The Journal of Experimental Biology **199**, 3–8 (1996)
Printed in Great Britain
JEB0120

THE FLEXIBLE MIGRATORY ORIENTATION SYSTEM OF THE SAVANNAH SPARROW (*PASSERCULUS SANDWICHENSIS*)

KENNETH P. ABLE AND MARY A. ABLE
Department of Biology, State University of New York, Albany, NY 12222, USA

Summary

The orientation system of the Savannah sparrow (*Passerculus sandwichensis*) is typical of nocturnal migrant passerine birds. It is based on a system of interacting compass senses: magnetic, star, polarized light and, perhaps, sun compasses. The magnetic compass capability develops in birds that have never seen the sky, but the preferred direction of magnetic orientation may be calibrated by celestial rotation (stars at night and polarized skylight patterns during the day). This ability to recalibrate magnetic orientation persists throughout life and enables the bird to compensate for variability in magnetic declination that may be encountered as it migrates. The polarized light compass may be manipulated by exposing young birds to altered patterns of skylight polarization. There is some evidence that the magnetic field may be involved in calibration of the polarized light compass. In short-term orientation decision-making during migration, visual information at sunset overrides both stars and magnetic cues, and polarized skylight is the relevant stimulus in dusk orientation. The star pattern compass seems to be of little importance. This extremely flexible orientation system enables the birds to respond to spatial and temporal variability in the quality and availability of orientation information.

Key words: migratory orientation, development, Savannah sparrow, *Passerculus sandwichensis*.

Introduction

Among North American migratory birds, the orientation behavior of the Savannah sparrow (*Passerculus sandwichensis*) has been more extensively studied than that of any other species. Moore (1978, 1980, 1982, 1985) studied visual and magnetic orientation in a series of cue-conflict experiments that revealed the importance of visual cues at sunset in the orientation of this species. Beginning with the work of Bingman (1983), our laboratory has been examining the development of orientation capabilities, using the Savannah sparrow as our model system. Its orientation behavior seems to be typical for nocturnal passerine migrants and in this regard it is now one of the two or three best known species in the world. Here we will discuss our current understanding of the orientation mechanisms in this species, how they interact during development in young birds and in mature individuals, and the similarities and differences between the orientation behavior of Savannah sparrows and other species.

Development of capabilities prior to the first migration

To study the ontogeny of orientation mechanisms, we take birds from nests during the first few days of life and hand-rear them under laboratory conditions. In this way, the birds' experience with relevant orientation cues can be controlled and manipulated so as to reveal the relationships amongst orientation capabilities. This has turned out to be a productive approach because the number of stimuli involved in bird orientation is large (the sun, skylight polarization patterns, the stars, the magnetic field) and the ontogenetic approach reduces some of the complexity that can obscure relationships in adult birds.

Migratory songbirds enter the world with two apparently innate representations of the direction of the first migration, one coded with respect to the magnetic field, the other with respect to the axis of celestial rotation (Wiltschko *et al.* 1987). An ability to orient in an appropriate migratory direction based on the magnetic field develops in young birds raised entirely indoors with no exposure to relevant visual orientation information. This ability has been demonstrated in several species of European passerines (Wiltschko and Gwinner, 1974; Gwinner and Wiltschko, 1978; Wiltschko *et al.* 1980; Bingman *et al.* 1985) and in the Savannah sparrow (Bingman, 1983; Able and Able, 1993*a*). Growing up within the ambient earth's magnetic field and a light:dark cycle is sufficient for this development, but little is known about the necessary conditions. Presumably some restricted range of field intensities might be effective (Wiltschko, 1978) and, inasmuch as the avian magnetic compass is based on inclination, proper development might be dependent upon the inclination of the local field. Recent experiments by Weindler *et al.* (1995) have shown that the development of magnetic orientation may be impaired if the experience of young birds is confined to fields of steep inclination (73 ˚) and, in theory, very shallow inclination should also be problematical.

Savannah sparrows taken from the field before their eyes open and reared entirely indoors exhibit magnetic orientation, during their first autumn migration, that is axial and oriented northwest–southeast (Bingman, 1981, 1983; Able and Able, 1993*a*). These birds nearly always orient in a unimodal direction on any given night; the bimodality is the result of birds reversing direction from night to night. This behavior does not seem to result from the laboratory rearing conditions nor from the restricted experience of the birds. Both young Savannah sparrows reared in the field and adults captured from the wild show equally strong bimodal magnetic orientation in autumn (Able and Able, 1995*a*, and unpublished data).

