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Clock-shift experiments with Savannah sparrows, *Passerculus sandwichensis*, at high northern latitudes

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Abstract Orientation can be difficult for nocturnal bird migrants at high northern latitudes because of the large changes of magnetic declinations, rapid longitudinal time-shifts experienced during a long-distance flight and the invisibility of stars during the polar summer. Both sunset cues as well as geomagnetic cues have been shown to be of great importance in the orientation system of Savannah sparrows, *Passerculus sandwichensis*. We used clock-shift experiments to investigate whether geomagnetic and sunset cues were used for migratory orientation by wild-caught young Savannah sparrows at high geomagnetic latitudes in Northern Canada. We exposed birds to a 4-h slow clock-shift, expecting a 60° clock-wise shift in orientation after the treatment. Under natural clear skies in the local geomagnetic field, the birds responded by showing a significant axial mean orientation directed towards the position of the setting sun in the NW and towards their preferred migratory direction in the SE. After exposure to the clock-shift for 6 days and nights the birds showed a clear response to the treatment and shifted significantly towards NNE. Birds that first oriented towards NW in the experiments before clock-shift tended to shift clock-wise, thus reacted to the clock-shift in the expected way. The reaction of the individual birds that originally oriented towards SE seems to vary. In summary, our birds did not select a constant angle (menotaxis) in relation to the sun's position during the experiments, but presumably were affected by the sun showing phototaxis or followed their magnetic compass. Possible explanations of the unexpected experimental results are discussed.

Keywords Clock-shift · Magnetic orientation · Migratory orientation · *Passerculus sandwichensis* · Savannah sparrow

Introduction

Nocturnally migrating birds use different cues for orientation. They possess a magnetic compass based on the inclination angle of the geomagnetic field as well as celestial compasses that translate information from the azimuth position of the sun, the polarisation pattern of skylight and from the rotating stars into an inherited migration direction (for reviews see, for example, Emlen 1975; Able 1980; Wiltschko and Wiltschko 1995).

Birds starting their autumn migration from high northern geographic and geomagnetic latitudes face several orientation difficulties: (1) the stars are not visible during the light nights of the polar summers and can therefore not be used for orientation during the initial part of migration; (2) close to the geomagnetic poles the magnetic field lines cross the surface of the Earth at very steep inclination angles (Skiles 1985) and the birds might have problems in translating this information into a migratory direction (Wiltschko and Wiltschko 1995; see also Åkesson et al. 2001); (3) orientation might be difficult because of large geomagnetic declinations and the birds will be exposed to rapid and large changes in declination during flights at high latitudes; and (4) a time-compensated sun compass can be difficult to use because of the rapid longitudinal shifts birds will experience during long-distance migratory flights (for review see Alerstam 1990; Alerstam and Gudmundsson 1999; Alerstam et al. 2001).

Cage experiments with migratory songbirds at high northern latitudes have demonstrated that birds are capable of selecting a magnetic compass course based on very steep angles of inclination (Sandberg et al. 1991, 1998; Åkesson et al. 1995, 2001). However, in order to be able to cope with the large changes in declinations between areas, the birds can be expected to recalibrate their magnetic direction according to celestial cues (Bingman 1983a; Able and Able 1999). This possibility provides the birds with a way to bring magnetic and visual compass information into conformity, but updates are necessary during the course of migration when geographic and

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magnetic compass information diverge because of changing declinations (Able and Able 1999).

