

Effects of magnetic manipulations on orientation: comparing diurnal and nocturnal passerine migrants on Capri, Italy in autumn

Effekter av magnetiska manipulationer på orientering: jämförelser mellan dag- och nattflyttande tättingar på Capri, Italien under hösten

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Abstract

Orientation cage experiments were performed on Capri in Italy, with a diurnal passerine migrant (Tree Pipit *Anthus trivialis*), and a nocturnal passerine migrant (Garden Warbler *Sylvia borin*), to study the use of magnetic compass information during autumn passage migration. The experiments were performed outdoors at sunset in: (1) the local geomagnetic field under natural clear skies, (2) a shifted magnetic field (mN -90°) under clear skies, and (3) a shifted magnetic field (mN -90°) under simulated overcast skies. Day migrating Tree Pipits showed a clear shift in orientation compared to controls (i.e. local geomagnetic field and clear sky conditions) corresponding roughly with the magnetic shift (mN -90°) under clear as well as overcast skies, while the Garden Warbler migrating at night, did not respond

to the same magnetic manipulations by shifting their preferred directions in the cages. The mean orientation of Tree Pipits did not differ from the sun's position during experiments, while it was clearly different in Garden Warblers. Species-specific orientation responses to experimental manipulations in caged compared to free-flying migrants is discussed.

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Introduction

Migratory songbirds are able to use geomagnetic information and celestial cues based on the sun, the pattern of skylight polarization, and stars for orientation (e.g. Emlen 1975, Able 1980, Wiltschko & Wiltschko 1995). Passerine migrants born in the Northern Hemisphere have been shown to possess an inherited tendency to orient away from the rotation centre of the sky, i.e. the pole star in the Northern Hemisphere, in autumn (for review see Emlen 1975), and also an inherited magnetic compass based on the angle of inclination (Wiltschko & Wiltschko 1972). However, the combination of the two sources of information are important for the bird to experience during the ontogenetic phase, to guide a bird from the site where it is born to the population specific wintering area (Weindler et al. 1996).

However, what specific compasses are used under certain phases of the migration route, and if species with different migration strategies and

destination areas differ in how they respond to the same type of manipulations of external compass information, and thus if they rely on the same compasses to select a migration course in the same ecological situation, is not clear (Helbig 1990, Able 1993, Åkesson 1994). Different species of songbirds seem to respond differently to cue-conflict experiments (for review, Muheim et al. 2006). In this study we compare the orientation in two species of migrants with different migration strategies, a diurnal migrant, the Tree Pipit *Anthus trivialis*, and a nocturnal migrant, the Garden Warbler *Sylvia borin*. We exposed the birds to the same shift of the magnetic field and recorded their orientation, in circular cages under both clear and overcast skies. Earlier experiments with the same type of experimental set-up suggest that there might be species-specific differences in how the birds respond to the same type of manipulation of external information (e.g. Åkesson 1993, 1994, Åkesson et al. 2002, Sandberg et al. 1991, 2000).

Methods

Study species and study site

We used a diurnal and a nocturnal passerine migrant, Tree Pipit and Garden Warbler captured on Capri in southwestern Italy, to study the use of magnetic compass information for migratory orientation in autumn. The birds were captured in mistnets at Castello Barbarossa near Villa San Michele, Anacapri (44°33'N, 14°15'E) from end of August to the end of September (for further information on capture procedure see Pettersson et al. 1990, Jonzén et al. 2006). Experiments with Tree Pipits were performed in 1995 and 1996, while Garden Warblers were studied 1994–1996.

The birds were kept during the day in individual cages and were tested at local sunset in circular orientation cages (Emlen & Emlen 1966). In the cages the birds were fed with mealworms and water with vitamins. We recorded the birds' body mass to the nearest 0.1 g with a Pesola spring-balance (50 g) and classified the fat levels according to a 10-graded visual scale (0–9) for fat classification (Pettersson & Hasselquist 1985, and extended at Falsterbo Bird Observatory) immediately before the cage experiments were performed.