We have referred to this spontaneously developing orientation capability as the primary magnetic compass (Able and Bingman, 1987). In the first studies on the ontogeny of orientation in Savannah sparrows, Bingman (1983) discovered that the preferred direction of this primary magnetic orientation could be modified by exposure to celestial cues. Specifically, birds reared in situations in which magnetic compass directions and geographic directions differed (i.e. reared in a large magnetic declination) had altered magnetic orientation in autumn. They adopted a new preferred magnetic direction, one that corresponded to the appropriate geographic migratory direction. This result has been replicated in several species (Bingman *et al.* 1985; Prinz and Wiltschko, 1992). Thus, the two apparently innate representations of the migratory direction, celestial rotation and the magnetic field, may interact in birds growing up in natural situations with exposure to both the magnetic field and celestial cues. Geographic or true directions take precedence and calibrate the preferred magnetic direction. The primacy of geographic directions makes adaptive sense inasmuch as they are the ones most relevant to a bird required to move from high to low latitudes on its first migration, and many Savannah sparrows grow up in regions with large magnetic declination.

In Bingman's experiments, the birds were exposed to both day and night skies within the shifted magnetic field. Thus, it was impossible to infer anything about the specific visual cues involved in the calibration of magnetic orientation. Subsequently, we showed that exposure to either clear daytime or night skies was sufficient to alter the magnetic preference (Able and Able, 1990*a*), and that finding stimulated us to search for some common feature of the diurnal and nocturnal stimulus environment. Celestial rotation, already known to be important in the ontogeny of the star compass (Emlen, 1970; Wiltschko *et al.* 1987), can reveal geographic compass directions (e.g. true north) during day or night. We first tested whether celestial rotation of stars could calibrate magnetic orientation.

Four groups of hand-reared Savannah sparrows were exposed nightly to a small artificial 'sky' with an arbitrary pattern of 'stars'. Each group of birds viewed the sky from a small box cage at one of the four cardinal magnetic directions under the disc of simulated stars. The sky disc rotated about its center at 15 ˚ h^{-1} (the sense of rotation changed randomly from night to night), so each experimental group saw the center of rotation of the sky in a different magnetic direction. If the center of rotation of the artificial sky defines true north for the birds and provides the frame of reference for modification of the magnetic preference, then the groups of birds should differ in their magnetic orientation. Tests during the birds' first autumn in both shifted and unshifted magnetic fields showed that their magnetic orientation had been altered as predicted (Able and Able, 1990*b*). Thus, the axis of stellar rotation provides a sufficient stimulus to modify the developing magnetic directional preference.

During daytime, birds might assess celestial rotation using at least two visual cues: the path of the sun across the sky and either static or dynamic patterns of polarized skylight on clear days (Brines, 1980; Phillips and Waldvogel, 1982, 1988). Our initial attempt to investigate this problem involved removing one of the potential stimuli. Hand-raised birds were exposed to the clear sky, for 3–4 h at a time, throughout the day from sunrise to sunset. The experience of the four groups of birds differed with respect to whether they could see skylight polarization patterns and whether they viewed the sky in a shifted or unshifted magnetic field. Altered magnetic migratory orientation was observed only in the shifted field group that had visual access to the natural sky, including the sun itself as well as polarized skylight patterns. The shifted field group that viewed the sky through clear depolarizers showed no indication of altered magnetic orientation. Birds of all groups had similar opportunity to observe the sun's position and path across the sky. The results thus showed that skylight polarization is the necessary stimulus to produce calibration of magnetic orientation in daytime (Able and Able, 1993*b*).

