

CLOCK-SHIFT EXPERIMENTS WITH MIGRATORY YELLOW-FACED HONEYEATERS, *LICHENOSTOMUS CHRYSOPS* (MELIPHAGIDAE), AN AUSTRALIAN DAY-MIGRATING BIRD

URSULA MUNRO

Department of Zoology, The University of New England, Armidale, NSW 2351, Australia
and ROSWITHA WILTSCHKO*

FB Biologie der Universität, Zoologie, Siesmayerstraße 70, D 6000 Frankfurt a.M., Germany

Accepted 30 March 1993

Summary

The behaviour of an Australian day migrant, the yellow-faced honeyeater *Lichenostomus chrysops*, was studied in order to assess the role of the sun in migratory orientation. During autumn migration, all tests took place under a sunny sky; birds were tested while living in the natural photoperiod (control) and with their internal clock shifted 4h fast and 4h slow. In spring, all birds were shifted 3h fast; tests in overcast conditions, with the birds relying on their magnetic compass, served as controls. In control tests in both seasons, the birds preferred directions corresponding to those observed in the wild. When tested under sunny conditions with their internal clock shifted, the birds changed their directional tendencies. However, their preferred directions were different from those expected if a time-compensating sun compass was being used. After about 6 days, the shifted birds' directions were no longer different from the control direction. This behaviour argues against a major role of the sun compass in the orientation of day migrants. The dramatic changes of the sun's arc with geographic latitude might cause day-migrating birds to prefer a more constant orientation cue, such as the geomagnetic field. The initial response to the clock-shift might have occurred because the birds were confused by the conflicting information from solar and magnetic cues. This suggests that the sun is usually used as a secondary cue in combination with the magnetic field.

Introduction

Experiments with night-migrating birds revealed that nocturnal migrants use information from the geomagnetic field, stars and the setting sun to orient their migratory movements (for a summary, see Wiltschko and Wiltschko, 1991). In contrast, fairly little is known about the orientation mechanisms of diurnal migrants. Early observations on the

*To whom reprint requests should be addressed.

Key words: honeyeater, *Lichenostomus chrysops*, bird migration, day migrant, sun compass, clock-shift, internal clock, magnetic compass.

orientation of European starlings, *Sturnus vulgaris*, suggested the use of a sun compass (Kramer, 1950). Further studies on the use of the sun focused on directional training (Hoffmann, 1954; Kramer, 1957), homing of pigeons, *Columba livia domestica* (Schmidt-Koenig, 1958), and of displaced mallards, *Anas platyrhynchos* (Matthews, 1963). The true role of the sun in diurnal migratory orientation, however, remained largely unknown. Nevertheless, it became a widespread belief that the sun compass was the major orientation mechanism of day-migrating birds (e.g. Bellrose, 1972; Emlen, 1975).

Later studies with day-migrating birds, such as European starlings and meadow pipits *Anthus pratensis*, during autumn migration did not support this view. These birds did not show the typical deflections in response to manipulations of their internal clocks that had been observed in clock-shift experiments with homing pigeons (e.g. Schmidt-Koenig, 1958, 1972; cf. Wiltschko, 1983). While these day migrants did not show oriented behaviour when tested under clock-shift conditions on sunny days, they were well oriented under overcast sky (Orth and Wiltschko, 1981; Wiltschko, 1981; Helbig *et al.* 1987). Only in spring did the starlings respond to a shift of their internal clock with the expected deviation (Wiltschko, 1981). These findings left the role of the sun compass rather unclear, while suggesting that another mechanism might be involved.

In order to specify the orientation mechanisms used by day-migrating birds, we began a series of experiments to analyse the migratory behaviour of the yellow-faced honeyeater, *Lichenostomus chrysops*, an Australian diurnal migrant. Previous tests have shown that this species can use the magnetic field for directional orientation (Munro and Wiltschko, 1993); here we present the first results of outdoor tests designed to identify the role of the sun.

Materials and methods

Test birds

The yellow-faced honeyeater is a species of the family Meliphagidae which is characteristic of the Australo-Papuan faunal region (Sibley and Ahlquist, 1985). Yellow-faced honeyeaters are found in the southern parts of South Australia, Victoria, and in the eastern parts of New South Wales and Queensland. They perform conspicuous movements in autumn and spring along the eastern coastline and the adjacent mountain ranges (e.g. Hindwood, 1956; Robertson, 1965; Liddy, 1966). Usually, their migration takes place in fine weather. Movements increase on bright clear mornings, but come to a temporary halt during cloudy periods (Robertson, 1965; Robertson and Woodall, 1983).