Tree Pipits are mainly diurnal migrants breeding in northern Europe and wintering in an area from tropical West Africa across Central Africa south of 10°N latitude to East and Southeast Africa (Moreau 1972, Cramp 1988), with an expected migratory direction towards southwest to south at Capri. Garden warblers are night migrants and winter in an area from West and Central Africa south of 8°N latitude and also migrate to East and

South Africa (Moreau 1972, Cramp 1992). They are expected to migrate mainly towards southwest to south on Capri.

Experimental procedure and statistics

The migratory orientation of individual birds was recorded in circular cages, so-called Emlen funnels (Emlen & Emlen 1966; lined with Tipp-Ex paper), allowing the birds to see approximately 160° of the sky at zenith. The experiments were performed outdoors at Castello Barbarossa. The mean angle of orientation of individual birds was recorded for one hour under natural clear and simulated overcast (the top of the cage covered with a 3 mm diffusing Plexiglas sheet) skies. The recordings of the birds' activity started at local sunset. The mean orientation of the birds was recorded one time per individual per test category, between 10 and 30 September for Tree Pipits and between 30 August and 30 September for Garden Warblers. All birds were released after the experimental period.

Based on the bird's activity within 24 sectors in the cage, as recorded by claw marks crossing a horizontal line in the pigment of the Tipp-Ex paper (minimum set to 10 registrations, which is a measure of the distribution of the activity around the circle, but not a complete count of all registrations present), we calculated the mean angle of orientation relative to Geographic North by using vector addition (Batschelet 1981). Experiments for which the mean orientation of the individual were not significantly different from random ($p > 0.05$ according to Rayleigh test, Batschelet 1981) or with an activity below 10 registrations as scratch

Table 1. Number of Tree Pipits and Garden Warblers tested in orientation experiments on Capri under different experimental conditions (1–3) in autumn.

Antal trädpiplärkor och trädgårdssångare vars orientering registrerats i orienteringsburar på Capri under hösten för olika experimentförhållanden: 1) Klar himmel, lokalt magnetfält, 2) Klar himmel, magnetfält vridet -90°, 3) Simulerat mulen himmel, magnetfält vridet -90°)

Species Art	Experiment	Inactive	Disoriented	Included	Total
Tree Pipit <i>Anthus trivialis</i>	1) Clear skies, local geomagnetic field	4	0	10	14
	2) Clear skies, mN -90°	5	0	12	17
	3) Simulated overcast skies, mN -90°	6	0	7	13
	Total all three <i>Summa alla tre</i>	15	0	29	44
	Per cent <i>Procent</i>	34.1	0	65.9	100)
Garden Warbler <i>Sylvia borin</i>	1) Clear skies, local geomagnetic field	2	3	62	67
	2) Clear skies, mN -90°	3	3	34	40
	3) Simulated overcast skies, mN -90°	6	3	36	45
	Total all three <i>Summa alla tre</i>	11	9	132	152
	Per cent <i>Procent</i>	7.2	5.9	86.8	100

Table 2. Mean fat class (0–9) and mass (g) for Tree Pipits and Garden Warblers for each experimental category as recorded prior to orientation experiments on Capri in autumn. Given is also median±sd activity (number of registrations per test hour) as calculated for all experiments in each category (1–3). For details on visual fat classification see Pettersson & Hasselquist (1986). The visual fat classification scale has been extended by three grades (7–9) at Falsterbo Bird Observatory.

Medelfettklass (0–9) och vikt (g) för trädpiplärkor och trädgårdssångare noterade direkt innan orienteringsexperimenten startades för respektive experimentkategori. Angivet är också median aktiviteten (antal registreringar per timme) och ±sd beräknat för respektive experimentkategori (see Tabell 1). För detaljer angående den visuella fettskalan see Pettersson & Hasselquist (1986). Skalan har utökats med tre fettklasser (7–9) vid Falsterbo Fågelstation.

