahmad, L. Peichl, W. Wiltschko, R. Wiltschko, *J.R. Soc. Interface* **10**, 20130630 (2013)
- R. Wiltschko, M. Ahmad, C. Nießner, D. Gehring, W. Wiltschko, R. Wiltschko, *J.R. Soc. Interface* **13**, 20151010 (2016)
- J.B. Phillips, S.C. Borland, *Ethol. Ecol. Evol.* **4**, 33 (1992)
- K.J. Lohmann, C.M.F. Lohmann, *Biol. Bull.* **185**, 149 (1993)
- T.P. Quinn, R.T. Merrill, E.L. Brannon, *J. Exp. Biol.* **21**, 137 (1981)
- P. Thalau, T. Ritz, H. Burda, R.E. Wegner, R.E. Wiltschko, *J. R. Soc. Interface* **3**, 583 (2006)
- Y. Wang, Y. Pan, S. Parsons, M. Walker, S. Zhang, *Proc. R. Soc. Lond. B* **274**, 2901 (2007)
- K. Lohmann, N.D. Pentcheff, G.A. Nevitt, G.D. Stetten, R.K. Zimmer-Faust, H.E. Jarrard, L.C. Boles, *J. Exp. Biol.* **198**, 2041 (1995)

53. M. Vácha, D. Drštková, T. Půžova, *Naturwissenschaften* **95**, (2008)
54. P.A. Guerra, R.J. Gegeer, S.M. Reppert, *Nat. Commun.* **5**, 4164 (2014)
55. F. Santschi, *Revue Suisse de Zoologie* **19**, 303 (1911)
56. L. Pardi, *Cold Spring Harbour Sym. Quant. Biol.* **25**, 395 (1960)
57. K. von Frisch, *Tanzsprache und Orientierung der Bienen* (Springer, Berlin, 1965)
58. K. Schmidt-Koenig, *Migration and Homing in Animals, Zoophysiology and Ecology 6* (Springer, Berlin, 1975)
59. S.M. Perez, O.R. Taylor, R. Jander, *Nature* **387**, 29 (1997)
60. K. Warburton, *Mar. Biol.* **23**, 93 (1973)
61. A. Hasler, R.M. Horral, W.J. Wisby, W. Braemer, *Limnol. Oceanogr.* **3**, 353 (1958)
62. T. Waterman, in *Animal Orientation and Navigation* edited by S.R. Galler, K. Schmidt-Koenig, G.J. Jacobs, R.E-Belleville (NASA SP-262, Washington, D.C., 1972), p. 437
63. K. Fischer, *Naturwissenschaften* **47**, 287 (1960)
64. R.T. Newcomer, D.H. Taylor, S.L. Guttman, *Herpetologia* **30**, 194 (1974)
65. J.S. Robinson, G.G. Murphy, *J. Tenn. Acad. Sci.* **51**, 59 (1976)
66. K. Fischer, *Verh. Dtsch. Zool. Ges.* **1965**, 546 (1965)
67. C.T. DeRosa, D.H. Taylor, *Am. Zool.* **16**, 245 (1976)
68. P.A. Murphy, *Copeia* **3**, 638 (1981)
69. D.E. Ferguson, *Ann. N. Y. Acad. Sci.* **188**, 30 (1971)
70. S.L. Fluharty, D.H. Taylor, G.W. Barrett, *J. Mammal.* **57**, 1 (1976)
71. J. Aschoff, *Naturwissenschaften* **41**, 49 (1954)
72. K. Schmidt-Koenig, *Z. Tierpsychol.* **18**, 221 (1961)
73. R. Wehner, B. Lanfranconi, *Nature* **293**, 731 (1981)
74. W. Braemer, *Cold Spring Harbour Sym. Quant. Biol.* **25**, 413 (1960)
75. D.A.T. New, J.K. New, *J. Exp. Biol.* **39**, 363 (1962)
76. F.C. Dyer, J.A. Dickinson, *Proc. Natl. Acad. Sci. USA* **91**, 4471 (1994)
77. H.O. Schwassmann, W. Braemer, *Physiol. Zool.* **34**, 273 (1961)
78. R. Wiltschko, M. Walker, W. Wiltschko, *J. Exp. Biol.* **203**, 889 (2000)
79. M. Lindauer, *Z. Vergl. Physiol.* **42**, 43 (1959)
80. R. Wehner, M. Müller, *Naturwissenschaften* **80**, 331 (1993)
81. R. Jander, *Z. Vergl. Physiol.* **40**, 162 (1957)
