ORIGINAL ARTICLE

Early evening activity of migratory Garden Warbler *Sylvia borin*: compass calibration activity?

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Abstract It has been shown that songbird migrants can use several compass cues for orientation (e.g. sun position at sunset and possibly sunrise and related polarised light cues, stars and the geomagnetic field); therefore, the obtained information is redundant. This suggests that compasses of migratory birds must have certain hierarchical relationships and be calibrated. Currently, it is not known how avian compass calibration is accomplished. We report the results of our experiments with Garden Warblers *Sylvia borin*, long-distance songbird migrants. We tested the birds in two experimental conditions: in a local magnetic field with access to a starry sky (Control group) and in a vertical magnetic field that does not provide magnetic compass information with access to stars (Clear sky experimental group) or without it (Overcast experimental group), and analysed locomotor activity and orientation in all three groups. For the Garden Warblers from the control and experimental groups, we revealed two periods of activity separated by a quiescent period: twilight and nocturnal periods. The average direction for both periods of activity showed no significant difference in the control group. Birds from the experimental group were disoriented in both periods. Birds from the clear sky and overcast groups were also disoriented. These data suggest that long-distance songbird migrants, particularly the Garden Warbler, need information from the geomagnetic field, but not from the stars, at sunset and during twilight in order to choose the correct migratory direction. The nocturnal period of migratory activity probably represents actual migratory flight, while the nature of the twilight period remains unknown. The results of the present work and data from prior cue-conflict experiments on other species suggest that the twilight period may correspond to compass calibration activity.

Keywords Garden Warbler · *Sylvia borin* · Migration · Orientation · Vertical magnetic field · Compass calibration · Songbird migrant

Zusammenfassung

Dient die frühabendliche Aktivität ziehender Gartengrasmücken *Sylvia borin* der Kompasskalibrierung?

Es ist bekannt, dass Singvögel auf dem Zug verschiedene Kompassinformationen (zum Beispiel den Sonnenstand bei Sonnenuntergang und möglicherweise bei Sonnenaufgang sowie damit zusammenhängende Polarisationsverhältnisse, die Sterne und das Erdmagnetfeld) zur Orientierung nutzen können; daher beinhalten diese Informationen eine gewisse Redundanz. Dies legt nahe, dass die Kompasssysteme von Zugvögeln einer bestimmten Hierarchie unterliegen und kalibriert werden müssen. Derzeit ist nicht bekannt, wie Vögel diese Kompasskalibrierung bewerkstelligen. Hier stellen wir die Ergebnisse unserer Versuche an Gartengrasmücken *Sylvia borin*, einer langstreckenziehenden Singvogelart, vor. Die Vögel wurden unter zwei verschiedenen Versuchsbedingungen getestet: in einem lokalen

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Magnetfeld mit Zugang zum Sternenhimmel (Kontrollgruppe) beziehungsweise in einem vertikalen Magnetfeld, welches keine magnetischen Kompassinformationen liefert, jeweils mit (Versuchsgruppe bei klarem Himmel) oder ohne (Versuchsgruppe bei bewölktem Himmel) Zugang zum Sternenhimmel; die lokomotorische Aktivität und die Orientierungsrichtung aller drei Gruppen wurden anschließend analysiert. Gartengrasmücken aus Kontroll- und Versuchsgruppen zeigten zwei von einer Ruheperiode unterbrochene Aktivitätsphasen, jeweils zur Dämmerung beziehungsweise während der Nacht. Die Durchschnittsrichtung beider Aktivitätsphasen wies bei der Kontrollgruppe keinen signifikanten Unterschied auf. Die Vögel der Versuchsgruppen zeigten während beider Phasen Desorientierung. Sowohl die Vögel bei klarem als auch die bei bewölktem Himmel waren desorientiert. Diese Befunde legen nahe, dass langstreckenziehende Singvögel, speziell die Gartengrasmücke, bei Sonnenuntergang und in zur Dämmerungszeit zwar erdmagnetische Informationen benötigen, um die richtige Zugrichtung zu wählen, aber dafür nicht auf den Sternenhimmel angewiesen sind. Die nächtliche Phase der Zugaktivität repräsentiert möglicherweise den eigentlichen Migrationsflug, während die Funktion der Dämmerungsphase unbekannt bleibt. Die Ergebnisse aktueller Versuche und Daten aus früheren Sinneskonflikt-Experimenten an anderen Arten legen nahe, dass die Dämmerungsphase möglicherweise Aktivität zur Kompasskalibrierung widerspiegelt.

Introduction

Every year, billions of songbirds migrate from their breeding areas to wintering grounds and back. In order to determine the seasonally appropriate migratory direction, they are believed to use at least three orientation cues: parameters of the geomagnetic field (Wiltschko and Wiltschko 1972); the motion of the sun and its position at sunset (Kramer 1950; Moore 1986; Cochran et al. 2004) and related polarised light patterns (Moore and Phillips 1988); and stellar cues (Sauer 1957; Emlen 1967, 1975). Information perceived from these references is apparently redundant, which suggests that compass information must be integrated (Muheim et al. 2006a; Liu and Chernetsov 2012).