Species	Experiment	Mean fat class±sd	Mean mass (g) ±sd	Median activity ±sd	N
Tree Pipit <i>Anthus trivialis</i>	1) Clear skies, local geomagnetic field	6.0±1.4	25.8±3.2	22±50.5	14
	2) Clear skies, mN –90°	6.0±1.4	27.0±3.6	29±42.8	17
	3) Simulated overcast skies, mN –90°	6.1±1.5	26.2±4.5	16±38.0	13
Garden Warbler <i>Sylvia borin</i>	1) Clear skies, local geomagnetic field	5.5±1.6	20.6±3.6	41±54.6	67
	2) Clear skies, mN –90°	5.7±1.6	21.5±4.0	29±55.6	40
	3) Simulated overcast skies, mN –90°	5.3±2.0	20.5±4.3	43±76.6	45

marks crossing a horizontal line per test hour, were not included in further analyses. Number of experiments classified as inactive, disoriented and included (classifications given above) are given in Table 1. We used circular statistics to calculate the mean orientation of a group of birds recorded for each test category, and the Rayleigh test to analyse if the mean orientation differed from a random distribution (Batschelet 1981). For individuals with a significant axial mean orientation (Tree Pipits: 3 (10.3%) out of 29 experiments; Garden Warbler: 16 (12.1%) out of 132), we used only the side of the axis with the majority of the registrations for further statistical analyses. Differences between groups were compared with Watson's U²-test (U²; Batschelet 1981) and Mardia's one-way classification test (F_{1,df}; Mardia 1972). We used STATISTICA (StatSoft, Inc 2005) for analysing non-circular data. We used 95% Confidence Interval (95% CI; Batschelet 1981) to analyse if the mean orientation differed from the sun's position in the middle of the test hour calculated relative to Geographic North for each experimental site.

Results

Both Tree Pipits and Garden Warblers carried large fat reserves at the time of the experiments (Table 2), suggesting they were prepared for long-distance flights across the Mediterranean Sea, and perhaps also directly across the Sahara. There were no differences in fat class between the dif-

ferent experimental categories (Median test, Tree Pipits: $\chi^2=0.14$, df=3, P>0.05, Garden Warblers: $\chi^2=0.43$, df=3, P>0.05). We found no difference in mass between the three different experimental categories, neither for Tree Pipits (ANOVA, F_{2,41}=0.37, p>0.05) nor for Garden Warblers (ANOVA, F_{2,148}=0.81, p<0.05). The Tree Pipits showed slightly lower activity in the cages than Garden Warblers (Table 2), but there was no significant difference in median activity between the different experimental categories for Tree Pipits (Median test, $\chi^2_2=1.22$, df=2, P>0.05) or for Garden Warblers (Median test, $\chi^2_2=0.14$, df=3, P>0.05).

Orientation under natural clear skies in the local geomagnetic field

The mean orientation under clear skies in the local geomagnetic field for Tree Pipits were directed towards west to northwest (Figure 1A), while Garden Warblers showed a mean orientation towards southwest (Figure 2A). The mean orientation was significantly different from the position of the sun in the middle of the test hour for Garden Warblers (95% Confidence Interval, 95% CI, ±17°, p<0.05, Batschelet 1981), but not for Tree Pipits (95% CI, ±41°, p>0.05).

Effects of magnetic manipulations on orientation

The mean orientation recorded for Tree Pipits under clear skies in a shifted magnetic field (mN

