SKYLIGHT POLARIZATION DOES NOT AFFECT THE MIGRATORY ORIENTATION OF EUROPEAN ROBINS[1]

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Among birds, only the Rock Dove (*Columba livia*) has been shown so far to be able to perceive the E-vector direction of linearly polarized light (Kreithen and Keeton 1974, Delius et al. 1976). The adaptive significance of this ability remains largely unknown, but may be related to the birds' capacity for orientation (Brines 1980, Brines and Gould 1982). Recently, Able (1982) reported that the orientation of nocturnally migrating White-throated Sparrows (*Zonotrichia albicollis*), is affected by manipulations of skylight polarization patterns at dusk, and Moore (1986) demonstrated that polarized light influences the early morning (dawn) orientation of night migrants tested during spring on the southwest coast of Louisiana in a similar way. In addition, recent data on the relationship between sunset orientation and polarized light, includes the Yellow-rumped Warbler (*Dendroica coronata*) as a species which responds to polarized light (F. Moore, pers. comm.). Orientation experiments have indicated that there may be significant differences between bird species in their use of sun-related cues, the stars, and the geomagnetic field for the establishment and maintenance of nocturnal orientation (Wiltschko and Wiltschko 1978, Able and Cherry 1985, Moore 1987). In contrast to North American Savannah Sparrows (*Passerculus sandwichensis*) and White-throated Sparrows, the European Robin (*Erithacus rubecula*) seems to rely more extensively on the geomagnetic field for their orientation during the night (Wiltschko et al. 1971, Wiltschko and Wiltschko 1975, but cf. Katz and Michelson 1978 and Wallraff and Gelderloos 1978 for some conflicting evidence), as well as during the twilight period after sunset (Sandberg et al., in press a). Katz (1985), however, found that robins displayed uniform orientation during twilight tests under total overcast as well as after sunset under starry skies whereas in twilight tests under clear skies, the robins were able to select an appropriate fall migratory direction. I have undertaken experiments with migrating robins captured at the Falsterbo Bird Observatory (FBO, 55°23'N, 12°50'E) in south Sweden in order to investigate the possible influence of skylight polarization patterns on the dusk orientation of this species.

METHODS

The tests were performed during the spring (April and May) and autumn (September and October) migration periods in 1986. Experimental birds captured at FBO were transported by car approximately 55 km to the northeast, to a test site at the ecological field station Stensoffa (55°42'N, 13°25'E), close to Lund. The robins were housed indoors in individual cages under the natural photoperiod and the local geomagnetic field. During the tests, the birds were placed in modified "Emlen-funnels" with automatic counter registration of the activity in eight sectors (see Sandberg et al., in press b for details of experimental setup and equipment) and tested for 1 hr beginning 10 min after local sunset. The birds were never allowed to see the disc of the setting sun during tests, and the sunset sky below approximately 45° elevation was screened off from view. Orientation cages were covered by a linear dichroic polarizer, having a total light transmittance of 38% (Plexiglas laminated HN-38; Polaroid). Only one test per individual and condition is included in the analysis. The four different experimental conditions were:

(1) Clear skies (<⅝ cloud cover); (a) polarizer E-vector oriented in the seasonally normal direction at the associated test night ("E-vector = C") and (b) polarizer E-vector oriented 90° in relation to the seasonally normal direction, parallel to the sunset azimuth ("E-vector = C + 90°").

(2) Simulated total overcast. A panel of 3-mm opaque diffusing Plexiglas was placed on top of the screening shield surrounding the orientation cage i.e., above the polarizer, which thereby introduced an E-vector axis in an otherwise visually cueless situation; (a) E-vector = C and (b) E-vector = C + 90°.

