Meddelande nr....l.b.1.... från Falsterbo fågelstation

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Migratory Orientation of Passerines at Dusk, Night and Dawn

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Abstract

The orientation of four different species of nocturnal passerine migrants was investigated in spring and autumn by orientation-cage experiments at dusk, night, and dawn under natural clear skies. Our objective was to examine the orientation behaviour at different periods of a nocturnal migration flight, and to relate the orientation to visual orientation cues (the position of the sun). In robins, the mean orientation was W (autumn) and NW (spring) in the evening tests, N (both autumn and spring) in the middle of the night, and NE (both autumn and spring) at sunrise. The northerly mean orientation at night in both spring and autumn, agreed well with the expected migratory direction for robins (re-oriented migration in autumn) as shown by ringing recoveries. A clockwise shift in mean orientation throughout a nocturnal migration flight period (spring and autumn) indicates that the birds may not compensate fully for the azimuthal change of either sun or stars at the horizon. Migratory activity was highest at dusk and dawn, with a reduction in activity in the middle of the night. Spring tests revealed a significantly higher incidence of migratory activity during the second h after sunset than in the autumn tests, indicating longer flights in spring when the birds are approaching the breeding areas. For pied flycatchers, redstarts and lesser whitethroats, the directional choices during spring were between NW and N in evening tests while the dawn experiments showed mean directions towards NE or E. A compromise orientation was observed during both spring and autumn between the expected migratory direction for the season and the position of the sun at both sunset and sunrise, resulting in orientation more to the north of the sun in spring and more to the south of the sun in autumn.

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Introduction

The important role of the sunset position and the skylight polarization pattern for twilight orientation of nocturnal passerine migrants has been confirmed in a number of recent studies (ABLE 1982, 1989; MOORE 1978, 1980, 1982, 1987a;

MOORE & PHILLIPS 1988; HELBIG & WILTSCHKO 1989; HELBIG 1990, 1991; OTTOSSON et al. 1990; SANDBERG 1991). In addition to solar cues, migratory birds are also able to use the geomagnetic field for orientation (MERKEL & WILTSCHKO 1965; WILTSCHKO & WILTSCHKO 1972, 1988) and during the dark part of the night birds have been demonstrated to orient themselves by the aid of stars (SAUER 1957; EMLEN 1967a, b; RABØL 1988).

Most cage studies conducted under natural clear skies have focused on the orientation behaviour of night migrants at the sunset period before and during the expected migratory take-off (ABLE 1982; MOORE 1985, 1987a; SANDBERG et al. 1988; SANDBERG 1991; ÅKESSON 1994), while only a few studies have dealt with the birds' orientation at night (WILTSCHKO & WILTSCHKO 1975a, b) or during the early morning at sunrise (WILTSCHKO & HÖCK 1972; ABLE 1977; MOORE 1986).

Orientation experiments during the evening twilight period have shown possible sunset attraction (SANDBERG et al. 1988; SANDBERG 1991; ÅKESSON 1994) as well as orientation in the expected migratory direction (MOORE 1985; BINGMAN & WILTSCHKO 1988; SANDBERG et al. 1988; HELBIG 1990; SANDBERG 1991; ÅKESSON 1993). At night, directional responses in agreement with the expected migratory direction have been observed under natural clear skies and, under these circumstances, magnetic cues have been shown to play an important role in the birds' orientation (WILTSCHKO & WILTSCHKO 1975a, b). Under a full moon, when savannah sparrows (*Passerculus sandwichensis*) were exposed to the clear night sky without first being allowed to see the evening twilight sky, the birds oriented towards the direction of the moon, thus demonstrating a phototactic response rather than orienting in the expected migratory direction. In contrast, birds that were allowed to experience the natural-sunset sky oriented in the expected migratory direction (MOORE 1987b). In early morning tests, migrating robins (*Erithacus rubecula*) have been shown to orient in the expected migratory direction and to respond to shifts of the magnetic field under natural clear skies, but only when they showed migratory activity during the night preceding the tests (WILTSCHKO & HÖCK 1972). Morning orientation experiments with night-migrating warblers revealed orientation in northerly migratory directions during spring, and a clear response to shifts of the polarization pattern in the sky (MOORE 1986). These experiments indicate that nocturnal bird migrants may also perform migration flights during the early morning, and that both magnetic and visual cues may be involved in the orientation. However, the orientation behaviour of individual birds during the complete period of possible migratory night flights, i.e. from evening twilight throughout the night until sunrise, has only been studied to a limited extent.

