

## Response to R. Wiltschko et al. (J. Ornithol.): Contradictory results on the role of polarized light in compass calibration in migratory songbirds

Rachel Muheim · Susanne Åkesson ·  
John B. Phillips

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In a recent review of the cue conflict literature (Muheim et al. 2006a), we summarized all of the published studies in which migratory birds were exposed to a shifted magnetic field relative to the natural celestial cues. We concluded that the birds recalibrated the magnetic compass with respect to celestial cues if they had a view of the sky down to the horizon at sunrise or sunset. When the view of the horizon was obstructed during exposure (e.g., when exposure to the cue conflict was carried out in an orientation funnel or automatic registration cage), the birds recalibrated the celestial cues with respect to the magnetic field. We found no other variables, e.g., migratory phase (before vs. during migration), season, species or location, that could explain the otherwise highly variable and seemingly contradictory results from the different studies. In all of the studies cited by Wiltschko et al. as contradictory to our theory (Wiltschko and Wiltschko 1975a, b; Bingman 1987; Bingman and Wiltschko 1988; Wiltschko et al. 1998; Sandberg et al. 2000), the birds were exposed to the cue conflict in funnels or registration cages, restricting the view

of the horizon, the section of sky that we suggest is critical for magnetic compass calibration. It is likely that the birds could obtain a view of the horizon in some of the funnel/cage designs when hovering near the top of the cage. However, our survey of the literature suggests that recalibration of the magnetic compass does not occur under these conditions, perhaps because birds must remain stationary during the calibration process.

To test the conclusions of our literature survey, that polarized light cues present at sunrise and sunset provide the calibration reference used to recalibrate the magnetic compass, we carried out orientation experiments with Savannah Sparrows, *Passerculus sandwichensis*, in Alaska (Muheim et al. 2006b, 2007). We exposed birds caught during migration to a shifted artificial polarization pattern at sunrise or sunset and tested their magnetic compass orientation. The comparison between each bird's initial control orientation and its orientation after the exposure clearly showed that Savannah Sparrows recalibrate their magnetic compass after a 1-h exposure to a rotated polarization axis at either sunrise or sunset. The results supported earlier findings by Able and Able (1995) and Cochran et al. (2004) that also reported recalibration of the magnetic compass when the birds were exposed to a rotated magnetic field while simultaneously provided with a view of sunset cues down to the horizon. We have recently corroborated these results with White-throated Sparrows, *Zonotrichia albicollis*, in New York State, showing that these sparrows recalibrate their magnetic compass after exposure to either a shifted artificial polarization pattern in the ambient (unshifted) geomagnetic field or a shifted magnetic field under natural celestial cues (R Muheim, ME Deutschlander, JB Phillips, unpublished data). These experiments were carried out during both spring and autumn migration and confirm that migratory season and phase do not explain the difference

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R. Muheim · J. B. Phillips  
Department of Biological Sciences,  
Virginia Polytechnic Institute and State University,  
Derring Hall, Blacksburg, VA 24061, USA

*Present Address:*  
R. Muheim (✉)  
Department of Animal Ecology, Lund University,  
Ecology Building, 223 62 Lund, Sweden  
e-mail: Rachel.Muheim@zoekol.lu.se

S. Åkesson  
Department of Animal Ecology, Lund University,  
Ecology Building, 223 62 Lund, Sweden

between studies, and that there is no difference in the response of the birds to a cue conflict produced by rotating an artificial polarization pattern versus one produced by rotating the magnetic field.

Wiltshcko et al. argue that the paper by Cochran et al. (2004) cannot be regarded as support for recalibration of the magnetic compass, since the experiments were not carried out in orientation funnels, but instead are based on release experiments. This argument strongly contradicts a study by Sandberg et al. (2000), who exposed four species of birds to a shifted magnetic field while they were tested in orientation funnels during sunset, and then released these birds and observed their vanishing bearings. In agreement with the overall pattern found in the literature (Muheim et al. 2006a), the birds did not recalibrate their magnetic compass, since their view of the celestial cues near the horizon was obscured by the funnels during the exposure. Instead, two species recalibrated their celestial compasses in the funnel experiments, while the other two species did not show a reaction to the exposure (Sandberg et al. 2000). In the release experiments that occurred within 1 h after the funnel experiments, the departure directions of the birds of all four groups showed that they had recalibrated their celestial compasses. Neither the funnel experiments nor the subsequent release experiments provided evidence for recalibration of the magnetic compass, nor was there evidence that birds show opposite responses in funnel and release experiments. Thus, the results of Sandberg et al. and Cochran et al. are in full agreement with our interpretation. Wiltshcko et al. (1983) also argue that the findings from the study by Cochran et al. (2004) cannot be interpreted as evidence for recalibration of the magnetic compass because the birds may have been “overcompensating” after exposure to the cue conflict, citing their earlier work on homing pigeons. They exposed homing pigeons to a rotated magnetic field in a home loft which provided an undisturbed view of celestial cues. When first tested under the sun, the birds shifted in a direction consistent with calibration of the sun compass relative to the magnetic field, but then “overcompensated” (i.e., shifted in the opposite direction), presumably as a result of the feedback they received during their first flight under the sun. Interpretation of these findings is complicated by the fact that the same deflection of the initial orientation would result from the magnetic compass being calibrated relative to celestial cues if the pigeons used magnetic compass cues to determine the direction of displacement (Phillips and Waldvogel 1988). Regardless of the explanation for the magnetic loft experiments, there is no reason to believe that these findings suggest a reinterpretation of Cochran et al.’s findings, since these birds were tracked on their first release after exposure to the cue conflict, and showed the deflected orientation immediately upon release. In conclusion, it is