In this study, we designed a clock-shift experiment to investigate the relative importance of geomagnetic and sunset cues for migratory orientation in wild-caught young Savannah sparrows, *Passerculus sandwichensis*, reared at high geomagnetic latitudes. Both cues have been shown to be very important when selecting the initial migratory direction in Savannah sparrows, although experiments suggest that sunset cues are of primary importance (Bingman 1981; Moore 1982, 1985; Able and Able 1993b). It has been shown that it is the polarisation pattern of the setting sun rather than the position of the sun itself that provides the birds with visual orientation cues (for review see Able and Able 1996). We assumed that if young birds predominantly rely on celestial sunset cues and if they calibrate their magnetic compass before their first autumn migration is initiated using celestial cues, as described for Savannah sparrows by Able and Able (1995a, 1999), they should be especially sensitive to changes of the sun's position relative to the magnetic compass course and respond to the manipulations by shifting their preferred orientation according to the shifted position of the sun. Savannah sparrows seem to be able to calibrate their magnetic compass repeatedly during the course of migration (Able and Able 1995a) which could, however, not be confirmed in other species (Wiltschko et al. 1999). The reason for this difference in response might be related to species-specific differences or to at what time during the ontogenetic or migratory phase the birds were exposed to a cue-conflict situation (cf. Wiltschko et al. 1998, 1999). We investigated the effect of clock-shift on the orientation behaviour of young Savannah sparrows caught and tested during their first autumn migration period in the breeding area in Inuvik, north-western Canada. Slow-shifting the internal clock of the birds by 4 h relative to the local time is expected to result in a 60° clock-wise shift of the birds' orientation compared to the control experiments where the birds' orientation was recorded under natural clear skies.

Methods

Experimental birds and clock-shift procedure

We used 21 night-migrating Savannah sparrows of the subspecies *P. s. anthinus* as experimental birds. This subspecies breeds across

most of northern and western North America (Wheelwright and Rising 1993) and winters along coastal western United States from south-western British Columbia south to northern and western Mexico (Byers et al. 1995). The experimental birds were captured with mistnets in deciduous scrub and open grassland close to the town of Inuvik (68°21'N, 133°43'W), Northwest Territories, Canada, between 22 July and 10 August 1999. Each individual bird was ringed, measured and aged according to Pyle et al. (1987). We selected only juvenile birds for the experiments.

Prior to the clock-shift the birds were held indoors in individual cages in a room with large windows pointing towards geographic west and exposed to the natural light regime. Artificial lights were used to increase the light intensity inside the room during daytime. The birds were fed mealworms, seeds, fruit and vitaminised water ad libitum.

Before the birds were exposed to a clock-shift, the mean migratory direction (control direction) of the 21 Savannah sparrows was recorded by testing each individual 1–2 times between 12 and 15 August 1999 (Table 1). Prior to the experiments, the birds were exposed to the experimental situation in an orientation funnel for one initial experiment (6 August) and once under simulated overcast conditions (8 August; Table 1).

The clock-shift started on 15 August when the birds were moved to a room without windows where no natural light was available and their internal clock was shifted 4 h slow relative to local time by changing the artificial light regime. Since the natural night had not started yet, i.e. the sun was never lower than -4° below the horizon (cf. Åkesson et al. 1996a), we introduced a 4-h artificial night in order to be able to clock-shift the birds such that they experienced an artificial night from 0200 to 0600 hours local time (corresponds to 0400–0800 hours Mountain Standard time). This period was prolonged to 5 h from 24 August and onwards in order to simulate the natural light regime of the season. On 31 August the dark period was changed once more so that the birds experienced a 6-h night from 0100 to 0700 hours local time, which was in good agreement with the natural night shifted 4 h slow. The Savannah sparrows were allowed to adapt to their shifted internal clock for 6 days and nights before the experiments started. Each of the 21 clock-shifted birds was tested 3 times under clear skies between 21 August and 1 September 1999 (Tables 1, 2). All birds were released in the breeding area close to Inuvik on 2 September.

Experimental procedure

All orientation experiments were carried out in Emlen funnels lined with typewriter correction paper (Tipp-Ex paper; see Emlen and Emlen 1966). The funnels had a top diameter of 300 mm and a height of 150 mm and were built from non-magnetic material so as not to influence the birds' magnetic compass. They were set up in the backyard of the Aurora Research Institute in Inuvik where the birds experienced an incident geomagnetic field of approximately 58'255 nT, a declination of +33.8°E and an inclination of +81.7°, calculated from IGRF 1995 (IAGA Division V 1995; for 19 August 1999), in the middle of the experimental period. Experiments started after local sunset and lasted for 1 h, during which time the birds' activity was recorded as scratch marks in the Tipp-Ex paper. The clock-shift experiments were performed during the late local sunset period, which corresponds to the birds' subjective