82. W. Wiltschko, R. Wiltschko, W.T. Keeton, *Behav. Ecol. Sociobiol.* **1**, 229 (1976)
83. R. Wiltschko, D. Nohr, W. Wiltschko, *Science* **214**, 343 (1981)
84. R. Wiltschko, W. Wiltschko, *Behav. Ecol. Sociobiol.* **9**, 135 (1981)
85. W. Wiltschko, R. Wiltschko, W.T. Keeton, R. Madden, *Behav. Ecol. Sociobiol.* **12**, 135 (1983)
86. W. Braemer & Schwassmann, *Ergebn. Biol.* **26**, 182 (1963)
87. C. Groot, *Behaviour. Suppl.* **14**, 198 (1965)
88. S.G. Miles, *J. Fish. Res. Bd. Canada* **25**, 2143 (1968)
89. K. Schmidt-Koenig, *Adv. Study Behav.* **1**, 217 (1965)
90. U. Munro, R. Wiltschko, *J. Exp. Biol.* **181**, 233 (1993)
91. R. Wehner, *Ann. Rev. Entomol.* **29**, 277 (1984)
92. T.H. Watermann, in *Photorection and Vision in Invertebrates* edited by M.A. Ali (Plenum, 1984), p. 63
93. E.R. Baylor, F.E. Smith, *Am. Naturalist* **87**, 97 (1953)
94. R. Jander, K. Daumer, T.H. Waterman, *Z. Vergl. Physiol.* **46**, 363 (1963)
95. K. von Frisch, *Experientia* **5**, 142 (1949)
96. P. Duelli, R. Wehner, *J. Comp. Physiol.* **86**, 17 (1973)
97. R. Wehner in *The Biology of Photoreception* edited by D.J. Cosens, D. Vince-Price (Society for Experimental Biology 1983)
98. R. Wehner in *Orientation and Communication in Arthropods* edited by M. Lehrer (Birkhäuser, Basel 1997)
99. M. Dacke, M. Byrne, E. Baird, C.H. Schot, E.J. Warrant, *Proc. R. Soc. Lond. B.* **271**, 361 (2004)
100. T.H. Waterman in *Light as an Ecological Factor*, Vol II edited by G.C. Evans, R. Bainbridge, O. Rackham (Blackwell, Oxford, 1975), p. 305
101. D.H. Taylor, J.S. Auburn, in *Animal Migration, Navigation, and Homing* edited K. Schmidt-Koenig, W.T. Keeton (Springer, Berlin, Heidelberg, New York 1978), p. 334
102. K. Adler, J.B. Phillips, *J. Comp. Physiol. A* **156**, 547 (1985)
103. M.J. Freake, *J. Exp. Biol.* **202**, 1159 (1999)
104. S. Greif, I. Borissov, Y. Yovel, R. Holland, *Nat. Commun.* **5**, 4488 (2014)
105. M.L. Kreithen, W.T. Keeton, *J. Comp. Physiol.* **89**, 83 (1974)
106. K.P. Able, *Nature* **299**, 550 (1982)
107. F.R. Moore, J.B. Phillips, *Anim. Behav.* **36**, 1770 (1988)
108. K.P. Able, M.A. Able, *Nature* **375**, 230 (1995)
109. R. Muheim, J.B. Phillips, S. Åkesson, *Science* **313**, 837 (2006)
110. A.J. Helbig, W. Wiltschko, *Naturwissenschaften* **76**, 227 (1989)
111. N. Chernetsov, D. Kishkinev, V. Kosarev, C.V. Bolshakov, *J. Exp. Biol.* **214**, 2540 (2011)
112. S. Åkesson, C. Odin, R. Hegedüs, M. Ilieva, C. Sjöholm, A. Farkas, G. Horvath, *Biol. Open* **4**, 35 (2015)
113. W. Wiltschko, R. Wiltschko, U. Munro, H. Ford, *J. Comp. Physiol. A* **182**, 521 (1998)
114. U. Munro, R. Wiltschko, *J. Comp. Physiol. A* **177**, 357 (1995)
115. K.P. Able, M.A. Able, *Nature* **364**, 523 (1993)
116. S.T. Emlen, *Auk* **84**, 309 (1967)