To determine whether polarized light patterns in the sky are sufficient to effect calibration of magnetic orientation, we performed a direct manipulation of patterns of polarized light seen by the birds at dawn and dusk (Able and Able, 1995*b*). Hand-raised sparrows were allowed to observe the clear sky for 1 h prior to local sunrise and for 1 h following local sunset. They never saw the sun or the stars. The birds observed the sky through bands of polarizing material covering domes atop Emlen funnel cages. For each group of birds, the **e**-vector axis of the polarizing material was aligned in one of three orientations with respect to the azimuth of sunrise and sunset: (1) 90 ˚; (2) 45 ˚ clockwise; or (3) 45 ˚ counterclockwise. When tested for magnetic orientation in autumn, the directions chosen by the three groups differed significantly and as predicted by a model in which static patterns of polarized skylight are used to localize true north (Phillips and Waldvogel, 1982, 1988). The static patterns used in these experiments are, of course, snapshots of the rotation of skylight polarization about the celestial pole. Although quite simplified, they appear to be sufficient to provide the geographic reference necessary for calibration of magnetic orientation.

Relatively much less is known about the development of visual orientation mechanisms in the Savannah sparrow. Although Moore (1978, 1980) could find no compelling evidence that Savannah sparrows possess a star compass, Bingman's (1983) hand-raised birds that grew up outdoors showed axial northeast–southwest orientation when tested under starry skies in a vertical magnetic field (i.e. no magnetic orientation information available). A group of sparrows raised outdoors within a shifted magnetic field showed identical orientation under stars, indicating that the development of stellar orientation is unaffected by magnetic influences. Similar results have been found in other species (Bingman, 1984; Wiltschko, 1982; Wiltschko *et al.* 1987; but see Katz *et al.* 1988). There is no reason to doubt that the star pattern compass of the Savannah sparrow develops in the same way that it does in other species, although no direct studies have been performed. Configurational star patterns acquire learned directional meaning from the axis of stellar rotation. On the basis of an internal rule, the pole star is defined as true north. Once learned, rotational information is no longer required, and the static relationships between stars are sufficient for meaningful orientation (Emlen, 1970; Wiltschko *et al.* 1987).

Visual information at sunset is of primary importance in the pantheon of orientation mechanisms possessed by Savannah sparrows (Moore, 1978, 1980, 1982, 1985). As in other night migrants (blackcap, *Sylvia atricapilla*, Helbig, 1990*a*; European robin, *Erithacus rubecula*, Helbig, 1991), polarized skylight patterns at sunset, rather than the sun itself, seem to provide the relevant directional information. To examine how this orientation develops, we exposed hand-raised Savannah sparrows to clear daytime skies in cages covered with sheet polarizers such that each of three groups of birds observed a different directional relationship between sun azimuth, **e**-vector of skylight polarization and magnetic directions. In their first autumn, under clear skies (no polaroids) and in the normal magnetic field, the migratory orientation at dusk of these birds showed that they had learned compass directions relative to the manipulated patterns of polarized light. They selected the directions indicated by this polarized light compass in preference to magnetic directions and seemed unable to select appropriate directions when sunset position was the only available visual cue (tests under depolarizing material) (Able and Able, 1990*c*).

Young birds might learn to perform compass orientation using the **e**-vector of polarized skylight on the basis of some internal set of rules analogous to those involved in the establishment of the star compass (Brines, 1980; Phillips and Waldvogel, 1988). Our results are consistent with this hypothesis. However, the visual stimulus might be calibrated by some other directional cue. We also obtained some results (Able and Able, 1990*c*) suggesting that the magnetic field might be involved in calibrating the polarized light compass. The sample size in this experiment was small and, in the light of subsequent work that has revealed a robust calibrating effect of polarized skylight patterns upon magnetic orientation (Able and Able, 1993*b*, 1995*b*), the result is somewhat paradoxical. Further experiments are required to elucidate the development of sunset orientation mechanisms.

Interaction of orientation capabilities in 'adults'

Most of what we know about the relationships among orientation cues in Savannah sparrows of migratory age has come from experiments performed by Moore (1978, 1980, 1982, 1985). His work was the first to document clearly the overriding importance of visual cues at sunset in the directional decision-making process. He concluded (Moore, 1978) that directional information at sunset was necessary and sufficient for migratory orientation and could find no compelling evidence that Savannah sparrows possess an independent star compass. A similar picture has since emerged for a number of other species (for reviews, see Moore, 1987; Able, 1993). Although Bingman (1983) showed that hand-raised Savannah sparrows develop a functional star compass, it certainly appears to rank low in the hierarchy of orientation cues. More work is needed to understand the development of the star compass in this species and its role, if any, in the orientation of migrants.

