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The role of skylight polarization in the orientation of a day-migrating bird species

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Abstract To assess the role of skylight polarization in the orientation system of a day-migrating bird, Yellow-faced Honeyeaters (*Lichenostomus chrysops*, Meliphagidae) were tested in funnel cages for their directional preferences. In control tests in the natural local geomagnetic field under the clear natural sky, they preferred their normal migratory course. Manipulations of the *e*-vector by depolarizing the skylight or rotating the axis of polarization failed to affect the orientation as long as the natural geomagnetic field was present. When deprived of magnetic information, the birds continued in their normal migratory direction as long as they had access to information from the natural sky, or when either the sun or polarized light was available. However, when sun was hidden by clouds, depolarizers caused disorientation. – These findings indicate that polarized skylight can be used for orientation when no other known cues are available. However in the hierarchy of cues of this species, the polarization pattern clearly ranks lower than information from the geomagnetic field.

Key words Bird migration · Orientation · Polarized light · Magnetic field · Yellow-faced honeyeater

Introduction

The ability to perceive polarized light has been described for many animals, including vertebrates (cf. Waterman 1981). This ability has often been connected with the need of animals to orient in their environment; social hymenoptera, like bees and ants, provide the most prominent examples (e.g. von Frisch 1949, 1968; Wehner 1982). In birds, however, the role of polarized light is not entirely clear. Positive conditioning experiments (Kreithen and Keeton 1974; Delius et al. 1976) were questioned by Coemans et al. (1990) who attributed these results to artifacts resulting from minute differences in brightness and/or flickering caused by the polarizers themselves or by reflections of light in the experimental chamber (comp. Martin 1991). The observation that the orientation of nocturnal migrants at dusk could be influenced by the position of polarizers (e.g. Able 1982, 1989; Moore and Phillips 1988; Helbig 1991; Phillips and Moore 1992) suggested that polarized light was an important cue when the birds start their nocturnal flight. However, the test birds often tended to align their activity parallel to the axis of the *e*-vector so that their response to the artificially polarized light differed markedly from the orientation under the natural sky (Helbig and Wiltschko 1989). Hence it is unclear whether the tests under polarizers reflect the natural role of polarized light correctly. Clearcut indications that birds can indeed derive orientational information from polarized light of the natural sky are provided by findings that depolarization of the skylight caused a breakdown in orientation under certain conditions (Helbig 1990, 1991), and by recent ontogenetic experiments demonstrating that celestial rotation during daytime can recalibrate the set course of the magnetic compass, provided that the test birds have access to the polarized light pattern of the natural sky (Able and Able 1993, 1994).

So far, all experiments indicating a role of polarized light in the orientation of migratory birds involved nocturnal migrants. The ontogenetic study by Able and Able (1993) focussed on a long-term effect of polarized light on the orientation system during the premigratory period. All studies analysing the significance of polarized light for orientation during migration involve

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tests around sunset or sunrise (Moore 1986), when the natural light is most strongly polarized, with a conspicuous band of maximal polarization running perpendicular to the sun through the zenith (comp. Brines 1980). During daytime, the pattern of polarization is much more complex and changes according to the sun's movements. Insects like bees and ants are known to use the pattern of polarization alone or in combination with sun for orientation (v. Frisch 1968; Wehner 1962). Whether day migrating birds can also derive information from the complex diurnal patterns of polarization, was not yet known. Here we report first results of experiments designed to clarify the role of polarized light in the orientation of a day migrant, the Australian Yellow-faced Honeyeater, *Lichenostomus chrysops* (Meliphagidae).

Material and methods

Test birds

Yellow-faced Honeyeaters occur along the eastern coastline of Australia and the adjacent mountains of the Great Dividing Range. The southern populations are migratory and perform noticeable seasonal movements through eastern New South Wales and eastern Queensland (for summary, see Liddy 1966). In autumn and early winter, i.e. March till July, they migrate northward, while in spring they return on a southward course to their breeding areas. They prefer to migrate in fine weather during the morning and early afternoon, with a peak of migration between 8.00 and 12.00 (Robertson 1965; Robertson and Woodall 1983). Previous studies have shown that yellow-faced honeyeaters use the magnetic field and the sun for orientation (Munro and Wiltschko 1993a,b).