To investigate if and how directional choices of passerine night migrants may change during the night, and whether the orientations differ between evening and the early morning, we performed orientation cage experiments under natural clear skies with four different species of bird migrants (robin, redstart (*Phoenicurus phoenicurus*), pied flycatcher (*Ficedula hypoleuca*) and lesser whitethroat (*Sylvia curruca*)) during the spring and autumn migration periods in South Sweden.

Materials and Methods

Experimental Birds

The robin and the redstart have the most extensive breeding ranges from approximately 37 °N to 70 °N (VOOUS 1960; CRAMP 1988). Pied flycatchers show a slightly more northerly centre of gravity in their breeding distribution (from 39 °N and northwards to 64 °N) while the breeding area of the lesser whitethroat is more to the northeast (37 °N – 66 °N; VOOUS 1960; CRAMP 1992, 1993). All four species pass southern Sweden in both their spring and autumn migration, and are captured at Falsterbo Bird Observatory (55 °23′N, 12 °50′E) in relatively large numbers. In spring, the birds are heading for their northerly breeding areas. In autumn, lesser whitethroats migrate towards southeast/south to their winter quarters in tropical East Africa, while redstarts and pied flycatchers migrate to western Africa on SW courses, and finally, robins head for wintering areas in southwestern Europe (ZINK 1973).

The experimental birds were captured at Falsterbo Bird Observatory during the spring seasons of 1985, 1986, and 1988–1992 (Apr. and May) and on autumn migration in 1985–1987 and 1989–1992 (Sep. and Oct.), and they were tested in an open area close to the capture site, or transported approximately 55 km NE by car to a test site at Stensoffa Ecological Field Station (55 °42′N, 13 °25′E). At capture, the age of the birds was determined by criteria given in SVENSSON (1984). Test birds were held in captivity for 1 or a few days, during which time the birds' orientation was investigated either in experiments lasting for 8–13 h (whole-night experiments, robins only) or 2 h, i.e. 1 h immediately after capture in the morning and a second h later in the evening the same day. In a few cases, owing to overcast conditions, the tests were postponed until the next clear-sky period. Each bird was tested only once in each test period. During the time between tests, the birds were kept indoors and separately in spacious cages (350 × 350 × 450 mm) in a room with windows, and thus were exposed to the natural photoperiod. The birds were fed *ad libitum* with mealworms and vitaminized water.

Experimental Setup and Procedure

The directional behaviour of the birds was recorded in two types of circular orientation cages with sloping walls (modified Emlen funnels: EMLEN & EMLEN 1966; SANDBERG et al. 1988), with a top diameter of 300 mm and an inner height of 125 mm or 150 mm. The cages were constructed out of non-magnetic materials and the top of the cages was covered with fine-meshed plastic net, giving the birds visual access to the natural clear sky. In one of the cage types, with automatic registration, the walls were subdivided into eight 45 ° sectors. Under each sector a microswitch was placed and when the bird jumped on the sector, the microswitch closed and the jump was recorded at a specific counter. In addition to the 'automatic-cage type' described above, cages in which the birds' directional activity was recorded as clawmarks in the pigment of typewriter correction paper (Tipp-Ex® paper; RABØL 1979) or in dark pigment sprayed on glossy paper, were used. After the experiments, the paper was subdivided into 24 sectors and the claw scratches across a certain line, between 20 mm and 100 mm height above the cage floor and crossing the majority of the registrations, were counted in each sector. Based on the bird's activity in the 8 or 24 sectors, standard methods were used to calculate the mean direction of individual birds (BATSCHELET 1981).

Orientation experiments were performed under natural clear skies (≤⅜ of cloud cover) with the direction towards sunset or sunrise clearly visible. In the evening, experiments were initiated 10–20 min after local sunset, while the morning experiments were conducted immediately after capture, either before or shortly after sunrise.