We have no simple answer to the question of how migratory birds calibrate their compasses, and we may never have a universal answer that would apply to all birds. The pre-migratory period has been reported to be characterised by domination of the celestial compass over the magnetic one, as it has been suggested in Pied Flycatchers *Ficedula hypoleuca* (Prinz and Wiltschko 1992) and

Savannah Sparrows *Passerculus sandwichensis* (Able and Able 1990; see Muheim et al. 2006a for a review). During migration, birds show various types of relationship between compasses: calibration of the magnetic compass from solar (sunset) cues (Cochran et al. 2004; Muheim et al. 2006b, 2007) or vice versa (Sandberg et al. 2000); and plain domination of one of the compasses without any calibration (Chernetsov et al. 2011; Schmaljohann et al. 2013a). As a rule, the magnetic compass dominates during these periods and other compasses are calibrated by the magnetic cues. This has been suggested in cue–conflict experiments in Dunnocks *Prunella modularis*, Australian Silvereyes *Zosterops lateralis*, Red-eyed Vireos *Vireo olivaceus* and other avian species (Bingman and Wiltschko 1988; Wiltschko et al. 1998, 2001; Sandberg et al. 2000).

On the other hand, several species, e.g. Savannah Sparrows (during pre-migratory and migratory periods), Grey-cheeked Thrushes *Catharus minimus* and Swainson's Thrushes *C. ustulatus*, demonstrate a different strategy: their magnetic compass is calibrated by celestial cues (Able and Able 1995a, b; Cochran et al. 2004). It should be mentioned that, in the work of Cochran and co-workers, they analysed orientation of free-flying radio-tagged birds. This methodological aspect makes the results of this research especially convincing.

A few studies have brought evidence that some migratory species do not calibrate their compasses at all and are characterised by simple domination of magnetic or solar compasses (Gaggini et al. 2010; Rabøl 2010; Chernetsov et al. 2011; Schmaljohann et al. 2013a). Noteworthy, most cue–conflict experiments were carried out on captive birds in Emlen funnels (Bingman and Wiltschko 1988; Wiltschko et al. 2008; Gaggini et al. 2010), and just a few of them were performed using free-flying birds (Cochran et al. 2004; Chernetsov et al. 2011; Schmaljohann et al. 2013a).

In the present study, we aimed to find out which pattern of activity in nocturnal migratory restlessness of a European–African long-distance migrant, Garden Warbler *Sylvia borin*, in captive conditions may correspond to compass calibration activity in the wild. To accomplish this, we analysed the behaviour and orientation of Garden Warblers in two magnetic conditions: a local magnetic field and an artificial vertical magnetic field that contains no compass information.

Materials and methods

Study site and experimental birds

Orientation experiments were carried out at Rybachy (Courish Spit, Kaliningrad region, Russia; 55°09′N, 20°51′E) in mid August–late September of 2010 (control

group, $n = 52$), 2011 (experimental group, $n = 34$, magnetic parameters: magnetic intensity 50, 535 nT, magnetic inclination 90°) and 2012 (experimental group, $n = 10$, magnetic parameters: magnetic intensity 50, 569 nT, magnetic inclination 90°). As a model species, we used Garden Warblers, common passage migrants in this region. This species breeds in Europe and Western Siberia; its wintering areas are located in tropical and southern Africa between the latitudes of about 10°N to 30°S (Moreau 1972; Svensson 2009). All birds were caught by mist-netting at the Biological Station Rybachy during autumn migration (in early August–middle September) and kept in an aviary outdoors (in small wooden cages) in the local geomagnetic field with full access to natural celestial cues for several days before experiments. We used only first-year Garden Warblers (juveniles). The birds were provided with food (mealworms, *Tenebrio molitor*) and fresh vitaminised water ad libitum. All Garden Warblers were released after the experiments.

Experimental procedure

Orientation tests took place under good weather conditions with no or light wind (0–3 m/s) and under clear starry sky (maximum 60 % cloud cover). Birds were tested in modified Emlen funnels (top diameter 300 mm, bottom diameter 100 mm, wall slope 45°; Emlen and Emlen 1966). The cage was made of aluminium and its top covered with cotton netting. Each test was started 20 min before sunset. Funnels with birds from the experimental groups were put in an artificial vertical magnetic field which did not provide magnetic compass information. The total intensity of this artificial field was identical to the total intensity of the local geomagnetic field. The vertical magnetic field was created by $1 \times 1 \times 1$ m magnetic coils (Helmholtz coil system with two coils per axis) which were custom-built by Pushkov Institute of Terrestrial Magnetism, Ionosphere and Radiowave Propagation (Russian Academy of Sciences, St. Petersburg, Russia). Each magnetic coil contained one funnel. The coils were managed by custom-written software. Constant power supply (car battery) was used to create magnetic field in the centre of the coil (within a space of $40 \times 40 \times 40$ cm). The heterogeneity of the artificial magnetic field within this space was <1 %. A Helmholtz coil system like this generates an artificial magnetic field with <1 % heterogeneity within a similar space ($\pm 0.33 \times \pm 0.33 \times \pm 0.33$ d, d is the diameter of coil; see Mouritsen 2013 for more details). The parameters of the vertical magnetic field were recalibrated before the beginning of every test.