On the basis of current knowledge, the relationships among orientation cues, or compasses, in this species seem to be very similar to those of other nocturnal migrants, although comparable studies are few (Able, 1993). In short-term orientation decision-making, visual information at sunset overrides both stars and magnetic cues, and polarized skylight is the relevant stimulus in dusk orientation (but see Bingman and Wiltschko, 1988). In several European species, there is evidence that the magnetic compass takes precedence over stars in the short term and that artificial star patterns may be calibrated by magnetic directions (Wiltschko and Wiltschko 1975*a*,*b*, 1976). Moore's cue-conflict experiments (1982, 1985) found no such effect in Savannah sparrows.

We have tended to think that the types of interactions between innate predispositions and programmed learning that characterize the early development of orientation mechanisms come to an end when birds reach migratory age. In 'adult' birds, experiments have sought to discover the hierarchical relationships among what were presumed to be inflexible orientation mechanisms. Results from some of our experiments on the calibration of magnetic orientation in young birds caused us to re-examine this issue. Celestial rotation provides information about true compass directions that calibrates the direction of migration selected using the magnetic compass. Because true compass directions are those most relevant to a migratory bird, it should often be advantageous to be able to adjust the magnetic preference by a geographic reference, especially at high northern latitudes where magnetic declination is large. Paradoxically, however, magnetic orientation so calibrated will be reliable only within a region of similar declination: a bird traveling into a region of different declination would find its magnetic preference inappropriate. To cope with this problem, magnetic orientation would have to remain open to recalibration in older birds. Earlier studies suggested that this was not the case (for reviews, see Wiltschko and Wiltschko, 1991; Able, 1993).

To examine this question, we captured Savannah sparrows

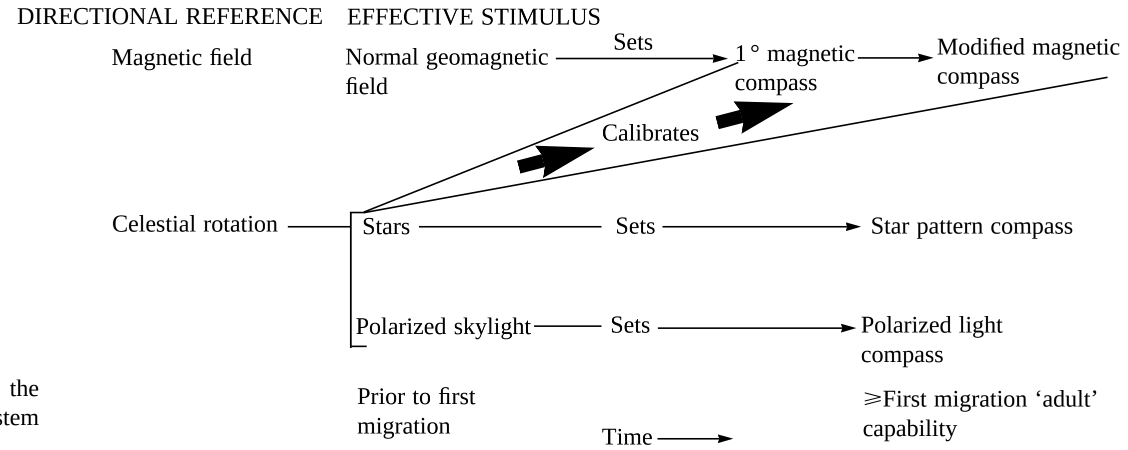

Fig. 1. Interactions in the migratory orientation system of the Savannah sparrow.

in the field at the end of the nesting season. Both adult birds with prior migratory experience and birds born during the previous summer and reared in the wild were used. During the autumn migration season, we placed these birds in an outdoor cage within a shifted magnetic field. We attempted to simulate a typical migration stop-over by requiring the birds to experience four clear days and nights within the shifted field. We then compared their magnetic orientation with that following similar exposure to the day and night sky in an unshifted magnetic field. The results of this experiment showed that the same sort of calibration of magnetic orientation found in very young birds also occurs in adults (Able and Able, 1995*a*). That magnetic orientation may be calibrated repeatedly and apparently indefinitely suggests that the plasticity that characterizes early development persists throughout the life of these birds. Celestial rotation assessed *via* visual cues appears to be of overriding importance in both early development and in adulthood.