In the experiments with robins (spring and autumn), lasting from sunset throughout the night until sunrise, the orientation cages were placed inside large plastic tubes, restricting the birds' view of the sky above to a sector of approximately 90 ° centered around the zenith (SANDBERG et al. 1988). All other experiments were conducted without screens, thus allowing the birds to see approximately 160 ° of the sky above (SANDBERG 1991). There was no difference in the orientation behaviour between tests performed with a restricted view of the sky (experiments at Stensoffa) as compared to tests without screens (tests at Falsterbo; robins control condition, sunset, spring, $F_{1,169} = 0.003$, p > 0.05; sunrise hour, spring, $F_{1,98} = 1.32$, p > 0.05; sunset, autumn, $F_{1,142} = 2.91$, p > 0.05, one-way classification test; MARDIA 1972; cf. below), except for morning tests in autumn where there was an increase in

Table 1: Number of birds classified as active, inactive, disoriented and total number of birds used in the orientation-cage experiments under clear skies in spring and autumn. The experiments were performed in the evening-twilight period (vector 1), during the night (vector 2–4 for robins) and in the early morning around sunrise (vector 5)

Species, season	Vector no.	Active tests	Inactive tests	Disoriented tests	Total no. of tests
Robin, spring	1	171	34	2	207
	2	51	43	1	95
	3	18	6	2	26
	4	17	9	0	26
	5	101	7	3	111
Robin, autumn	1	144	57	10	211
	2	30	120	4	154
	3	29	6	2	37
	4	22	9	1	32
	5	49	15	4	68
Redstart, spring	1	66	4	8	78
	5	23	2	0	25
Pied flycatcher, spring	1	45	0	2	47
	5	18	0	1	19
Lesser whitethroat, spring	1	17	3	1	21
	5	8	0	0	8
		809 (69 %)	315 (27 %)	41 (4 %)	1165 (100 %)

scatter in the experiments without screens compared to tests with screens ($t = 2.06$, $p < 0.05$, test for the homogeneity of concentration parameters; MARDIA 1972). However, since the angle of orientation did not differ significantly between screened and unscreened tests (tests performed at Stensoffa and Falsterbo, respectively), experiments from the two categories were pooled in the analysis.

Data Analysis and Statistics

We quantified the activity of the birds in the orientation cages as the number of counter registrations or scratches (minimum set at 40) during 1 test h. The orientation experiments at night were performed using the cages with automatic registration and the birds' activities were divided into 1-h periods throughout the night. Because of the reduced activity of robins tested in the middle of the night, 3 or more test h were combined into one test period in the analysis.

By vector addition we calculated a mean heading of each bird tested. Experiments which failed to demonstrate a reasonable well-defined orientation (the limit was arbitrarily set to $p > 0.05$ according to the Rayleigh test; BATSCHELET 1981) were excluded. Based on this criterion only 41 (3.5 %) disoriented and unreliable orientation results were excluded (Table 1).

For each test period we calculated a mean angle of orientation (α) based on individual mean headings (Table 2). Mean vector lengths (r), ranging between 0 and 1, give a measure that is inversely related to the angular scatter. The Rayleigh test (BATSCHELET 1981) was used to determine whether the circular distribution was significantly different from random.

Differences in orientation scatter (indicated by t) or in the angle of mean orientation (indicated by $F_{1,df}$) between test periods were analysed by using MARDIA's 'test for the homogenity of concentration parameters' and 'one-way classification test', respectively (MARDIA 1972). For the experiments at sunset and sunrise (skylight glow at the horizon clearly visible), the mean direction towards the position of the sun in the middle of the test h was calculated. We used the 95 % confidence interval to analyse whether the birds mean orientation differed from the direction towards the mean position of the sun.

Table 2: Mean angle of orientation (α), vector lengths (r) and numbers of birds (n) tested in orientation experiments under natural clear skies in South Sweden during spring and autumn, respectively. Significance levels: ***p < 0.001; **p < 0.01; *p < 0.05; ns p > 0.05) are according to the Rayleigh test (BATSCHELET 1981) and the 95 % confidence interval (CI: p-values denote significant or non-significant deviations from mean sun azimuth). Mean directions towards the position of the sun in the middle of the test h are given. Vector numbers refers to mean vectors of orientation in Figs. 1, 2 and Table 1

| Species	Season	Vector no	α	n	r(p)	Sun position	95 % CI (p)
Robin	spring	1	314°	171	0.69***	305°	± 9° ns
		2	345°	51	0.66***	324°	±15° ns
		3	17°	18	0.58**	340°	±32° ns
		4	36°	17	0.71***	21°	±24° ns
		5	47°	100	0.44***	71°	±17°*
Robin	autumn	1	270°	144	0.68***	272°	± 9° ns
		2	343°	30	0.32*	283°	±54° ns
		3	348°	29	0.36*	320°	±45° ns
		4	348°	22	0.54**	24°	±32° ns
		5	32°	49	0.23 ns	98°	—
Redstart	spring	1	328°	63	0.58***	312°	±17° ns
		5	47°	23	0.72***	75°	±21°*
Pied flycatcher	spring	1	355°	43	0.68***	314°	±16°*
		5	85°	18	0.69***	98°	±24° ns
Lesser whitethroat	spring	1	348°	17	0.65***	315°	±25°*
		5	37°	8	0.85**	64°	±29° ns