Previous experiments outdoors and in the laboratory revealed that yellow-faced honeyeaters tested in cages showed directional tendencies corresponding to those observed in the wild. They preferred northerly to northeasterly directions during the first stage and northwesterly directions during the second stage of autumn migration (Munro and Wiltschko, 1992, 1993; Munro *et al.* 1993).

The experimental birds were caught in spring and autumn between 1989 and 1991 in Armidale, New South Wales (30°30' S, 151°40' E). At those times of the year, the density of yellow-faced honeyeaters in the region is increased, indicating heavy migration (see

McFarland, 1986). The birds were first housed in an outside aviary, but were later moved into individual cages inside a windowless room (see below), where the photoperiod always corresponded in its length to the natural day and night cycle of Armidale.

Clock-shift tests in autumn 1990

All autumn experiments were performed outdoors under sunny conditions in the local geomagnetic field between 1 May and 24 July 1990. Nineteen birds were involved.

The control tests, with the birds living in the outdoor aviary, took place between 07:50h and 11:00h. Eleven birds produced one, and eight birds produced two usable recordings under these conditions. The birds' internal clock was shifted by subjecting them in the laboratory to an artificial day and night cycle for at least 5 days (see Schmidt-Koenig, 1958, 1990). We conducted two types of clock-shift experiments. (1) A group of nine birds was exposed to a 4h fast shift, i.e. their internal clock was advanced 4h, which means that their subjective day started 4h before natural sunrise and ended 4h before natural sunset. These birds were tested outdoors between 07:30h and 09:30h, i.e. between 11:30h and 13:30h according to their subjective time. (2) The other 10 birds experienced a corresponding 4h slow shift, i.e. their internal clock was delayed 4h. Their subsequent testing time was between 13:00h and 15:30h, i.e. between 09:00h and 11:30h of their subjective time.

Owing to unsettled weather, the tests took place on 25 days over a period of 85 days. For most birds, the series began with a control test. They were again tested under control conditions after the clock shift had ended. During the clock shift, they were tested once per day up to six times in sunny weather.

Clock-shift tests in spring 1991

The spring experiments were performed from 25 October to 10 November 1991, under sunny as well as under overcast conditions. Eighteen birds were involved; sixteen had been moved into indoor cages in the course of other experiments, between 1 month 22 days and 9 months 14 days before the clock-shift tests; the other two birds had lived indoors for about 2 years. Hence, all of these birds had had no access to the natural sun for a considerable time. The birds' internal clock was shifted 3h fast, i.e. their subjective day began 3h before natural sunrise and ended 3h before natural sunset. The critical tests began after they had lived under the fast-shifted light regime for at least 5 days.

Yellow-faced honeyeaters show maximal migratory activity between approximately 08:00h and 12:00h (Robertson and Woodall, 1983; U. Munro, unpublished data). In spring, however, outside temperatures rise very fast in the morning. The 3h fast shift allowed us to test the birds shortly after sunrise, between 05:00h and 07:00h, i.e. at a subjective time of 08:00h and 10:00h, when temperatures were still low. Orientation tests with non-shifted birds in sunshine between 08:00h and 10:00h, however, were impossible without endangering the birds' life. Therefore, the data obtained on the two overcast mornings, 1 and 2 November 1991, serve as controls, in the sense that they provide the reference direction. The birds were tested once each day or at least each second day.

Methods used to record orientation

The birds' directional preferences were recorded in funnel cages (Emlen and Emlen, 1966). The inclined walls of these funnels were lined with typewriter correction paper (Tipp-Ex, Germany; see Munro and Wiltschko, 1992, for a more detailed description). A single bird was placed in each funnel for approximately 75min. In its attempts to escape, it left scratch marks on the Tipp-Ex lining of the walls. These scratch marks are a measure of the bird's directional movements.

Data analysis and statistics

After each experiment, the funnel paper was divided into 24 15° sectors, and the number of scratches counted. Tests with fewer than 35 scratches were excluded from the statistical analysis because activity was insufficient. The bird's heading was calculated from the distribution of the scratches (see Munro and Wiltschko, 1992).

Based on the headings, a mean vector with the direction α_m and the length r_m was calculated. The mean vector was tested against randomness with the Rayleigh test. The directional preferences shown by clock-shifted birds in the course of the test series required a detailed analysis. Since the sample sizes of all first, second and consecutive tests were usually too small for an appropriate statistical analysis, the data from the first and the second tests, from the third and fourth tests etc., were pooled (compare Tables 1 and 2) and were then compared with the control sample. The confidence interval was used to test for differences from the expected direction (see below). Directional distributions were tested using the Mardia–Watson–Wheeler test (Batschelet, 1981). Activity levels were compared by the Mann–Whitney test.