Conclusions

To the extent that comparable data exist, the orientation system of the Savannah sparrow appears to be typical of nocturnal migrants. Indeed, largely because of the small number of studies performed and differences in experimental design among them, it is not possible to make a convincing case for species differences in orientation behavior among night migrants (Helbig, 1990*b*; Able, 1993; Åkesson, 1994). The picture that emerges from this well-studied species is of a navigation system based upon multiple compass mechanisms that interact throughout the life of the bird. The large amount of behavioral plasticity that seems to persist indefinitely provides individuals with the flexibility to respond to spatial and temporal variability in orientation information that they may encounter while *en route*.

Spatial variability in the quality or availability of orientation information may come in various forms. As described above, birds may encounter substantial changes in magnetic declination as they move. The capacity to recalibrate magnetic orientation with visual cues provides a means of coping with this problem. The inclination magnetic compass of birds will not function properly at the magnetic equator, where field lines are parallel to the earth’s surface, and inclination reverses when one passes from the northern to southern magnetic hemispheres. Recent studies have shown that exposure to a horizontal magnetic field somehow reverses the response of trans-equatorial migrants to field inclination (Wiltschko and Wiltschko, 1992; Beason, 1992). For migrants that move a large distance in latitude, familiar star patterns will disappear below the northern horizon and new, unfamiliar ones will become visible to the first-time migrant. In this situation, the calibration of star patterns by magnetic directions described by Wiltschko and Wiltschko (1975*a*,*b*, 1976) might play a role. Temporal variability may occur in the form of cloud cover that can temporarily obscure visual orientation cues. At such times, it may be important to have available alternative mechanisms. Visual cues such as sunset position will change over the migration season. Sunset azimuth changes most rapidly around the equinoxes, a time of year when many birds are migrating. In adult yellow-rumped warblers (*Dendroica coronata*), sunset position seems to be calibrated by polarized skylight patterns (Phillips and Moore, 1992).

Perhaps the most important conclusion is that, contrary to the long-standing consensus in the field, plasticity in migratory orientation is not confined to a sensitive period in the early life of the Savannah sparrow. The interactions as we currently understand them are outlined in Fig. 1. Only the initial calibration of star patterns by stellar rotation seems to be irreversible once the bird reaches migratory age. Indigo buntings (*Passerina cyanea*) exposed to an unnatural center of rotation of a planetarium sky learned an incorrect star pattern compass. These birds were subsequently held for several months in an outdoor aviary where they were exposed to the natural rotation of the starry sky. In their second autumn, they continued to orient in the same direction as in their first, i.e. they did not recalibrate the star compass (Emlen, 1972). This result is perhaps not surprising because, under natural conditions, stellar rotation provides an invariant source of true compass directions and star patterns calibrated on the basis of stellar rotation should not require recalibration.

It has become apparent that the same stimuli may be employed in very different roles in the development and day-to-day operation of orientation systems. For example, celestial rotation monitored *via* stars, polarized skylight patterns or, perhaps, the sun plays a pre-eminent role in the calibration of orientation mechanisms. These same visual stimuli may be employed in short-term, snapshot compass roles in which observation of rotation is not required. In this latter context, they are essentially fixed landmarks that derive directional meaning from more or less frequent calibration by some other reference (see also Wiltschko and Wiltschko, 1976).

Work in our laboratory on the orientation of Savannah sparrows has been supported over the years by the National Science Foundation (grants BNS 7923711, BNS 8217633, BNS 8608653, BNS 8909886, IBN 9119508 and IBN 9419664) and awards from the E. N. Huyck Preserve, Frank M. Chapman Fund and Sigma Xi to V. P. Bingman. Charles Walcott has been generous in allowing us to use his magnetometer and Giorgio Trapani of Polaroid Corporation has been very helpful in obtaining polarizing material and providing advice on its use.

References

ABLE, K. P. (1993). Orientation cues used by migratory birds: A review of cue-conflict experiments. *Trends Ecol. Evol*. **8**, 367–371.