Before the orientation tests, we weighed our birds and visually estimated their fat score according to the 9-class scale (from $0 = $ no fat to $8 = $ maximum fat; Kaiser 1993). Birds from the control group were tested in Emlen funnels for 4 h after sunset with full access to the local geomagnetic field

and celestial cues in the course of orientation tests. All experimental birds were divided into two subgroups: birds from the first subgroup (Clear sky group) saw a clear starry sky during the experiment. The magnetic coils' setup with birds from the second subgroup (Overcast group) was covered with semi-transparent polyethylene film to imitate cloudy weather conditions for 45 min after sunset. The magnetic coils were turned off upon the end of nautical twilight (100 min after sunset) after which the birds' orientation was video-recorded for 2 more hours. Each bird's orientation was tested only once to avoid pseudo-replication. Birds were released after the experiment.

To record the behaviour of the test birds in the funnels, we used infrared monochrome cameras SK–2020/SO (Sunkwang Electronics, South Korea). The video cameras were placed under the coil above the Emlen funnels and connected to a surveillance monitor for real-time observation. Video was recorded with a PC using Video Viewer 1.1 (AV-Tech, Taiwan) and used for further analysis of migratory restlessness.

Data analysis and statistics

Locomotor activity was categorised into four types: jumps, flushes, cage crawling and head scanning. We defined a jump as a movement without the use of the wings from the centre of a funnel towards its periphery, flushes as jumps with use of the wings, cage crawling as the moving of birds on the cotton netting, and head scanning as turns of the head of the bird from its body axis position to an angle of more than 60° to the left or right, similar to the study by Mouritsen et al. (2004). The video was divided into 5-min intervals, where all types of locomotor activity were counted. In order to analyse the orientation of the test birds, we counted the numbers of jumps and flushes in each of sixteen 22.5° sectors. Rayleigh test (with p value of 0.05) was used to determine statistically significant directional preferences of our test birds (Batschelet 1981). Inactive birds (<20 jumps and/or flushes) and disoriented birds (orientation was not significantly different from random) were excluded from further analysis of orientation. Statistical differences between the orientations of control birds during two periods of activity were calculated using the non-parametric Mardia–Watson–Wheeler test. The Mann–Whitney U test was applied to compare the number of head scans in the natural magnetic field (NMF) and the vertical magnetic field (VMF). Statistical tests and data analysis were performed with Oriana 2.02 (Kovach Computing Services, Inc., Anglesey, UK), STATISTICA 8.0 (StatSoft, Tulsa, USA) and R 2.15.2 (www.r-project.org). Average sunset azimuths, sunset times and the end of nautical twilight for our experimental place were computed in Stellarium 0.11.3 (Free Software Foundation, Inc., Boston, USA).

Results

Test birds

The weights of the birds from the control group varied from 17.7 to 25.1 g [average 21.7 g $\pm$ 2.5 (SD)]. The weights of the birds from the experimental group varied from 17.3 to 30.2 g [average 23.9 g $\pm$ 2.2 (SD)]. The weights of birds significantly differed between the control and experimental groups (t test: $t = -5.3$, $p < 0.001$). The fat scores for the control birds varied from 4 to 7 according to the 9-class scale of Kaiser (1993), and the average value was 6. The fat scores of all experimental birds varied from 3 to 7, and the average value was 6. We did not use lean individuals (fat score 0–3) to avoid reduced activity of experimental birds and reverse orientation that is characteristic of lean birds (Sandberg 1994; Sandberg and Moore 1996).

Locomotor activity

Garden Warblers from the control group (with access to the local geomagnetic field and natural celestial cues) showed two periods of restlessness in cage conditions. The first