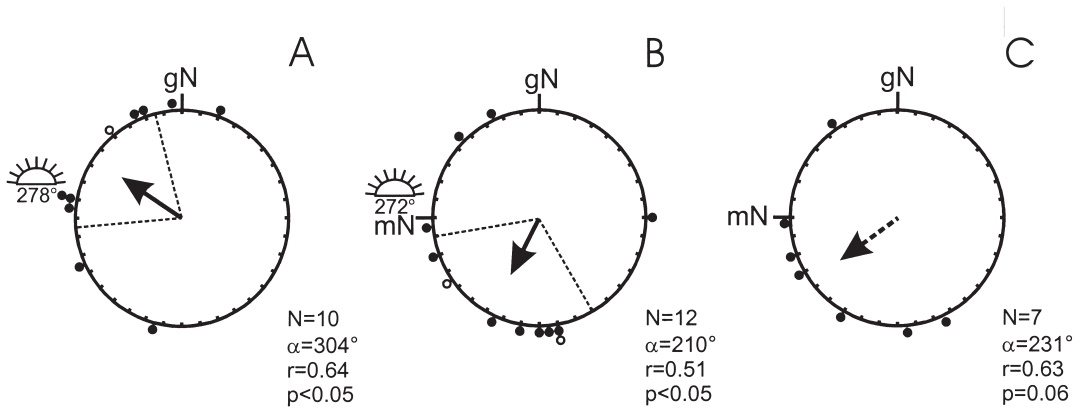


Figure 1. Results of orientation experiments with Tree Pipits under clear sky (A, B) and simulated overcast conditions (C) on Capri in autumn. The experiments were performed in the local geomagnetic field (A), and in a deflected magnetic field (magnetic North, mN corresponds to geographic West, mN -90° , B and C). Each symbol (filled: unimodal, open: bimodal) denotes the mean orientation of an individual bird. The mean angle of the group (α) indicated by the arrow, vector length (r) ranging between 0 and 1, and number of birds (N) tested is given for each circular distribution. Broken arrow indicates distribution not significantly different from random. Significance levels (p) are given according to the Rayleigh test (Batschelet 1981). Mean angle towards the sun in the middle of the test period is indicated for the clear sky experiments. 95% Confidence limits are given as broken lines.

Resultat från orienteringsexperiment med trädpiplärkor under naturligt klar (A, B) och simulerat mulen himmel (C) på Capri under hösten. Experimenten genomfördes i ett naturligt opåverkat magnetfält (A), samt i ett vridet magnetfält (magnetiskt norr vridet till geografisk väster, mN -90° , B och C). Varje symbol (fylld: unimodal fördelning, öppen: bimodal fördelning) visar medelriktningen för en individ. Medelriktningen (α) som visas av en pil med längden (r) och varierande mellan 0 och 1, samt antal fåglar (N) som testats anges för respektive cirkeldiagram. Signifikansnivåerna (p) ges enligt Rayleigh testet (Batschelet 1981). Medelriktningen mot solens position i mitten av experimenttimmen anges för respektive test under klar himmel. 95% konfidens intervall anges som streckade linjer.

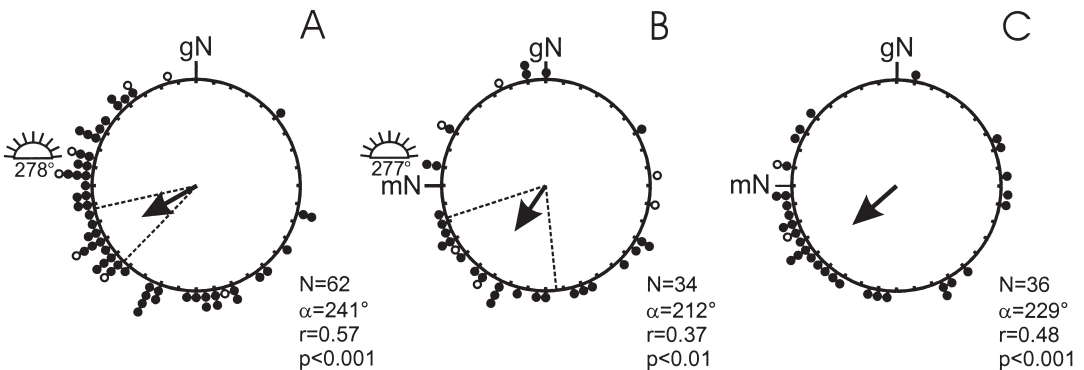


Figure 2. Results of orientation experiments with Garden Warblers under clear sky (A, B) and simulated overcast conditions (C) at Capri in autumn. The experiments were performed in the local geomagnetic field (A), and in a deflected magnetic field (magnetic North, mN corresponds to geographic West, mN -90° ; B, C). For further information on symbols and calculated values see Figure 1.

Resultat från orienteringsexperiment med trädgårdssångare under klar himmel (A, B) och simulerat mulen himmel (C) på Capri under hösten. Experimenten genomfördes i ett lokalt magnetfält (A), samt i ett vridet magnetfält (mN -90° ; B, C). För information om symboler och statistik se Figur 1.

