Evidence for calibration of magnetic migratory orientation in Savannah sparrows reared in the field

Kenneth P. Able* and Mary A. Able

Department of Biological Sciences, University at Albany, State University of New York, Albany, NY 12222, USA

The orientation system of migratory birds consists of a magnetic compass and compasses based upon celestial cues. In many places, magnetic compass directions and true or geographic compass directions differ (referred to as magnetic declination). It has been demonstrated experimentally in several species that the innate preferred direction of magnetic orientation can be calibrated by celestial rotation, an indicator of geographic directions. This calibration process brings the two types of compass into conformity and provides the birds with a mechanism that compensates for the spatial variation in magnetic declination. Calibration of magnetic orientation has heretofore been demonstrated only with hand-raised birds exposed to very large declination (90° or more). Here we show that the magnetic orientation of wild birds from near Albany, New York, USA (declination = 14° W) was N–S, a clockwise shift of 26° from the NNW–SSE direction of birds raised entirely indoors. Hand-raised birds having visual experience with either the daytime sky or both day and night sky orientated N–S, similar to wild-caught birds. These data provide the first confirmation that calibration of magnetic orientation occurs under natural conditions and in response to modest declination values.

Keywords: Savannah sparrows; magnetic calibration; orientation system; migratory orientation

1. INTRODUCTION

Orientation in nocturnally migrating birds is based on magnetic, polarized light and star pattern compasses (e.g. Wiltschko & Wiltschko 1994). Studies of the compass mechanisms have revealed a complex web of interactions, both during the development of orientation behaviour in young birds and in mature individuals exhibiting migratory activity (for reviews, see Able & Able 1998, 1999). With respect to ontogeny, migratory birds are born with two apparently innate representations of the direction of the first migration, one coded with respect to the magnetic field and the other with respect to the axis of celestial rotation (Wiltschko *et al.* 1987). The magnetic compass, which develops to a functional level even in birds raised without any exposure to the natural sky, is one of the foundation components of the migratory orientation system (Wiltschko & Wiltschko 1995).

Bingman (1983) discovered that the spontaneously developing preferred magnetic orientation direction of Savannah sparrows (*Passerculus sandwichensis*) could be modified by exposure to the sky. Specifically, birds reared in conditions in which magnetic and geographic compass directions differed (i.e. reared in a large magnetic declination) adopted a new preferred magnetic direction, one that corresponded to the appropriate geographic direction. Termed calibration of magnetic orientation, the phenomenon has been demonstrated in several species (Bingman *et al.* 1985; Prinz & Wiltschko 1992). In all

cases, geographic or true compass directions took precedence and calibrated the preferred magnetic direction of migratory orientation. This primacy of geographic directions makes adaptive sense because it provides birds born in regions with large magnetic declination a means of bringing their magnetic and visual compasses into conformity.

Calibration of magnetic orientation by visual cues is based on celestial rotation of star patterns at night (Able & Able 1990a) and of patterns of polarized skylight during the day (Able & Able 1993, 1995a; Weindler *et al.* 1998). All of the experiments demonstrating calibration of magnetic orientation during ontogeny were performed on birds hand raised under controlled conditions where exposure to celestial rotation took place in situations in which geographic and magnetic directions differed by 90° or more. Within the breeding range of the Savannah sparrow, magnetic declination values may reach ± 40 – 50° , but over most of its range the difference is much smaller. Most migratory birds born in temperate latitudes will grow up in areas with a declination of less than 30° . If calibration of magnetic orientation is an adaptive mechanism, it should occur under natural conditions in all declinations. Therefore, it is important to learn whether calibration occurs in young wild birds that grow up in typical natural declination values. To do this, we compared the orientation of birds reared in the field in Upstate New York (where local declination is 14° W) with birds from the same population reared entirely indoors and with hand-raised birds that had limited and controlled experience with celestial orientation cues.

*Author for correspondence (kpa@cnsunix.albany.edu).