ABLE, K. P. AND ABLE, M. A. (1990*a*). Ontogeny of migratory orientation in the Savannah sparrow, *Passerculus sandwichensis*: Calibration of the magnetic compass. *Anim. Behav.* **39**, 905–913.

ABLE, K. P. AND ABLE, M. A. (1990*b*). Calibration of the magnetic compass of a migratory bird by celestial rotation. *Nature* **347**, 378–380.

ABLE, K. P. AND ABLE, M. A. (1990*c*). Ontogeny of migratory orientation in the Savannah sparrow, *Passerculus sandwichensis*: mechanisms at sunset. *Anim. Behav.* **39**, 1189–1198.

ABLE, K. P. AND ABLE, M. A. (1993*a*). Magnetic orientation in the Savannah sparrow. *Ethology* **93**, 337–343.

ABLE, K. P. AND ABLE, M. A. (1993*b*). Daytime calibration of magnetic orientation in a migratory bird requires a view of skylight polarization. *Nature* **364**, 523–525.

ABLE, K. P. AND ABLE, M. A. (1995*a*). Interactions in the flexible orientation system of a migratory bird. *Nature* **375**, 230–232.

ABLE, K. P. AND ABLE, M. A. (1995*b*). Manipulations of polarized skylight calibrate magnetic orientation in a migratory bird. *J. comp. Physiol.* A **177**, 351–356.

ABLE, K. P. AND BINGMAN, V. P. (1987). The development of orientation and navigation behavior in birds. *Q. Rev. Biol.* **62**, 1–29.

ÅKESSON, S. (1994). Comparative orientation experiments with different species of passerine long-distance migrants: Effects of magnetic field manipulation. *Anim. Behav.* **48**, 1379–1393.

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

BINGMAN, V. P. (1981). Savannah sparrows have a magnetic compass. *Anim. Behav.* **29**, 962–963.

BINGMAN, V. P. (1983). Magnetic field orientation of migratory naive Savannah sparrows with different first summer experience. *Behaviour* **87**, 43–53.

BINGMAN, V. P. (1984). Night sky orientation of migratory pied flycatchers raised in different magnetic fields. *Behav. Ecol. Sociobiol.* **15**, 77–80.

BINGMAN, V. P., BECK, W. AND WILTSCHKO, W. (1985). Ontogeny of migratory orientation: A look at the pied flycatcher, *Ficedula hypoleuca*. In *Migration: Mechanisms and Adaptive Significance* (ed. M. A. Rankin), pp. 543–552. Austin: Contrib. Marine Sci. Suppl., vol. 27, Marine Sci. Inst., University of Texas.

BINGMAN, V. P. AND WILTSCHKO, W. (1988). Orientation of dunnocks (*Prunella modularis*) at sunset. *Ethology* **77**, 1–9.

BRINES, M. L. (1980). Dynamic patterns of skylight polarization as clock and compass. *J. theor. Biol.* **86**, 507–512.

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

EMLEN, S. T. (1972). The ontogenetic development of orientation capabilities. In *Animal Orientation and Navigation* (ed. S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs and R. E. Belleville), pp. 191–210. Washington, DC: NASA SP-262, U.S. Government Printing Office.

GWINNER, E. AND WILTSCHKO, W. (1978). Endogenously controlled change in the migratory direction of the garden warbler, *Sylvia borin*. *J. comp. Physiol.* A **125**, 267–273.

HELBIG, A. J. (1990*a*). Depolarization of natural skylight disrupts orientation of an avian nocturnal migrant. *Experientia* **46**, 755–758.

HELBIG, A. J. (1990*b*). Are orientation mechanisms among migratory birds species-specific? *Trends Ecol. Evol.* **5**, 365–366.

HELBIG, A. J. (1991). Dusk orientation of migratory European robins, *Erithacus rubecula*: The role of sun-related directional information. *Anim. Behav.* **41**, 313–322.

KATZ, Y., LIEPA, V. AND VIKSNE, J. (1988). Orientation research in the Latvian SSR in 1982–1985. In *Acta XIX Congressus Internationalis Ornithologicus* (ed. H. Ouellet), pp. 1919–1931. Ottawa: University of Ottawa Press.

