

The Earth's Magnetic Field as a Navigational Cue

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INTRODUCTION

It is well known by biologists, paraprofessionals and lay persons that many birds and a variety of other vertebrates (e.g., fishes, marine mammals) migrate annually. This means that these species make an annual round trip between their breeding and nonbreeding ranges. In many instances the distances traversed can be measured in thousands of kilometers and the goals at each end of the migration route frequently are precise, with individual birds, for example, returning to the same hectare of habitat year after year. Numerous studies involving marked animals, either banded or otherwise individually recognizable, have documented the distances traveled, the seasonal ranges of particular species and individuals, and the seasonal periodicity of such movements (1, 2). The migratory ability of birds and the associated direction-finding methodologies have been studied more thoroughly than similar behavior in other vertebrates. Most of this review, therefore, will be devoted to the state of our knowledge about avian orientation and navigation.

Perhaps two-thirds of temperate North America's bird species make annual round trips between their seasonal ranges which average 2000-6000 km (3). Individuals of some species travel much farther, and the transequatorial journeys of some shorebirds exceed 20,000 km annually. These seasonal migratory flights are weather dependent, and often the route is broken into a series of discrete segments. Usually the journey will take several weeks but considerable inter- and intraspecific variability exists.

Some avian species migrate nocturnally, others are diurnal migrants, and some are capable of migrating during day or night. The altitude at which migrating birds fly varies greatly and is related to species and weather conditions. Radar evidence indicates that most migrants fly at elevations below 3000 meters but some, such as shorebirds and geese, may migrate at altitudes up to about 10,500 meters (3).

Because of the nature of these feats, it follows that migratory birds must possess some mechanism for determining and maintaining a given direction of travel. They should possess, in other words, an internal *compass* which uses one or more of the

available environmental cues (e.g., geomagnetism, stars, sun) to know and follow a particular heading. It appears equally necessary that migrants possess some means of recognizing where they are spatially, and the relationship between a given location and the preferred destination; that is, for a bird to accurately navigate between two distant points a *map* component seems essential. Investigators have used a variety of approaches over the last 35 years or so to determine which of the available sources of environmental information are used as navigational cues, how they are used, and when (seasonally or developmentally) particular cues are used.

It is worth emphasizing that all species do not have the same direction-finding needs and abilities. Even within a species, orientational ability may vary from season to season, day to day, and bird to bird. For example, the orientation mechanisms used during local foraging flights are probably different from those used during long-distance migratory travel.

Griffin (4) described three types of homing ability which require increasingly sophisticated mechanisms. The following homing types of Griffin (4) discern between piloting, compass orientation, and true navigation: Type 1, or piloting, is the finding of a goal by referring to familiar landmarks during random or systematic searches; Type 2, or compass orientation, is the ability to orient in a given compass direction without use of landmarks; and Type 3, or true navigation, is the ability to select a direction toward a goal or home, thus necessitating a map and a compass.

During the 1950's and 1960's there was a tendency among researchers to seek a single solution to the orientation puzzle; that is, there was a tendency to believe that a common denominator existed and that all or most birds used the same mechanism for orienting or navigating. When I entered the field in the early 1960's, the findings of Matthews (5) and Sauer (6) were heralded as solutions to the avian navigation riddle. Matthews' sun arc hypothesis was envisioned as the answer to how diurnal migrants navigated, and Sauer's findings about the use of stellar cues were considered the answer to the question of how nocturnal migrants navigated. This is far from being the consensus of opinion today.

Later studies revealed that the problem was much more complex than originally believed. It became apparent that some or all avian migrants, as well as homing pigeons, possess the ability to use more than one kind of environmental information for orientational or navigational purposes. A system of multiple cues enables birds to navigate under a variety of environmental conditions and in different geographical areas. It is likely that a redundancy of cues exists which provides birds with improved accuracy as well as flexibility. It appears that the array of cues birds may use for navigational purposes (e.g., landmarks, wind direction, sun, stars, geomagnetism, polarized light) are hierarchically arranged in the bird's repertoire. Those used most regularly, possibly because they result in higher accuracy or are more dependably available, appear to be at

the top of the hierarchy.

Before it was generally recognized that birds had backup systems for direction finding, investigators were besieged by contradictory evidence from similarly designed studies. For example, controversy resulted from the inability of any other investigator to replicate the findings of Yeagley (7), which showed that pigeons were using magnetic cues during homing flights. This brought most studies dealing with magnetism to an end, and it was not until about 24 years later that Keeton (8) repeated part of Yeagley's experiment and found that pigeons used backup cues (e.g., the sun) when the Earth's magnetic field was disrupted. Thus, latency in our ability to comprehend that birds might be able to use more than a single type of environmental information for direction-finding purposes resulted in most hypotheses dealing with geomagnetic cues being placed on the shelf by all but a few tenacious investigators. The revival of the hypothesis that birds possessed a magnetic compass occurred in the late 1960's, and it came into its own during the next decade.

In this chapter, I review the studies that have contributed to our understanding of the avian magnetic compass, and attempt to place this method of orientation within the hierarchy of cues we recognize as being available to birds. Although I will generalize frequently and refer to birds as a group, it must be recognized that we have experimental data for only a few migrant species and variations on this theme are to be expected.

This is not the first review of this subject as several authors (5, 9-19) have included a discussion of magnetic cues as part of reviews of avian orientation or as papers. To my knowledge only one other review has been devoted solely to the subject of bird orientation and geomagnetic cues (20). This chapter provides an updated review, elaborates on some of the studies, and places in chronological order a majority of the contributions leading to the present, although cautious, acceptance of the hypothesis that birds possess a magnetic compass. Evidence for a magnetically-based map is still circumstantial, although experiments clearly show that birds are able to solve navigational-type problems.

HISTORICAL PERSPECTIVE

Although the homing and navigational abilities of birds were not tested experimentally until well into the twentieth century, the importance of a compass to migrants was apparent to several nineteenth-century investigators. The likelihood that geomagnetism served as the source of directional information was proposed by Middendorff in 1859 (21), Viguier in 1882 (22), and Thauzies in 1898 (23). Viguier suggested that birds could detect and measure magnetic intensity, inclination, and declination which would provide a complex grid of the isolines. This contention was pursued by other investigators during the next three or four decades (24-26).

Opposition to the notion that birds could sense and use the Earth's magnetic field for orientational purposes developed during the 1920's and 1930's, and the results of experiments supported such views. Casamajor (27) and Wodzicki et al. (28) attached magnets to the heads of homing pigeons and storks and found that this had no effect on their homing ability. Rochon-Duvigneaud and Maurain (29) also argued against the possibility, but on theoretical rather than experimental grounds. The opposing viewpoints were force fully presented and as a consequence the contention that birds possessed a magnetic compass was shelved until Yeagley (7) addressed the subject.

Yeagley's (7) first experiment was conducted in 1943. At that time he attached hyflux-chrome magnets (0.172 Oersted) to the underside of both wings of the experimental pigeons. The control birds carried similarly attached copper plates of comparable mass. Twenty pigeons (10 experimental and 10 controls) were released singly on the same date at a site about 104 km from their loft. Eight (80%) of the controls returned within two days following release whereas only two (20%) of the pigeons bearing magnets returned. Notable differences also were recorded at the time each bird was released in the homing trial. The controls showed better initial orientation with their departure bearings deviating only 10-50 degrees from a direct line between the release site and the loft. In contrast, the experimental birds showed deviations in headings ranging between 45 and 180 degrees from the homeward bearing. In 1944, Yeagley (7) released 122 pigeons in similar experiments but different methods were used for presenting results. Rather than indicating the number of birds returning and not returning, he summed the vectors for the pigeons used in each release. Six (75%) of the total flight vectors supported the hypothesis that pigeons used the Earth's magnetic field during homing.

Yeagley (30) postulated that three factors were essential to pigeon navigation: 1) sensitivity to the effect of flying through the vertical component of the Earth's magnetic field; 2) sensitivity to the magnitude of the Coriolis effect which results from a natural relationship between the Earth's rotational speed and the speed of an object moving over the Earth's surface; and 3) visual sensitivity to velocity over the Earth's surface (ground speed). Yeagley proposed that by correlating the results of the first and third of these sensitivities, a bird could detect its magnetic latitude. By a similar correlation of the second and third sensitivities, the bird would be able to detect the true latitude of its location.

In spite of his early success, Yeagley's contention that pigeons were capable of using the Earth's magnetic field for orientational purposes soon encountered serious problems. Other investigators (31-33) working with pigeons and even Yeagley himself (34) were unable to reproduce his earlier results. In addition, studies with other species also produced negative results (35, 36) and attempts to detect magnetic sensitivity in birds were unsuccessful (37-47).