inappropriate to exclude Cochran et al.’s (2004) results when discussing cue conflict experiments.

The paper by Wiltshcko et al. shows interesting new findings that appear to contradict our results. They report that Australian Silvereyes, *Zosterops lateralis*, did not show recalibration of the magnetic compass after exposure to a shifted magnetic field for 90 min at sunset and for 90 min the following sunrise, even though the birds has access to natural celestial cues, including the horizon. Instead, their birds oriented in the same direction as before the exposure, which is interpreted by the authors as a demonstration of that polarized light cues are not the primary compass cues, but instead that the magnetic field calibrates the celestial compasses during migration. Unfortunately, Wiltshcko et al. did not test whether the silvereyes had recalibrated their celestial compasses. Since the birds were held in an outdoor aviary for about two - weeks prior to the start of the experiments (see below), they may have completed calibration of their compass systems prior to the cue conflict exposures. Previous studies have shown that once calibration of a compass system is completed, updating the calibration (e.g., when the birds are exposed to a new cue conflict) may require several days of exposure (Bingman 1987; Wiltshcko and Wiltshcko 1975b).

In their recent paper, Wiltshcko et al. discuss a number of possible explanations for their contradictory results that we would like to address:

*Different bird species* Wiltshcko et al. point out that species-specific differences in the control of migration could explain the differences observed between the Savannah Sparrows in North America and Silvereyes in Australia, i.e., that birds of different phylogenetic origin may have evolved different migration strategies. To date, published records of recalibration of the magnetic compass has been shown for the following species: Savannah Sparrow (Bingman 1983; Able and Able 1990, 1993, 1995; Muheim et al. 2006b, 2007), Pied Flycatcher, *Ficedula hypoleuca* (Weindler and Liepa 1999; Prinz and Wiltshcko 1992) and Swainson’s and Gray-cheeked Thrush, *Catharus ustulatus* and *minimus* (Cochran et al. 2004). Moreover, Bingman (1984) (Pied Flycatcher) and Able and Able (1997) (Savannah Sparrow) reported no recalibration of the celestial compasses when testing birds in a vertical magnetic field after exposure to a shifted magnetic field in an open cage, indicating that the magnetic field is likely to have been recalibrated instead. Thus, a variety of species from both North America and Europe recalibrated their magnetic compass when exposed to a cue conflict with access to polarized light cues near the horizon. Further work is needed to determine whether Silvereyes are an exception to this general pattern or, instead, whether

methodological differences can account for the difference in the responses of the birds in the experiments carried out by Wiltschko et al. (see earlier discussion and below).

*Different phases of migration* Contrary to the conclusions of earlier authors that birds use celestial cues to recalibrate their magnetic compass before the onset of migration, but then switch to using the magnetic compass to recalibrate the celestial compasses during migration (Wiltschko and Wiltschko 1999), we did not find that the phase of migration was a factor in our review of the cue conflict literature (Muheim et al. 2006a). This was based on two studies (Able and Able 1995; Cochran et al. 2004) that showed recalibration of the magnetic compass during migration. Cochran et al. (2004) tested long-distance migrants captured en route during spring migration, and so they used birds that were well underway in their migratory journey. Able and Able (1995) used both juvenile and adult birds captured at their breeding site before migration, but did not start with the exposures and experiments before later during the migration season. Wiltschko et al. argue that both Able and Able's and our study was carried out at the start of the migratory season, with birds that had not previously experienced changing relationships between compass cues. This is surprising, because the Silvereyes used in their study were captured near the northern edge of their wintering area two weeks before the start of spring migration. The Savannah Sparrows we tested in Alaska (Muheim et al. 2006b) had all accumulated subcutaneous fat, a clear sign of migratory disposition, and it is very likely that they had been migrating up to several 100 km before reaching our research station. When considered along with the study by Cochran et al. (2004), showing recalibration of the magnetic compass during migration, these findings make it unlikely that phase of migration or migratory disposition can explain the discrepancies between the studies. The argument that the Silvereyes might have used true navigation and therefore did not recalibrate their compasses might be a valid interpretation of the current results, but then adult birds tested in both our and Able and Able's study would also have been expected to show a different response to that of the juvenile birds, which they did not. Therefore, further consideration should be given to the possibility that the Silvereyes in Wiltschko et al.'s study calibrated their compasses during the two weeks they were held in the outdoor aviary (a significant departure from the other studies) and did not calibrate their compasses again when exposed to the shifted magnetic field in the familiar environment. If this explanation is correct, we would expect that there would be no recalibration of the magnetic or celestial compasses. Another departure from most, if not all, previous studies is that Wiltschko et al. held birds between exposure to the cue conflicts and testing in a room