In spring and autumn from 1989 to 1991, 23 Yellow-faced Honeyeaters were captured in mistnets in Armidale, New South Wales (30°30′ S, 151°40′ E), at times of the year when the abundance of the species increases due to an influx of migrants. The birds were housed in the natural magnetic field in outside aviaries so that they were subjected to the natural photoperiod and had access to the natural sky.

Test conditions

Series 1 was performed in the local geomagnetic field of Armidale (56000 nT, −62° incl.). In series 2, the birds were deprived of meaningful magnetic information by compensating the horizontal component of the test field with Helmholtz coils (49500 nT, −90° incl.). All tests of series 1 and part of series 2 were performed under clear weather when the sun was visible. The remaining tests of series 2 took place under partly overcast conditions when 70% to 90% of the sky were cloud-covered and the sun was hidden behind clouds.

Clear plexiglass covers were used to give the birds largely unrestricted access to the natural sky. To depolarize the natural skylight, we used clear sheets consisting of two pseudodepolarizers of Hostaphan (= polyethylene terephthalate), Hoechst AG Wiesbaden, Germany, (thickness: 0.18 mm) stapled together. These sheets decreased the polarization of incident light by over 90%, while at the same time the distribution of skylight intensity was not altered (for details, see Helbig 1990). To alter the polarization pattern, we used polarizer sheets of Dodwell Hi-Tech, Tokyo, (thickness: 0.40 mm) which restrict transmission of unpolarized light to 0.01%. Consequently, incoming light was almost 100% linearly polarized in one direction. The polarizers decreased the intensity of incoming light in the visible spectrum up to about 60–65%, depending on wavelengths (for details, see Helbig and Wiltschko 1989; Helbig 1991).

Specifically, we tested the birds under the following conditions:

Series 1: Tests in the natural geomagnetic field and under clear sky (in 1990):
(1.1) with clear plexiglass - simulating the natural situation
(1.2) with depolarizers, i.e. only the magnetic field and the sun were available as cues
(1.3) with polarizers in three different orientations (see below), i.e. magnetic field, sun and polarized light gave conflicting information.

Series 2: Tests in a partially compensated magnetic field which did not provide meaningful directional information (in 1991):
(2.1) with clear plexiglass under clear sky, i.e. the sun and polarization were available as cues
(2.2) with depolarizers under clear sky, i.e. the sun was the only cue available
(2.3) with clear plexiglass under partially cloudy sky with the sun not visible, i.e. polarization was the only cue available
(2.4) with depolarizers under partially cloudy sky with the sun not visible, i.e. neither the magnetic field, nor the sun nor polarization were available.

Orientation tests

The tests were performed from 15 March to 31 July 1990 and 1991, in the morning between 7.00 and 11.45. Registration time was about one hour. The birds were tested one at a time in funnel-shaped cages (see Emlen and Emlen 1966) which were lined with typewriter-correction paper (TippEx, Germany). When moving around, the birds left scratches on the coating of the walls which were later counted and analysed (see below; for details see Munro and Wiltschko 1992). The cages were covered with plexiglass, polarizers or depolarizers, according to the test conditions.

Data analysis and statistics

After each test, the TippEx lining was removed from the cage and was divided into 24 sectors of 15° each. The scratches per sector were counted on a light-table. Tests with fewer than a total of 35 scratches were excluded from the statistical analysis. From the distribution of the scratches from each test, a heading was determined. For birds used in more than one test per test series, a single mean heading was calculated. These headings were then used to calculate a mean vector with length r_m and direction α_m for each test condition. The directions are given with respect to local magnetic north = geographic 11°. The vectors were tested for significant directional preferences with the Rayleigh test. The data of the various test conditions were compared by the Mardia Watson Wheeler test (Batschelet 1981); differences in scatter were analysed using the Mann Whitney test.

Results

The numerical data from all conditions are presented in Table 1.