The preponderance of negative results during this period contributed to the subject being tabled by all but a few researchers. Persistent work by biologists on invertebrates repeatedly produced results indicating that various species, ranging from planarian worms to insects, responded to weak magnetic fields (48-52). During the 1950's and early 1960's, the only proponents of the magnetic compass in birds were Merkel and his associates in Germany (53-56). These authors consistently found that European robins (*Erithacus rubecula*), during periods of migratory unrest (Zugunruhe), showed preferences for their natural migratory direction (SW in fall, NE in spring) when tested in orientation cages in the absence of celestial cues. Birds placed in an all-steel chamber, which had a shielding effect, were unable to maintain these bearings. The directional choice of the birds was reinstated when the investigators generated a magnetic field of the Earth's intensity in the steel chamber with Helmholtz coils. The findings of these investigators were not readily accepted because (a) the negative results produced by attempts to reproduce Yeagley's (7) early results convinced most researchers that birds could not perceive magnetic stimuli, (b) a receptor for magnetic stimuli had not been identified in birds, and (c) other investigators (57, 58) were unable to duplicate the results reported by Merkel, Wiltschko, and their colleagues. Later, however, it was shown that methodological problems were responsible for the inability of some researchers to duplicate the results of Merkel and Wiltschko (55, 59, 60). The persistence of Merkel, Roswitha, and Wolfgang Wiltschko and their co-workers forced other investigators to seriously reconsider the possibility that birds, other than the European robin, were using a magnetic compass during orientation.

During 1962–1966, I obtained the first evidence suggesting that natural disturbances in the Earth's magnetic field might disrupt the orientational ability of free-flying wild birds (61). A total of 429 adult herring gulls (*Larus argentatus*) and ring-billed gulls (*L. delawarensis*) were transported in darkened containers to locations at various directions and distances from their breeding colony. Releases were made under a variety of environmental conditions (e.g., clear and overcast skies) in an attempt to determine which factors influenced homing success and speed of return. Some individuals were radio-tracked following release. The results showed that these experienced migrators were capable of homing under environmental conditions that were believed to render particular, supposedly essential, cues unavailable to them (e.g., heavy overcast obscuring solar cues) (62-66). This prompted the hypothesis that adult gulls, because of experience gained from using a variety of cues during previous migratory trips, possessed the ability to use more than one type of environmental information for direction-finding purposes. If a particular type of directional information was unavailable (e.g., the sun), they used the next most accurate method available to them. To test this hypothesis, 56 juvenile ring-billed gulls were released at sites 11–29 km from their breeding colony in 1964 and 1965. This was the maiden flight for each of the young gulls as they had never flown outside the confines of the colony site. The departure bearings

of these individuals was principally to the east and southeast, which was not the case for adults of the same species (61, 67). Such headings corresponded with the direction ring-billed gulls would take to reach their major winter range (68-70). If fledgling gulls (35+ days old) expressed preference for their future migrational bearing, it seemed possible that even younger gulls might respond similarly. This was tested by placing ring-billed gull chicks (about 3-20 days old) in a circular cage and plotting the route they walked when exposed to selected environmental conditions. The results from an initial set of trials with 294 chicks showed that they possessed an innate ability for selecting a course suitable for reaching the primary winter range of the population (67, 70). There was no evidence that solar cues were being used as directional information by the gulls and so the possible effect of naturally-occurring geomagnetic disturbances was examined.

The National Geomagnetic Observatory's K-indices were used as a measure of magnetic disturbance. These values, ranging from 0-9, reflect the amount of disturbance in the Earth's field that is caused by solar flares, solar storms, and related phenomena. K-values occurring at release times, or the mean value for the preceding 12 hours, were compared with the responses of gull chicks to determine if the bearings selected by the birds varied in accordance with different levels of geomagnetic disturbance. All but 8 of the initial trials were conducted during low levels of disturbance, and it was not clearly evident that modifications in the geomagnetic field were influencing directional responses. Additional tests were conducted and the results from these 333 trials were combined with the earlier data for analysis. During the second series of tests, K-values ranged between 0 and 7, with 7 representing a moderately severe magnetic storm. At this time, it was clearly demonstrated that although ring-billed gull chicks were able to select a preferred bearing of SE during minor disturbances (0-3 K) in the Earth's field, they were unable to do so during higher intensity storms (4-7 K) (71). Similarly tested herring gull chicks (a more sedentary species than ring-billed gulls) from an adjacent colony did not show as much disorientation as ring-billed gulls (72). There was, however, a difference between the mean directional preferences of the experimental and control birds, and the experimental group also showed greater variance in the direction chosen. Moore (72) concluded that magnetic stimuli altered but did not completely disrupt herring gull chick orientation. Later ring-billed gull experiments involving magnets and a magnetically-shielded room (Earth's field reduced by a factor of 25) also produced disorientation. Results from trials using Ruben's coils to simulate the Earth's field within the shielded chamber were inconclusive because of lighting and ventilation problems within the apparatus (73).

Keeton et al. (74) examined the directional tendencies of pigeons during periods of naturally-occurring magnetic disturbances. The results showed a significant inverse correlation with K-values. Since most of the magnetic fluctuations during their releases were less than 70 gamma, Keeton et al. (74) concluded that the sensitivity of pigeons to magnetic cues probably approached that already demonstrated for honeybees (0-300

gamma) (75). In contrast, ring-billed gulls did not exhibit disorientation prior to disturbances measuring about 500 gamma ($K=4$) (73).

As the body of evidence grew in support of birds being able to derive directional information from the Earth's magnetic field, other investigators became interested. Old approaches were retested, and new methodology was applied. Keeton (8, 76) replicated Yeagley's (7, 30) experiment by placing magnets on the backs (instead of the wings as done by Yeagley) of experimental pigeons and brass weights on the controls. In contrast to Yeagley, however, Keeton also considered sky condition at the time of release. He found that both the experimentals and controls oriented homeward when released under sunny conditions. But when the experimental and control birds were released under overcast conditions, the controls oriented homeward but the experimentals usually departed randomly. This was the first solid experimental demonstration of the possible redundancy of cues, i.e., that birds could use both solar and magnetic cues. Young untrained pigeons wearing magnets were unable to orient homeward under either clear or overcast conditions, suggesting that (a) young pigeons are dependent upon a magnetic compass, and (b) the sun compass develops through experience. Keeton and Gobert (77) concluded that inexperienced pigeons required both sun cues and magnetic cues to orient homeward. This also may be the case with young ring-billed gulls (78, 79).

Other studies during the 1970's supported the contention that birds indeed must be capable of perceiving the Earth's magnetic field and using it as a compass. Walcott (80) equipped pigeons with two small Helmholtz coils, one glued to the top of the bird's head and the other around its neck. The power supply was attached to the bird's back. This arrangement produced a magnetic field of approximately 0.1 gauss between the coils in the vicinity of the bird's head. Experimental birds exhibited vanishing bearings under sun that were usually more scattered than bearings of control birds wearing an unenergized set of coils. Larkin and Keeton (81) compared the responses of pigeons with attached magnets and those with brass weights during periods of natural magnetic disturbance. Both magnets and natural disturbances caused pigeons to shift their bearings slightly to the left. Following these results, Larkin and Keeton concluded there was a direct cause-and-effect relationship between fluctuations in the Earth's magnetic field and the variations in initial bearings of pigeons.

Particularly important were the results from the continuing and increasingly refined studies of W. Wiltschko and his colleagues. These studies indicated that European robins and Old World warblers (*Sylvia* spp.) showed oriented nocturnal migratory activity (Zugunruhe) in a seasonally appropriate direction even when deprived of vision of the natural environment (e.g., stars or sun), provided they were exposed to a magnetic field comparable to that of the Earth (82-93). Working in cooperation with the Wiltschkos, Emlen et al. (60) found that indigo buntings (*Passerina cyanea*) were able to orient in the appropriate migratory direction when exposed to a minimum of visual cues and normal

geomagnetic stimuli. When the horizontal component of the magnetic field was deflected clockwise 120° with Helmholtz coils, the buntings shifted their orientation clockwise. Emlen et al. (60) concluded from these results that indigo buntings are able to detect the Earth's magnetic field and to use the resultant information in determining their migratory direction.

It is particularly difficult to design studies that will test for the effects of naturally occurring geomagnetic disturbances on free-flying migrants. Such studies, however, are extremely important. Moore (94) provided the first direct visual evidence that the orientation of free-flying nocturnal migrants was affected by natural fluctuations in the geomagnetic field. He found that the variability in flight directions of nocturnal migrants was significantly correlated with increasing geomagnetic disturbance as measured by both the K-index and various components of the Earth's magnetic field. As with all studies involving modifications in the geomagnetic stimuli birds receive (superimposing other fields with magnets or coils), these results do not show conclusively that birds use geomagnetism as an orientational cue. They do show, however, that disturbances in the Earth's field are in some way detected by birds and that in response they alter their direction of travel. Intuitively, it would make sense for migrant birds, which are specialized for long-distance travel, to have evolved filters for weak background disturbances (such as magnetic fluctuations measuring up to perhaps 1000 gamma) that affected the efficiency of migration. The fact that they have not done so suggests that this type of environmental information is important to them rather than being solely disruptive. The evidence available makes attractive the assumption that the Earth's magnetic field provides information essential to the avian compass or to the apparently necessary navigational map.