Results

Numbers of birds used in the orientation experiments, and numbers of birds excluded owing to inactivity or disorientation (see Materials and Methods) are given in Table 1. Mean angles of orientation (α), mean vector lengths (r) and number of birds (n) included in the analysis are shown in Table 2. Vector numbers refer to the different mean vectors shown in Figs 1 and 2.

Orientation Experiments with Robins: Spring and Autumn

The mean orientation of robins was significantly different from random in all experimental periods, except for the sunrise test period in autumn (p = 0.07; Fig. 1, Table 2).

In spring, the mean orientation recorded during the first test hour immediately after sunset differed from the expected migratory direction towards north and was not significantly different from the direction towards the sun in the middle of the test h (p > 0.05, Table 2). Morning tests revealed a mean orientation towards NE which was significantly different from the position of the sun (p < 0.05, Table 2). The mean orientation in the first test hour at sunset (vector 1, Fig. 1) was significantly different from the mean orientation in the 2nd test h (vector 2: Mardia's one-way classification test, $F_{1,220} = 11.5$, p < 0.01), and also significantly different from the other two succeeding test periods (vector 3: $F_{1,187} = 16.4$,
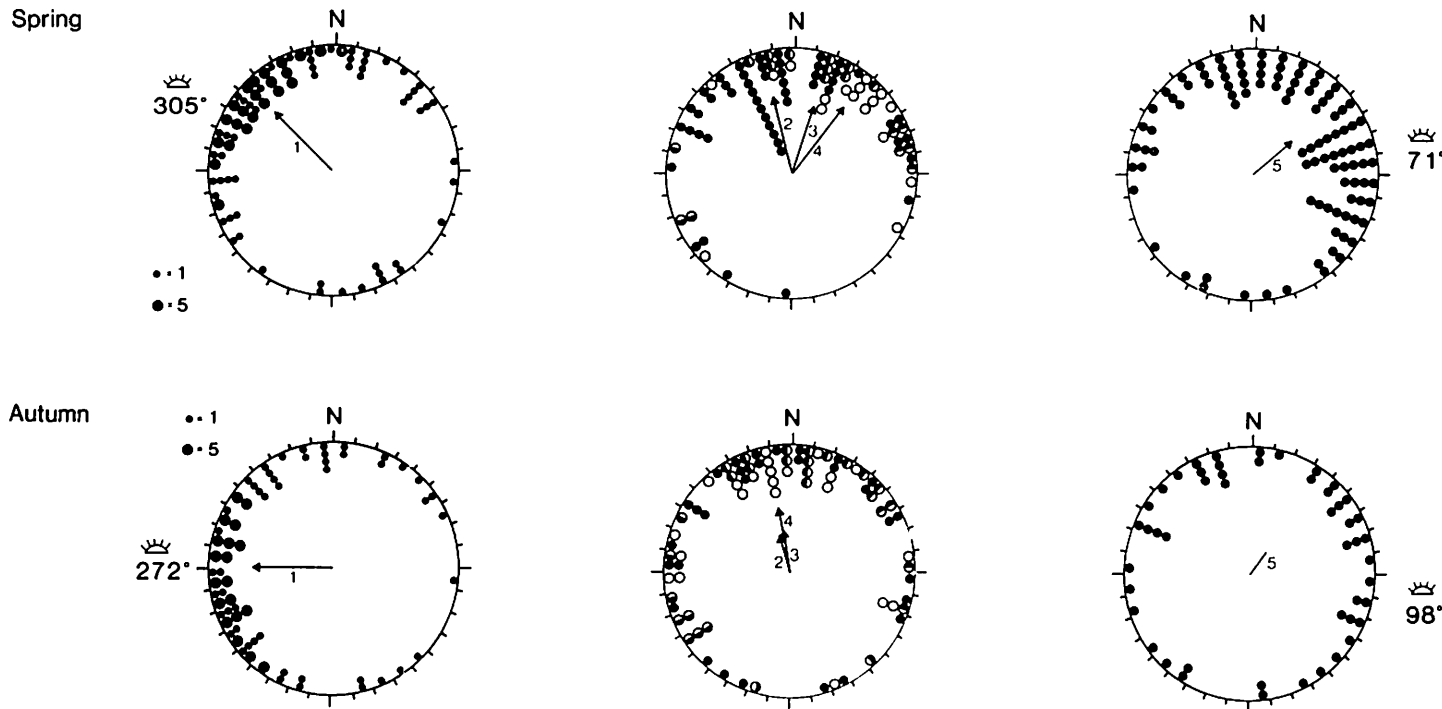
Spring