Estimation of the expected directional deviations resulting from clock-shifts

Sun-compass orientation requires compensation for the apparent movement of the sun. Earlier experiments with clock-shifted birds (e.g. Hoffmann, 1954; Schmidt-Koenig, 1958, 1972) indicated that the sun compass is based on the sun azimuth. Therefore, we may expect the deviation to be proportional to the difference in sun azimuth between the objective time and the subjective time of day of clock-shifted birds.

In the southern hemisphere, the sun moves counterclockwise from east *via* north to west. This means that advancing the internal clock should lead to a clockwise deflection, while a retardation should result in a corresponding counterclockwise deflection. Since the city of Armidale is situated rather close to the tropic of Capricorn, the movements of the sun vary considerably during the day, with slow azimuth changes early in the morning and late in the evening, and rapid changes around noon. In addition, seasonal changes have to be taken into account. In autumn, the expected deviation varied for the 4h fast-shifted birds between +51° and +55° at the beginning of the tests at 07:30h, while they ranged between +63° and +69° at the end at 09.30 h. For the 4h slow-shifted birds tested between 13:00h and 15:30h, the expected deviation varied between –61° and –71° at the beginning and between –57° and –63° at the end of the tests. The spring experiments took place shortly after sunrise between 05:10h and 06:30h; in this case, the corresponding deviation for 3h fast-

shifted birds only ranged between between $+22^\circ$ and $+23^\circ$ at the beginning and between $+25^\circ$ and $+28^\circ$ at the end of the tests.

In summary, the expected deviations are in the range 55° – 60° for the autumn experiments and around 25° for the spring experiments.

Results

Activity

In autumn, the birds showed little activity, so that more than one-third of all attempted tests did not yield evaluable results. There was no difference between the controls (16 negative tests from 43 attempted tests) and the fast- and slow-shifted birds (17 of 41 and 13 of 40, respectively). In spring, the birds were generally more active, and only 19 of 115 attempted tests under sunny conditions and one of 26 attempted tests under overcast conditions were excluded from the analysis because of too little activity.

Autumn experiments

Fig. 1 summarizes the headings of the birds tested outdoors under a sunny sky, while living in the natural day (control) and in a 4h shifted day.

The birds showed a significant directional preference of 316° NW while living in the natural photoperiod (see Table 1). The data for the 4h clock-shifted birds do not present a clear picture, as there are changes in the course of repeated exposure to the test situation. Fig. 2 presents the deviation from the direction of the controls in subsequent tests. Although many samples are based on very few data points, there appears to be a marked difference between fast-shifted and slow-shifted birds.

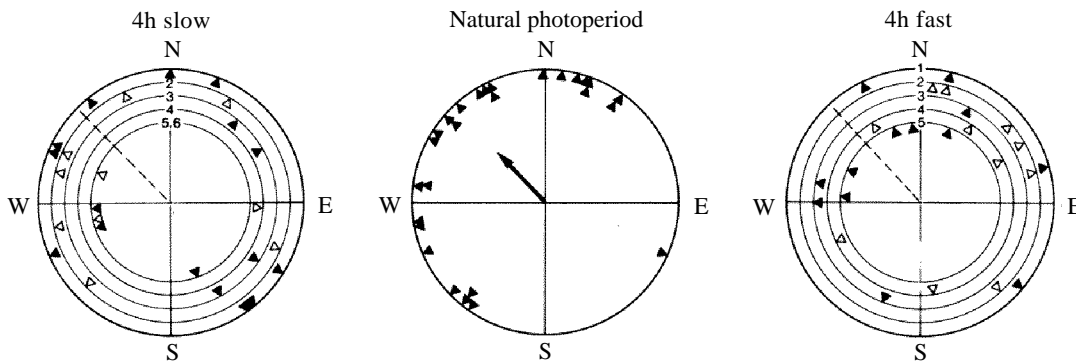


Fig. 1. Orientation behaviour of yellow-faced honeyeaters recorded under sunny conditions during autumn migration. The triangles at the periphery of the circles represent the headings. The headings recorded in successive tests under clock-shifted conditions are placed at different distances from the centre, starting with all data from the first tests at the periphery, alternating filled and open symbols for easier identification. The arrow represents the mean vector of the test under the natural photoperiod, with the radius of the circle having a value of 1; this direction is indicated as a dashed radius in the other diagrams. For numerical data, see Table 1.