Fig. 1 Behavioural activities performed by Garden Warblers from the control group during experiment: in **a** the activity of the birds is illustrated as a function of time. In **b** the activity of the birds is illustrated as a function of the elevation of the Sun above the horizon. Four types of activities were quantified: jumps (*filled circle*), flushes (*filled triangle point-up*), cage crawling (*filled square*) and head scanning (*filled diamond*). Jumps are movements of the birds without use of wings from the centre of a funnel towards its periphery, flushes are jumps with use of wings, cage crawling are movements on the cotton netting, and head scanning are turns of the head by more than 60° to the left or right from the body axis. Control Garden Warblers had access to all celestial cues and the geomagnetic field during the whole period of the experiment. *Symbols* indicate the proportion of Garden Warblers which showed one of types of activity in a specific 5-min interval or in a given one-degree sun elevation interval. *Vertical dashed line* indicates sunset. *The elevation of the sun relative to the horizon* indicates sun position relative to the celestial horizon
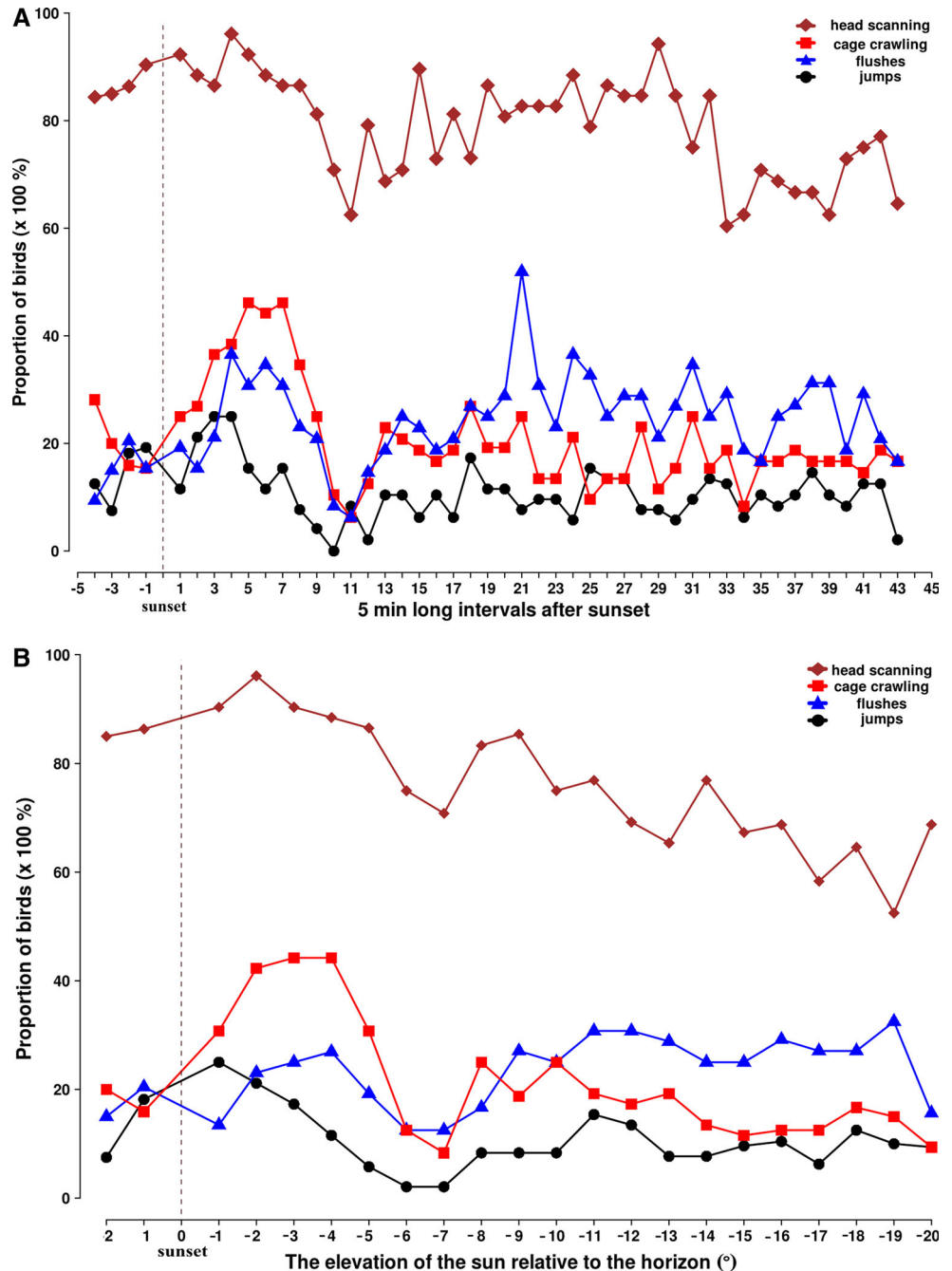
(twilight) period lasted for 33 ± 13 (SD) min after sunset and was separated from the second (nocturnal) one by a quiescent period (Fig. 1). The quiescent period represents a decrease in total activity of birds in cage conditions and lasts for 44 ± 27 (SD) min. Variations of activity of control birds significantly differed from random, as shown by χ^2 tests: jumps ($\chi^2 = 117$, $p < 0.001$), flushes ($\chi^2 = 77.1$, $p < 0.001$), cage crawling ($\chi^2 = 118$, $p < 0.001$), and head scanning ($\chi^2 = 46$, $p < 0.05$). Segmented regression analysis showed that the sun 6–7° below the horizon and the eleventh 5-min interval after sunset were the breakpoint for all four types of activity in control Garden Warblers. In the experimental conditions, the sun 6° below the horizon and the ninth 5-min interval after sunset were the breakpoint for