Table 1. *Rearing conditions, amount of exposure to the ambient geomagnetic field in the local magnetic declination (14°W) and conditions during magnetic orientation tests*

(CW, clockwise; CCW, counterclockwise.)

year	rearing condition	<i>n</i>	exposure to visual cues	duration of exposure	magnetic field during tests
1990	field	17	day and night sky	several weeks	ambient
1994	field	29	day and night sky	several weeks	ambient
1997	field	29	day and night sky	several weeks	ambient
1988	hand raised	10	none	—	ambient and 92° CW shifted
1990	hand raised	25	none	—	ambient and 90° CCW shifted
1987	hand raised	9	day sky only	25–32 h	ambient
1992	hand raised	10	day sky only	28 h	ambient and 90° CCW shifted
1995	hand raised	22	day sky only	≥5 days	ambient
1989	hand raised	16	day and night sky	54 days	ambient and 90° CW shifted

2. METHODS

(a) *General methods, orientation tests and analysis*

All tests were performed with Savannah sparrows captured in Albany County, New York, USA. Birds referred to as wild-caught birds were captured in mist-nets in local breeding areas at the end of the breeding season and prior to the onset of migration. Hand-raised birds were removed from nests in the field before their eyes opened and were reared in the laboratory under the conditions specified below for each group. General details of hand rearing are given in Able & Able (1990b). All orientation tests were performed between mid-September and mid-November in Emlen funnel orientation cages (Emlen & Emlen 1966). The funnel tops were covered with white translucent plastic sheets preventing the birds any view outside the cage. A dim fluorescent light passing through two diffusers and the cage cover provided a light intensity of 0.2–0.4 lux within the cage. This variation in light intensity occurred across the array of test cages; the light intensity within each orientation cage was uniform.

Orientation tests were performed in a wooden frame building in which the ambient magnetic field was 5.6×10^4 nT with an inclination of 71° (for more details on orientation tests see Able & Able (1990a, 1993)). Each bird was tested repeatedly (3–13 times). The mean of the individual nightly modal directions of each bird was used in the analysis, i.e. each bird is represented only once in the analysis. Data were analysed as described by Cherry & Able (1986), Batschelet (1981) and Able & Able (1993). All directions are magnetic.

(b) *Experimental groups, treatment and testing conditions (see table 1)*

(i) *Wild-caught birds*

Three groups of wild sparrows were tested in the ambient magnetic field ($n = 75$ birds): (i) birds captured 12–13 September 1990 ($n = 17$), (ii) birds captured 11–12 September 1994 ($n = 29$), and (iii) birds captured 10–11 September 1997 ($n = 29$). Twenty-two of these birds were adults (by skull ossification), with the remainder born during the previous summer. There were no differences of any kind in the orientation behaviour of the two age groups and their data were pooled.

(ii) *Hand-raised birds, indoors*

Birds raised during summer 1988 ($n = 10$) and summer 1990 ($n = 25$) had no visual experience with the night- or daytime sky. These birds were tested in both the ambient magnetic field and a field of ambient intensity with the horizontal component shifted 92° clockwise (1988) or 90° counterclockwise (1990) by Helmholtz coils. The orientation of the birds did not differ in the two field conditions (Watson's U^2 -test), so tests in shifted and unshifted fields were pooled to eliminate pseudo-replication.

(iii) *Hand-raised birds, daytime sky only*

Three groups of hand-raised birds had controlled exposure to the natural daytime sky in a normal magnetic field (5.5×10^4 nT, inclination 70° and declination 14° W). Birds raised during summer 1987 ($n = 9$) had 25–32 h of exposure to the clear sky, spread over the course of a day (see Able & Able (1990b) for more details). Birds raised during summer 1992 ($n = 10$) had 28 h of exposure to the clear sky (see Able & Able (1993) for details). Birds raised during summer 1995 ($n = 22$) had exposure to at least five days of clear or nearly clear skies (see Able & Able (1997) for more details). Birds raised during 1987 and 1995 were tested only in the ambient magnetic field, while birds raised in 1992 were tested in both unshifted and shifted (90° counterclockwise produced by a 1.8-m Merritt square coil) magnetic fields and the orientation data pooled as above.

(iv) *Hand-raised birds, night- and daytime skies*

Birds raised during summer 1989 ($n = 16$) lived outdoors in a group cage from 8 August to 1 October. Tests in unshifted and shifted (90° clockwise produced by Helmholtz coil) magnetic fields were pooled for each bird.