117. Y. Katz, H. Michelsons, H. in *Orientazija Ptiz (Orientation of Birds)* edited by H. Michelsons, P. Blüm & J. Baumaris (Riga, Zinatne 1978), p. 180
118. W. Wiltschko & Wiltschko, *Z. Tierpsychol.* **37**, 337 (1975)
119. W. Wiltschko & Wiltschko, *Z. Tierpsychol.* **39**, 265 (1975)
120. V.P. Bingman, *Behav. Ecol. Sociobiol.* **15**, 77 (1984)
121. S.T. Emlen, *Auk* **84**, 463 (1967)
122. S.T. Emlen, *Science* **170**, 1198 (1970)
123. W. Wiltschko, P. Daum, A. Fergenbauer-Kimmel, R. Wiltschko, *Ethology* **74**, 285 (1987)
124. K.P. Able, M.A. Able, *Nature* **347**, 378 (1990)
125. R. Wehner, F. Rüber, *Experientia* **35**, 1569 (1979)
126. T.S. Collett, *Philos. Trans.* **337**, 295 (1992)

127. M. Müller, R. Wehner, Proc. Natl. Acad. Sci. USA **85**, 5287 (1988)
128. G. Hartmann, R. Wehner, Biol. Cybern. **73**, 483 (1995)
129. R. Weher, M.V. Srinivasan, J. Comp. Physiol. **142**, 315 (1981)
130. R. Wehner, B. Michel, P. Antonsen, J. Exp. Biol. **199**, 129 (1996)
131. F.C. Dyer, N.A. Berry, A.S. Richards, Anim. Behav. **45**, 1028 (1993)
132. T.S. Collett, J. Baron, Nature **368**, 137 (1994)
133. R. Wiltschko, W. Wiltschko, Naturwissenschaften **65**, 112 (1978)
134. R. Wiltschko, W. Wiltschko, Anim. Behav. **33**, 583 (1985)
135. W. Wiltschko, E. Gwinner, Naturwissenschaften **61**, 406 (1974)
136. M.E. Shumakov, in *Baltic Birds 5* edited by J. Viksne, I. Vilks (Riga 1990), p. 146
137. E. Gwinner, W. Wiltschko, J. Comp. Physiol. A **125**, 267 (1978)
138. A.C. Perdeck, Ardea **46**, 1 (1958)
139. K. Thorup, I.-A. Bison, M.S. Bowlin, R.A. Holland, J.C. Wingfield, M. Ramenofsky, M. Wikelski, Proc. Natl. Acad. Sci. USA **104**, 18115 (2007)
140. K.J. Lohmann, B.E. Witherington, C.M.F. Lohmann, M. Salmon, in *The Biology of the Sea Turtles* edited by P.L. Lutz, J.A. Musick (CRC Press, Marine Science Series, Boca Raton, New York 1997), p. 107
141. M.J. Fuxjager, B.S. Eastwood, K.J. Lohmann, J. Exp. Biol. **214**, 2504 (2011)
142. C. Groot, in *Proc. Salmon Trout Migration Behavior Symposium* edited by E.L. Brannon, E.O. Salo Univ. of Washington, Seattle 1982), p. 1
143. R.J. Miller, E.L. Brannon, in *Proc. Salmon Trout Migration Behavior Symposium* edited by E.L. Brannon, E.O. Salo University of Washington, Seattle 1982), p. 296
144. N.F. Putman, M.N. Scanlan, E.J. Billman, J.P. O'Neil, R.B. Couture, T.P. Quinn, K.J. Lohmann, D.L. Noakes, Curr. Biol. **24**, 446 (2014)
145. F.W. Tesch in *Environmental Physiology of Fishes* edited by M.A. Ali (NATO Adv. Study Inst. Ser A Life Sci 35, 1980), p. 569
146. K.J. Lohmann, N.F. Putman, C.M.F. Lohmann, Proc. Natl. Acad. Sci. USA **105**, 19096 (2008)
147. A.R. Hasler, W.J. Wisby, Am. Naturalist **85**, 223 (1951)
148. G.V.T. Matthews, J. Navig. **4**, 250 (1951)
149. E.G.F. Sauer, E.M. Sauer, Cold Spring Harbor Sym. Quant. Biol. **25**, 463 (1960)