Fig. 2 Behavioural activities performed by Garden Warblers from the experimental group during experiment: in **a** the activity of the birds is illustrated as a function of time. In **b** the activity of the birds is illustrated as a function of the elevation of the Sun above the horizon. Four types of activities were quantified: jumps (*filled circle*), flushes (*filled triangle point-up*), cage crawling (*filled square*), and head scanning (*filled diamond*). A jump is defined as the movements of the birds without use of wings from the centre of a funnel towards its edge, flushes are defined as jumps but with the use of wings, cage crawling is defined as moving of the birds on the cotton netting, and head scanning is defined as turns of the head of the bird from its body axis position to an angle turned more than 60° to the left or right. *Symbols* indicate the proportion of Garden Warblers which showed the specific types of activity in each specific 5-min interval or in a given one degree sun elevation interval. *Vertical dashed line* indicates sunset. *The elevation of the sun relative to the horizon* indicates the sun position relative to the celestial horizon
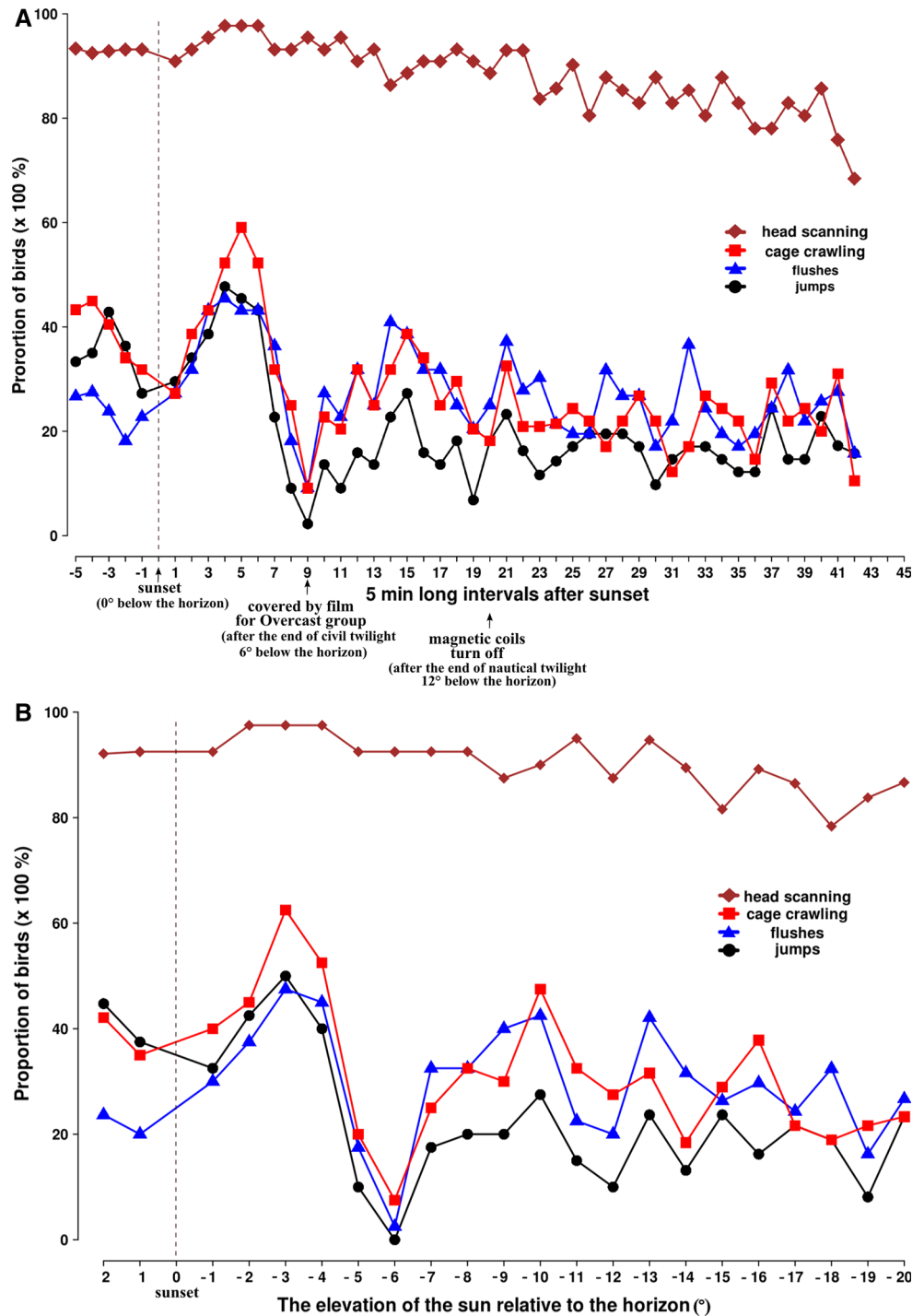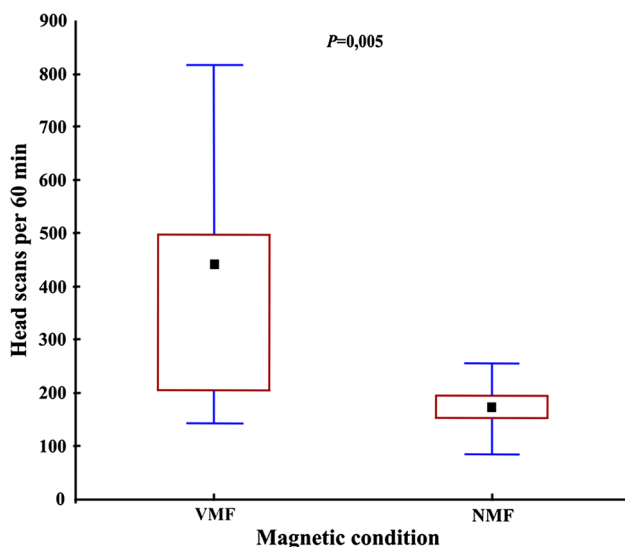
Fig. 3 Number of head scans performed by Garden Warblers in a normal magnetic field (*NMF*) and in a vertical magnetic field (*VMF*). The head scanning rate of birds from the experimental group (in the vertical magnetic field) significantly differs from the head scanning rate of control birds (in the normal magnetic field; Mann–Whitney *U* test: $U = 12.5$, $p = 0.005$). *Black square* is the median. *Boxes* are 25–75 % quartile. *Plots* indicate min–max values. *p* is the significance level

jumps, flushes and cage crawling, whereas head scanning showed no apparent breakpoint, i.e. it did not drop significantly throughout the testing period.