3. RESULTS

(a) *Orientation of wild-caught birds*

The magnetic orientation of the wild-caught Savannah sparrows was axial, orientated N–S: modes = 7 and 187°, $r_2 = 0.452$, $p < 0.001$, Rayleigh test, $n = 75$ birds and 95% CI = 21° (figure 1a).

Figure 1. Autumn magnetic orientation of Savannah sparrows. (a) Orientation of wild-caught sparrows tested in the normal geomagnetic field. Solid dots, autumn 1990 tests; plus signs, autumn 1994 tests; solid squares, autumn 1997 tests. (b) Orientation of sparrows raised indoors with no view of the night- or daytime sky. Solid dots, autumn 1990 tests; plus signs, autumn 1988 tests. The arrows indicate the mean direction of orientation and their length is proportional to the length of the mean vector. The broken and solid inner circles represent the 5 and 1% significance levels for the Rayleigh test, respectively. Each point represents the mean of the modal directions of each bird (each bird tested 3–13 times).

(b) Orientation of birds raised indoors

The magnetic orientation of hand-raised birds that had no visual experience with either night- or daytime sky was also axial, but orientated NNW–SSE:

modes = 161° and 341°, $r_2 = 0.417$, $p < 0.005$, $n = 35$ birds and 99% CI = 31° (figure 1b). The orientation of this group differed from that of the wild-caught birds by 26° and the two distributions differ statistically (Watson's U^2 -test, $p < 0.005$) (figure 1b).

(c) Orientation of hand-raised birds exposed to the daytime sky

Hand-raised birds that had visual experience with the daytime sky in the ambient earth's magnetic field orientated N–S: modes = 179° and 359°, $r_2 = 0.436$, $p < 0.001$, $n = 41$ birds and 95% CI = 28° (figure 2a). The orientation of this group differs from that of the birds reared indoors by 18° and from the wild birds by 8°; the distribution is not statistically different from either.

(d) Orientation of hand-raised birds exposed to night- and daytime skies

Hand-raised birds having visual experience with both day and night skies in the ambient geomagnetic field orientated N–S: modes = 180° and 360°, $r_2 = 0.454$, $p < 0.04$, $n = 16$ birds and 95% CI = 75° (figure 2b). The orientation of this small group is essentially identical to that of § 3(c) and is likewise not statistically different from the other groups.

4. DISCUSSION

Since the discovery that magnetic orientation was open to calibration by indicators of true compass directions, the adaptive explanation has been put forward that such plasticity provides birds born in places with magnetic declination a means of bringing their visual and magnetic compasses into conformity (Bingman 1983; Able & Able 1990a,b, 1993). The primacy of indicators of true compass directions is expected because they are invariant, whereas magnetic directions are quite variable in space. Across the extensive breeding range of the Savannah sparrow, magnetic declination may vary by as much as 90°, so the potential for conflicts between compasses based on celestial rotation and the magnetic compass is great. However, all demonstrations of calibration of magnetic orientation were conducted with hand-raised birds exposed to visual cues within coils that produced artificial magnetic fields with large declinations. It is important to find out whether calibration occurs under natural conditions and in more typical values of magnetic declination.

In the vicinity of Albany, New York, where these experiments were performed, magnetic north lies *ca.* 14° west of true north. The calibration hypothesis predicts that the magnetic orientation of wild-caught birds should be shifted *ca.* 14° clockwise relative to birds raised indoors with no experience with celestial cues. The wild-caught birds used in these tests showed a shift of 26° in the predicted direction relative to birds raised entirely indoors and, thus, provide the first confirmation that calibration of magnetic orientation occurs under natural conditions. The magnitude of the difference in direction between the two groups is somewhat larger, but is not statistically different from the predicted difference. The fact that the same result was obtained with groups of wild-caught birds captured in three different years indicates that the result is robust even though the predicted difference is small. To complete the

Figure 2. Autumn magnetic orientation of hand-raised Savannah sparrows having visual experience with celestial cues. (a) Orientation of sparrows exposed to the clear daytime sky within the normal geomagnetic field. Plus signs, autumn 1987 tests; solid dots, autumn 1992 tests; solid squares, autumn 1995 tests. (b) Orientation of sparrows exposed to both clear day and night skies within the normal geomagnetic field. Other symbols and conventions as in figure 1.

picture, it would be interesting to obtain magnetic orientation data from wild Savannah sparrows that grew up in localities with very large declination values, though these situations are more similar to the experimental manipulations that have been performed.