Table 1. *Tests with yellow-faced honeyeaters in autumn under sunny sky*

Treatment	Test period	<i>N</i>	<i>n</i>	Activity	α_m (degrees)	r_m	ΔC (degrees)	Significance
Natural photoperiod		19	27	93	316	0.52***		
4 h fast shift	1, 2	7	10	51	50	0.66*	+94	$P < 0.05$
	3, 4	6	9	81	297	0.24	-19	NS
	5, 6	5	5	171	329	0.78*	+13	NS
4 h slow shift	1, 2	10	17	66	297	0.19	-19	NS
	3, 4	4	5	81	93	0.76*	+137	$P < 0.01$
	5, 6	3	5	76	251	0.74	-64	NS

N, number of birds involved; *n*, number of tests. Activity, total number of scratches (see Materials and methods); α_m , direction, and r_m , length of mean vector; asterisks at r_m indicate significance by the Rayleigh test. ΔC , angular difference from the mean of the sample recorded with birds living in natural daylight; the last column indicates the significance of this difference by the Mardia–Watson–Wheeler test. NS, not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

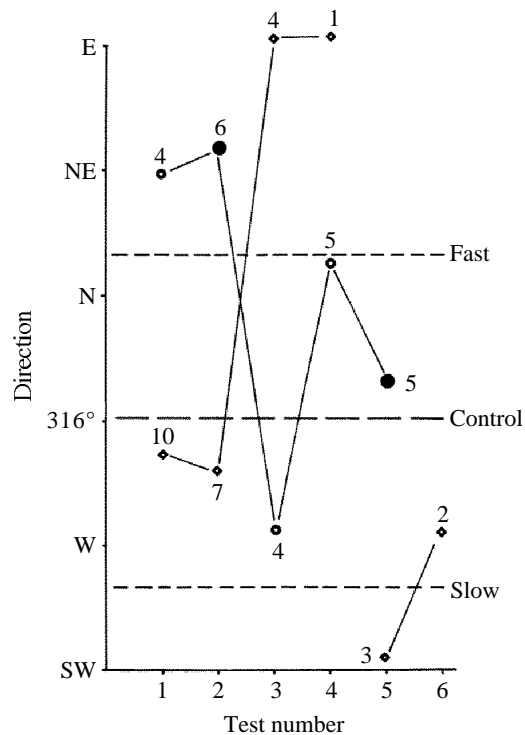


Fig. 2. Mean direction of the clock-shifted groups in successive tests. Circles, 4h fast-shifted birds; diamonds, 4h slow-shifted birds; the numbers indicate the number of headings on which the respective mean is based. Filled circles indicate means significantly different from the control (compare Table 1). The mean of controls, 316° NW, is indicated by a dashed line; the other two lines indicate the directions expected assuming that the birds use a time-compensating sun compass.

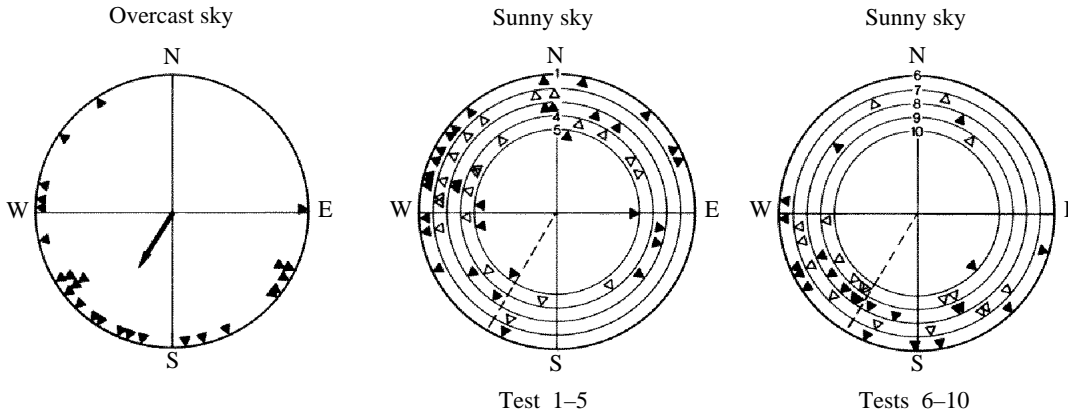


Fig. 3. Orientation behaviour of yellow-faced honeyeaters whose internal clock has been shifted 3h fast during spring. The triangles at the periphery of the circles represent the headings; other symbols as in Fig. 1. The arrow represents the mean vector of the data recorded under overcast skies, with the radius of the circle having a value of 1. For numerical data, see Table 2.

The numerical data are presented in Table 1. During the first two tests, the fast-shifted birds showed a large deviation of 94° towards the expected direction, which was followed by increased scatter in the third and fourth tests. In the fifth test, their directional tendency approached the control direction. The slow-shifted birds, in contrast, showed increased scatter in the first two tests. In the third and fourth tests, they preferred a direction deviating by 137° from the controls in the opposite direction from the expected direction, while in the fifth and sixth tests, they showed a pronounced tendency to deviate by 64° from the controls in the expected direction.

