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Orientation Behavior of Garden Warblers (*Sylvia borin*) Under Monochromatic Light of Various Wavelengths

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A little more than 30 years ago, a study revealed that migratory European Robins (*Erithacus rubecula*) could use the earth's magnetic field for directional orientation (Merkel and Wiltschko 1965, W. Wiltschko 1968). Today, magnetic compass orientation has been demonstrated in more than 15 other species of migratory birds and in homing pigeons, and it seems to be a rather widespread mechanism among birds (R. Wiltschko and Wiltschko 1995). Yet, it is still unclear how birds perceive the geomagnetic field and obtain directional information.

One hypothesis under investigation is that magnetoreception occurs via light-dependent processes parallel to the processes of vision in the avian eye (Leask 1977, 1978; Schulten and Windemuth 1986). This hypothesis assumes that incident light elevates certain macromolecules into an excited state, where they may be transferred to an excited triplet state and where further reactions are determined by the direction of the ambient magnetic field. This would mean that light is essential for magnetoreception. Results from early experiments with homing pigeons are in agreement with this prediction. Inexperienced young pigeons derive their home direction from information obtained with their magnetic compass during the outward journey (R. Wiltschko and Wiltschko 1978); pigeons transported to the release site in total darkness respond like birds transported without meaningful magnetic information, which indicates that light is indeed necessary for magnetic compass orientation (W. Wiltschko and Wiltschko 1981).

Similar experiments with migratory birds in total darkness proved impossible. Directional tendencies of migrants can be recorded only when the birds show a certain amount of activity, but Zugunruhe (i.e. migratory activity) is suppressed by darkness (Gwinner 1974). However, another approach allows testing the hypothesis of light-dependent magnetoreception in migrants. Leask (1977) suggested that exposing birds to monochromatic light at various wavelengths might modify the excitation transfer probability to the excited triplet state, allowing one

to look for possible effects on orientation behavior as indicators of magnetoreception. Previous experiments with Australian Silvereyes (*Zosterops lateralis lateralis*; W. Wiltschko et al. 1993, Munro et al. 1997) and European Robins (W. Wiltschko and Wiltschko 1995, 1999) were in accordance with light-dependent processes of magnetoreception: the birds were well oriented in their migratory direction under blue light of 443 nm and under green light of 565 nm, whereas they failed to orient under red light with a peak at 630 nm.

Given the importance of these experiments in understanding magnetoreception, it is desirable to test additional species under various wavelengths of light, in particular species with different migratory behaviors. Because the two species tested previously were short-distance migrants, we chose the Garden Warbler (*Sylvia borin*), which is a nocturnal migrant that breeds in northern and central Europe and migrates long distances to wintering sites in Africa south of the Sahara. In addition to blue, green, and red light, we used yellow-orange light with a peak wavelength of 590 nm to narrow the range of wavelengths at which magnetic orientation is no longer possible.

Methods.—Twelve young Garden Warblers hatched near Radolfzell at Lake Constance between 3 and 10 June 1994 were taken from their nests and moved to our Frankfurt laboratory on 17 June 1994, where they were hand raised and kept in closed rooms in a magnetic field that was close to normal. The photoperiod simulated the natural one, with a daylight level of 550 lux produced by fluorescent lamps.

The test lights included blue light with a peak at 443 nm and $\lambda/2$ at 402 and 472 nm, produced by a cool beam lamp and a glass filter, and green, orange-yellow, and red lights produced by sets of 25 LEDs each (see W. Wiltschko et al. 1993). Green had a peak at 565 nm, with $\lambda/2$ at 550 and 583 nm. The yellow LEDs were somewhat variable with peaks between 584 and 592 nm, but mostly at 590 nm and $\lambda/2$ at 572 and 609 nm (see W. Wiltschko and Wiltschko 1999: fig. 1). The peaks of the red LEDs lay between 626 and 635 nm; most of them had their peak at 630 and 631 nm and $\lambda/2$ at about 613 and 656 nm. Blue, green, and red were the same lights that were used in pre-