In the course of performing experiments on the ontogeny of orientation mechanisms in the Savannah sparrow

over a number of years, we have had occasion to expose hand-raised birds to the natural night- and/or daytime sky in the ambient geomagnetic field. These birds experienced much less exposure to the sky than individuals born and raised in the field. However, similar durations of exposure were sufficient to induce calibration in experimental birds exposed to large declination (90° or more). Therefore, unless very large declinations are a more potent calibration stimulus, we should expect that birds with limited exposure to celestial rotation in the ambient field would also exhibit a 14° clockwise shift in orientation. In fact, both birds experienced only with the clear daytime sky and those with experience with both day and night sky showed the predicted shifts: 18° clockwise in the case of the daytime sky group and 19° in the case of the day plus night sky group. Given the typical variability in cage orientation data and the sample sizes involved, it is not surprising that neither group is statistically different from the birds raised indoors. That the shifts are of the predicted direction and magnitude indicates that limited experience is sufficient to produce calibration, even with the small declinations found in most natural situations.

Autumn migratory orientation in Savannah sparrows, particularly magnetic orientation, is consistently axial. This is the case with hand-raised as well as wild-caught birds and adults with migratory experience as well as hatching-year birds that have not migrated for the first time (Bingman 1983; Able & Able 1990a,b, 1993, 1996). The birds nearly always orientate in a unimodal direction on a given night; the bimodality is the result of birds reversing direction from night to night. If tested a sufficient number of times in autumn, virtually every Savannah sparrow will exhibit axial orientation. Spring magnetic migratory orientation is unimodal, even in birds that were bimodal in autumn and were held in captivity until spring (Able & Able 1996). Axial orientation has been observed in other species (Berthold *et al.* 1990; Weindler *et al.* 1995, 1998), but seems to be of more frequent occurrence in Savannah sparrows. Studies with pied flycatchers (*Ficedula hypoleuca*) have shown that axial orientation developed when birds grew up in a magnetic field with steep inclination (73°) (Weindler *et al.* 1995, 1998). Savannah sparrows in the Albany, New York area grow up in a magnetic field with 70° inclination, but this explanation does not readily account for the seasonal change from bimodality to unimodality and other complexities of Savannah sparrow migratory orientation.

The development of compass orientation mechanisms in migratory birds involves a complex interaction of innate information and programmed learning governed by sets of rules (Able & Able 1999). The direction of the first migration is coded with respect to celestial rotation and with respect to the magnetic field. Recent studies on the garden warbler (*Sylvia borin*) have shown that the congenital information represented with respect to the magnetic field may contain more precise details concerning the migratory track of the population, whereas that coded with respect to celestial rotation may be less specific (Weindler *et al.* 1996). However, celestial rotation provides an invariant source of true compass directions and can thus be employed to nullify the effects of magnetic declination that could otherwise render the more precise innate magnetic migration directions

useless. At least for species with breeding ranges that encompass a wide range of declination values, this sort of learning plasticity could be of significant advantage to individual migrants.

Problems caused by temporal and spatial variability of orientation cues only compound as a bird embarks upon migration. As migrants travel southward, familiar star patterns disappear and new ones become visible. Changing day length and season alter the relationships between visual cues (star and skylight polarization patterns), direction and time. Celestial rotation continues to provide an inexorable beacon indicating true north, but magnetic declination will change as the bird moves, generally tending towards smaller values as it progresses southward. Magnetic orientation calibrated to compensate for the large declination of a high latitude birthplace will become increasingly in error as the bird moves to areas with ever smaller declination. In species with breeding ranges that contain a wide range of magnetic declination, the only option would seem to be to employ celestial rotation repeatedly to recalibrate magnetic orientation during the whole course of migration. This sort of behaviour has been demonstrated experimentally in Savannah sparrows (Able & Able 1995b), but does not seem to characterize some other species tested (Wiltschko *et al.* 1997).

We thank the Becker family of Knox, New York, for allowing us to capture birds on their farm. Support for this work was provided by the National Science Foundation (BNS8217633, BNS8608653, BNS8909886, IBN9119508 and IBN9419644).

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