Orientation in the natural geomagnetic field

The orientation in the tests under clear sky in the local geomagnetic field is summarized in Fig. 1. Under

Table 1 Orientation behavior of Yellow-faced Honeyeaters (*N*, number of birds; α_m, r_m direction and length of mean vector, respectively. *Asterisks* at r_m indicate significant directional preferences. *Asterisks in the last column* indicate significant differences to the samples 1.1 and 2.1, respectively, recorded under sunny sky and clear plexiglass

Test condition	*N*	Mean vector		Different from sample 1
		α_m	r_m	
Series 1: Tests under sunny sky in the local geomagnetic field				
1.1 Under clear plexiglass	23	350°	0.46**	
1.2 Under depolarizers	22	26°	0.53**	n.s.
1.3 Under polarizers, *e*-vector E-W	18	357°	0.52**	n.s.
Under polarizers, *e*-vector NE-SW	16	327°	0.49*	n.s.
Under polarizers, *e*-vector NW-SE	21	352°	0.41*	n.s.
Series 2: Tests in a partially compensated magnetic field				
2.1 Sunny sky, clear plexiglass	11	22°	0.69**	
2.2 Sunny sky, depolarizers	12	14°	0.52*	n.s.
2.3 Sun obscured, clear plexiglass	10	351°	0.73**	n.s.
2.4 Sun obscured, depolarizers	10	236°	$0.12^{n.s.}$	*

Significance levels:* = $P < 0.05$; ** = $P < 0.01$; *n.s.* = not significant

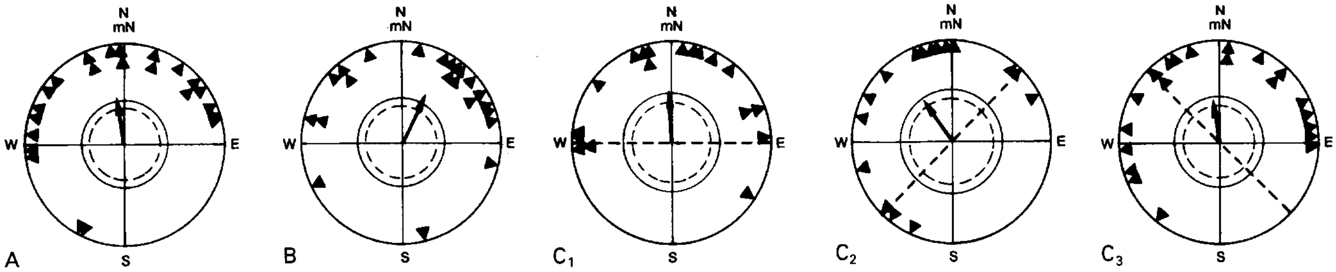

Fig. 1 Orientation of yellow-faced honeyeaters tested in the local geomagnetic field under a clear sky, **A** under clear plexiglass allowing the birds to see the sun and the polarized light of the natural sky; **B** under depolarizers, and $\mathbf{C}_1$, $\mathbf{C}_2$ and $\mathbf{C}_3$ under polarizers; the various orientations of the *e*-vector are indicated by a *dashed diameter*. The headings of individual birds are symbolized by *black dots* at the periphery of the circle. The mean vectors are represented by *arrows* drawn in relation to the radius of the unit circle. The two inner circles represent the 5% (*broken line*) and the 1% (*unbroken line*) significance level of the Rayleigh test. For numerical data, see Table 1

control conditions with all cues available, yellow-faced honeyeaters showed a northerly tendency (Fig. 1a) which is seasonally appropriate and corresponds well with the directions preferred by their free-flying conspecifics during autumn and early winter. Neither depolarizers (Fig. 1b) nor polarizers (Fig. 1, 2, 3) caused a change in the birds' directional preferences (comp. Table 1). In summary, an influence of polarized light and the *e*-vector axis was not observed as long as the magnetic information and the sun were available.

Orientation in the absence of meaningful magnetic information

Figure 2 presents the results of the tests in which the horizontal component of the magnetic field was compensated. When magnetic cues were removed, but the natural sky, including sun and polarized light, was visible through plexiglass, the birds oriented in their normal northerly migratory direction (Fig. 2a). Orientation in an appropriate direction was also evident when the clear sky was viewed through depolarizers (Fig. 2b) or under a partly cloudy sky with the sun hidden, viewed through plexiglass (Fig. 2c), i.e. as long as *either the sun or polarized light* was available. However, when the sun was hidden behind clouds and, in addition, polarization was abolished by depolarizers (Fig. 2d), the birds were no longer oriented. They exhibited significantly more scatter than under the other three conditions ($P < 0.01$ resp. $P < 0.001$).