MOORE, F. R. (1978). Sunset and the orientation of a nocturnally migrating bird. *Nature* **274**, 154–156.

MOORE, F. R. (1980). Solar cues in the migratory orientation of the Savannah sparrow (*Passerculus sandwichensis*). *Anim. Behav.* **28**, 684–704.

MOORE, F. R. (1982). Sunset and the orientation of a nocturnal bird migrant: A mirror experiment. *Behav. Ecol. Sociobiol.* **10**, 153–155.

MOORE, F. R. (1985). Integration of environmental stimuli in the migratory orientation of the Savannah sparrow, *Passerculus sandwichensis*. *Anim. Behav.* **33**, 657–663.

MOORE, F. R. (1987). Sunset and the orientation behaviour of migrating birds. *Biol. Rev.* **62**, 65–86.

PHILLIPS, J. B. AND MOORE, F. R. (1992). Calibration of the sun compass by sunset polarized light patterns in a migratory bird. *Behav. Ecol. Sociobiol.* **31**, 189–193.

PHILLIPS, J. B. AND WALDVOGEL, J. A. (1982). Reflected light cues generate the short-term deflector-loft effect. In *Avian Navigation* (ed. F. Papi and H. G. Wallraff), pp. 190–202. Berlin: Springer-Verlag.

PHILLIPS, J. B. AND WALDVOGEL, J. A. (1988). Celestial polarized light patterns as a calibration reference for sun compass of homing pigeons. *J. theor. Biol.* **131**, 55–67.

PRINZ, K. AND WILTSCHKO, W. (1992). Migratory orientation of pied flycatchers: Interaction of stellar and magnetic information during ontogeny. *Anim. Behav.* **44**, 539–545.

WEINDLER, P., BECK, W., LIEPA, V. AND WILTSCHKO, W. (1995). Development of migratory orientation in pied flycatchers in different magnetic inclinations. *Anim. Behav.* **49**, 227–234.

WILTSCHKO, W. (1978). Further analysis of the magnetic compass of migratory birds. In *Animal Migration*, *Navigation*, *and Homing* (ed. K. Schmidt-Koenig and W. T. Keeton), pp. 302–310. Berlin: Springer-Verlag.

WILTSCHKO, W. (1982). The migratory orientation of garden warblers, *Sylvia borin*. In *Avian Navigation* (ed. F. Papi and H. G. Wallraff), pp. 50–58. Berlin: Springer-Verlag.

WILTSCHKO, W., DAUM, P., FERGENBAUER-KIMMEL, A. AND WILTSCHKO, R. (1987). The development of the star compass in garden warblers, *Sylvia borin*. *Ethology* **74**, 285–292.

WILTSCHKO, W. AND GWINNER, E. (1974). Evidence for an innate magnetic compass in garden warblers. *Naturwissenschaften* **61**, 406.

WILTSCHKO, W., GWINNER, E. AND WILTSCHKO, R. (1980). The effect of celestial cues on the ontogeny of non-visual orientation in the garden warbler (*Sylvia borin*). *Z. Tierpsychol.* **53**, 1–8.

WILTSCHKO, W. AND WILTSCHKO, R. (1975*a*). The interaction of stars and magnetic field in the orientation system of night migrating birds. I. Autumn experiments with European warblers (gen. *Sylvia*). *Z. Tierpsychol.* **37**, 337–355.

WILTSCHKO, W. AND WILTSCHKO, R. (1975*b*). The interaction of stars and magnetic field in the orientation system of night migrating birds. II. Spring experiments with European robins (*Erithacus rubecula*). *Z. Tierpsychol.* **39**, 265–282.

WILTSCHKO, W. AND WILTSCHKO, R. (1976). Interrelations of magnetic compass and star orientation in night-migrating birds. *J. comp. Physiol.* **109**, 91–99.

WILTSCHKO, W. AND WILTSCHKO, R. (1991). Magnetic orientation and celestial cues in migratory orientation. In *Orientation in Birds* (ed. P. Berthold), pp. 16–37. Basel: Birkhauser.

WILTSCHKO, W. AND WILTSCHKO, R. (1992). Migratory orientation: Magnetic compass orientation of garden warblers (*Sylvia borin*) after a simulated crossing of the magnetic equator. *Ethology* **91**, 70–74.