The initial deflection of the 4h fast-shifted birds is considerably larger than predicted, despite the fact that the expected deviation of about 60° still lies within the 5% confidence interval. The directional behaviour of the 4h slow-shifted birds from the first to the fourth tests also differs from the predictions; only the directional tendency observed

Table 2. Tests with 3h fast-shifted yellow-faced honeyeaters in spring

Sky cover	Test period	N	n	Activity	α_m (degrees)	r_m	ΔC (degrees)	Significance
Overcast		15	25	136	211	0.48**		
Sunny sky	1, 2	18	27	97	302	0.63***	+91	$P < 0.001$
	3, 4	14	23	120	330	0.20	+119	$P < 0.05$
	5, 6	12	15	99	222	0.46*	+11	NS
	7, 8	14	22	119	213	0.50**	+2	NS
	9, 10	8	9	268	200	0.55	-11	NS

ΔC , angular deviation from the mean, recorded under overcast skies. Other symbols and abbreviations as in Table 1.

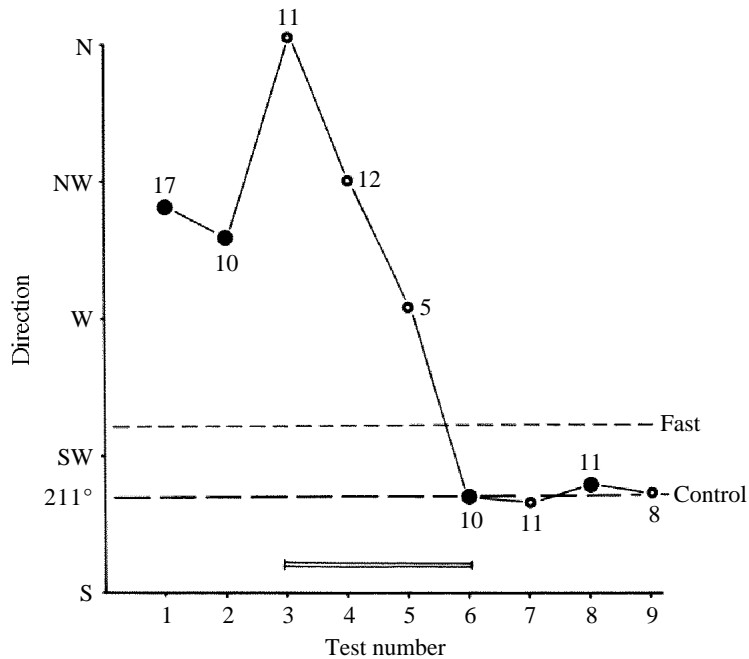


Fig. 4. Mean directions of successive tests of 3h fast-shifted birds under sunny conditions. Symbols as in Fig. 2. The mean direction under overcast skies, 211° SSW, is indicated by a dashed line; the other line indicates the direction expected assuming that the birds use a time-compensating sun compass. The bar marks the period when the control data under overcast skies were recorded.

during the fifth and sixth tests agrees with the prediction of a model based on a time-compensating sun compass.

Spring experiments

All birds were tested under 3h fast-shifted conditions.

The data recorded under solid overcast skies provided the reference direction (Fig. 3, left); they were obtained between the third and sixth recordings from individual birds (see Fig. 4). The birds preferred a significant mean direction of 211° SSW.

In fine weather, with the sun visible, they showed a change in directional tendencies similar to that of the fast-shifted birds in autumn (see Fig. 4 and Table 2). During their first and second tests, the mean direction deviated significantly by 91° from the direction recorded under overcast skies. This deflection pointed in the expected direction, but was significantly larger than expected. Scatter increased during the third and the fourth tests and, from the fifth and sixth tests onwards, the mean directions roughly coincided with the one measured under overcast sky.

Discussion

The mean directions under control conditions in autumn and spring coincide with the

migratory direction of yellow-faced honeyeaters observed in the wild during these seasons (Hindwood, 1956; Robertson, 1965; Liddy, 1966). The results recorded with birds living in the natural photoperiod during autumn also correspond to the directional preference of 321° shown by yellow-faced honeyeaters in indoor tests during the late stage of autumn migration (Munro and Wiltschko, 1993). The mean direction of 211° in spring under overcast skies represents a reversal of the direction recorded in previous tests during the first part of autumn migration (Munro and Wiltschko, 1993; Munro *et al.* 1993). Thus, the control data provide a firm baseline for assessing the effects of manipulation of the internal clock on orientation behaviour.