150. H.G. Wallraff, *Das Navigationssystem der Vögel (Schriftenreihe, Kybernetik“* (R. Oldenbourg, München, Wien, 1974)
151. W.T. Keeton, J. Comp. Physiol. **86**, 1 (1973)
152. C.J. Mead, J.D. Harrison, Bird Study **26**, 73 (1979)
153. H. Löhrl, J. Ornithol. **100**, 132 (1959)
154. M. Willemoes, J. Blas, M. Wikelski, K. Thorup, Sci. Rep. **5**, 16402 (2015)
155. C. Walcott in *Orientation in Birds* edited by P. Berthold (Birkhäuser, Basel, 1991)
156. N. Blaser, S.I. Guskov, V.A. Entin, D.P. Wolfer, V.A. Kanevskiy, H.P. Lipp, J. Exp. Biol. **217**, 4057 (2014)
157. J.T. Hagstrum, J. Exp. Biol. **216**, 687 (2013)
158. F. Papi, Monit. Zool. Ital. (N.S.) **20**, 471 (1986)
159. H.G. Wallraff, Anim. Behav. **67**, 189 (2004)
160. R.C. Beason, W. Wiltschko, J. Comp. Physiol. A **201**, 961 (2015)
161. J. Boström, S. Åkesson, T. Alerstam, Ecography **35**, 1039 (2012)
162. N. Chernetsov, A. Pakhomov, D. Kobylkov, D. Kishkinev, R. Holland, H. Mouritsen, Curr. Biol. **27**, 2647 (2017)
163. N. Chernetsov, A. Pakhomov, A. Davydov, F. Collarius, H. Mouritsen, PLoS One **15**, eo232136 (2020)
164. D. Kishkinev, F. Packmor, T. Zechmeister, H.-C. Winkler, N. Chernetsov, H. Mouritsen, R.A. Holland, Curr. Biol. **31**, P1563 (2021)
165. C. Walcott, in *Animal Migration, Navigation, and Homing* edited by K. Schmidt-Koenig, W.T. Keeton (Springer, Berlin, 1978), p. 143
166. J. Kiepenheuer, in *Avian Navigation* edited by H.G. Wallraff, F. Papi (Springer, Berlin, Heidelberg, 1982), p. 120
167. T.E. Dennis, M.J. Rayner, M.M. Walker, Proc. R Soc. Lond. B **274**, 1153 (2007)
168. R. Wiltschko, I. Schiffner, W. Wiltschko, J. Exp. Biol. **212**, 2983 (2009)
169. R.C. Beason, R. Wiltschko, W. Wiltschko, Auk **114**, 405 (1997)
170. W. Wiltschko, U. Munro, H. Ford, R. Wiltschko, J. Exp. Biol. **201**, 3257 (1998)
171. R.A. Holland, B. Helms, J. R. Soc. Interface **10**, 20121047 (2013)
172. L.C. Boles, K.J. Lohmann, Nature **421**, 60 (2003)
173. K.J. Lohmann, C.M.F. Lohmann, L.M. Ehrhart, D.A. Bagley, T. Swing, Nature **428**, 909 (2004)
174. P. Luschi, S. Benhamou, C. Girard, S. Ciccione, D. Roos, J. Sudre, S. Benvenuti, Curr. Biol. **17**, 126 (2007)
175. D. Kishkinev, N. Chernetsov, A. Pakhomov, D. Heyers, H. Mouritsen, Curr. Biol. **25**, R822 (2015)
176. N. Chernetsov, D.D. Kishkinev, H. Mouritsen, Curr. Biol. **18**, 188 (2008)
177. J.H. Fischer, M.J. Freake, S.C. Borland, J.B. Phillips, Anim. Behav. **62**, 1 (2001)
178. R.C. Beason, N. Dussourd, M.E. Deutchlander, J. Exp. Biol. **198**, 141 (1995)
179. A.F. Davila, G. Fleissner, M. Winklhofer, N. Petersen, Phys. Chem. Earth **28**, 647 (2003)
180. R.C. Beason, P. Semm, J. Exp. Biol. **199**, 1241 (1996)
181. D. Heyers, M. Zapka, M. Hoffmeister, J.M. Wild, H. Mouritsen, Proc. Natl. Acad. Sci. USA **107**, 9394 (2010)
182. A. Pakhomov, A. Anashina, D. Heyers, E.D. Kobylkov, H. Mouritsen, N. Chernetsov, Sci. Rep. **1**, 2018 (1975)