Ontogenetic studies involving young inexperienced migrants or homing pigeons have the potential for showing the innate ability of birds to orient or navigate. Such studies are based on the premise that young birds have a programmed directional choice or they develop an early attachment for the home loft. Studies have shown that the young of a number of avian species show apparently innate preferences for seasonally appropriate migratory bearings, although the goals at the ends of such routes must be learned (9, 61, 70, 95, 96). I demonstrated that the directional preferences expressed by young ring-billed gulls (preflight chicks and first-flight juveniles) corresponded to the bearing appropriate for reaching the winter range of the population of gulls studied (70). Selection of these bearings was influenced by changes in the Earth's magnetic field (magnetic storms) and by induced fields (magnets), and I proposed that young ring-billed gulls first used a magnetic compass and then developed an ability to use other environmental information to establish redundancy in the system and to increase accuracy (70, 71, 78, 79, 97). The relationship between the magnetic compass and cues learned during development were presented as a model (97).

Wiltschko et al. (98) have shown that the magnetic compass is involved in the learning process associated with establishment of the sun compass, but as yet they have not been able to unravel completely the complex relationship that apparently exists. Existence of the sun compass is well documented (15); the mechanism, which is based on a relationship between sun azimuth, time, and geographic direction, is learned rather than being innate. The magnetic compass is used by young pigeons before the sun compass is established, and it apparently provides the basis for the sun compass' geographic component which develops through experience (99-103). A similar mechanism has been reported for night-migrating birds wherein the star compass is influenced by, and possibly calibrated by, information obtained from the Earth's magnetic field (104). The evidence produced by R. Wiltschko and W. Wiltschko (105) demonstrates that the most important orientation mechanism during the first flights by young pigeons is the magnetic compass. Their studies show that young inexperienced pigeons use route reversal to find their way between an unfamiliar release site and the home locality. This means the birds use the magnetic field to determine the direction of the outward journey, and for determining the home direction upon release. Pigeons transported in a distorted magnetic field apparently were unable to obtain the necessary information while en route. Magnets attached to the pigeons upon release also caused disorientation.

The magnetic compass enables birds to establish and maintain a course but it does not provide them with the "map" component of a navigational system. This apparently is based upon learned information (106). Studies by Beck and Wiltschko (107, 108) with pied flycatchers (*Ficedula hypoleuca*) show that the magnetic compass develops independent of any exposure to the sky, and that it provides an adequate mechanism for selecting the migratory direction. Selection and maintenance of a migratory bearing are two separate and independent processes. Determination of a particular bearing is dependent upon a compass, in this case the magnetic compass, but maintenance of a direction strongly depends on the presence of other cues such as stars in the case of nocturnal migrants (93). The stars do not contain directional information in themselves, but they are secondary sources of orientation when information from the magnetic field has been transferred to them (88). In situations where information provided by stars and experimental magnetic fields was contradictory, the garden warbler (*Sylvia borin*) selected its bearing according to information provided by the altered magnetic field (96). This suggests that the magnetic compass is of primary importance to this species. Rabol (109), on the other hand, considered any tendency for sylvilid warblers to use the Earth's magnetic field for orientation in the absence of stellar cues to be weak at best. It seems that we are far from being able to weigh the various cue systems with respect to their relative importance within a species, let alone among species.

A considerable amount of evidence indicates that at least some birds apparently possess a magnetic compass. But if they do, work by W. and R. Wiltschko (86) suggests that the avian compass is functionally different from the mechanical device familiar to

humans. The magnetic compass of the European robin does not use the polarity of the Earth's magnetic field for detecting north. Instead, the robins derive north direction from interpreting the inclination of the axial direction of the magnetic field lines in space, and then taking the direction on the magnetic north-south axis for north where the field lines and the gravity vector form the smaller angle. The involvement of gravity (or some other secondary reference point) in the system is essential if a bird is to determine where north is along the north-south axis of the magnetic field lines. Such a mechanism would provide birds with a highly flexible direction-finding system as it would be able to adjust to the varying intensity ranges encountered geographically in the Earth's field.

The magnetic compass described by Wiltschko (82) is not consistent with what would be expected on the basis of the findings of Southern (71, 78, 79), Keeton (10), Moore (72), and Wagner (110). Magnetic storms and magnetic anomalies involve only small distortions in the total magnetic field, yet both events have been shown to affect orientation by pigeons, gulls, and migrating passerines. Wiltschko (82) contends that changing the intensity of the magnetic field by as much as 10% had no effect on the orientation of captive European robins. Since the field changes reported during geomagnetic storms or at anomalies were less than 10%, the possibility exists that the effects reported by myself (61, 67) and the others were not the result of the magnetic compass being disrupted (82). If such high sensitivity to geomagnetism is not an essential component of the avian magnetic compass, what role does magnetism play in the orientation or navigation process? This brings us to the possibility that geomagnetic information also may play a role in the experimentally elusive map that is essential to true navigators.

Walcott (111) suggested that the Earth's magnetic field could provide at least some information about position and hence contribute to the avian map component (i.e., a grid of coordinates). Objections to such a contention were raised in response to Yeagley's (30) conclusion that pigeons used a grid of latitudinal and longitudinal lines produced by the geomagnetic field and Coriolis effect. Similar objections also have been raised more recently by Kreithen and Keeton (112), Griffin (113), and Schmidt-Koenig (15). Several studies, however, have made the possibility of a map based on geomagnetic information worthy of further consideration (114). Much of the disagreement about this possibility has centered on the relative lack of *physiological* evidence indicating that pigeons or other birds actually are sensitive to magnetic stimuli. To date, a magnetic receptor has not been identified in birds and most of the data pointing to the existence of such a capability are from behavioral studies.

Because pigeons and some migratory birds apparently respond to small changes in the Earth's magnetic field (see studies dealing with K-values and anomalies), Walcott (111) suggested that these effects possibly were the result of the navigational map having a magnetic component. If this is correct, these effects provide a measure of avian

magnetic sensitivity. The angular deviations reported by myself (67, 73, 79) and Keeton et al. (74), and the magnetic anomaly results suggest that a change in field strength of about 10 gamma is detectable by birds (111). This would provide the map resolution (1-mile accuracy) proposed by Schlichte and Schmidt-Koenig (115) and Schmidt-Koenig and Walcott (116). Walcott (111) also pointed out that there is roughly a 10 gamma/mile change in the Earth's magnetic field strength which could provide positional information. Perception of these subtle differences in field strength indeed could contribute to the map component but the results of studies designed to test for such ability have done little to resolve the problem.

Another, but even less convincing, possibility has been proposed by Wallraff and Foa (117). They concluded that olfaction was an integral part of the pigeon's navigation mechanism, but anosmic birds that showed rudimentary homeward orientation relied on magnetic cues. There is, however, only circumstantial evidence showing that birds, other than the domesticated homing pigeon, may be capable of navigating over long distances by olfactory cues. Furthermore, the evidence for pigeons navigating by this means is far from convincing (118). Some birds, however, use olfaction during foraging activities (e.g., vultures, shearwaters) and possibly for recognizing their home locality (e.g., petrels) (119, 120).

GEOMAGNETIC SENSITIVITY AND THE SEARCH FOR A RECEPTOR

The results from four studies at the organ or cellular level suggest that pigeons may be able to perceive magnetic stimuli, but studies reporting negative results also exist (44, 47, 58, 121, 122). Reille (123) reported successful cardiac conditioning to a field intensity of 0.8 Oersted. Yakovleva and Medvedeva (124) also reported conditioning of the heart but at much higher intensity magnetic fields (520 Oe), which makes their results of questionable relevance to the orientation question. Bookman (125, 126) used a different approach to test for sensitivity to Earth-intensity field strengths. A Y-maze was installed in a metal room which reduced the natural field intensity to about 0.02 Oe. Pigeons were trained to travel a flight tunnel and select the compartment containing food. The absence or presence of food was linked with a 0.5 Oe magnetic field produced by Helmholtz coils. Some birds discriminated between the presence and absence of the magnetic field. These individuals fluttered rather than walked down the tunnel, and correctly selected the part of the maze with an Earth-intensity magnetic field.

The results from these types of studies have not shown conclusively that birds possess a sensitivity to magnetic fields because: (a) only a small proportion of the sample tested responded positively (e.g., Bookman's study), and (b) other investigators (e.g., Kreithen and Keeton) (112) have failed in their attempts to replicate the results from some of the conditioning experiments (e.g., Reille's). One piece of evidence, however,

suggests that with improved methodologies investigators may be able to determine conclusively whether or not magnetic sensitivity exists in potential receptor sites. Semm et al. (127, 128) reported that the firing rates of some cells in the pigeon's pineal organ were altered when exposed to Earth-strength magnetic fields. The remaining evidence pointing to a sensitivity to magnetic stimuli is indirect, being based on results from studies wherein birds were subjected to fields produced by magnets or coils (8, 71, 78, 79, 129, 130), naturally-occurring magnetic anomalies (110, 131-135), or man-made electromagnetic disturbances (136, 137).