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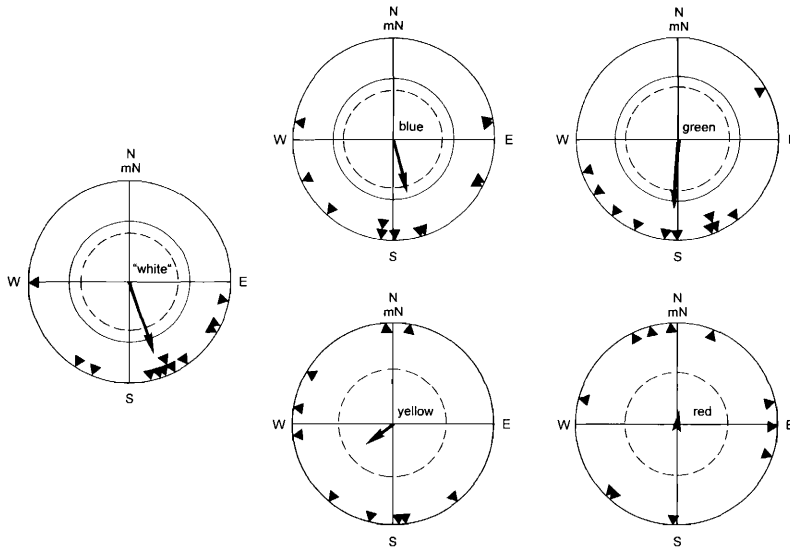


FIG. 1. Orientation behavior of Garden Warblers under light of various wavelengths. Symbols at the periphery of the circle give the mean directions (α_b) of the individual birds; arrows represent the grand mean vectors drawn proportional to the radius of the circle = 1. The two inner circles mark the 5% (dotted) and the 1% (solid) significance border based on the Rayleigh test. See Tables 1 and 2 for numerical data.

vious studies (e.g. W. Wiltschko et al. 1993, Munro et al. 1997, R. Wiltschko and Wiltschko 1998). The lights passed through a set of three diffusers before they reached the birds in the test cages (see below); they were adjusted to be of equal quantal flux of 8.7×10^{15} quanta per s and m^2 (see W. Wiltschko et al. 1993). Tests under "white" light provided by a 15-watt incandescent light bulb served as a control. Each bird was tested under the various lights in a pseudorandom sequence. One bird escaped after the first three tests, and another produced no usable recordings under yellow light and only one under red light.

The experiments were performed between 15 August and 16 October 1994. The birds were tested in wooden huts in the garden of the institute building in the local geomagnetic field (46,000 nT, 66° inclination) and in the absence of visual cues. The tests took place in the first part of the night; they began after the end of the daylight period and lasted for approximately 1 h 15 min. The directional tendencies of the birds were recorded in funnel-shaped cages (Emlen and Emlen 1966) lined with typewriter correction paper. The birds were put into the cages from random directions, which normally does not result in marks on the paper. When the birds were active and hopping up the inclined walls, however, their claws removed the coating of the paper, leaving visible scratch marks that reflected their directional preferences.

For evaluation, the paper was subdivided into 24 sectors, and the number of scratches per sector was counted on a light table. From this distribution, the

heading of the recording was determined by vector addition, with the vector length indicating the concentration of activity. Recordings with fewer than 35 scratches were excluded because of low activity, which involved about 30% of the recordings.

For the headings of each bird in each test condition, we calculated that bird's mean vector with direction α_b and length r_b , which, when n was at least 4, was tested with a Rayleigh test (Batschelet 1981) for directional preferences. The median amount of activity and the median concentration of the bird were also determined. In a second-order analysis, we calculated grand mean vectors (with direction α_N and length r_N) for each test condition, based on the mean headings (α_b) of the individual birds. The grand mean vectors were tested with a Rayleigh test for directional preference, and the distributions in the various conditions were compared using the Mardia Watson Wheeler test (Batschelet 1981). Median activity, median concentration, and vector length (r_b) per bird were compared using the Wilcoxon test for matched pairs.

Results.—Under "white" control light, birds showed a significant preference for a southerly migratory direction (Table 1). Similar orientation in southerly directions was observed under blue and green light. Under yellow and red light, significant directional preferences were not observed (Fig. 1). The distribution of the birds' mean headings under red light was significantly different from that under the "white" control light (Mardia Watson Wheeler test, $U = 11.2$; $P < 0.01$); the other samples were not

TABLE 1. Orientation behavior of individual Garden Warblers under light of various wavelengths. Shown are mean length (r_b) and direction (α_b) of each bird's vector. Asterisks denote significant directional preference based on the Rayleigh test.