If birds had no access to the normal magnetic field at sunset and twilight, their behaviour was similar to that of the control birds. Figure 2 shows the total activity of Garden Warblers from the experimental group. Birds tested in the VMF demonstrated an increase in activity after sunset [twilight period with duration of 30 ± 8 (SD) min], after which their activity decreased [quiescent period with duration of 29 ± 13 (SD) min]. Afterwards, the birds again increased their nocturnal restlessness (Fig. 2). Variations of the activity of the experimental birds significantly differed from random (χ^2 test: jumps ($\chi^2 = 117.5$, $p < 0.001$), flushes ($\chi^2 = 101.3$, $p < 0.001$), cage crawling ($\chi^2 = 101$, $p < 0.001$), head scanning ($\chi^2 = 49$, $p = 0.02$)). We also found that the number of head scans differed between control and experimental Garden Warblers. Garden Warblers tested in the NMF (control birds) made 169 ± 45 (SD) head scans per 60 min, whereas birds in the VMF (experimental birds) made 397 ± 203 (SD) head scans per 60 min (Fig. 3). The head scanning rate was significantly higher in the experimental condition (Mann–Whitney *U* test: $U = 12.5$, $p = 0.005$), and, as mentioned earlier, it did not significantly drop during the 'quiescence' period between the twilight and the nocturnal activity, as did other types of activity.

Orientation of test birds

Control group

As many as 27 individuals of the total of 52 birds were significantly oriented in the twilight period, 20 were disoriented and 5 were inactive. In the night period, 31 birds were significantly oriented, 18 were disoriented and 3 were inactive. Control birds were oriented towards the southwest in both periods: $\alpha = 218°$, $r = 0.568$, $n = 27$, $p < 0.001$, 95 % confidence intervals (CI) $= 194°–242°$ for the first period (Fig. 4a); $\alpha = 256°$, $r = 0.426$, $n = 31$, $p < 0.001$, 95 % CI $= 224°–288°$ for the second period (Fig. 4b). The Mardia–Watson–Wheeler test did not show any differences between the mean vectors ($W = 1.251$, $p = 0.535$).
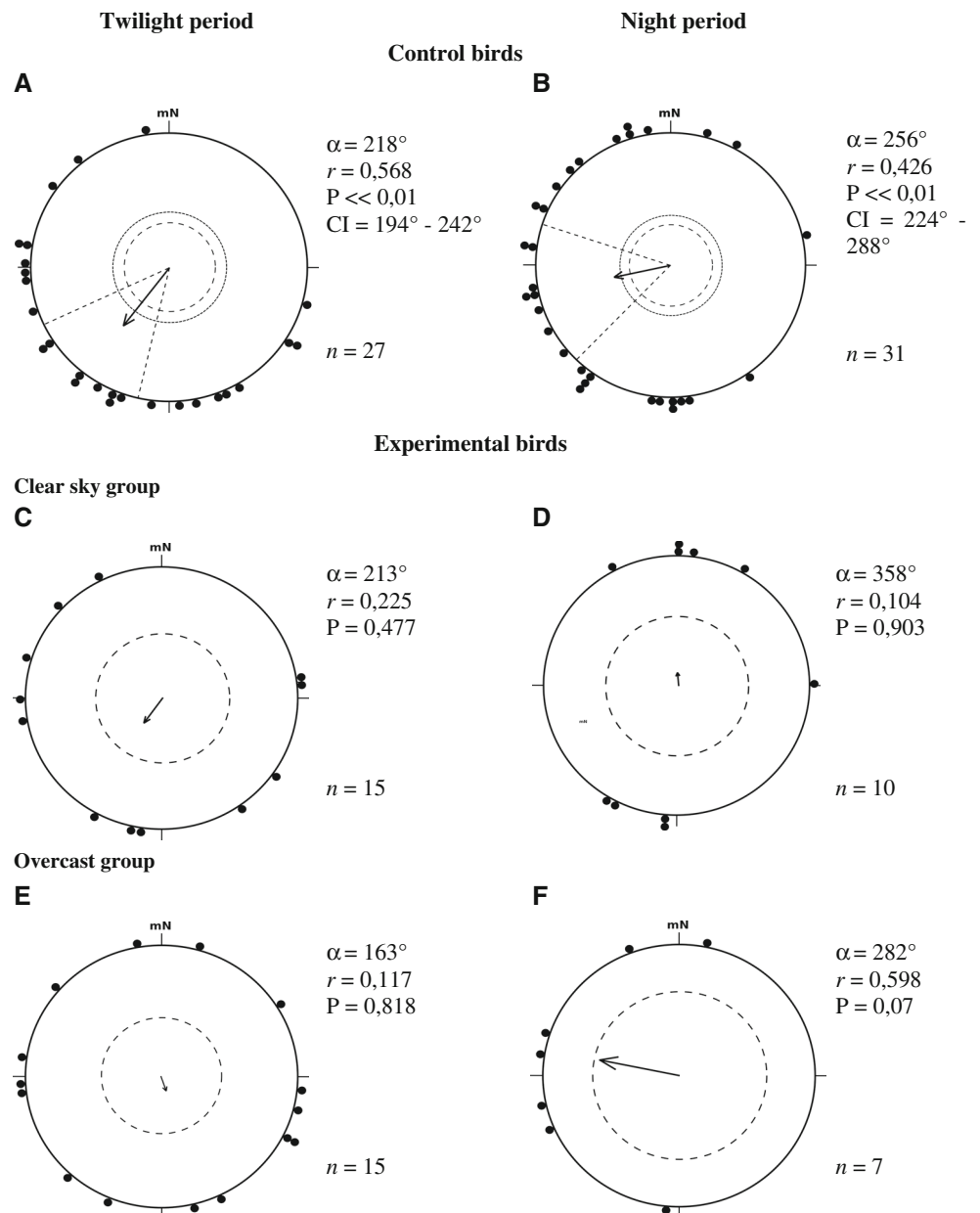
Experimental group