Vector calculation based on counter registrations yielded a mean heading for each individual and test night. Bird-hours with less than 40 registrations were excluded from analysis, as were tests which showed a highly scattered and unreliable orientation with $P > 0.05$ according to the Rayleigh test (Batschelet 1981). This selection led to acceptance of 83% of the total number of control tests (without polarizer, cf. below) that were conducted, and of 81% of the total number of experimental tests. There was no significant difference in the proportion, of accepted tests (1), of tests excluded because of inactive birds (2), or excluded because of scattered and unreliable orientation (3), between control and experimental categories ($\chi^2 = 0.3$, df = 2, $P > 0.5$). Second order mean vectors and axes of orientation were calculated on the basis of individual mean headings for each condition. A mean axis of
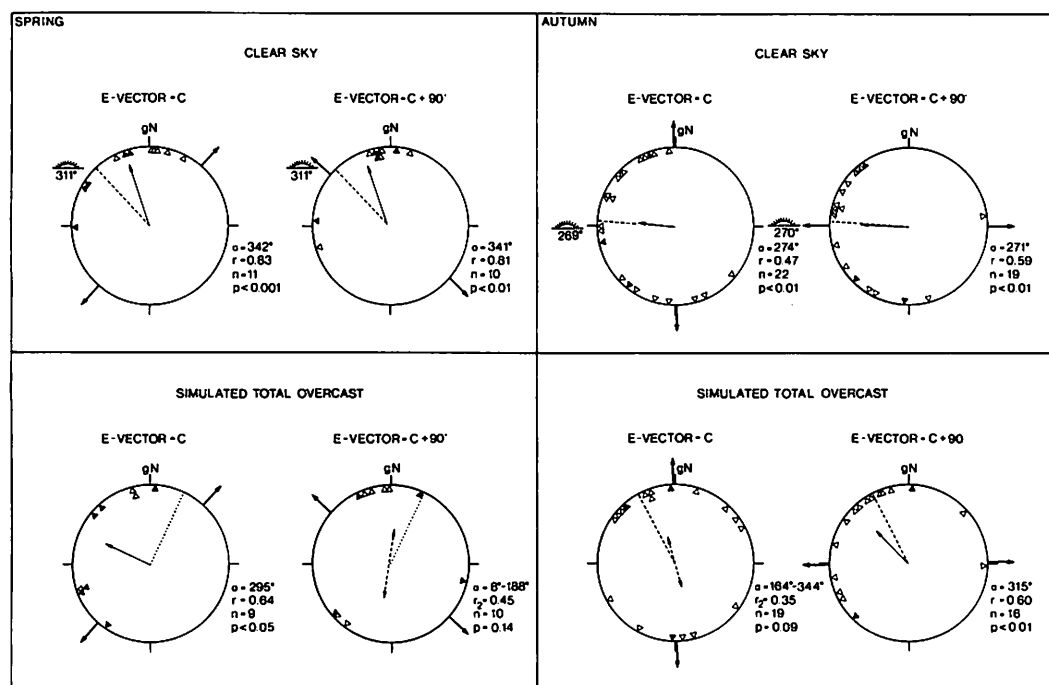
FIGURE 1.   The orientation of European Robins tested under four different experimental conditions during spring and autumn migration, respectively. Polarizer E-vector directions were either in the seasonally normal direction (E-vector = C), i.e., situated 90° from the sunset azimuth, or shifted 90° from normal (E-vector = C + 90°) resulting in a polarization axis directed towards the setting sun. Experiments with the two E-vector conditions were performed under clear skies as well as under simulated total overcast. The mean direction towards the setting sun 40 min after sunset (i.e., in the middle of the test hour) is indicated for the experiments under clear skies. Open symbols denote significant headings of birds in their first year of life, and filled symbols the corresponding headings of migratory-experienced robins. Second order mean vectors (or axes) with direction (α) and length (r) are shown in the circular diagrams, and vector lengths are drawn relative to the radius of the circle = 1. Arrows outside the circles indicate the alignment of E-vectors. The preferred mean orientation of controls under natural skies is represented by broken (significant directionality according to the Rayleigh test), or dotted (mean orientation not significant) lines.

orientation is considered when it provides a better fit to the data than the unimodal mean vector (see Batschelet 1981).

If robins are able to perceive polarized light and use it for their orientation, they may be expected either to orient directly in relation to the E-vector axis, or to use the polarization patterns indirectly to localize and orient according to the position of the setting sun. This could be of particular relevance when the sun is hidden behind clouds, or situated below the horizon as is the case during twilight. In either case, the expected directions of the robins will not differ from controls under E-vector = C, but will deviate by approximately ±90° from the control direction under E-vector = C + 90°.

Robins tested at Stensoffa during the spring and autumn seasons in 1983 to 1986 under clear and simulated overcast skies, without polarizer manipulations, were used as controls. There were no statistical differences between the total sample of controls tested at this site and the subsample of controls tested during 1986 (simultaneously with polarization tests) in either

directions or scatter (according to Mardia's [1972] "one-way classification test" and "the test for the homogeneity of the concentration parameters," respectively).