Many of the objections to the idea that birds can use geomagnetic cues for orienting or navigating stem from the fact that a receptor for magnetic stimuli has not been described. Studies of some non-avian species, however, have shown that the existence of such a receptor in birds is possible. Three methods of magnetic-field detection by living organisms have been described (138): (a) induction; (b) the presence of some type of paramagnetic material that will react to the geomagnetic field; (c) the existence of permanent magnets, such as magnetite particles, that will align themselves with the earth's magnetic field.

Induction occurs in some marine fishes. Kalmijn (139-142) described how sharks locate prey through electroreceptors (143) which register current flow generated by the prey (a conductor) passing through the Earth's magnetic field. The ability of skates to sense magnetic stimuli *per se* was suggested by Kalmijn's successfully training individuals to select a hiding place in a laboratory tank on the basis of stimuli from the Earth's magnetic field (141, 142). These studies do not prove that elasmobranchs are using the induction process for orientation, however, as they do not rule out the possibility of some yet unknown magnetic detector system (111). The induction strategy represents a difficult approach for terrestrial vertebrates since they are not immersed in saltwater which serves as the return current path for sharks (134).

Search for an avian magnetic receptor was revitalized by the discovery that mud bacteria contain small magnetic inclusions of magnetite (Fe_3O_4) which act as single magnetic domains and result in the organisms being magnetotactic (144-149). These bacteria contain a chain-like alignment of magnetite particles (referred to as magnetosomes) which function as a compass. The cellular inclusions cause the organism to orient in the same direction as the lines of force of the geomagnetic field. Torque exerted on this biomagnetic compass by the magnetic field passively steers the swimming bacterium, and the field's inclination directs it down into the mud substrate. In the southern hemisphere, the bacteria's magnetic polarity is reversed, thereby producing the same relationship between the compass and the behaviorally relevant direction of orientation (145, 150, 151). The earlier report of magnetite in the radula of chitons (152), however, also should alert investigators to the possibility that this dense substance may be used within organisms for functions totally unrelated to orientation (153).

Positive results have been reported from some of the searches for iron-rich particles, magnetite or precursors thereof (e.g., hydrous iron oxides) in other animals. Gould et al. (138) and Kuterbach et al. (154) reported such substances in honeybees, and similar discoveries have been made in vertebrates, such as pigeons (155, 156) and dolphins (157). The magnetite-containing tissue of pigeons was found, by using a magnetometer, on the inner surface of the dorsal cranium in an area just posterior to the orbits (156), but a later effort to expand upon this discovery produced only negative results (158). Changes in methodology again produced positive results. Stained serial sections of the pigeon's head were examined from the beak posteriorly. This approach thus far has revealed three major sites in the head with iron-containing tissue. The locations of the sites are: (a) the harderian gland which is positioned medial to each eye within the orbits; (b) the base of the beak; and (c) a sheet of cells more centrally positioned in the brain near the olfactory lobes (158).

The eye pecten, an intraocular pleated and highly vascular structure, has been suggested as a possible magnetic sensor (159), but this possibility has been ruled out in at least one species by de tailed his to logical examination of the pecten's ultrastructure and the absence of magnetite-containing cells (160, 161).

The search goes on to identify structures that may serve as the receptor of geomagnetic stimuli in birds. At this time, the search is concentrating on the head region and some positive results to date justify this approach. The finding of magnetite in pigeons has provided the first solid evidence that a potential component of a magnetic compass exists in vertebrates. Still lacking, however, are physiological data showing that these structures are indeed functioning as receptors. The results from mud bacteria suggest that magnetite-containing cells could function as a magnetic compass in birds, but the map component of the navigational system remains as elusive as ever.

MAGNETISM AND OTHER VERTEBRATES

A number of studies with fishes, in addition to those previously mentioned, have demonstrated responses to magnetic fields (162-167). Amphibians also have shown an ability to perceive magnetic stimuli. Phillips (168) trained salamanders to respond directionally according to geomagnetic stimuli and Phillips and Adler (169) documented magnetic sensitivity in two species of salamander. There is also evidence that reptiles are sensitive to magnetic fields. Rodda (170-172) concluded that alligators are not only true navigators, but that they use a geomagnetic map to select homeward directions when displaced. A few reports also indicate that mammals, ranging from rodents (173, 174) to humans (175, 176), are capable of perceiving and orienting by geomagnetic cues. The results reported for humans have been subjected to criticism as other investigators have been unable to duplicate the findings (e.g., Gould and Able) (175-177). Such controversy is not new, however, as it has existed in the bird literature for decades. As has been

clearly shown for birds, it may be counterproductive to immediately dismiss evidence showing an effect in a carefully designed experiment simply because another investigator has been unable to reproduce the findings. Methodologies appear to be extremely important in this field, and subtle changes in apparatus or treatment of subjects have been causes for some of the disagreement.

The amount of evidence for these non-avian groups is small compared to what is available for birds. It is impossible, therefore, to pass judgment on the importance of magnetism in the orientation and navigation of representatives of these groups. It is interesting, however, that the apparent ability to perceive and use geomagnetic information appears to be so widespread. This suggests the ability may have been essentially universal among vertebrates at some point in their evolutionary history, but that the degree to which it is used today is contingent upon their orientational requirements. Long-distance migrants may have evolved increasing dependence upon supplemental cue types (e.g., sun, stars), particularly those which enhance efficiency, thereby obscuring the underlying sensitivity to geomagnetism and the magnetic compass.

CONCLUDING REMARKS AND SUMMARY

Almost 40 years have passed since Yeagley's (7) first publication on the subject of pigeons navigating by geomagnetic cues. We have gone full circle since then with respect to our willingness to accept the possibility that organisms can perceive and use geomagnetic information. Critical examination of the literature on the subject, with its contradictions and ambiguities, leads one to conclude that the road to scientific truth often is serpentine.

In the foregoing sections I have emphasized the positive results and provided the picture of a developing consensus favoring: (a) a great variety of organisms being able to perceive the Earth's magnetic field, (b) representatives from several major taxa having a magnetic compass, and (c) the magnetic field, in some way, possibly influencing the map component of the avian navigational system. Much of the available evidence strongly supports the first two possibilities, with the third being less well documented. The riddle of how birds navigate and the actual role of geomagnetism in the process is far from being answered (16). There are reasons for being cautious about accepting some of the more prevalent views until more evidence becomes available.

The consistent results which the Wiltschkos have produced over the years would appear, at first glance, as a breakthrough toward solving the avian orientation riddle. The findings, however, have not been readily accepted by ornithologists, either justly or unjustly. The cautionary approach of investigators is based on: (1) the difficulty others have had in replicating the results; (2) the statistical methods that are required to show positive effects; (3) the absence of conclusive physiological evidence showing that birds

have a magnetic receptor; and (4) the tendency of the Wiltschkos to place the magnetic compass in the dominant position in the hierarchical arrangement of orientational cues. As a result, the mood appears to be that of tolerance rather than acceptance of the contention that birds are navigating by geomagnetic cues. Ornithologists are closer to agreeing on the existence of a magnetic compass which would establish a bird's general direction of travel during migration (i.e., orientation) than they are to accepting geomagnetism as the basis for a true navigational ability in birds (i.e., the basis for both the compass and map components). But until more comparative studies are conducted, so as to provide a broader species base for the apparent ability to orient by geomagnetic cues, the uncertainties will persist.

A brief discussion of some of the concerns that have been raised appears in order. Firstly, when tests similar to the Wiltschko's are conducted in other than their exact cage design, or if the perch arrangement within the cage is different, negative results usually are obtained (57, 178). Positive results appear possible only if the cage is eight-sided and has radially aligned perches. If perch arrangement is tangential, for example, other researchers (179) have been unable to replicate the Wiltschko's findings. Why should cage design be so important in such tests unless the cage itself is contributing to the responses obtained? This question has been raised repeatedly, and no acceptable answer is available although other investigators who have switched to Merkel and Wiltschko's cage design or collaborated with the Wiltschkos have obtained comparable results at other locations.

The second, and potentially more serious problem, pertains to the statistical procedures necessary to show positive effects in Wiltschko-type experiments. It is necessary to pool data and the practice used is to calculate nightly means for birds tested, and then to group these means and calculate a grand mean (3). This procedure of using second-order statistics obscures how individual birds respond, and high variance around such grand means is usually ignored. It is difficult to envision directional preferences (i.e., orientation) which are so weakly expressed that they can only be documented in this manner (i.e., second-order means) being useful to migratory birds. Evidence pertaining to the effects of naturally-occurring magnetic disturbances (e.g., storms and anomalies), however, has relied upon first-order means, suggesting that naturally occurring changes in the Earth's magnetic field have a more pronounced effect on orienting birds than the methods used by the Wiltschkos. Until the magnetic compass they propose is documented by other methods and in other species, it must be accepted with reservation.