A clock-shift causes a situation where cues that change in the course of the day, such as the sun, and constant cues, such as the magnetic field, provide conflicting information. Homing pigeons clearly prefer their sun compass when clock-shifted, which results in a typical deflection from the mean direction of controls (e.g. Schmidt-Koenig, 1972, 1990). The clock-shifted migrants in our tests behaved differently; their data do not agree with the predictions derived from the traditional sun compass concept.

The slow shift led at first to disorientation, which was followed by inexplicable directional tendencies. The reasons for the lack of directional preference during the first two tests are unknown. Lower motivation, for example, does not seem probable, since the amount of activity and the percentage of inactive tests were not different from those of the controls. The disoriented behaviour observed when solar and magnetic cues provide conflicting information corresponds with results of earlier experiments with European starlings and meadow pipits (Orth and Wiltschko, 1981; Wiltschko, 1981). It remains uncertain whether the slow-shifted birds' (non-significant) tendency to deflect in the predicted direction observed after five tests reflects sun-compass orientation. Such a reaction would have been expected immediately, but not at a time when the fast-shifted birds were no longer affected by the clock shift.

The behaviour of fast-shifted birds is also difficult to interpret. In the first two tests, they showed deflections to the expected side, but of considerably greater extent than predicted. After a short period of disorientation, they preferred directions that started to approach those of the controls. The fast-shift tests in autumn and in spring differed in a number of important aspects: (1) the size of the shift, 4 h *versus* 3 h, (2) the subjective time of testing, 11:30h–13:00h *versus* 08:00h–10:00h, (3) the expected deflection, 60° *versus* 25° , and (4) the duration of time the birds had spent inside without access to the natural sun before the critical tests, 5–11 days *versus* 52 days and up to more than 1 year. Despite these differences, the responses of the birds in the two seasons were remarkably similar.

The responses of the clock-shifted birds indicate that the sun is involved; however, the kind of response clearly argues against control of orientation by a time-compensating sun compass. Attempts to interpret the birds' behaviour when solar and magnetic cues are giving conflicting information have to take other responses to the sun into account. The disoriented behaviour observed in the first two tests with slow-shifted birds might suggest that the birds were confused when faced with conflicting cues. The fast-shifted birds, however, showed a deflection of their directional tendencies. In autumn, the mean direction during the first two tests is close to the azimuth of the sun at the beginning of the

tests. This might mean that the birds attempted to move towards the sun. In spring, when the sun was still low above the horizon, the direction of 302° is roughly opposite to the sun's azimuth, which could indicate that the birds move towards the lightest part of their funnel cage. Hence, the tendencies of the fast-shifted birds during the first 2 days might suggest a simple positive phototactic behaviour.

Only birds in spring were tested more than six times under clock-shifted conditions. From test 6 onward, their directional tendencies coincided with the direction recorded under overcast sky. This suggests that the birds were no longer affected by the clock shift. A similar phenomenon was observed in homing pigeons when they were repeatedly exposed to the natural environment while living in a shifted photoperiod: their initial orientation ceased to differ from that of control birds living in the natural photoperiod (Wiltschko *et al.* 1976, 1984). In migratory birds, the behaviour of yellow-faced honeyeaters has a parallel in the response of nocturnal migrants tested under the stars while receiving contradictory information from the magnetic field. After a few tests, the birds followed the magnetic field and apparently ignored the stars (e.g. Wiltschko and Wiltschko, 1975*a,b*; Beason, 1987; Bingman, 1987). There is little doubt that the honeyeaters also used their magnetic compass to orient in their seasonally appropriate migratory direction after six tests, since in subsequent outdoor tests the birds reversed their directional tendencies when the vertical component of the local magnetic field was inverted (see Fig. 2 in Munro and Wiltschko, 1993).

These results indicate that the magnetic compass also plays an important role in day migrants. The decrease of migratory movements under overcast skies that is frequently observed in the wild (e.g. Robertson, 1965; Robertson and Woodall, 1983) seems to have motivational rather than orientational causes, as overcast skies are normally associated with adverse weather conditions such as rain, strong winds, etc. The reduced migration of a day migrant like the yellow-faced honeyeater under overcast skies has a parallel in nocturnal migrants, where migration is also generally reduced under overcast skies. The birds that migrate under these conditions, however, are well oriented (e.g. Bellrose, 1967).