Discussion

Our data provide some insight into the role of polarized light in the migratory orientation of Yellow-faced Honeyeaters: Figure 2c clearly shows that polarized skylight can be used to orient their diurnal migration. However, Fig. 1 indicates that polarization patterns are not a cue of major importance and receive less attention than the geomagnetic field when both sources of information are available. This applies to the artificial patterns produced by polarizers, which mimic the natural pattern only imperfectly, but it seems to be also true for the natural skylight, since these honeyeaters readily responded to changes of magnetic north when tested outdoors under clear sky (Munro and Wiltschko 1993b).

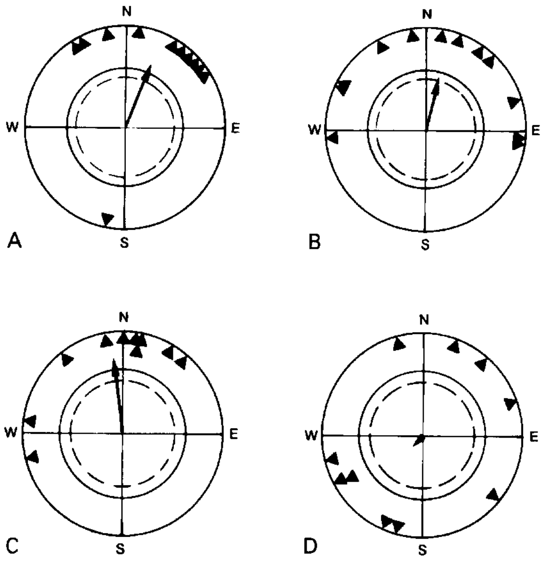

Fig. 2 Orientation of Yellow-faced Honeyeaters in a magnetic field which did not provide meaningful orientation information. The tests were performed **A** under a clear sky in cages covered with clear plexiglass so that sun and polarized light were available as orientation cues, **B** under clear sky in cages covered with depolarizers so that the sun was the only orientation cue; **C** under partially cloudy sky with the sun hidden in cages covered with clear plexiglass so that polarized light was the only orientation cue; **D** under partially cloudy sky with the sun hidden in cages covered with depolarizers, i.e. neither the sun nor polarized light were available. *Symbols* as in Fig. 1; for numerical data, see Table 1

In the presence of meaningful magnetic information and when the sun was visible, manipulations of the *e*-vector axis did not affect the birds' behavior significantly. This is in marked contrast to previous reports that several species of nocturnal migrants altered their directional tendencies when the *e*-vector axis was rotated by polarizers in the presence of the natural magnetic field (e.g. Able 1982; Moore 1986; Moore and Phillips 1988; Helbig 1991). This seemed to suggest a predominant role of polarization as an orientation factor. The findings of Sandberg (1988) were the only exception. Wiltschko and Wiltschko (1975a, b) and Bingman and Wiltschko (1988), on the other hand, found that birds followed a deflection of magnetic north in spite of contradicting information from the natural polarization pattern. This leads to the question of how the response to the artificial polarization pattern is to be interpreted. The 100% polarization produced by polarizers may have increased the saliency of this cue as compared to the natural sky and thus may have altered the natural hierarchy of cues. The altered response to the artificially polarized light reported by Helbig and Wiltschko (1989) suggests that the behavior under polarizers might not represent normal migratory orientation. All the experiments mentioned above involved nocturnal migrants tested at dawn or dusk. Polarizers might have caused differences in the light intensity within the cage. Able (1989) tried to test against such artefacts by lining sectors of the cage walls with darker material and found the orientation under polarizers unaffected. Still, it cannot be excluded that the test birds responded to the distribution of light from above rather than to the *e*-vector, e.g. aligning their orientation along the brightest axis of their 'sky'. Since our tests were performed in bright daylight, any minute difference in light intensity caused by polarizers might lose significance against the much higher general light level.