Autumn

Fig. 1: Results of orientation experiments with robins under natural clear skies during spring and autumn migration. Mean vectors of orientation during the evening twilight (vector 1), night (vector 2, 2nd test h after sunset; vector 3, test h 2–4 combined in spring and 2–6 in autumn; vector 4, test h 5–7 combined in spring and 7–12 in autumn) and early-morning periods (vector 5, corresponds to test h 8 in spring and 13 in autumn) are given. Test periods 1–3 refer to tests before midnight (spring and autumn). Samples showing significant mean orientation according to the Rayleigh test are represented by arrows and non-significant groups with a line. Experiments performed during the night (central figure), vector 2, 3 and 4 are represented by filled circles, half-filled circles and open circles, respectively. The mean direction towards the position of the sun in the middle of the test periods at sunset (SS) and sunrise (SR) are indicated. Values for mean vector lengths, mean angles of orientation and numbers of birds are given in Table 2

$p < 0.01$; vector 4: $F_{1,186} = 31.2$, $p < 0.01$). Individual mean headings were significantly more scattered in morning tests, as compared to evening-twilight tests (vector 5 vs. vector 1: $t = 3.8$, $df = 269$, $p < 0.05$).

In the autumn, there was a significant westerly mean orientation in tests performed immediately after sunset (Table 2), and the orientation was not significantly different from the sunset position ($p > 0.05$, Table 2). The mean orientation in the 2nd, 3rd, and 4th test periods at night were towards northerly directions falling between the orientation recorded at sunset and in the morning experiments (Fig. 1). The concentration was significantly reduced in the 2nd, 3rd and 5th test periods compared to the first test period in the evening (vector 2: $t = 3.0$, $p < 0.05$; vector 3: $t = 2.7$, $p < 0.05$; vector 5: $t = 4.5$, $p < 0.05$), while there was a significant difference in mean angle of orientation between test period 1 and 4 ($F_{1,164} = 25.1$, $p < 0.01$).

Orientation Experiments with Redstarts, Pied Flycatchers and Lesser Whitethroats: Spring

During experiments around sunset, the redstarts showed a northwesterly mean direction (Fig. 2), which corresponded rather well with the expected northerly migratory direction, but which was not significantly different from the sunset position ($p > 0.05$, Table 2). The morning tests (vector 5) were oriented towards northeast and differed significantly from the mean orientation in the evening ($F_{1,84} = 26.3$, $p < 0.01$) and this mean direction was also significantly separated from the position of the sun ($p < 0.05$, Table 2).

Pied flycatchers demonstrated a well concentrated northerly mean direction during evening tests (Fig. 2, Table 2), in good agreement with the expected migratory direction and clearly separated from the sunset position ($p < 0.05$, Table 2). Dawn experiments yielded a mean orientation towards east, coinciding with the position of the sun ($p > 0.05$, Table 2). The mean orientation obtained in evening tests was significantly different from the orientation during morning tests ($F_{1,59} = 29.6$, $p < 0.001$).

Northerly directional choices were recorded in evening tests with lesser whitethroats (Fig. 2, Table 2), significantly different from the sunset point ($p < 0.05$, Table 2) and corresponding closely with the expected migratory direction in spring. The mean orientation at dawn was significantly different from the mean orientation at dusk ($F_{1,17} = 4.5$, $p < 0.05$), but was statistically inseparable from the position of the sun ($p > 0.05$, Table 2).