Other types of problems are associated with some of the research approaches, and these have been reviewed by others (20). One group of problems relates to magnetic-field characteristics. Ossenkopp and Barbeito (20) aptly point out that over the years investigators have used two approaches; one assumes that the stronger the stimulus, the stronger the response, whereas the other attempts to simulate the Earth's field

characteristics as closely as possible and looks for more subtle effects. It is possible that high-intensity fields may stress systems other than, or in addition to those associated with orientation thereby camouflaging any possible effect on direction-finding ability. The point is that the right stimulus must be used to test for a specific response or effect. Another set of problems is associated with the physiological or psychological state of the organism being tested. Emlen (180) and others have shown that orientation behavior changes according to the endogenous state of the organism. Failure to take this into account can lead to tests and results that do not accurately address the question being asked. Similarly, I found that the homing tendencies of individual gulls was influenced by their reaction to the test procedures themselves (61). Some individuals that were trapped and released, but not transported away from their nesting colony, showed tendencies similar to those usually used as measures of homing success. For example, some immediately abandoned their nest sites (this would equate with unsuccessful homers), others disappeared for several hours (slow homers), and some returned immediately to their nests as if nothing had happened (rapid homers). It can be misleading, therefore, for investigators to assume that the quantifiable responses of their test subjects are solely in reaction to the variable for which they want to test. In other words, control subjects are required. These types of design problems were more frequent in the past than they are now, but they must be placed in perspective when reviewing and evaluating the published accounts.

If we accept the precautionary stance which seems appropriate at this time, where does this leave us with respect to understanding the role of geomagnetic cues in vertebrate orientation? In the case of birds, the answer seems to be that it leaves us in a state of turmoil (16). It is now widely accepted that birds are capable of using a multiplicity of environmental information for orientational purposes. This realization was a significant advancement, but it also made it more difficult to design ways of testing for the importance of specific cues. The list of types of environmental information that could provide for redundancy in the system is lengthy, including the sun, stars, wind, odors, magnetic field, infrasound and landmarks (16). Not only is it possible that such cues may be used alternately for direction-finding purposes, but the use of two or more could be integrated in some way so as to improve accuracy. The difficulties that have been encountered have greatly slowed advances in this field during the 1980's. A possible contributor to the slowdown may have been our overreaction to the possibility that multiple cues are used by some birds. It may be that we have lost sight of the forest because of the trees.

The results from homing and migration studies indicate that an array of avian species is capable of solving navigational-type problems. At this point in time, however, it is impossible to describe the complete mechanism that enables any bird to accomplish such feats (for reviews of the role of various cues see (3, 16)). The likelihood that magnetism plays an integral role in the orientation of some avian species is supported by

a number of studies discussed in this review. It remains to be discovered whether this apparent ability to sense and use geomagnetism is widespread among species and, if so, how they actually perceive and process such information.

REFERENCES

- (1) Dorst, J.: The Migration of Birds. Houghton Mifflin Co., Boston, 1962.
- (2) Gauthreaux Jr., S.A.: Animal Migration, Orientation, and Navigation. Academic Press, New York, 1980.
- (3) Emlen, S.T. Migration: Orientation and navigation. In: Farner, D.S., King, J.R. and Parkes, K.C. eds., Avian Biology. Academic Press, New York, 129-219, 1975.
- (4) Griffin, D.R. Bird navigation. In: Wolfson, A. ed., Recent Studies in Avian Biology. University of Illinois Press, Champaign, 154-197, 1955.
- (5) Matthews, G.V.T.: Bird Navigation. Cambridge University Press, Cambridge, 1955.
- (6) Sauer, E.G.F.: Die sternorientierung nachlich ziehender grasmucken (*Sylvia atricapilla*, *borin* und *curruca*). Z. Tierpsychol. 14: 29-70, 1957.
- (7) Yeagley, H.L.: A preliminary study of a physical basis of bird navigation. J. Appl. Phys. 18: 1035-1063, 1947.
- (8) Keeton, W.T.: Magnets interfere with pigeon homing. Proc. Natl. Acad. Sci. USA 68: 102-106, 1971.
- (9) Matthews, G.V.T.: Bird Navigation, Second Edition. Cambridge University Press, Cambridge, 1968.
- (10) Keeton, W.T. The orientational and navigational basis of homing in birds. In: Lehrman, D.S., Hinde, R. and Shaw, E. eds., Advances in the Study of Behavior, Vol. 5. Academic Press, New York, 47-132, 1974.
- (11) Keeton, W.T.: Avian orientation and navigation. Ann. Rev. Physiol. 41: 353-366, 1979.
- (12) Keeton, W.T.: Avian orientation and navigation: a brief overview. Brit. Birds 72: 451-470, 1979.
- (13) Keeton, W.T. Pigeon navigation. In: Granda, A.M. and Maxwell, J.H. eds., Neural Mechanisms of Behavior in the Pigeon. Plenum Publishing Corp., New York, 5-20, 1979.
- (14) Schmidt-Koenig, K. and Keeton, W.T. eds. Animal Migration, Navigation, and Homing. Springer-Verlag, New York, 1978.
- (15) Schmidt-Koenig, K.: Avian Orientation and Navigation. Academic Press, New York, 1979.
- (16) Able, K.P. Mechanisms of orientation, navigation, and homing. In: Gauthreaux Jr., S.A. ed., Animal Migration, Orientation, and Navigatin. Academic Press, New York, 283-373, 1980.

- (17) Papi, F. and Wallraff, H.G.: Avian Navigation. Springer-Verlag, New York, 1982.
- (18) Baker, R.R.: Bird Navigation: The Solution to a Mystery? Holmes & Meier Publ. Inc., New York, 1984.
- (19) Wallraff, H.G. Migration and navigation in birds: a present-state survey with some digressions to related fish behaviour. In: McCleave, J.D., Arnold, G.P., Dodson, J.J. and Neill, W.H. eds., Mechanisms of Migration in Fishes. Plenum Publishing Corp., New York, 509-544, 1984.
- (20) Ossenkopp, K. and Barbeito, R.: Bird orientation and the geomagnetic field: a review. *Neurosci. Behav. Rev.* 2: 255-270, 1978.
- (21) Middendorff, A.: Die isepipetesen russlands. Grundlagen zur erforschung der zugzeiten und zugrichtungen der vogel russlands. *Mem. L'Acad. Imp. Sci., St. Petersburg, Sixth Series* 10 8: 1-144, 1859.
- (22) Viguiet, C.: Le sens d'orientation et ses organes chez les animaux et chez l'homme. *Rev. Phil.* 14: 1-36, 1882.
- (23) Thauzies, A.: L'orientation. *Rev. Sci. (4th Series)* 9: 392-397, 1898.
- (24) Stresemann, E.: Haben die Vogel einen Ortssinn? *Ardea* 24: 213-226, 1935.
- (25) Daanje, A.: Haben die vögel einen sinn für den erdmagnetismus, wie deklination, inklination, und intersitat? *Ardea* 25: 107-111, 1936.
- (26) Daanje, A.: Heimfindeversuche und erdmagnetismus. *Vogelzug* 12: 15-17, 1941.
- (27) Casamajor, J.: Le mysterieux "sens de l'espace". *Rev. Sci.* 65: 554-556, 1927.
- (28) Wodzicki, K., Puchalski, W. and Liche, H.: Untersuchungen über die orientation und geschwindigkeit des fluges bie vögeln. V. Weigtere versuche an storchen. *J. Ornithol.* 87: 99-114, 1939.
- (29) Rochon-Duvigneaud, A. and Maurain, C.: Enquete sur l'orientation du pigeon voyageur et son mecanisme. *Nature (London)* 51: 232-238, 1923.
- (30) Yeagley, H.L. Final Scientific Report on Bird Navigation, Unpublished report. Department of the Army, Signal Corps Engineering Lab, File No. 3664-PH-47-91 (756), 1949.
- (31) Gordon, D.A.: Sensitivity of the homing pigeon to the magnetic field of the Earth. *Science* 108: 710-711, 1948.
- (32) Matthews, G.V.T.: The experimental investigation of navigation in homing pigeons. *J. Exp. Biol.* 28: 508-536, 1951.
- (33) van Riper, W. and Kalmbach, E.R.: Homing not hindered by wing magnets. *Science* 115: 577-578, 1952.
- (34) Yeagley, H.L.: A preliminary study of a physical basis of bird navigation. II. *J. Appl. Phys.* 22: 746-760, 1951.
- (35) Matthews, G.V.T.: An investigation of homing ability in two species of gulls. *Ibis* 94:

- 243-264, 1952.
- (36) Bochenski, Z., Dyslewska, M., Gieszczykiewicz, J. and Sych, L.: Homing experiments on birds. XI. Experiments with swallows *Hirundo rustica* L. concerning the influence of earth magnetism and partial eclipse of the sun on their orientation. Zesz. Nauk, W.J. Zool. 5: 125-130 (In Polish, English Summary), 1960.
- (37) Griffin, D.R.: Homing experiments with Leach's petrels. Auk 57: 61-74, 1940.
- (38) Griffin, D.R.: Bird navigation. Biol. Rev. Cambridge Phil. Soc. 27: 359-400, 1952.
- (39) Henderson, G.H.: Physical basis of bird navigation. Science 107: 597-598, 1948.
- (40) Clark, C.L., Peck, R.A. and Hollander, W.F.: Homing pigeon in electromagnetic fields. J. Appl. Phys. 19: 1183, 1948.
- (41) Kramer, G. Über richtungstendenzen bei der nächtlichen zugruhe gekäfigten vögel. In: Mayr, E. and Schuz, E. eds., Ornithologie als biologische Wissenschaft. Winter, Heidelberg, 269-283, 1949.
- (42) Kramer, G.: Orientierte zugaktivität gekäfigter singvögel. Naturwissenschaften 37: 188, 1950.
- (43) Wilkinson, D.H.: Some physical principles of bird orientation. Proc. Linn. Soc. London 160: 94-99, 1949.
- (44) Orgel, A.R. and Smith, J.C.: Test of the magnetic theory of homing. Science 120: 891-892, 1954.
- (45) Neville, J.R.: An Experimental Study of Magnetic Factors Possibly Concerned with Bird Navigation, Ph.D. thesis. Stanford University, Palo Alto, CA, 1955.
- (46) Fromme, H.G.: Untersuchungen über das orientierungsvermögen nächtliche ziehender kleinvögel (*Erithacus rubecula*, *Sylvia communis*). Z. Tierpsychol. 18: 205-220, 1961.
- (47) Meyer, M.E. and Lambe, D.R.: Sensitivity of the pigeon to changes in the magnetic field. Psychon. Sci. 5: 349-350, 1966.
- (48) Becker, G.F.: Ruheeinstellung nach der himmelsrichtung eine magnetfeld-orientierung bei termiten. Naturwissenschaften 50: 455, 1963.
- (49) Brown, F.A. and Park, Y.H.: Phase-shifting a lunar rhythm in planarians by altering the horizontal magnetic vector. Biol. Bull. 129: 79-86, 1965.
- (50) Lindauer, M. and Martin, H.: Die schwereorientierung der bienen unter dem einfluss des erdmagnetfeldes. Z. Vergl. Physiol. 60: 219-243, 1968.
- (51) Bennett, M.F. and Huguenin, J.: Geomagnetic effects on a circadian difference in reaction times in earthworms. Z. Vergl. Physiol. 63: 440-445, 1969.
- (52) Brown, F.A.: Some orientational influences of nonvisual terrestrial electromagnetic fields. Ann. N.Y. Acad. Sci. 188: 224-241, 1971.
- (53) Merkel, F.W. and Fromme, H.J.: Untersuchungen über das orientierungsvermögen nächtlich ziehender rotkehlchen (*Erithacus rubecula*). Naturwissenschaften 45: 499-500,

- 1958.
- (54) Merkel, F.W., Fromme, H.J. and Wiltshcko, W.: Nichtvisuelles orientierungsvermögen bei nächtlich zugunruhigen rotkehlchen. Vogelwarte 22: 168-173, 1964.
- (55) Merkel, F.W. and Wiltshcko, W.: Magnetismus und richtungsfinden zugunruhiger rotkehlchen (*Erithacus rubecula*). Vogelwarte 23: 71-77, 1965.
- (56) Wiltshcko, W. and Merkel, F.W.: Orientierung zugunruhiger rotkehlchen im statischen magnetfeld. Verh. Deut. Zool. Ges. Jena 1965: 362-367, 1966.
- (57) Perdeck, A.C.: Does navigation without visual clues exist in robins? Ardea 52: 91-104, 1963.
- (58) Emlen, S.T. The influence of magnetic information on the orientation of the indigo bunting, *Passerina cyanea*. In: Galler, S.R., Schmidt-Koenig, K., Jacobs, G.J. and Belleville, R.E. eds., Animal Orientation and Navigation. NASA SP-262, 191-210, 1970.
- (59) Wallraff, H.G.: Nichtvisuelle orientierung zugunruhiger rotkehlchen (*Erithacus rubecula*). Z. Tierpsychol. 30: 374-383, 1972.
- (60) Emlen, S.T., Wiltshcko, W., Demong, N.J., Wiltshcko, R. and Bergman, S.: Magnetic direction finding: evidence for its use in migratory indigo buntings. Science 193: 505-508, 1976.
- (61) Southern, W.E.: The role of environmental factors in ring-billed and herring gull orientation, Ph.D. thesis. Cornell University, Ithaca, 1967.
- (62) Southern, W.E.: Gull orientation behavior: influence of experience, sex, age, and group releases. Jack-Pine Warbler 47: 34-43, 1969.
- (63) Southern, W.E.: Sky conditions in relation to ring-billed and herring gull orientation. Trans. Ill. State Acad. Sci. 62: 342-349, 1969.
- (64) Southern, W.E.: Influence of disturbances in the Earth's magnetic field on ring-billed gull orientation (Abstract). Am. Zool 10: 23, 1970.
- (65) Southern, W.E.: En route behavior of homing herring gulls as determined by radio-tracking. Wilson Bull. 82: 189-200, 1970.
- (66) Southern, W.E.: Orientation in gulls: effect of distance, direction of release, and wind. Living Bird 9: 75-95, 1970.
- (67) Southern, W.E.: Orientation behavior of ring-billed gull chicks and fledglings. Condor 71: 418-425, 1969.
- (68) Southern, W.E.: Colony selection, longevity, and ring-billed gull populations: preliminary discussion. Bird-Banding 8: 52-60, 1967.
- (69) Southern, W.E.: Seasonal distribution of Great Lakes region ring-billed gulls. Jack-Pine Warbler 52: 154-179, 1974.
- (70) Southern, W.E.: Migrational orientation in ring-billed gull chicks. Auk 93: 78-85, 1976.
- (71) Southern, W.E.: Influence of disturbances in the Earth's magnetic field on ring-billed gull

- orientation. *Condor* 74: 102-105, 1972.
- (72) Moore, F.R.: Influence of solar and geomagnetic stimuli on the migratory orientation of herring gull chicks. *Auk* 92: 655-664, 1975.
- (73) Southern, W.E.: The effects of superimposed magnetic fields on gull orientation. *Wilson Bull.* 86: 256-271, 1974.
- (74) Keeton, W.T., Larkin, T.S. and Windsor, D.M.: Normal fluctuations in the Earth's magnetic field influence pigeon orientation. *J. Comp. Physiol.* 95: 95-103, 1974.
- (75) Lindauer, M. and Martin, H. Magnetic effect on dancing bees. In: Galler, S.R., Schmidt-Koenig, K., Jacobs, G.J. and Belleville, R.E. eds., *Animal Orientation and Navigation*. NASA SP-262, 559-567, 1972.
- (76) Keeton, W.T. Effects of magnets on pigeon homing. In: Galler, S.R., Schmidt-Koenig, K., Jacobs, G.J. and Belleville, R.E. eds., *Animal Orientation and Navigation*. NASA SP-262, 579-594, 1972.
- (77) Keeton, W.T. and Gobert, A.: Orientation by untrained pigeons requires the sun. *Proc. Natl. Acad. Sci. USA* 65: 853-856, 1970.
- (78) Southern, W.E.: Magnets disrupt the orientation of juvenile ring-billed gulls. *BioScience* 22: 476-479, 1972.
- (79) Southern, W.E. Orientation responses of ring-billed gull chicks: a re-evaluation. In: Schmidt-Koenig, K. and Keeton, W.T. eds., *Animal Migration, Navigation, and Homing*. Springer-Verlag, New York, 311-317, 1978.
- (80) Walcott, C. The navigation of homing pigeons: do they use sun navigation? In: Galler, S.R., Schmidt-Koenig, K., Jacobs, G.J. and Belleville, R.E. eds., *Animal Orientation and Navigation*, NASA SP-262. U.S. Govt. Printing Office, Washington, DC, 283-292, 1972.
- (81) Larkin, T.S. and Keeton, W.T.: Bar magnets mask the effect of normal magnetic disturbances on pigeon orientation. *J. Comp. Physiol.* 110: 227-231, 1976.
- (82) Wiltschko, W. The influence of magnetic total intensity and inclination on directions preferred by migrating European robins (*Erithacus rubecula*). In: Galler, S.R., Schmidt-Koenig, K., Jacobs, G.J. and Belleville, R.E. eds., *Animal Orientation and Navigation*, NASA SP-262, 569-578, 1972.
- (83) Wiltschko, W.: Der magnetkompass der gartengrasmücke (*Sylvia borin*). *Vogelwarte* 29: 76-82, 1974.
- (84) Wiltschko, W. and Merkel, F.W.: Zugorientierung von dorngrasmücken (*Sylvia communis*) im erdmagnetfeld. *Vogelwarte* 26: 245-249, 1971.
- (85) Wiltschko, W.: Der magnetkompass der zugvögel und seine biologische bedeutung. *Vogelwarte* 29: 76-82, 1977.
- (86) Wiltschko, W. and Wiltschko, R.: Magnetic compass of European robins. *Science* 176: 62-64, 1972.
- (87) Wiltschko, W. and Wiltschko, R.: Grasmücken benutzen den magnetkompass auch bie