At this point, it might seem necessary to consider the general role of the sun compass in bird orientation, in particular in that of diurnal migrants. Most evidence for sun-compass orientation has been obtained from clock-shift experiments with directionally trained birds (e.g. Hoffmann, 1954; Saint Paul, 1956; Able and Dillon, 1977), displaced pigeons (e.g. Schmidt-Koenig, 1958, 1972, 1990; Wiltschko and Wiltschko, 1981) and mallards (Matthews, 1963, 1984). Furthermore, studies on scrub jays, *Aphelocoma coerulescens*, have shown that these birds use the sun compass for the recovery of food caches (Wiltschko and Balda, 1989). All of these orientation tasks have in common that they do not involve large spatial movements as does migration. The changes in geographic latitude during migration require a permanent adjustment of the sun compass to the local situation, which makes an independent reference system such as the geomagnetic field essential (see Wiltschko, 1981, for a discussion). The sun compass thus does not seem to be adequate for the orientation of large-scale movements, and might be less important for migration than for movements within the home range, such as homing, searching for food, etc.

Our clock-shift tests with yellow-faced honeyeaters clearly speak against a dominant

role of the sun compass in their orientation. At the same time, they indicate that the sun is involved in the orientation of diurnal migrants, since the birds seemed to realize the conflict between magnetic and solar information. However, they followed their magnetic compass after six tests. This can best be explained by the assumption that the sun represents a secondary cue and derives its significance from the magnetic field. The sun thus may be used as a 'celestial landmark' in migratory orientation. Whether it is sufficient to direct the birds' movements in the absence of other conflicting cues remains to be tested.

This work was supported by the Deutsche Forschungsgemeinschaft in the program SFB 45 'Vergleichende Neurobiologie des Verhaltens' and a Commonwealth Postgraduate Research Award to U.M. Part of the computer work was carried out at the Hochschulrechenzentrum der Universität Frankfurt a.M. Special thanks go to Hugh A. Ford, John Munro, Helen Sink, Geoff Barrett and Stuart Cairns for their support and valuable discussion.

References

- ABLE, K. P. AND DILLON, P. M. (1977). Sun compass orientation in a nocturnal migrant, the White-throated Sparrow. *Condor* **79**, 393–395.
- BATSCHLET, E. (1981). *Circular Statistics in Biology*. London: Academic Press.
- BEASON, R. C. (1987). Interaction of visual and non-visual cues during migratory orientation by the Bobolink (*Dolichonyx oryzivorus*). *J. Ornithol.* **128**, 317–324.
- BELLROSE, F. C. (1967). Radar in orientation research. In *Proc. XIV Int. Ornith. Congr. Oxford 1966* (ed. D. W. Snow), pp. 281–309. Oxford, Edinburgh: Blackwell Scientific Publishing.
- BELLROSE, F. C. (1972). Possible steps in the evolutionary development of birds' navigation. In *Animal Orientation and Navigation*. NASA SP-262 (ed. S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs and R. E. Belleville), pp. 223–258. Washington, DC: US Government Printing Office.
- BINGMAN, V. P. (1987). Earth's magnetism and the nocturnal orientation of migratory European Robins. *Auk* **104**, 523–525.
- EMLÉN, S. T. (1975). Migration: Orientation and Navigation. In *Avian Biology*, vol. V (ed. D. S. Farner and J. R. King), pp. 129–219. New York, San Francisco, London: Academic Press.
- EMLÉN, S. T. AND EMLÉN, J. T. (1966). A technique for recording migratory orientation of captive birds. *Auk* **83**, 361–367.
- HELBIG, A., ORTH, G., LASKE, V. AND WILTSCHKO, W. (1987). Migratory orientation and activity of the Meadow Pipit (*Anthus pratensis*): a comparative and experimental field study. *Behaviour* **103**, 276–293.
- HINDWOOD, K. A. (1956). The migration of the White-naped and Yellow-faced Honeyeater. *Emu* **56**, 421–425.
- HOFFMANN, K. (1954). Versuche zu der im Richtungsfinden der Vögel enthaltene Zeiteinschätzung. *Z. Tierpsychol.* **11**, 453–475.
- KRAMER, G. (1950). Weitere Analyse der Faktoren, welche die Zugaktivität des gekäfigten Vogels orientieren. *Naturwissenschaften* **37**, 377–378.
- KRAMER, G. (1957). Experiments in bird orientation and their interpretation. *Ibis* **99**, 196–227.
- LIDDY, J. (1966). Autumnal migration of the Yellow-faced Honeyeater. *Emu* **66**, 87–104.
- MATTHEWS, G. V. T. (1963). The astronomical bases of 'nonsense' orientation. *Proc. XIII Int. Ornith. Congr., Ithaca, New York, 1962*. pp. 415–429.
- MATTHEWS, G. V. T. (1984). 'Nonsense' orientation in mallards: a resume and an investigation of the mechanism of a sun-compass. *Wildfowl* **35**, 81–92.
- McFARLAND, D. C. (1986). The organization of a honeyeater community in an unpredictable environment. *Austr. J. Ecol.* **11**, 107–120.