Orientation in Relation to Sun Azimuth

The number of individual tests oriented within $120°$ to the left or to the right of the sun in the middle of the test h at sunset and at sunrise were analysed using χ^2 tests. As a null hypothesis, we considered the birds to be oriented towards the position of the sun in the middle of the test period (sun attraction), and under these conditions we expected no difference in the distributions of individual mean headings on either side of the sun azimuth, when dusk and dawn tests or when autumn and spring experiments were compared. If the birds, apart from sun
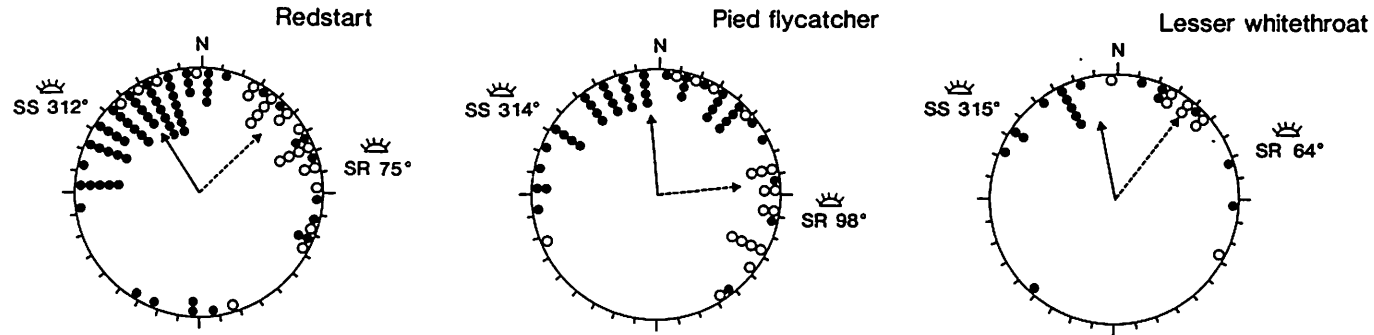
Fig. 2: Results of orientation cage experiments with redstarts, pied flycatchers and lesser whitethroats under clear skies in spring. Tests were performed in the evening-twilight period (vector 1) and at sunrise (vector 5). For further details on symbols used and calculated values (Fig. 1, Table 2)

Table 3:   Number of individual tests oriented to the left (S of sun at sunset and N of sun at sunrise) or to the right side of the sun position in the middle of the test h are given for experiments performed at sunset and sunrise, with different species of nocturnal bird migrants in spring and autumn, respectively. Individual headings within ± 120° from the sun position are included in this analysis. χ^2 values and significance levels (p) are given

Species, season	Sunset		Sunrise		
	Left of sun	Right of sun	Left of sun	Right of sun	χ^2, p
Robin, spring	62	98	51	36	8.2, p < 0.01
Robin, autumn	73	63	22	13	0.6, p > 0.05
Redstart, spring	19	36	16	6	7.8, p < 0.01
Pied flycatcher, spring	9	31	11	6	7.6, p < 0.01
Lesser whitethroat, spring	4	12	7	1	6.1, p < 0.02

Table 4:   Number of birds orienting to the left (S of sun) or to the right (N of sun) of the sun in the middle of the test h during sunset tests in spring and autumn. Only individual headings within ± 120° from the direction towards the sun are considered in this analysis. χ^2 values and significance levels (p) are given

Species, reference	Spring		Autumn		
	Left of sun	Right of sun	Left of sun	Right of sun	χ^2, p
Robin: this study	62	98	73	63	6.0, p < 0.02
Redstart: this study; ÅKESSON 1994	19	36	8	14	0.01, p > 0.05
Pied flycatcher: this study; ÅKESSON 1994	9	31	40	20	17.0, p < 0.001

attraction, demonstrated orientation to the north of the sun (in spring) and to the south of the sun (in autumn), the null hypothesis was rejected. A northerly preference would lead to orientation to the right of the sun in dusk experiments and to directions mainly to the left of the sun at dawn. Southerly preferences would, instead, lead to orientation to the left of the sun at sunset.

In spring, all birds oriented slightly north of the sun at sunset as well as at sunrise (Table 3), however this difference was not significant for robins. In dusk experiments, robins and pied flycatchers were significantly oriented to the north of the sun in spring and south of the sun in autumn (Table 4; this study; ÅKESSON 1994). For redstarts there was no significant difference in orientation to the right or to the left side of the sun at sunset in spring as compared to autumn tests (Table 4).