Table 1 Experimental conditions, dates and local times with the respective sunset azimuths and elevations for orientation cage experiments carried out with young Savannah sparrows, *Passerculus sandwichensis*, in NW Canada during autumn migration

Experimental condition	Date	Local time (hours)	Cloud cover	Sun azimuth	Sun elevation
Simulated overcast	8/8/99	2130–2230	8/8 simulated	–	–
Control	12/8/99	2100–2200	7/8	324°	-1.7°
Control	14/8/99	2100–2200	0/8	324°	-2.4°
Control	15/8/99	2030–2130	6/8	317°	-0.9°
Clock-shift	21/8/99	2150–2250	1/8	336°	-7.9°
Clock-shift	29/8/99	2115–2215	0/8	327°	-9.5°
Clock-shift	1/9/99	2050–2150	0/8	321°	-8.9°

Table 2 Mean orientation of Savannah sparrows tested under simulated overcast and before and after clock-shift. For each experimental day the unimodal direction (α) or axial direction (α_2) is given for each individual bird. All directions are given relative to geographic North. Furthermore, the first- and second-order mean directions (α , α_2) and mean vector lengths (r , r_2) are given for experiments performed before and after clock-shift. The mean direc-

tions used in the discussion are marked in bold font. The individual shift represents the change in orientation for each bird as recorded before compared to after clock-shift (second-order direction before clock-shift set to 0°). *n.s.* Not significantly oriented, *n.a.* no activity (<40 scratches in funnel), – no experiment. For further information see Fig. 1

Date	Simulated overcast	Before clock-shift			After clock-shift									Individual shift
	8/8/99	12/8/99	14/8/99	15/8/99	Second-order statistics			21/8/99	29/8/99	1/9/99	Second-order statistics			
Bird no.	α , α_2	α , α_2	α	α	α , α_2	r , r_2	n	α , α_2	α	α , α_2	α , α_2	r , r_2	n	α
503	83°	n.s.	127°	–	127°	1.00	1	114°	116°	51°	95°	0.87	3	328°
504	156°	297°	188°	–	243°	0.58	2	36°	n.s.	78°	57°	0.93	2	174°
506	348°– 168°	306°	337°	–	322°	0.96	2	334°	353°	n.s.	344°	0.99	2	22°
509	129°	324°– 144°	269°	–	297°	0.89	2	13°	56°	63°	44°	0.93	3	107°
510	107°– 287°	280°	304°	–	292°	0.98	2	44°	267°	84°	73°– 253°	0.78	3	141°
511	308°– 128°	119°	135°	–	127°	0.99	2	83°	56°	352°	45°	0.79	3	278°
512	n.s.	103°	51°	–	77°	0.90	2	22°	223°	284°	289°	0.45	3	213°
514	158°– 338°	323°	n.s.	–	323°	1.00	1	263°	7°	36°	350°	0.57	3	27°
516	n.s.	193°	–	142°	168°	0.90	2	288°– 108°	47°	348°	348°	0.67	3	180°
518	n.s.	88°	n.a.	–	88°	1.00	1	257°	353°	137°	320°– 140°	0.27	3	232°
519	n.s.	306°	254°	–	280°	0.90	2	322°	155°	21°	343°– 163°	0.64	3	63°
521	87°	279°	340°	–	310°	0.86	2	248°	270°	323°	280°	0.86	3	330°
523	166°	318°	160°	–	149°– 329°	0.92	2	267°	212°	242°	240°	0.92	3	91°
524	100°	354°	235°	–	295°	0.51	2	304°	249°	119°– 299°	287°– 107°	0.66	3	352°
526	49°	1°	n.s.	–	1°	1.00	1	48°	356°	327°	3°	0.84	3	2°
527	163°– 343°	172°– 352°	106°	–	139°	0.84	2	124°	106°	109°	114°	0.99	3	335°
531	–	118°– 298°	–	124°	121°	1.00	2	60°	11°	30°	34°	0.94	3	273°
532	–	–	–	30°	30°	1.00	1	285°	107°	28°	96°– 276°	0.39	3	66°
533	–	–	–	279°	279°	1.00	1	267°	144°	46°	84°– 264°	0.25	3	165°
535	–	–	–	142°	142°	1.00	1	25°	6°	341°	4°	0.95	3	222°
537	–	–	–	27°	27°	1.00	1	175°	203°	67°	158°	0.55	3	131°
<i>n</i>	12	16	12	6	21			21	20	20	21			21
α , α_2	113°	310°– 130°	127°– 307°	97°	305°– 125°			341°	27°– 207°	35°	18°			175°– 355°
r , r_2	0.52	0.53	0.23	0.34	0.45			0.28	0.18	0.53	0.43			0.15
<i>P</i>	0.03	0.01	0.53	0.50	0.01			0.19	0.53	0.004	0.02			0.65
95% CI	±43°				±37°						±38°			(±118°)