- sternsicht. *Naturwissenschaften* 12: 1-3, 1973.
- (88) Wiltschko, W. and Wiltschko, R.: The interaction of stars and magnetic field in the orientation system of night migrating birds. *Z. Tierpsychol.* 37: 337-355, 1975.
- (89) Wiltschko, W. and Wiltschko, R.: Die bedeutung des magnetkompasses für die orientierung der vögel. *J. Ornithol.* 117: 362-387, 1976.
- (90) Wiltschko, W. and Wiltschko, R.: Interaction of magnetic compass and star orientation in night-migrating birds. *J. Comp. Physiol.* 109: 91-99, 1976.
- (91) Wiltschko, W. and Wiltschko, R.: A theoretical model for migratory orientation and homing in birds. *Oikos* 30: 177-187, 1978.
- (92) Wiltschko, W. and Wiltschko, R.: Orientation behavior of night-migrating birds (European robins) during late afternoon and early morning hours. *Wilson Bull.* 84: 149-163, 1972.
- (93) Wiltschko, R. and Wiltschko, W.: Relative importance of stars and the magnetic field for the accuracy of orientation in night-migrating birds. *Oikos* 30: 195-206, 1978.
- (94) Moore, F.R.: Geomagnetic disturbance and orientation of nocturnally migrating birds. *Science* 196: 682-684, 1977.
- (95) Bingman, V.P.: Savannah sparrows have a magnetic compass. *Anim. Behav.* 29: 962-963, 1981.
- (96) Wiltschko, W. The migratory orientation of garden warblers. In: Papi, F. and Wallraff, H.G. eds., *Avian Navigation*. Springer-Verlag, Berlin, 50-58, 1982.
- (97) Southern, W.E. Comparative distribution and orientation in North American gulls. In: Burger, J., Olla, B.L. and Winn, H.E. eds., *Behavior of Marine Animals*, Vol. 4. Plenum Publishing Co., New York, 449-498, 1980.
- (98) Wiltschko, W., Wiltschko, R., Keeton, W.T. and Madden, R.: Growing up in an altered magnetic field affects the initial orientation of young homing pigeons. *Behav. Ecol. Sociobiol.* 12: 135-142, 1983.
- (99) Wiltschko, W., Wiltschko, R. and Keeton, W.T.: Effects of a "permanent clock-shift" on the orientation of young homing pigeons. *Behav. Ecol. Sociobiol.* 1: 229-243, 1976.
- (100) Wiltschko, R. and Wiltschko, W.: The development of sun compass orientation in young homing pigeons. *Behav. Ecol. Sociobiol.* 9: 135-141, 1981.
- (101) Wiltschko, R., Nohr, D. and Wiltschko, W.: Pigeons with a deficient sun compass use the magnetic compass. *Science* 214: 343-345, 1980.
- (102) Walcott, C.: Magnetic orientation in homing pigeons. *IEEE Trans. Magnetics* MAG 16: 1008-1013, 1980.
- (103) Viehmann, W. Interrelation of magnetic compass, star orientation, and the sun in the orientation of blackcaps and robins. In: Papi, F. and Wallraff, H.G. eds., *Avian Navigation*. Springer-Verlag, Berlin, 59-67, 1982.

- (104) Wiltschko, W.: The Earth's magnetic field and bird orientation. *Trends Neurosci.* 1980: 140-144, 1980.
- (105) Wiltschko, R. and Wiltschko, W. The development of the navigational system in young homing pigeons. In: Varju, D. and Schnitzler, H.-U. eds., *Localization and Orientation in Biology and Engineering*. Springer-Verlag, Berlin, 337-343, 1984.
- (106) Wiltschko, R.: The ontogeny of orientation in young pigeons. *Comp. Biochem. Physiol.* 76A: 701-708, 1983.
- (107) Beck, W. and Wiltschko, W.: Trauerschnapper (*Ficedula hypoleuca* Pallas) orientieren sich nickvisuell mit hilfe des magnetfeldes. *Vogelwarte* 31: 168-174, 1981.
- (108) Beck, W. and Wiltschko, W.: The magnetic field as a reference system for genetically encoded migratory direction in pied flycatchers (*Ficedula hypoleuca* Pallas). *Z. Tierpsychol.* 60: 41-46, 1982.
- (109) Rabol, J.: Magnetic orientation in night-migrating passerines. *Ornis Scandinavia* 10: 69-75, 1979.
- (110) Wagner, G.: Das orientierungsverhalten von brieftauben im erdmagnetisch gestorten geviete des chasserai. *Rev. Suisse Zool.* 83: 883-890, 1976.
- (111) Walcott, C. Is there evidence for a magnetic map in homing pigeons. In: Papi, F. and Wallraff, H.G. eds., *Avian Navigation*. Springer-Verlag, Berlin, 99-108, 1982.
- (112) Kreithen, M.L. and Keeton, W.T.: Attempts to condition homing pigeons to magnetic stimuli. *J. Comp. Physiol.* 129: 355-362, 1974.
- (113) Griffin, D.R.: The sensory physiology of animal orientation. *Harvey Lect. Ser.* 71: 133-172, 1978.
- (114) Moore, F.R.: Is the homing pigeon's map geomagnetic? *Nature (London)* 285: 69-70, 1980.
- (115) Schlichte, H.J. and Schmidt-Koenig, K.: Zum heimfindevermogen der brieftaube bei erschwerter optischer Wahrnehmung. *Naturwissenschaften* 58: 329-330, 1971.
- (116) Schmidt-Koenig, K. and Walcott, C.: Tracks of pigeons homing with frosted lenses. *Anim. Behav.* 26: 480-486, 1978.
- (117) Wallraff, H.G. and Foa, A.: The roles of olfaction and magnetism in pigeon homing. *Naturwissenschaften* 69: 504-505, 1982.
- (118) Phillips, J.B. and Waldvogel, J.A. Reflected light cues generate the short-term deflector-loft effect. In: Papi, F. and Wallraff, H.G. eds., *Avian Navigation*. Springer-Verlag, Berlin, 190-202, 1982.
- (119) Grubb Jr., T.C.: Olfactory navigation to the nesting burrow in Leach's petrel (*Oceanodroma leucorhoa*). *Anim. Behav.* 22: 192-202, 1974.
- (120) Wenzel, B.M. Chemoreception in seabirds. In: Burger, J., Olla, B.L. and Winn, H.E. eds., *Behavior of Marine Animals, Vol. IV*. Academic Press, New York, 41-67, 1980.

- (121) Beaugrand, J.P.: An attempt to confirm magnetic sensitivity in the pigeon, *Columba livia*. J. Comp. Physiol. 110: 343-355, 1976.
- (122) Orgel, A.R. and Smith, J.C.: A test of the magnetic theory of homing in pigeons. J. Genet. Psychol. 88: 203-210, 1956.
- (123) Reille, A.: Essai de mise en evidence d'une sensibilite du pigeon au champ magnetique a l'aide d'une conditionnement nociceptif. J. Physiol. Paris 60: 85-92, 1968.
- (124) Yakovleva, M.I. and Medvedeva, M.V.: Conditioned control of cardiac activity and respiration and morphological changes in the brain of pigeons under the effect of a constant magnetic field. Zh. vyssh. nerv. Deyat. I.P. Pavlova 22: 288-293 (NTIS No. AD-784-798), 1972.
- (125) Bookman, M.: Sensitivity of the homing pigeon to an Earth-strength magnetic field. Nature (London) 267: 340-342, 1977.
- (126) Bookman, M. Sensitivity of the homing pigeon to an Earth-strength field. In: Schmidt-Koenig, K. and Keeton, W.T. eds., Navigation and Homing. Springer-Verlag, Berlin, 127-134, 1978.
- (127) Semm, P., Schneider, T. and Vollrath, L.: Effects of an Earth-strength field on electrical activity of pineal cells. Nature (London) 288: 607-608, 1980.
- (128) Semm, P., Schneider, T., Vollrath, L. and Wiltschko, W. Magnetic sensitive pineal cells in pigeons. In: Papi, F. and Wallraff, H.G. eds., Avian Navigation. Springer-Verlag, Berlin, 329-337, 1982.
- (129) Visalberghi, E. and Alleva, E.: Magnetic influences on pigeon homing. Biol. Bull. 156: 246-256, 1979.
- (130) Walcott, C. and Green, R.: Orientation of homing pigeons altered by a change in the direction of an applied magnetic field. Science 184: 180-182, 1974.
- (131) Frie, U. and Wagner, G.: Die anfangsorientierung von brieftauben im erdmagnetisch gestören gebiet des mont jorat. Rev. Suisse Zool. 83: 891-897, 1976.
- (132) Graue, L.C.: Initial orientation in pigeon homing related to magnetic contours (Abstract). Am. Zool. 5: 704, 1965.
- (133) Talkington, L.: Bird navigation and geomagnetism (Abstract). Am. Zool. 7: 199, 1967.
- (134) Walcott, C. Anomalies in the Earth's magnetic field increase the scatter of pigeon's vanishing bearings. In: Schmidt-Koenig, K. and Keeton, W.T. eds., Animal Migration, Navigation, and Homing. Springer-Verlag, Berlin, 143-151, 1978.
- (135) Walcott, C.: Homing-pigeon vanishing bearings at magnetic anomalies are not altered by bar magnets. J. Exp. Biol. 86: 349-352, 1980.
- (136) Larkin, R.P. and Sutherland, D.J.: Migrating birds respond to project Seafarer's electromagnetic field. Science 195: 777-778, 1977.
- (137) Southern, W.E.: Orientation of gull chicks exposed to project Sanguine's electromagnetic field. Science 189: 143-145, 1975.