Bird	n^a	"White"		Blue		Green		Yellow		Red					
		r_b	α_b	n	r_b	α_b	n	r_b	α_b	n	r_b	α_b			
G1	5	0.95**	168°	5	0.30	78°	4	0.82	250°	4	0.67	220°	5	0.53	91°
G2	2	0.80	162°	1	1.00	162°	—	—	—	—	—	—	—	—	—
G3	5	0.67	202°	5	0.26	80°	5	0.89**	188°	5	0.49	264°	5	0.31	183°
G4	5	0.14	270°	4	0.58	246°	3	0.18	205°	3	0.93	356°	5	0.38	225°
G5	7	0.57	145°	5	0.11	280°	5	0.85*	180°	5	0.29	280°	6	0.22	222°
G6	7	0.59	154°	5	0.33	221°	5	0.73	144°	5	0.16	10°	5	0.26	334°
G7	5	0.68	213°	3	0.56	179°	3	0.72	157°	—	—	—	1	1.00	286°
G8	6	0.55	101°	5	0.38	114°	5	0.16	60°	5	0.60	302°	5	0.34	345°
G9	6	0.79*	156°	5	0.70	164°	6	0.55	222°	4	0.87*	173°	5	0.35	77°
G10	7	0.58	120°	5	0.63	116°	5	0.20	235°	5	0.52	141°	5	0.31	109°
G11	7	0.74*	116°	4	0.51	187°	5	0.71	160°	4	0.29	194°	5	0.72	356°
G12	6	0.45	159°	5	0.88**	187°	5	0.35	158°	5	0.39	177°	5	0.25	21°

* $P < 0.05$; ** $P < 0.01$.

^a Number of recordings that could be evaluated.

significantly different from each other because of considerable scatter (Table 2).

The vector lengths r_b of individual birds varied considerably (Table 1). The medians were longest under green and "white" lights and shortest under red light, with the difference between "white" and red being significant (Table 2). Three birds showed significant tendencies under "white" light, two birds under green light, and one bird each under blue and yellow lights.

The activity under "white" was significantly higher than under blue, green, yellow, and red lights (Table 2). The only difference found between the colored lights was between blue and red (Wilcoxon test, $t = 11.5$, $P < 0.05$). Thus, although activity tended to be lower under red light, it was not significantly different from that under green or yellow lights. The concentration of activity in the cages was similar under all five conditions (Wilcoxon test, $P > 0.05$; Table 2).

Discussion.—Our data clearly show a wavelength dependency in magnetic compass orientation by

Garden Warblers, which is consistent with the existence of light-dependent mechanisms of magnetoreception. Orientation appears to be possible only in a wavelength range from less than 443 nm blue to about 565 nm green; under 590 nm yellow-orange and 630 nm red, the birds were no longer oriented.

Nonsignificant orientation behavior at wavelengths of 590 nm and longer raises the question of whether Garden Warblers could see the light provided by yellow and red LEDs. Garden Warblers have been shown to become inactive in total darkness (Gwinner 1974), so the fact that we observed activity under yellow and red indicates that the yellow and red LEDs provided sufficient light for the birds to see. The amount of activity under yellow and red was similar to that under green, where the birds were well oriented. The birds were active and appeared to be motivated to migrate. Yet, they were not oriented, presumably because they lacked information about their migratory direction because the wavelengths of yellow and red light did not allow them to use their

TABLE 2. Summary of orientation behavior of Garden Warblers under light of various wavelengths.

Light	n^a	Median activity ^b	Median concentration ^b	Median vector length ^b	α_N^c	r_N^d
"White"	12	281	0.28	0.63	159°	0.75***
Blue	12	161*	0.29	0.51	166°	0.55*
Green	11	160*	0.25	0.71	183°	0.70**
Yellow	10	146**	0.26	0.51	236°	0.34
Red	11	116***	0.27	0.33**	5°	0.14

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

^a Number of birds producing recordings that could be evaluated.