sunset period, just before the lights were switched off in the dark room (for experimental times, sun azimuth and elevation see Table 1). After the end of each experiment we recorded the fat score of each individual bird (according to Pettersson and Hasselquist (1985), upgraded to 10 grades), which was used to analyse if fat score had any influence on the birds' orientation.

Data analysis

Each Tipp-Ex paper was divided into 24 sectors to evaluate the activity and the preferred migratory directions of the birds. The

number of scratches left by the bird was counted along a horizontal line within each 15° sector. A bird was considered inactive when the total number of scratches crossing the line was less than 40. The mean direction (α) of an active individual was calculated by vector addition (Batschelet 1981). We applied the method of doubling the angles to test for axiality. The orientation of a bird was considered axial when the mean vector length (r_2) of the distribution of scratches with doubled angles was larger than the one with single angles (r ; Batschelet 1981). In these cases the part of the mean vector closer to the one of the unimodal distribution was included in further analyses. Birds whose mean direction was not significantly different from random according to the Rayleigh test

($P > 0.05$) were excluded (Batschelet 1981). It has to be noted, however, that the Rayleigh test was only used as a guideline and does not provide accurate probability estimates in this case because the single scratches on the Tipp-Ex paper are not independent of each other.

Mean direction (α) and scatter (r) of groups of birds tested before and after clock-shift were analysed using second-order statistics. We calculated a second-order mean direction and scatter for each individual tested more than once under a treatment and then the mean directions alone were used to calculate a grand mean direction and scatter for the whole group (Batschelet 1981). Groups were tested for axiality as explained above for individuals. In case of an axial distribution, both axial directions are given (α_2).

The mean sun position was calculated for each individual bird by taking the azimuth and elevation of the sun in the middle of the experiment and calculating the mean sun position for the experiments performed before and after clock-shift. Experiments performed under complete overcast (cloud cover 8/8) were not included in further analyses since the sun was not available for orientation. Experiments during which the sun was visible at least for a short time (cloud cover $\leq 7/8$) were included in further analyses.

Results

The Savannah sparrows showed a significant axial mean control direction towards geographic NW-SE, with one end of the axis pointing towards the setting sun and the other end pointing towards the expected migratory direction (Fig. 1a, Table 2). The mean azimuth position of the setting sun (322°) lay well within the 95% confidence interval (CI) of the mean group direction.

When tested under simulated overcast the Savannah sparrows were significantly unimodally directed towards magnetic E (=geographic ESE, Fig. 1c, Table 2); 41.7% of the individuals were axially distributed within the funnel. The SE axis of the mean group direction chosen under clear skies (125°) lies within the 95% CI of the mean direction chosen under simulated overcast.