- MUNRO, U. AND WILTSCHKO, W. (1992). Orientation studies on Yellow-faced Honeyeaters, *Lichenostomus chrysops* (Meliphagidae), during autumn migration. *Emu* **92**, 181–184.
- MUNRO, U. AND WILTSCHKO, W. (1993). Magnetic compass orientation in the Yellow-faced Honeyeater, *Lichenostomus chrysops*, a day-migrating bird from Australia. *Behav. Ecol. Sociobiol.* **32**, 141–145.
- MUNRO, U., WILTSCHKO, W. AND FORD, H. A. (1993). Changes in the migratory direction of Yellow-faced Honeyeaters, *Lichenostomus chrysops* (Meliphagidae), during autumn migration. *Emu* **93**, 59–62.
- ORTH, G. AND WILTSCHKO, W. (1981). Die Orientierung von Wiesenpiepern (*Anthus pratensis* L.). *Verh. dt. zool. Ges.* **74**, 252.
- ROBERTSON, J. S. (1965). Migration of Yellow-faced Honeyeaters. *Austr. Bird Bander* **3**, 33–34.
- ROBERTSON, J. S. AND WOODALL, P. F. (1983). The status and movements of honeyeaters at Wellington Point, South-east Queensland. *Sunbird* **13**, 1–14.
- SAINT PAUL, U. (1956). Compass directional training of Western Meadow Larks (*Sturnella neglecta*). *Auk* **73**, 203–210.
- SCHMIDT-KOENIG, K. (1958). Experimentelle Einflußnahme auf die 24-Stunden-Periodik bei Brieftauben und deren Auswirkungen unter besonderer Berücksichtigung des Heimfindevermögens. *Z. Tierpsychol.* **15**, 301–331.
- SCHMIDT-KOENIG, K. (1972). New experiments on the effect of clock-shifts on homing in pigeons. In *Avian Orientation and Navigation*. NASA SP-262 (ed. S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs and R. E. Belleville), pp. 275–282. Washington, DC: US Government Printing Office.
- SCHMIDT-KOENIG, K. (1990). The sun compass. *Experientia* **46**, 336–341.
- SIBLEY, C. G. AND AHLQUIST, J. E. (1985). The phylogeny and classification of the Australo-Papuan passerine birds. *Emu* **85**, 1–14.
- WILTSCHKO, R. (1981). Die Sonnenorientierung der Vögel. II. Entwicklung des Sonnenkompaß und sein Stellenwert im Orientierungssystem. *J. Ornithol.* **122**, 1–22.
- WILTSCHKO, R. AND WILTSCHKO, W. (1981). The development of sun compass orientation in young homing pigeons. *Behav. Ecol. Sociobiol.* **9**, 135–141.
- WILTSCHKO, W. (1983). Compasses used by birds. *Comp. Biochem. Physiol.* **76A**, 709–718.
- WILTSCHKO, W. AND BALDA, R. P. (1989). Sun compass orientation in seed-caching Scrub Jays (*Aphelocoma coerulescens*). *J. comp. Physiol. A* **164**, 717–721.
- WILTSCHKO, W. AND WILTSCHKO, R. (1975a). The interaction of stars and magnetic field in the orientation system of night migrating birds. I. Autumn experiments with European warblers (Gen. *Sylvia*). *Z. Tierpsychol.* **37**, 337–355.
- WILTSCHKO, W. AND WILTSCHKO, R. (1975b). The interaction of stars and magnetic field in the orientation system of night migrating birds. II. Spring experiments with European Robins (*Erithacus rubecula*). *Z. Tierpsychol.* **39**, 265–282.
- WILTSCHKO, W. AND WILTSCHKO, R. (1991). Magnetic orientation and celestial cues in migratory orientation. In *Orientation in Birds* (ed. P. Berthold), pp. 16–37. Basel: Birkhäuser Verlag.
- WILTSCHKO, W., WILTSCHKO, R. AND KEETON, W. T. (1976). Effects of a 'permanent' clock-shift on the orientation of young homing pigeons. *Behav. Ecol. Sociobiol.* **1**, 229–243.
- WILTSCHKO, W., WILTSCHKO, R. AND KEETON, W. T. (1984). The effects of a 'permanent' clock-shift on the orientation of experienced homing pigeons. I. Experiments in Ithaca, New York, USA. *Behav. Ecol. Sociobiol.* **15**, 263–272.