RESULTS AND DISCUSSION

The results are shown in Figure 1. From them, the following conclusions can be drawn.

Under clear skies, the robins showed almost exactly the same mean orientation whether the E-vector was in the control (C) or shifted (C + 90°) direction. The mean angles of orientation during spring and autumn are not significantly different from the corresponding directional choices of unmanipulated controls at this site (cf. Sandberg et al., in press b). These results provide clear indications that the robins do not use E-vector directions as orientational cues. This is in sharp contrast to the results presented by Able (1982) and Moore (1986), who found profound effects of imposed patterns of skylight polarization on the orientation of their test birds. White-throated Sparrows (Able 1982) as well as Northern Waterthrushes, Seiurus nov-

eboracensis, and Kentucky Warblers, *Oporornis for-
mosus* (Moore 1986), all responded by orienting their
activity parallel to the introduced E-vectors. It should
be noted that the experimental design differed between
my study and those of Able (1982) and Moore (1986)
in that the vector alignment (C and C + 90°) in the
present case did not exclude light transmittance and
color variations between experimental categories (cf.
also below). This difference is partly reduced by the
fact that a greater proportion of the sky was screened
off from the birds' view in my study.

During autumn tests under clear skies, the robins are
not oriented in a seasonally appropriate migratory di-
rection (expected direction = SW/SSW, based on ring-
ing recoveries). A possible reason for the lack of re-
sponse to E-vector manipulations may be that the birds
show a nonmigratory escape orientation directed at the
position of the setting sun or at the brighter part of the
sky (phototactic response). This is supported by the
fact that robins caught as passage migrants during au-
tumn at FBO have low fat reserves and often engage
in reoriented movements (cf. Sandberg et al., in press
b). The experiments under polarizers resulted in a
markedly higher degree of scatter in mean headings as
compared to controls under natural twilight skies (r =
0.79), but it was statistically significant only between
controls and the E-vector = C category ($P < 0.05$, test
for the homogeneity of concentration parameters,
Mardia 1972:165–167). This may be an effect of the
limited light transmission through the polarizers which
in effect creates less variation in skylight intensity un-
der E-vector = C thereby making it more difficult for
the birds to detect the brighter parts of the sky. Below
E-vector = C + 90°, there will be a dark band overhead,
but it is still possible to recognize where the sun or the
brighter part of the sky is situated (for photographs
illustrating this effect, see Wehner 1976).

On the other hand, during spring tests with a clear
sky overhead, the birds oriented in a seasonally ap-
propriate direction, significantly to the right of the sun-
set azimuth (95% Confidence Intervals = ±24° and
±27°, respectively), under both polarizer conditions.
Earlier experiments with artificially shifted magnetic
fields have shown that the orientation of Falsterbo rob-
ins during spring is significantly influenced by manip-
ulations of geomagnetic cues (Sandberg et al., in press
a). This suggests that the spring orientation of robins
at this site is related to migratory behavior. Conse-
quently, the fact that robins under the two experimen-
tal polarizer conditions (E-vector = C and E-vector =
C + 90°) select almost exactly the same directions clear-
ly indicates that they do not use skylight polarization
patterns in their migratory orientation.

Under simulated overcast, the introduction of an
E-vector axis in an otherwise visually cueless situation
was expected to produce clear differences in directional
choice between experimental categories, if the robins
use polarization patterns for their orientation. As can
be seen in Figure 1, the experimental outcome is not
consistent with this expectation. There are no statistical
differences between experimental treatments or be-
tween birds tested under polarizers and controls. Ob-
viously, the polarization patterns have not facilitated
or changed the orientation of the robins in any decisive

way. The orientation results under simulated overcast
are too scattered to allow a detailed evaluation whether
there are any less pronounced effects of the imposed
E-vectors.

In comparison with the clear demonstrations by Able
(1982) and Moore (1986) concerning the influence of
skylight polarization on the orientation of White-
throated Sparrows, Kentucky Warblers, and Northern
Waterthrushes, my negative results suggest that there
are important differences between these species and
the robin. Further support for fundamental differences
between species in the mechanisms of migratory ori-
entation is indicated by the demonstrated sensitivity
of robins to the geomagnetic field (cf. Wiltschko and
Wiltschko 1975; Sandberg et al., in press a), in contrast
to the frequent failures to detect any involvement of
magnetic cues in the orientation of North American
emberizines (Moore 1985; Able and Cherry 1986; but
see Bingman 1981, 1983).

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