The mean orientation of the clock-shifted group was significantly unimodally directed towards geographic NNE (Fig. 1b, Table 2). The mean azimuth position of the setting sun during the experiments (328°) was different from the 95% CI of the mean group direction. The distribution of data points from individual experiments over the four quadrants of the circle (NE, SE, SW, NW) before clock-shift was significantly different from the distribution after clock-shift ($\chi^2 = 7.80$, $df = 3$, $P = 0.05$). Each individual bird seems to have reacted to the clock-shift treatment in a different way since the distribution of data points of the individual birds' directional changes was not different from random (Table 2). However, the birds orienting towards the NW sector (between 225° and 45°) before clock-shift tended to shift their orientation clock-wise ($\alpha = 69^\circ$, $r = 0.42$, $P = 0.12$, $n = 12$) whereas the birds orienting towards SE (between 45° and 225°) tended to shift their orientation counterclock-wise ($\alpha = 252^\circ$, $r = 0.46$, $P = 0.15$, $n = 9$; Fig. 1d). We could not detect significant differences in fat score between the two groups (mean fat score \pm SD before clock-shift, NW group: 5.4 ± 0.9 , $n = 19$; SE group: 5.4 ± 1.1 , $n = 15$; Mann-Whitney U -test: $U = 136.5$, $P = 0.84$) that could explain the difference in the birds' orientation (i.e. reverse orienta-

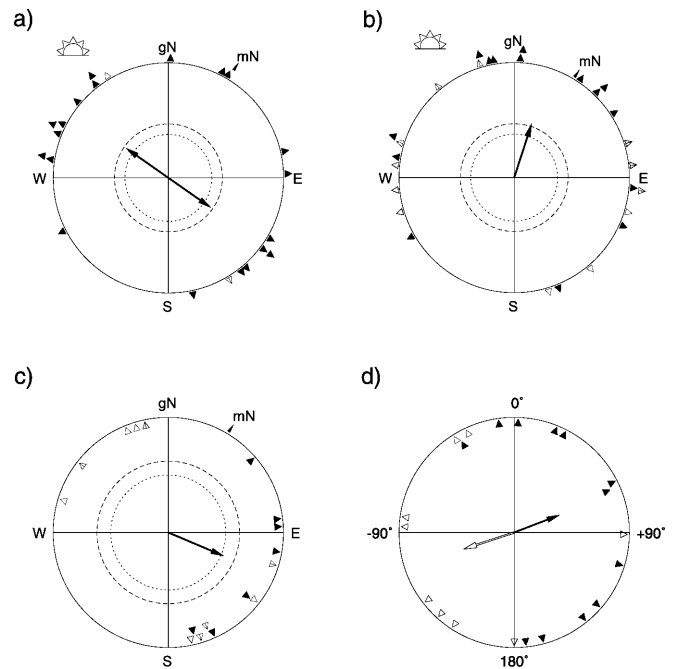


Fig. 1a–d Mean orientation of Savannah sparrows, *Passerculus sandwichensis*, tested in Inuvik. **a, b** Second-order directions of the individual birds tested under natural clear skies before (**a**) and after (**b**) clock-shift. Each *triangle* outside the *circle* represents the mean direction of an individual bird. Axial individuals are marked with two *white triangles* 180° apart. The direction closer to the unimodal direction and thus included in the statistical analyses is marked with a *line*. The *arrows* give the respective mean direction (α , α_2) of the groups and are drawn according to the mean vector lengths (r , r_2) relative to the radius of the circle = 1. The *inner dotted circle* gives the 5%, the *outer broken circle* the 1% significance level according to the Rayleigh test. The *sun* indicates the mean position of the setting sun in the middle of the experimental period. **c** Orientation of Savannah sparrows under simulated overcast. Each *triangle* inside the *circle* represents the direction of one individual bird. **d** Directional responses of individual Savannah sparrows to clock-shift. Each *triangle* gives the individual shift of a bird's second-order mean direction after clock-shift relative to the second-order mean direction before the treatment (second-order mean direction before clock-shift set to 0°), clock-wise shifts are expressed as positive angles (to the right), counterclock-wise shifts as negative angles (to the left). *White triangles* indicate birds that oriented to the SE between 45° and 225° , *black triangles* birds that oriented to the NW between 225° and 45° in their second-order mean direction before clock-shift. *gN* Geographic North, *mN* magnetic North. For more details see Table 2

tion in lean birds and forward orientation in fat birds, cf. Sandberg et al. 1998).