-90°), showed orientation towards southwest, significantly different from the position of the sun (95% CI, $\pm 50^\circ$, $p < 0.05$) (Figure 1B). Thus, under clear skies there was a significant difference in mean orientation in a shifted magnetic field compared to in the local geomagnetic field (Mardia's one-way classification test, $F_{1,20} = 8.39$, $p < 0.01$, Mardia 1972). The mean orientations recorded under simulated overcast skies did not differ between tests in the local geomagnetic field and the shifted magnetic field (Watson's U^2 -test, $U^2 = 0.12$, $p > 0.05$, Batschelet 1981, Figure 1B & C). Furthermore, we found no difference between clear sky experiments in the local geomagnetic field and experiments under simulated overcast skies in a shifted magnetic field (Watson's U^2 -test, $U^2 = 0.04$, $p > 0.05$, Figure 1A & C).

The Garden Warblers showed a mean orientation under clear skies in a shifted magnetic field (mN-90°) that was directed towards southwest (Figure 2B), significantly different from the position of the sun in the middle of the test hour (95% CI, $\pm 39^\circ$, $p < 0.05$). This mean orientation recorded for the Garden Warblers did not differ from the clear sky experiments in the local geomagnetic field (Mardia's one-way classification test, $F_{1,94} = 2.30$, $p > 0.05$, Figure 2A & B), nor from the mean orientation in a shifted magnetic field under simulated overcast skies (Mardia's one-way classification test, $F_{1,68} = 0.54$, $p > 0.05$, Figure 2B & C). We found no difference in orientation in Garden Warblers between clear sky experiments in the local geomagnetic field and simulated overcast experiments in a shifted magnetic field (Mardia's one-way classification test, $F_{1,96} = 0.54$, $p > 0.05$, Figure 2A & C).

Discussion

Orientation under natural clear skies

Diurnally migrating Tree Pipits in our study clearly showed a west to northwesterly mean orientation in autumn at Capri, under natural clear skies in the local geomagnetic field, directed distinctly more to the north than expected (Cramp 1988). However, the mean orientation was not different from the position of the sun during the experimental period at sunset, suggesting that the birds might have been influenced by the sunset during the experiments. Attraction towards the sun's position during experimentation at sunset has been observed for a number of passerine migrants in circular cage experiments (e.g. Åkesson 1993, 1994, Åkesson & Sandberg 1994, Åkesson & Bäckman 1999, Sand-

berg et al. 1991, Marchetti et al. 1998). It has been suggested that information available at the horizon is important for the bird's compass orientation during the twilight period (Sandberg 1991, see also Muheim et al. 2006), and free-flying North American *Catharus* thrushes seem to use twilight visual information for compass calibration prior to nocturnal flights (Cochran et al. 2004). Daytime celestial cues, and more specifically the skylight polarisation pattern have been shown to be used to calibrate the magnetic compass by birds (e.g. Able & Able 1990, 1993, 1995)

The experiments with the nocturnal migrant, the Garden Warbler, showed selection of southwesterly courses under natural clear skies in the local geomagnetic field, more or less in the expected migratory direction (Cramp 1992). The mean orientation for Garden Warblers was clearly different from the sun's position during the experiments, suggesting minor or no influence from the sun on the bird's orientation in the cages.

Experiments in cages with migratory passerines at twilight, throughout the night and in the sunset hours have demonstrated a shifted orientation in European robins *Erithacus rubecula*, and between sunrise and sunset also for some tropical nocturnal passerine migrants captured and tested on migration in South Scandinavia (Åkesson & Sandberg 1994). The birds' orientation in circular cages was to a large extent influenced by the position of the sun, during these test periods, suggesting a phototactic response. It is interesting to note the difference between the diurnal and the nocturnal migrant in our study, demonstrating a clear sun attraction in the diurnal migrants, but no such attraction in the nocturnal migrant. Could this difference be related to differences in the use of solar, and/or magnetic cues at the test period? The Tree Pipits predominantly migrate during the day, and are expected to depart from stopover sites in the morning (Cramp 1988). The experimental period used by us might therefore be out of phase with the timing of the natural migratory departure. We observed a slightly lower mean activity in Tree Pipits relative to Garden Warblers, which support these observations. However, observations of free-flying nocturnal migrants (Åkesson et al. 1996, 2001), expected to predominantly depart in the twilight period (for review, see Moore 1984), show that individuals might select to depart at a very wide range of times, covering up to 10h. Many passerine migrants are also selecting their time of departure in relation to the prevailing wind and weather conditions (Åkesson & Hedenström