Thirty birds of the total of 44 Garden Warblers were significantly oriented in the twilight period, 6 were disoriented and 8 were inactive. During the deep night, 17 birds were significantly oriented, 17 were disoriented and 10 were inactive. Birds from the clear sky group did not demonstrate any significant orientation during either period: $\alpha = 213°$, $r = 0.225$, $n = 15$, $p = 0.477$ in the twilight period (Fig. 4c) and $\alpha = 358°$, $r = 0.104$, $n = 10$, $p = 0.903$ in the night (Fig. 4d), out of 22 tested individuals. Garden Warblers from the overcast group were not oriented in the twilight period: $\alpha = 163°$ ($r = 0.117$, $n = 15$, $p = 0.818$, (Fig. 4e), whereas during the deep night, the mean orientation was marginally insignificant: $\alpha = 282°$, $r = 0.598$, $n = 7$, $p = 0.07$ (Fig. 4f). However, it is worth mentioning that just 7 birds were active and oriented during this period out of the 22 tested ones, which makes their nearly significant orientation vector even less reliable.

Discussion

Distinct period of twilight activity

Birds tested under natural conditions showed two periods of activity separated by a quiescent period. Similar results were obtained for birds with no access to the geomagnetic field at sunset and during twilight. We assume that this activity of the caged birds reflects some forms of activity in their free-living conspecifics. At the same time, there are differences between the activity of control and experimental Garden Warblers: birds did head scans more often when exposed to the VMF comparing to the NMF conditions (Fig. 3). Head scanning is a characteristic behaviour shown during nocturnal orientation tests in round arenas (Dolnik 1981), which is believed to be used

Fig. 4 Orientation of Garden Warblers from the control (during autumn 2010) and experimental groups (in autumn 2011 and 2012). *Top row* orientation of control birds. Control Garden Warblers had access to all celestial cues and the geomagnetic field during the twilight (**a**) and night (**b**) periods. *Middle row* orientation of birds from the clear sky experimental group during the twilight (**c**) and night (**d**) periods. Garden Warblers from this group had access to all celestial cues in both periods, but not to the normal magnetic field from sunset until the end of nautical twilight. *Bottom row* orientation of birds from the overcast experimental group during the twilight (**e**) and night (**f**) periods. Garden Warblers from this group did not have access to the stars in both periods and also not to the geomagnetic field from sunset to the end of nautical twilight. α is the direction of mean vector, r is the length of mean vector (r varies from 0 to 1), n is the number of birds, providing significant orientation results under the given condition, p is the significance level, *CI* is 95 % confidence intervals (95 % CI). *Dots* individual directions; *arrow* mean group vector; *inner and outer dashed circles* 1 and 5 % significance levels of the Rayleigh test respectively. *Radial lines* 95 % CI, *mN* magnetic north

Twilight period

Night period

Control birds

A
$\alpha = 218°$
$r = 0,568$
$P \ll 0,01$
$CI = 194° - 242°$
$n = 27$

B
$\alpha = 256°$
$r = 0,426$
$P \ll 0,01$
$CI = 224° - 288°$
$n = 31$

Experimental birds

Clear sky group

C
$\alpha = 213°$
$r = 0,225$
$P = 0,477$
$n = 15$

D
$\alpha = 358°$
$r = 0,104$
$P = 0,903$
$n = 10$

Overcast group

E
$\alpha = 163°$
$r = 0,117$
$P = 0,818$
$n = 15$

F
$\alpha = 282°$
$r = 0,598$
$P = 0,07$
$n = 7$

by migratory birds to detect the direction of the earth's magnetic field (Mouritsen et al. 2004). Our results independently support the suggestion of Mouritsen et al. (2004) who reported that garden warblers which have no access to useful geomagnetic compass cues increase their head scanning frequency. There is a possibility that birds use head scanning both to detect the direction of the geomagnetic field during compass calibration (which presumably occurs in the twilight period) and to maintain an appropriate migratory direction during nocturnal migratory flight. Our data showed that Garden Warblers maintained a high rate of head scanning throughout the periods of twilight activity, the quiescence phase and

nocturnal activity, but we cannot rule out the possibility that free flying birds may not need to make head scans and that head scanning thus may only be performed by caged birds.