^b Asterisks at median activity, median concentration, and median vector length per bird (r_b) indicate significant difference from "white" light based on Wilcoxon test.

^c Direction of grand mean vector.

^d Length of grand mean vector. Asterisks indicate significant directional preferences based on the Rayleigh test.

magnetic compass. This indicates an important difference between the wavelength dependency of magnetoreception and that of vision, because the range of magnetoreception appears to end between 565 and 590 nm, whereas that of vision extends considerably farther toward the long end of the spectrum (see Maier 1992, Maier and Bowmaker 1993).

Our findings with Garden Warblers are in agreement with previous findings with Silvereyes (W. Wiltschko et al. 1993, Munro et al. 1997) and European Robins (W. Wiltschko and Wiltschko 1995, 1999). Aside from Garden Warblers in the present study, the European Robin is the only other species that has been tested under yellow light. The 16 robins, tested in spring, showed a behavior under 590 nm yellow light that differed significantly from that observed under green and blue lights. The distribution of mean headings α_b under yellow light resulted in a nonsignificant grand mean vector of 229° and 0.40, whereas the grand mean vector was 360° and 0.90 under green light and 13° and 0.72 under blue light. At the same time, the vector lengths r_b of the individual robins under yellow light, with a median of 0.50, were significantly shorter than those recorded under green and blue lights, with medians of 0.91 and 0.88, respectively (W. Wiltschko and Wiltschko 1999). Our Garden Warblers were hand raised and showed generally more scatter, resulting in shorter vectors. However, it is interesting that the difference in behavior between yellow and green light appeared to be less pronounced than in robins. Although the warblers were significantly oriented under green light but not under yellow light, the difference in the lengths of the grand mean vectors and of the individual mean vectors was not significant between green and yellow lights. Bird G9 even showed a significant preference in migratory direction under 590 nm yellow light. This seems to suggest that for Garden Warblers, the 590 nm yellow light is just at the edge of the range that allows orientation, and some individuals might still be able to orient.

In view of the wavelength dependency of magnetic compass orientation in migratory birds, it must be mentioned that the various groups of vertebrates respond differently to the light regime. In contrast to birds, the fish, reptiles, and mammals that have been tested were able to use their magnetic compass in total darkness (Quinn 1980, Lohmann and Lohmann 1993, Marhold et al. 1997), indicating that their mechanisms of magnetoreception function independently of light. Amphibians, like birds, seem to require light, but the range of wavelengths in which normal orientation is possible differs markedly from that indicated in birds and appears to be restricted to short wavelengths (below 450 nm) at the blue-violet end of the spectrum (Phillips and Borland 1992, 1994). This suggests that the mechanisms of magnetoreception differ among vertebrates.

The data available from birds on wavelength dependency are in good agreement so far. This is true not only for migrant passerines, but also for homing pigeons. Recent experiments indicate that light of 565 nm green allows magnetic orientation in pigeons, whereas 630 nm red does not (R. Wiltschko and Wiltschko 1998). This means that the same wavelength dependency of magnetoreception is found in birds of different orders and among passerines from three different families (Zosteropidae, Turdidae, and Sylviidae). In addition, different behaviors were tested: homing in pigeons and migratory orientation in passerines, the latter involving both short-distance and long-distance migrants. This suggests that the wavelength dependency of magnetic compass orientation reported here is rather widespread among birds. We need more data from different taxa, however, before we can conclude that the wavelength dependency is the same for all bird species, which, in turn, would imply a uniform mechanism of magnetoreception within Aves.

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Facultative Nest Switching by Juvenile Ospreys

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When fledglings forego parental protection and provisioning to explore nests other than their own, they take a behavioral risk. In species whose young

generally cannot leave the nest prior to developing flight, such movements among nests are unlikely to occur. Yet, this facultative behavior, which we refer to as “nest switching,” has been noted in a variety of semialtricial species (e.g. Poole 1982, González et al. 1986, Newton 1986, Bustamante and Hiraldo 1989, Donazar and Ceballos 1989, Kenward et al. 1993).

Two models may explain facultative nest switching in semialtricial species: (1) switching may arise

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