1996, Åkesson et al. 2001, 2002), rather than strictly departing at a specific time in relation to the availability of celestial orientation cues (Åkesson et al. 1996). This clearly demonstrates their ability to select appropriate migratory conditions during a large range of times within their natural flight period.

Effect of magnetic manipulations on orientation

The Tree Pipits in our study responded to the shifted magnetic field (mN-90°) by shifting the mean orientation under clear skies to almost the same extent (observed angular shift: -94°). However, the Garden Warblers did not show a significant shift in their mean orientation (-29°) relative to the shifted magnetic field. The results suggest a difference in response to the magnetic manipulation between the two species. Why did the Tree Pipits follow the magnetic shift to a high extent, while the Garden Warblers did not follow the shift to any significant degree? Species-specificity in the use of alternative compass cues have been suggested and discussed several times in the literature (Helbig 1990, Able 1993, Åkesson 1994; see also Muheim et al. in press). Both our birds are migrating to tropical Africa for wintering (Cramp 1988, 1992), but may do so by using different migration strategies. The measurements of fat and mass suggest that species were prepared for long migration flights. But as the two species differ in their predominant time of migration, with the Tree Pipits migrating mainly at day and the Garden Warblers mainly at night (Cramp 1988, 1992), we suggest that the observed differences in orientation response relative to the magnetic field, are most likely related to the birds' use of and perhaps calibration of alternative compasses (solar, stellar and geomagnetic) during migration.

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Sammanfattning

Jämförande orienteringsexperiment genomfördes under höstflyttningen på Capri i Italien med två arter tättingar, en dagflyttare, trädpiplärka *Anthus trivialis*, och en nattflyttare, trädgårdssångare *Sylvia borin*, för att undersöka hur de olika arterna använder sig av magnetisk information för orientering (Tabell 1). Experimenten startade vid lokal solnedgång och genomfördes utomhus under: (1) naturligt klar himmel i ett lokalt magnetfält, och (2) naturligt klar himmel i ett vridet magnetfält (magnetisk nordriktning vriden mot geografisk väster, mN -90°), samt (3) simulerat mulen himmel i ett vridet magnetfält (magnetisk nordriktning vriden mot geografisk väster, mN -90°). Fåglarnas aktivitet registrerades som skrapmärken i pigment på Tipp-Ex papper som placerats på de sluttande sidorna i cirkelrunda burar, s.k. Em-len-trattar, och deras fett och vikt noterades inför varje experimenttillfälle. Båda arterna hade stora fettreserver vid experimenttillfällena, vilket visar att de var förberedda på flyttning över Medelhavet och Sahara (Tabell 2). De dagflyttande trädpiplärkorna (Figur 1) visade en nordvästlig orientering under klar himmel i ett opåverkat magnetfält, och ändrade sin orientering i samma utsträckning som den introducerade magnetfältsvridningen under klar himmel, vilket antyder att de skulle lita till sin magnetkompass för orientering under skymningsperioden. Trädgårdssångarna (Figur 2) valde däremot en mer sydvästlig riktning under klar himmel i opåverkat magnetfält, och ändrade inte sin orientering med magnetfältsvridningen. Resultaten visar på skillnader i orientering relativt ett vridet magnetfält mellan en dag- och en nattflyttande tätting som exponerats för samma experimentförhållanden. Skillnaderna i orientering antas vara kopplade till hur de olika arterna utnyttjar, och möjligen kalibrerar, sin magnetkompass relativt visuella orienteringshjälpmedel under flyttningen. Dessa skillnader är möjligen kopplade till de olika arternas flyttningstrategier.