Discussion

Migratory orientation before clock-shift

Our Savannah sparrows oriented axially towards NW-SE before clock-shift. The SE directions lie in the expected migratory direction as calculated along an initial great circle route leading from Inuvik to the expected wintering area located between south-western British Columbia

and northern and western Mexico (Byers et al. 1995; Muheim et al., in preparation). Other populations of Savannah sparrows tested in orientation cage experiments have been shown to select unimodal directions between SSW and SW, but these birds were caught at the onset of migration in North Dakota (Moore 1978, 1980, 1984, 1987a) or as nestlings in the area of New York (Able and Able 1997) and therefore belonged to more easterly populations. Possible explanations for the axial mean direction of our birds tested under clear skies before clock-shift can, for instance, be (1) that at least some of our birds might have relied more on their magnetic compass than on celestial cues, but had difficulties in deciding which was the correct side of the axis NW-SE or (2) that some individuals might have been attracted to the lighter part in the evening sky, since the sun was only a few degrees below the horizon during the experimental hour (for availability of celestial cues at dusk, see Åkesson et al. 1996a). Partial sun attraction responses have been observed in a number of different bird species captured and tested on migration (e.g. Åkesson and Sandberg 1994; Sandberg et al. 1998; Muheim et al. 1999), and might be at least partly related to the direction given by the birds exhibiting reverse migration (cf. Åkesson et al. 1996b). Reverse migration responses and partial sun attraction has also been observed in young snow buntings, *Plectrophenax nivalis*, captured and tested in high Arctic breeding areas at Resolute on Cornwallis Island, Canada (Sandberg et al. 1998). However, in these experiments it was only the lean birds that showed reverse orientation responses. We cannot confirm this pattern of reverse migration courses towards NW selected predominantly by lean birds, since there was no statistical difference in fat score between the birds orienting towards NW and the ones orienting towards SE in our experiments.

Simulated overcast experiments

Our experiment with Savannah sparrows under simulated overcast and other studies carried out at high northern latitudes in orientation cages under simulated or natural complete overcast clearly show that birds are able to orient without access to celestial cues at these high geomagnetic latitudes (Sandberg et al. 1991, 1998; Åkesson et al. 1995; Gudmundsson and Sandberg 2000; Åkesson et al. 2001). We cannot completely exclude the possibility that birds have access to other unknown cues when tested under completely overcast skies or under Plexiglas sheets simulating overcast, but according to current knowledge this is very unlikely. Many orientation cage experiments with Savannah sparrows reveal axial mean directions when the orientation of individual wild-caught as well as hand-raised birds is recorded several times under the same experimental condition and without access to visual cues during autumn migration (Bingman 1983b; Able and Able 1990a, b, 1993a, 1995a, b) In our simulated overcast experiments more than 40% of the

birds showed axial orientation, but the mean orientation of the group was significantly unimodal. The reason for this can be due to the fact that our birds were tested only once whereas the axial directions obtained by others were explained by a change of the preferred direction by the individual birds from one experiment to the other (reviewed by Able and Able 1999).

Clock-shift experiment

Exposing a bird to a clock-shift creates a cue-conflict situation since the directions given by sunset and geomagnetic cues do not agree. The bird presumably has to set priority to one of the cues to select its migratory course or alternatively may react by choosing a mean direction between the two cue-conflict directions. Our birds reacted to the clock-shift by shifting their orientation towards NNE after clock-shift. They did not seem to be attracted by the sun since the 95% CI of their mean direction does not include the mean azimuth position of the setting sun. This might be due to adjustment to the unnatural situation in captivity and strongly supports the fact that the change of the birds' internal clock seems to have had an effect on their orientation.