with a window that provided a partial view of the outside world, although not a direct view of the sky. Further work will be needed to determine whether a view of previously calibrated landmarks and/or indirect sun information might have interfered with the calibration of one or more of the birds' compass systems.

*Different regions of the Earth* We agree that the rapid changes of magnetic declination experienced in Alaska (11 min/year in the year of the experiments) compared to 0.2 min/year in eastern Australia could result in the evolution of an orientation system that primarily relies on celestial, rather than magnetic cues. However, magnetic declination does not change as dramatically in central North America (New York and Illinois, 3 and 7 min/year, respectively; changes that are similar to those observed in Germany, 7 min/year). Thus, if variation in declination in different regions of the Earth rather than access to celestial cues near the horizon explains the differences between studies, birds from central North America and Europe should use the same primary calibration cues. However, there are large discrepancies between studies carried out in regions with similar annual changes in declination, both within central North America (e.g., Able and Able 1995 and Cochran et al. 2004 versus Sandberg et al. 2000) and between Europe and central North America (e.g., Wiltschko and Wiltschko 1975a, b; Bingman 1987; Bingman and Wiltschko 1988 and Wiltschko et al. 1998 versus Able and Able 1995 and Cochran et al. 2004). Therefore, different regions of the Earth with different magnetic properties are unlikely to explain why the Silvereyes in Wiltschko et al.'s experiments responded differently to the cue conflict.

*Circumstances of experiments* As mentioned earlier, the birds in the experiments reported in Muheim et al. (2006b) had accumulated fat and showed migratory restlessness with a clear directional tendency (Mouritsen and Larsen 1998), which suggests that the birds were in migratory condition. In addition, most Savannah Sparrows had left the area in the second part of the experimental period, indicating that the experiments were carried out during the migratory period of the population of Savannah Sparrows migrating in this area.

Wiltschko et al.'s comparison of the exposures to polarizing filters in our study (Muheim et al. 2006b, 2007) with other studies fails to mention one important difference: while birds in the studies cited by Wiltschko et al. aligned their behavior along the e-vector axis of the polarizers, birds did not do this in our experiments (which would have resulted in a fixed axis of orientation relative to the polarization filter). Instead, individual birds in our study reoriented their direction of orientation relative to the magnetic field by an amount corresponding to the

difference between the natural polarization pattern and the rotated pattern produced with the polarization filters; a consistent axis of orientation was only observed when each bird's direction of orientation after exposure to the cue conflict was plotted as a deviation from their direction of orientation prior to the cue conflict exposure. Thus, unlike earlier studies using artificial polarization filters, the birds' orientation cannot be attributed to a fixed (i.e., parallel) alignment relative to the artificial polarization axis as Wiltschko et al. suggest, nor can an artifact resulting from the use of an unnaturally strong polarized light stimulus explain the results of experiments by Cochran et al. (2004) and Able and Able (1995), in which cue conflicts were created by exposing birds to natural celestial cues in a rotated magnetic field.

## Conclusions

In conclusion, we believe that the most likely explanation for the reported failure of Silvereyes to respond in the same manner as the other species tested to date lies in differences in the exposure protocol and/or the experiences of birds before or after exposure to the cue conflict, rather than in the arguments listed by Wiltschko et al. Their birds may have had ample opportunity to familiarize themselves with the surroundings and to recalibrate their compasses during the two weeks they spent in the outdoor aviary. They may not have updated the calibration of their compass systems when later exposed to the shifted magnetic field in the familiar surroundings if the aviary was situated close to the exposure site used later. The role of a familiar environment in the compass calibration process remains an interesting area of future research. Future studies might also examine other methodological differences between the studies. For example, if birds are exposed to a conflict between celestial and magnetic cues during successive day/night transitions, does the order of these exposures matter (e.g., for a nocturnal migrant, a typical daytime stopover would result in the bird experiencing a sunrise followed by a sunset at the same location)? Clearly, much is yet to be learned about the detailed mechanisms of compass calibration, especially in different species and geographic areas, and it remains a challenging area of future exploration.

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