Migratory Activity

The migratory activity during different periods of a whole night was recorded as number of counter registrations. These tests were performed with robins only, and the median activity (number of registrations per test h) is summarized in Fig. 3 for the five different test periods in spring and autumn, respectively. The activity
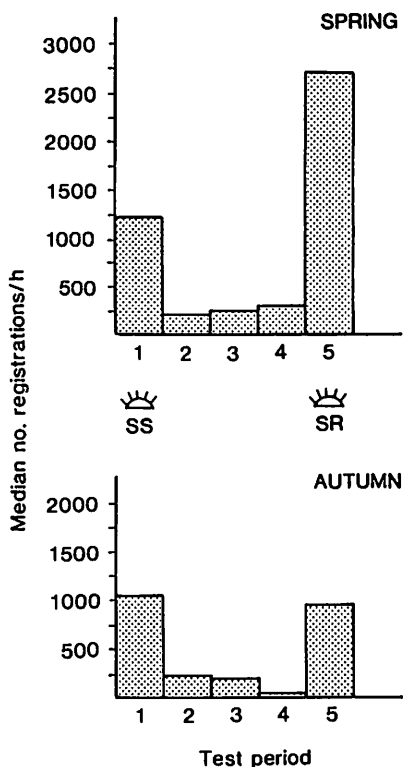
Fig. 3: Median activity in orientation cages (number of registrations per test h) of robins during different test periods at sunset (SS), night and sunrise (SR) in spring and autumn, respectively. Because of reduced activity at night, 3 or more test h have been combined for each test period (see Fig. 1)

was clearly higher in the first test h after sunset (period 1) and in early-morning tests (period 5) compared to the test periods in the middle of the night (Fig. 3). Furthermore, the robins showed higher activity in spring compared to the autumn experiments (Fig. 3). There were significantly more active tests compared to inactive tests (<40 registrations/h) during the 2nd test h in spring compared to autumn ($\chi^2 = 29.1$, p < 0.001; Table 1). In addition, the orientation result obtained during the 2nd h in autumn was significantly more scattered than during the corresponding period in spring (t = 2.5, p < 0.05).

Discussion

Radar and visual observations of free-flying nocturnal passerine migrants show that they normally initiate their migration flights approximately 30–40 min after local sunset (DRURY & NISBET 1964; DORKA 1966; PARSLOW 1969; HEBRARD 1971; GAUTHREAUX 1972; ALERSTAM 1976; RICHARDSON 1978; COCHRAN 1987). Nocturnal migrants have been shown to use both magnetic and visual cues for

orientation (MOORE 1987a; WILTSCHKO & WILTSCHKO 1988), and the period
around sunset is presumably important since, at this time, visual cues (i.e. the
polarization pattern in the sky and the sun azimuth) are prominent and the birds
have a chance to evaluate and integrate the available cues before the impending
migration flight. In a radiotelemetry study, migration flights of individual
Hylocichla thrushes were tracked from a car (COCHRAN et al. 1967; COCHRAN
1987), and the birds usually initiated their migration between 45 min up to 2 h
after sunset and terminated their flights at dawn. These results indicate that the
test period used in this study covers the normal flight period in free-flying birds
and may therefore demonstrate the preferred orientation throughout a migration-
flight period for individual birds.

In both spring and autumn, robins oriented towards northwest and west in
evening twilight experiments, while during the night they showed northerly
directions and, in the morning tests, they were oriented towards northeast–east.
This northerly mean orientation at night corresponds well with the expected
northerly migratory direction in spring. Short-distance recoveries of robins cap-
tured and ringed at Falsterbo during autumn migration, are, to a dominant extent,
found in northerly directions relative to the ringing site, thus demonstrating
reoriented migration flights (SANDBERG et al. 1988). This northerly orientation in
autumn has also been found in orientation-cage experiments with Falsterbo robins
(SANDBERG et al. 1988), and shows that the directional shift to northerly headings
during the autumn nights in this study agrees with what we might expect for re-
oriented robins at Falsterbo.

In this study, a clockwise mean directional shift of about 12° per h in spring
and about 9° per h in autumn was observed for the robins. This shift is slightly
smaller than the sun's apparent movement over the sky which is, on average, 15°
per h. Clockwise directional shifts in mean orientation, of approximately 15° per
h, have been observed also for free-flying nocturnal migrants in a ceilometer study
(LINDGREN & NILSSON 1975). Smaller clockwise shifts in mean angle of orientation
(in total 10°–30° throughout the night), have also been recorded by radar for
day-migrating birds (GEHRING 1963), as well as for nocturnal bird migrants
(STEIDINGER 1968; BRUDERER 1975). These results suggest that the migratory
direction selected by migratory birds in cages, as well as by free-flying birds, may
shift during a migration flight period and that this change in orientation may be
connected with visual, sunset, and night-sky orientation cues. One possibility is
that the birds do not completely compensate for the sun's apparent movement
over the sky during migration flights, but instead orient in a rather constant angle
in relation to the shifting sun azimuth, or possibly in relation to stars located close
to the horizon.