Interestingly, our data indicate that the two groups of birds orienting toward the NW and the SE sector, respectively, before clock-shift reacted to the clock-shift in different ways. The individual birds which initially oriented towards NW showed an on average about 70° clockwise shift relative to their preferred control direction, while the individuals initially oriented towards SE shifted by on average about 110° counterclockwise (see Fig. 1d). Birds initially oriented towards NW thus seem to have reacted to the clock-shift by shifting their course in the expected way, whereas birds initially oriented towards SE showed a different reaction. However, assuming that individual Savannah sparrows change axis from one experiment to the other, the 110° counterclockwise shift of the SE group might be explained by a 70° (180°–110°) clockwise shift followed by a change of the preferred axis (K. Able, personal communication). This might be true, at least for three individuals orienting towards the NE sector after clock-shift. Three individuals preferred SE, one SW and two NW directions. So, the most plausible explanation might be that the birds showed a mixture of different reactions. Unfortunately, we have no explanation for this difference in reactions, but the following suggestions can be proposed: Our results cannot be interpreted as a phototactic response since the birds did not seem to be attracted by the setting sun, neither before nor after clock-shift. The suggestion that Savannah sparrows show constant-angle responses rather than using a time-compensated sun compass (Moore 1980) is not supported either with the results from our study, since the birds showed a clear shift in orientation away from the sun. Furthermore, we cannot conclude that the birds used the magnetic compass as their primary orientation cue in the cue-conflict situation experienced, because the SE group

Table 3 Summary of clock-shift experiments with migrating birds published in the literature (homing pigeons are not included). The expected directional shifts of the birds are about 15° per hour of clock-shift, clock-wise (CW) after a slow shift and counterclock-wise (CCW) after a fast shift for birds tested in the northern hemisphere and into the opposite directions for birds tested in the southern hemisphere (i.e. yellow-faced honeyeater; Munro and

Wiltshcko 1993). The time of exposure to clock-shift before the start of the experiments (adaptation time), time of experiment and availability of orientation cues as well as expected and observed shifts are given for each experiment. For studies with results based on multiple experiments with the same individual birds, both the number of shifted birds and the total sample size are given

Clock-shift	Adaptation time	Experimental time	Availability of orientation cues during experiment	Expected shift	Observed shift	Number of shifted birds/sample size	Species	Reference
Expected shift clock-wise:								
3-hr slow	≥6 days	Approx. 3.5 hr after sunset ^a	No sunset cues	45°CW	No sign. orientation (exp. birds+ controls)	7/10	White-throated sparrow (<i>Zonotrichia albicollis</i>)	(Able and Cherry 1986)
3-hr slow	5 days	Local sunset	Sunset cues	45°CW	45°CW, increase in scatter	20/94	European robin (<i>Erithacus rubecula</i>)	(Helbig 1991)
3-hr fast	≥5 days	Morning hours	Sun	45°CW	91°CW (exp. 1, 2), then increase in scatter+return to control direction	9	Yellow-faced honeyeater (<i>Lichenostomus chrysops</i>)	(Munro and Wiltshcko 1993)
4-hr slow	5 days	Local sunset	Sunset cues	60°CW	Lean birds: 147°CCW; fat birds: 84°CW	20 lean=12; fat=5	Snow bunting (<i>Plectrophenax nivalis</i>)	(Sandberg et al.1998)
4-hr slow	6 days	Local sunset	Sunset cues	60°CW	All birds NE NW birds: tendency towards 69°CW SE birds: tendency towards 108°CCW	NW birds=12; SE birds=9	Savannah sparrow (<i>Passerculus sandwichensis</i>)	this study
4-hr fast	≥5 days	Morning hours	Sun	60°CW	94°CW (exp. 1, 2) then increase in scatter (exp. 3, 4), 13°CW (exp. 5, 6)	18	Yellow-faced honeyeater	(Munro and Wiltshcko 1993)
6-hr slow	8 days	Local sunset	Sunset cues, no stars	90°CW	No shift	5	Savannah sparrow	(Moore 1980)
6-hr slow	8 days	Local sunset	Sunset cues, stars	90°CW	No shift (one bird: 24°CW)	5	Savannah sparrow	(Moore 1980)
6-hr slow	?	Day	Sun	90°CW	Autumn: northerly direction, n.s., no shift spring: 69°CW	Autumn: ?/49 Spring: 6/49	European starling (<i>Sturnus vulgaris</i>)	(Wiltshcko 1980)
6-hr slow	5 days	Morning hours	Sun	90°CW	Autumn: bimodal orientation, but no shift spring: disorientation	Autumn: 13/63 Spring: 5/26	Meadow pipit (<i>Anthus pratensis</i>)	(Helbig et al. 1987)
Expected shift counter clock-wise:								
3-hr fast	≥6 days	Between sunset +civil twilight	Sunset cues	45°CCW	51°CCW	8/23	White-throated sparrow	(Able and Cherry 1986)
3-hr fast	5 days	Local sunset	Sunset cues	45°CCW	41°CCW	12/56	European robin	(Helbig 1991)
4-hr slow	≥5 days	Midday	Sun	60°CCW	Increase in scatter (exp. 1, 2), 137°CW (exp. 3,4), increase in scatter (exp. 5, 6)	10	Yellow-faced honeyeater	(Munro and Wiltshcko 1993)