The finding that depolarizers had no effect when magnetic information was available is not surprising, since Yellow-faced Honeyeaters are able to orient by the magnetic field (Munro and Wiltschko 1993b). Able (1989) reported similar results from White-throated Sparrows, *Zonotrichia albicollis*, a night-migrating species. The orientation observed in the absence of magnetic and solar information, which became random under depolarizers, shows that Yellow-faced Honeyeaters can use natural polarized light for direction finding when all other known cues are absent. This is in agreement with findings by Helbig (1990, 1991) and by Pettersson et al. (1991) on nocturnal migrants: European robins, *Erithacus rubecula*, and Blackcaps, *Sylvia atricapilla*, tested at dusk, were oriented in the absence of meaningful magnetic information when natural skylight was available. Their orientation was also disrupted when skylight was depolarized.

The precise role of polarized light in the migratory orientation of diurnal migrants is still open, and several possibilities might be considered. One of them involves the use of polarized skylight as an independent reference for migratory orientation. The pattern of polarization depends directly on the sun's arc and thus varies considerably with latitude and with season; hence its use as a reference would require rather complex mechanisms to locate the migratory direction in the course of migration with sufficient accuracy. In nocturnal migrants, the role of polarized light as reference is likewise unclear. Phillips and Moore (1992) claimed that information provided by the polarization pattern at sunset was used to calibrate the sun compass of a nocturnally migrating species. However, Bingman (1983) reported that young nocturnal migrants were well oriented only when magnetic information was available, in spite of previous experience with the natural sky. Findings by Able and Able (1990) also suggest an association between the magnetic field and the directional significance of sunset cues.

The polarization pattern may, together with the sun, represent a part of a general "skylight compass" mechanism, as has been proposed for insects, in particular for honey bees and ants (v. Frisch 1949, 1968; Wehner 1982); in that case, a limited view of the blue sky might provide the honeyeaters with similar information as the sun. Clock-shift experiments with nocturnal migrants at dusk (Able and Cherry 1986; Helbig 1991) indicate that the internal clock is involved in the orientation at sunset and might be taken to support such a view. Clock-shift experiments with Yellow-faced Honeyeaters, however, failed to produce clear evidence that a sun compass in the traditional sense is involved in the migratory orientation of this diurnal migrant (Munro and Wiltschko 1993a). The birds' responses rather suggested that the sun was used as a "sky mark", analogous to a landmark. This leaves the possibility that the pattern of polarized light, like the sun, acts as a secondary cue, receiving temporary significance from other sources of directional information. Our experimental birds were living in an outdoor aviary at the time of the tests and thus had ample opportunity to experience the natural sky together with the natural geomagnetic field. Hence, they might have associated the sun and the pattern of polarization with the direction of the geomagnetic field. When experimentally deprived of this primary cue, they switched over to memorized information from the sun and/or polarization to locate their migratory direction.

Aside from the tests under polarizers, which seemed to indicate a dominant role of polarization in nocturnal migrants, but possibly have to be interpreted as artifacts, the experiments with nocturnal migrants and our present tests with a day migrating species produced basically similar results: Polarized light can be used to locate the migratory direction, but it seems to be cue of minor importance, probably deriving its directional significance from the magnetic field (Bingman and Wiltschko 1988). This is surprising insofar as polarized light was found to mediate information on celestial rotation, which can recalibrate the innate course for the magnetic compass during the pre-migratory period (Able and Able 1993, 1994). Our findings might reflect a general decrease in the importance of celestial cues as compared to magnetic cues between ontogeny and actual migration (comp. Wiltschko et al. 1989).

In one aspect, there appears to be a difference between our findings on the day-migrating honey eater and nocturnal migrants: In Yellow-faced Honeyeaters, the sun and the pattern of polarization appeared to be largely equivalent, whereas in European Robins as well as in Blackcaps, the pattern of polarization could maintain orientation in the absence of magnetic information, while the view of the sun itself could not (Helbig 1991). The same was true for the long-term effect of the day-time sky on Savannah Sparrows passerculus sandwichensis during ontogeny (Able and Able 1993). Here, polarization at the time of sunrise and sunset may prove crucial (see Moore and Phillips 1988; Able and Able 1994), i.e., patterns which are much simpler than those formed during the day when the sun is high in the sky. The minor role of polarization in the orientation of day migrants may be caused by this complexity of the pattern and its dependency on the time of the day, season, and geographic latitude. Day-migrants would have to adjust this mechanism repeatedly to their current position, which drastically limits the use of polarized light as a cue for migratory orientation over long distances and does not allow a role as a directional reference for innate directional information (see also Munro and Wiltschko 1993a for discussion).

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