The preferred orientation seems to consist partly of an attraction towards the
position of the sun and partly of orientation in the preferred migratory direction
(ÅKESSON 1994). Long-distance migrants, i.e. the redstart, pied flycatcher and
lesser whitethroat, showed a similar orientation behaviour to the robins. In spring,
their mean orientations at dusk were directed towards northwest–north, partly
attracted towards the sunset point (redstart) and partly oriented in their expected

northerly migratory direction, while in autumn, the robins and the pied flycatchers were significantly more oriented to the south of the sun at sunset (Table 4). There was a significant difference in mean orientation between dusk and dawn experiments such that the birds oriented to the north of the sun azimuth in each test period (Table 3, not significant for robins during the autumn). This shift in orientation between dusk and dawn tests is probably caused by different urges to orient in the expected migratory direction (possibly by use of visual and/or magnetic orientation cues) and attraction towards the position of the sun. In autumn-dusk experiments, robins do not only behave as a north migrant (as has been demonstrated by short-distance ringing recoveries and cage experiments under overcast skies; SANDBERG et al. 1988), but instead were more oriented to the south of the sun at sunset. The sunset orientation responses in autumn seem to be complex and the birds' orientation is partly affected by sun attraction as well as orientation towards the wintering areas (robin and pied flycatcher), or possibly demonstrating re-oriented migration flights (redstart).

Why are the birds attracted to the position of the sun in orientation-cage experiments in the dusk and dawn periods? There may be at least two different explanations for the sun-attraction response. Firstly, birds may orient towards the brightest part of the sky as a basic escape response from the orientation cages (SANDBERG 1991; ÅKESSON 1994). The possibility that the birds may not have been used to the handling and test procedure and therefore behaved unnaturally and differently from birds being handraised or held in captivity for longer periods (acclimatization effect), cannot be completely ruled out. Secondly, the position of the sun at sunset and sunrise may be an important orientation cue for nocturnal bird migrants and they may need to get a clear view of the sun to be able to evaluate and integrate the different available orientation cues before initiating a migratory flight (COCHRAN 1987; SANDBERG 1991).

The activity recorded in the orientation cages for robins was highest during the sunset and the sunrise test periods, with a marked decrease in migratory activity in the middle of the night. This shows that robins in orientation cages are more active when the horizon glow from the sunset and sunrise, as well as the polarization pattern of the sky, is visible, than under starry skies. However, tests during the twilight period after sunset, especially during the 2nd test h after sunset and at sunrise yielded a higher activity in spring in comparison to autumn experiments. Together with the fact that robins also showed significantly more concentrated orientation during the 2nd spring h, the results may indicate important differences in migratory motivation and directional behaviour between autumn and spring, respectively (SANDBERG 1991). WILTSCHKO & HÖCK (1972) only reported well defined directional tendencies in morning tests during spring for robins which had shown migratory activity during the preceding night. The majority, if not all, of the birds used in this study were caught in the early morning at Falsterbo bird observatory after migratory flights the preceding night, and were therefore expected to demonstrate migratory orientation activity in the morning as well as in the evening tests.

To summarize, the birds examined in this study demonstrated orientation

tendencies partly in the expected migratory direction for the species and season, and partly towards the position of the sun at sunset and at sunrise, in both spring and autumn. Furthermore, the results indicate a compromise orientation between the position of the sun at sunset or at sunrise and the expected migratory direction, rather than a pure phototactic response. The results show that robins are more active when the sunset and sunrise horizon glow are visible compared to when tested under clear starry skies. This suggests that the birds may be more motivated to migrate when they have access to sun-related orientation cues. A clockwise orientation shift throughout the night was observed for robins in both spring and autumn tests, in agreement with the expected northerly-migration flight directions. This is interesting and suggests that the clockwise orientation shift may be partly related to the rotating celestial-orientation cues connected with the evening and night skies. Our results do not lend support to the use of a time-compensated sun or star compass, but instead indicate that birds may change their orientation along with the azimuthal change of the sun and the stars throughout the night.

Acknowledgements

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