- (138) Gould, J.L., Kirschvink, J.L. and Deffeyes, K.S.: Bees have magnetic remanence. *Science* 201: 1026-1028, 1978.
- (139) Kalmijn, A.J.: The electric sense of sharks and rays. *J. Exp. Biol.* 55: 371-383, 1971.
- (140) Kalmijn, A.J.: The electric and magnetic sense of sharks, skates and rays. *Oceanus* 20: 45-52, 1977.
- (141) Kalmijn, A.J. Electric and magnetic sensory world of sharks, skates, and rays. In: Hodgson, E.S. and Mathewson, R.F. eds., *Sensory Biology of Sharks, Skates and Rays*. U.S. Govt. Printing Office, Washington, DC, 507-528, 1978.
- (142) Kalmijn, A.J. Experimental evidence of geomagnetic orientation in elasmobranch fishes. In: Schmidt-Koenig, K. and Keeton, W.T. eds., *Animal Migration, Navigation and Homing*. Springer-Verlag, Berlin, 347-355, 1978.
- (143) Lissman, H.W.: On the function and evolution of electric organs in fish. *J. Exp. Biol.* 35: 156-191, 1958.
- (144) Blakemore, R.P.: Magnetotactic bacteria. *Science* 190: 377-378, 1975.
- (145) Blakemore, R.P. and Frankel, R.B.: Magnetic navigation in bacteria. *Sci. Am.* 245: 58-65, 1981.
- (146) Frankel, R.B., Blakemore, R.P., Torres de Araujo, F.F., Esquivel, D.M.S. and Dannon, J.: Magnetotactic bacteria at the geomagnetic equator. *Science* 212: 1269-1270, 1981.
- (147) Frankel, R.B., Blakemore, R.P. and Wolfe, R.S.: Magnetite in freshwater magnetotactic bacteria. *Science* 203: 1355-1356, 1979.
- (148) Kalmijn, A.J. and Blakemore, R.P.: Geomagnetic orientation in marine mud bacteria. *Proc. Int. Union Physiol. Sci.* 13: 364, 1977.
- (149) Kalmijn, A.J. and Blakemore, R.P. The magnetic behavior of mud bacteria. In: Schmidt-Koenig, K. and Keeton, W.T. eds., *Animal Migration, Navigation, and Homing*. Springer-Verlag, Berlin, 354-355, 1978.
- (150) Blakemore, R.P., Frankel, R.B. and Kalmijn, A.J.: South-seeking magnetotactic bacteria in the southern hemisphere. *Nature (London)* 256: 384, 1980.
- (151) Kirschvink, J.L.: South-seeking magnetic bacteria. *J. Exp. Biol.* 86: 345-348, 1980.
- (152) Lowenstam, H.A.: Magnetite in denticle capping in recent chitons (Polyplacophora). *Geol. Soc. Amer. Bull.* 73: 435-438, 1962.
- (153) Maugh II, T.H.: Magnetic navigation an attractive possibility. *Science* 215: 1492-1493, 1982.
- (154) Kuterbach, D.A., Walcott, B., Reeder, R.J. and Frankel, R.B.: Iron-containing cells in the honey bee (*Apis mellifera*). *Science* 218: 695-697, 1982.
- (155) Presti, D. and Pettigrew, J.D.: Ferromagnetic coupling to muscle receptors as a basis for geomagnetic field sensitivity in animals. *Nature (London)* 285: 99-101, 1980.
- (156) Walcott, C., Gould, J. and Kirschvink, J.: Pigeons have magnets. *Science* 215: 1027-1029,

- 1979.
- (157) Zoeger, J. and Fuller, M.: Magnetic material in the head of a dolphin. *Trans. Am. Geophys. Union* 61: 225, 1980.
- (158) Walcott, B. and Walcott, C. A search for magnetic field receptors in animals. In: Papi, F. and Wallraff, H.G. eds., *Avian Navigation*. Springer-Verlag, Berlin, 338-343, 1982.
- (159) Danilov, V., Demirochaglyan, G., Avetyan, Z., Aelakhnyerdyan, M., Grigoryan, S. and Saribekhyan, G.: Possible mechanisms of magnetic sensitivity in birds (in Russian). *Biol. Zh. Arm.* 23: 26-34, 1970.
- (160) Hanzely, L., Southern, W.E. and Molsen, D.: Ultrastructure of the ring-billed gull eye pecten. *Cytobios* 12: 191-201, 1975.
- (161) Southern, W.E., Hanzely, L., Bailey, R.L. and Molsen, D.V. Is the avian eye pecten a magnetic sensor? In: Papi, F. and Wallraff, H.G. eds., *Avian Navigation*. Springer-Verlag, Berlin, 344-351, 1982.
- (162) Andrianov, G.N., Brown, G.R. and Ilyinsky, O.B.: Responses of central neurons to electrical and magnetic stimuli of the ampullae of Lorenzini in the Black Sea skates. *J. Comp. Physiol.* 93: 287-299, 1974.
- (163) Branover, G.G., Vasil'yev, A.S., Gleyzer, S.I. and Tsinober, A.B.: A study of the behavior of cells in natural and artificial magnetic fields and an analysis of its reception mechanism. *J. Ichthyol.* 11: 608-614, 1971.
- (164) Kalmijn, A.J.: Electric and magnetic field detection in elasmobranch fishes. *Science* 218: 916-918, 1982.
- (165) Ovchinnikov, V.V., Gleyzer, S.I. and Alaktionov, G.Z.: Features of orientation of the European eel (*Anguilla anguilla*) (L.) at some stages of migration. *J. Ichthyol.* 13: 455-463, 1973.
- (166) Tesch, F.-W.: Influence of geomagnetism and salinity on the directional choice of eels. *Helgolander Wiss. Meeresunters* 26: 382-395, 1974.
- (167) Vasil'yev, A.S. and Gleyzer, S.I.: Changes in the activity of the freshwater eel (*Anguilla anguilla*) (L.) in magnetic fields. *J. Ichthyol.* 13: 322-324, 1973.
- (168) Phillips, J.B.: Use of the Earth's magnetic field by orienting cave salamanders (*Eurycea lucifuga*). *J. Comp. Physiol.* A121: 273-288, 1977.
- (169) Phillips, J.B. and Adler, K. Directional and discriminatory responses of salamanders to weak magnetic fields. In: Schmidt-Koenig, K. and Keeton, W.T. eds., *Animal Migration, Navigation, and Homing*. Springer-Verlag, Berlin, 325-334, 1978.
- (170) Rodda, G.H.: The orientation and navigation of juvenile alligators: evidence of magnetic sensitivity. *J. Comp. Physiol.* A154: 649-658, 1984.
- (171) Rodda, G.H.: Homeward paths of displaced juvenile alligators as determined by radiotelemetry. *Behav. Ecol. Sociobiol.* 14: 241-246, 1984.
- (172) Rodda, G.H.: Navigation in juvenile alligators. *Z. Tierpsychol.* 68: 65-77, 1985.

- (173) Baker, R.R. and Mather, J.G. A comparative approach to bird navigation: implications of parallel studies on mammals. In: Papi, F. and Wallraff, H.G. eds., *Avian Navigation*. Springer-Verlag, Berlin, 308-312, 1982.
- (174) Mather, J.G. and Baker, R.R.: Magnetic sense of direction in woodmice for route-based navigation. *Nature* 291: 152-155, 1981.
- (175) Baker, R.R.: Goal orientation by blindfolded humans after long-distance displacement: possible involvement of a magnetic sense. *Science* 210: 555-557, 1980.
- (176) Baker, R.R.: *Human Navigation and the Sixth Sense*. Hodder and Stoughton, London, 1981.
- (177) Gould, J.L. and Able, K.P.: Human homing: an elusive phenomenon. *Science* 212: 1061-1063, 1981.
- (178) Wallraff, H.G.: Versuche zur frage der gerichteten nachzug-aktivaitat von gekafigten singvögeln. *Verh. dt. zool Ges. Jena*: 339-356, 1965.
- (179) Howland, H.C.: Orientation of European robins to kramer cages. *Z. Tierpsychol.* 33: 295-312, 1973.
- (180) Emlen, S.T.: Bird migration: influence of physiological state upon celestial orientation. *Science* 165: 716-718, 1969.