The nocturnal period of activity most likely corresponds to nocturnal migratory flights performed by flee-flying birds. Recent telemetry studies on long-distance songbird migrants during autumn passage demonstrated that most species begin their migratory flights within 1–2 h after sunset (Åkesson et al. 1996; Bolshakov and Chernetsov 2004; Schmaljohann et al. 2013b; but see Bolshakov et al. 2007 for medium-distance migrants). Similar results have been shown in radar studies (Schmaljohann et al. 2007).

Importance of magnetic information at sunset
for orientation throughout the night

Even though we cannot be completely sure about the
function of the twilight period of activity of Garden War-
blers under test conditions, our orientation data suggest that
this period is of importance for selecting the appropriate
migratory direction. The birds from the control group with
access to celestial cues and the geomagnetic field during
the sunset period were oriented towards the south-west in
both periods. According to ringing recoveries (Bolshakov
et al. 2009), this direction is typical of Garden Warblers in
the Eastern Baltic during autumn migration. Orientation in
the second period (256°) probably also represents the
seasonally appropriate migratory direction. Orientation in
the twilight period (mean 218°) is consistent with the
migratory direction and does not seem to be influenced by
phototactic responses to the setting sun (the average sunset
azimuth was 290°).

If Garden Warblers have no access to geomagnetic
compass information at sunset and during nautical twilight
(i.e. if they cannot calibrate their compasses), they fail to
select an appropriate migratory direction during the night,
even when they get access to the geomagnetic field later in
the night (Fig. 4d, f). The fact that Garden Warblers were
disoriented during the period when they could receive the
correct directional information from the geomagnetic field
suggests that access to magnetic cues at sunset and twilight
plays a crucial role in their choice and maintenance of
direction during nocturnal migration. Surprisingly, experi-
mental birds under the clear sky were also disoriented in
the twilight and night periods (Fig. 4c, d), just as were
Garden Warblers tested in overcast conditions (Fig. 4e, f).
They seem not to have used cues from the starry sky to
select their migratory direction, even though this infor-
mation was available to them. Similar results were
obtained in cue–conflict experiments with Catharus thru-
shes in North America (Cochran et al. 2004). Grey-cheeked
and Swainson's Thrushes exposed to clockwise changes in
the magnetic field during the calibration phase, selected
and maintained a wrong direction (consistent with the
calibration of their magnetic compass from sunset cues)
during their first-night flight after experimental treatment,
despite the fact that they had access to the correct compass
information from the stars. However, other songbird
migrants, for example, Redstarts Phoenicurus phoenicurus
and European Robins Erithacus rubecula, can use a stellar
compass if they do not have access to other compass cues
(Mouritsen 1998; Zapka et al. 2009).

Previous studies have suggested that the star compass
plays a secondary role and is calibrated by information
from the magnetic field (Wiltschko and Wiltschko 1976).
Experiments with three Sylvia warblers (Garden Warblers,

Whitethroats S. communis and Subalpine Warblers S.
cantillans) suggested a domination of the magnetic com-
pass over the star compass. All three species when tested in
a magnetic field deflected by 120° clockwise altered their
direction preference correspondingly despite access to
information from the clear starry sky (Wiltschko and
Wiltschko 1975). Garden Warblers were also disoriented in
a vertical magnetic field with access to the local stars.

The presented data suggest that Garden Warblers do
not use their star compass as an independent orientation
system for selection and maintenance of the preferential
migratory direction in orientation cages. Instead, they
seem to use the sun compass to determine their migratory
direction and use the magnetic compass to maintain the
selected direction during nocturnal migration. The mag-
netic compass seems to be calibrated by the sun compass.
The twilight period of nocturnal activity demonstrated in
the present research can reflect this process. However, it
does not rule out the possibility that a stellar compass may
be of greater importance for some other passerine and
non-passerine migrants during nocturnal migration (Mou-
ritsen 1998).

Moreover, information from the starry sky seems to play
an important role in the development of the magnetic
compass during the pre-migratory period and the trans-
mission of innate direction information into an actual
migratory direction (Wiltschko and Gwinner 1974; Beck
and Wiltschko 1982; Weindler et al. 1995, 1998; Michalik
et al. 2014). Garden Warblers kept under a rotating artifi-
cial starry sky without geomagnetic and solar information
during the pre-migratory period, and then tested in the
same conditions but under stationary sky, used their stellar
compass to select the correct migratory direction (Wilt-
schko et al. 1987). The authors suggest that stellar and
magnetic compasses develop independently during ontog-
eny but control switches from celestial rotation to magnetic
compass during autumn migration.

In conclusion, access to geomagnetic information during
sunset and nautical twilight plays a crucial role for
selecting the appropriate migratory direction in migratory
Garden Warblers tested in orientation cages. The twilight
period of locomotor activity shown by Garden Warblers in
our experiments seems to reflect a calibration between their
solar and magnetic compasses. In addition, the role of the
stellar compass during autumn migration is not quite
obvious, and Garden Warblers seem to disregard the
information from starry skies for the selection and main-
tenance of their seasonal species-specific direction during
migration.

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