183. A.J. Lednor, C. Walcott, J. Exp. Biol. **111**, 259 (1984)
184. N. Blaser, S.I. Guskov, V. Meskenaite, V.I. Kanevskiy, H.P. Lipp, PLoS ONE **8**, e77102 (2013)
185. M.L. Kreithen, D.R. Quine, J. Comp. Physiol. A **129**, 1 (1979)
186. J.T. Hagstrum, J. Exp. Biol. **203**, 1103 (2000)
187. A. Mukhin, N. Chernetsov, D. Kishkinev, Behav. Ecol. **19**, 716 (2008)
188. J.T. Hagstrum, J. Exp. Biol. **216**, 687 (2013)
189. J.T. Hagstrum, G.A. Manley, J. Comp. Physiol. A **201**, 983 (2015)

190. F. Papi, L. Fiore, V. Fiaschi, S. Benvenuti, *Monit. Zool. Ital. (N.S.)* **6**, 85 (1972)
191. A. Gagliardo, *J. Exp. Biol.* **216**, 2165 (2013)
192. W.T. Keeton, M.L. Kreithen, K.L. Hermayer, *J. Comp. Physiol.* **114**, 289 (1977)
193. W. Wiltschko, R. Wiltschko, C. Walcott, *Behav. Ecol. Sociobiol.* **21**, 333 (1987)
194. R. Wiltschko, W. Wiltschko, *Behav. Ecol. Sociobiol.* **24**, 163 (1989)
195. R.A. Holland, K. Thorup, A. Gagliardo, I.A. Bisson, E. Knecht, D. Mizrahi, M. Wikelski, *J. Exp. Biol.* **212**, 4065 (2009)
196. M. Wikelski, E. Arriero, A. Gagliardo, R.A. Holland, M.J. Huttunen, R. Juvaste, I. Mueller, G. Teriaski, K. Thorup, M. Wild, M. Alanko, F. Bairlein, A. Cherenkov, A. Cameron, R. Flatz, J. Hannila, O. Hüppop, M. Kangasniemi, B. Kranstauber, M.L. Penttinen, K. Safi, V. Semashko, H. Schmid, R. Wistbacka, *Sci. Rep.* **5**, 17061 (2015)
197. R.F. Hartwick, A. Foa, F. Papi, *Behav. Ecol. Sociobiol.* **2**, 81 (1977)
198. S. Benvenuti, V. Fiaschi, *Comp. Biochem. Physiol.* **76A**, 719 (1983)
199. P. Luschi, P. Dall'Antonia, *Anim. Behav.* **46**, 1195 (1993)
200. P.E. Jorge, A.E. Marques, J.B. Phillips, *Curr. Biol.* **19**, 650 (2009)
201. P.E. Jorge, A.E. Marques, J.B. Phillips, *Proc. R. Soc. B* **277**, 45 (2010)
202. P.E. Jorge, J.B. Phillips, A. Gonçalves, P.A.M. Marques, P. Nêmec, *Proc. R. Soc. B.* **281**, 20140025 (2014)
203. R. Wiltschko, W. Wiltschko, *J. Exp. Biol.* **220**, 4347 (2017)
204. A.D. Hasler, A.T. Scholz, R.M. Horrall, *Am. Sci.* **66**, 347 (1978)
205. K. Schmidt-Koenig, C. Walcott, *Anim. Behav.* **26**, 480 (1978)
206. H.-J. Schlichte, *Z. Tierpsychol.* **32**, 257 (1973)
207. L.C. Graue, *Ohio J. Sci.* **63**, 214 (1963)
208. W.T. Keeton, *Adv. Study Behav.* **5**, 47 (1974)
209. R. Wiltschko, W. Wiltschko, *Adv. Study Behav.* **47**, 229 (2015)
210. C. Walcott, *Integr. Comp. Biol.* **45**, 574 (2005)
211. R.R. Baker, *Migration: Paths through Time and Space* (Hodder and Stoughton, London, 1982)
212. R. Wiltschko, I. Schiffner, P. Fuhrmann, W. Wiltschko, *Curr. Biol.* **20**, 1534 (2010)
213. E. Batschelet, *Circular Statistics in Biology* (Academic Press, London, 1981)
214. W. Wiltschko, M. Gesson, R. Wiltschko, *Naturwissenschaften* **88**, 387 (2001)
215. R. Wehner, S. Wehner, *Ethol. Ecol. Evol.* **2**, 27 (1990)