^a Subjective sunset for the birds (lights off)

also shifted their orientation. However, we cannot exclude the possibility that calibrations between different compass systems have been involved during the clock-shift procedure (cf. Wiltschko et al. 1999). Further experiments will be needed to clarify the mechanisms involved.

Other clock-shift experiments with Savannah sparrows during spring migration did not result in shifts of the expected degree, but the birds continued to orient in the same NW direction they chose in the control experiment or showed an axial response with one axis pointing towards the position of the moon in the SSE (Moore 1980; see Table 3). This suggests that the birds neither responded to nor used the sun for orientation. However, the sample size ($n=5$) was relatively small in these experiments.

Birds exposed to clock-shift seem to be very sensitive to both the availability of sunset cues and the experimental time, which can never be in agreement with the situation a bird meets under unshifted conditions. The availability of sunset cues, which includes the position of the setting sun and the polarisation pattern of the evening sky, has shown to be crucial for nocturnal migrants to select a migratory direction (Moore 1978, 1987b; Able and Cherry 1993a). The onset of the experiment seems to be important since the bird's motivation to show migratory restlessness and to choose a migratory direction is dependent on its internal clock (Berthold 1996). It might therefore not be suitable to record the migratory orientation of night-migrating birds during their subjective midday several hours before the subjective evening when the sunset cues are not visible and when migratory restlessness usually develops, which will be the result of a slow-shift (cf. Able and Cherry 1986). Likewise, fast-shifted birds are usually tested after their subjective sunset time, when sunset cues are not very prominent anymore and the availability of celestial cues typical of night-time are clearly visible. This might result in reduced motivation to show migratory orientation and might cause problems in the use of sunset cues. We tested our clock-shifted birds slightly later in the night with the sun on average -8.8° below the horizon, compared to sun elevations of -1.7° before clock-shift. The difference in availability of orientation cues might explain why the clock-shifted birds did not show any attraction towards the position of the setting sun. However, the polarisation pattern of the setting sun is to some degree expected to be accessible for orientation during both experimental periods. Complete darkness at night does not occur before the end of the Nautical Twilight period at a sun elevation of -12° , when sunset cues, brighter light at the horizon and the polarisation pattern are no longer visible (Åkesson et al. 1996a).

Results from other clock-shift experiments with migrating birds confirm the limited responses demonstrating expected shifts (see Table 3). In only a few experiments did the birds show the expected reaction to the clock-shift by shifting their orientation as predicted (Wiltschko 1980; Able and Cherry 1986; Helbig 1991). Most other studies resulted in very different responses, reporting either in-

creases in scatter, shifts into unexpected directions, or larger shifts than expected (Moore 1980; Able and Cherry 1986; Munro and Wiltschko 1993; Sandberg et al. 1998; this study; see also Table 3). Although clock-shift is an elegant experimental design to study sun compass orientation, especially in homing pigeons (Schmidt-Koenig 1990; Wiltschko et al. 1994), it does not seem to be suitable for studying sun compass orientation in nocturnal passerine migrants at high latitudes.

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