

Migrating songbirds tested in computer-controlled Emlen funnels use stellar cues for a time-independent compass

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Summary

This paper investigates how young pied flycatchers, *Ficedula hypoleuca*, and blackcaps, *Sylvia atricapilla*, interpret and use celestial cues. In order to record these data, we developed a computer-controlled version of the Emlen funnel, which enabled us to make detailed temporal analyses. First, we showed that the birds use a star compass. Then, we tested the birds under a stationary planetarium sky, which simulated the star pattern of the local sky at 02:35 h for 11 consecutive hours of the night, and compared the birds' directional choices as a function of time with the predictions from five alternative stellar orientation hypotheses. The results supported the

hypothesis suggesting that birds use a time-independent star compass based on learned geometrical star configurations to pinpoint the rotational point of the starry sky (north). In contrast, neither hypotheses suggesting that birds use the stars for establishing their global position and then perform true star navigation nor those suggesting the use of a time-compensated star compass were supported.

Key words: computer-controlled Emlen funnel, star compass, orientation, navigation, *Ficedula hypoleuca*, *Sylvia atricapilla*, bird migration, time dependence.

Introduction

The aim of the present paper was to investigate how pied flycatchers *Ficedula hypoleuca* and blackcaps *Sylvia atricapilla* use and interpret celestial cues. To collect these data, we developed computer-controlled Emlen funnels, which permit temporal analyses of orientation behaviour.

The migratory urge of night-migrating passerines is so strong that they will jump in their migratory direction even when confined to a cage (Kramer, 1949; Emlen and Emlen, 1966; Able and Terrill, 1987; Mouritsen, 1998a; Mouritsen and Larsen, 1998; Nievergelt et al., 1999). This observation led to the invention of the Emlen funnel (Emlen and Emlen, 1966). In the traditional Emlen funnel, ink marks (Emlen and Emlen, 1966) or scratches in typewriter correction paper (Rabøl, 1979) are used to measure the bird's directional choices. Despite the fact that the Emlen funnel has been a very important tool in the study of bird orientation and navigation (for recent reviews, see Helbig, 1991; Wiltschko and Wiltschko, 1996; Mouritsen, 1999), they do have their limitations. These are mainly the subjectivity involved in scoring the scratch marks (but see Mouritsen, 1998c), and the difficulty of recording temporal variations in the orientation behaviour (but see Åkesson and Sandberg, 1994). During 1995–1997 we therefore developed a computer-controlled version of the Emlen funnel, which enables the experimenter to manipulate relevant orientation cues while the orientation reactions of the birds are monitored

continuously without disturbing them, and which allows detailed temporal analyses afterwards. They also provide exact and completely non-subjective calculations of mean direction and concentration, and false positives from the escape reactions when the birds are put into and taken out of the funnels can be avoided, since registration is started and terminated by remote control. With this tool available, we investigated how migrating young pied flycatchers and blackcaps placed under an artificial planetarium sky interpret and use celestial cues.

Sauer (1957) performed the first planetarium experiments suggesting that birds use the stars for orientation. Sauer's data were based on a few experiments with either a single or very few individuals and were, therefore, somewhat anecdotal. The definite proof that birds can use the stars for orientation came in 1967 when Emlen published his classical planetarium experiments on indigo buntings *Passerina cyanea* (Emlen, 1967a,b, 1970, 1972, 1975). Later, it was shown that blackcaps (Viehmann, 1982), savannah sparrows *Passerculus sandwichensis* (Bingman, 1983), pied flycatchers (Bingman, 1984), garden warblers *Sylvia borin* (Wiltschko et al., 1987) and European redstarts *Phoenicurus phoenicurus* (Mouritsen, 1998a) can orient in a non-directional magnetic field, presumably by using directional cues from the stars (only night experiments are considered here, not sunset/twilight

experiments). In conclusion, it seems well established that night-migrating songbirds use the stars for orientation. But, what information do they extract from the starry sky and what is their migratory response? There are, in principle, at least five different ways birds could use celestial cues for migratory orientation. These five hypotheses are:

Hypothesis 1a: True star navigation

This hypothesis implies that birds deduce their true geographical position from the rotational phase of the stars. The height of the rotational point of the stars above the horizon could be a measure of latitude and the rotational phase of the stars combined with a dual time-sense could provide longitude information. They could use this stellar information to orient towards their goal (stop-over site or wintering quarter), travelling along a constant compass course route (a loxodrome course).

Hypothesis 1b

The same as Hypothesis 1a except that the birds orient towards their goal along great circle routes (an orthodrome route – the shortest distance between two points on the globe).

Hypothesis 1c

The same as Hypothesis 1a except that the birds do not orient towards their goal but towards the location where they expected to be at the given time, i.e. in this case, back towards the capture site.

Hypothesis 2: Time-dependent compass orientation

This hypothesis implies that the birds use the stars as part of a time-compensated star compass (similar to the sun compass) (see Schmidt-Koenig et al., 1991; Alerstam et al., 2001) but without being able to establish their geographical position (extract longitude and latitude information) from the rotational phase of the starry sky.

Hypothesis 3: Time-independent compass orientation

According to this hypothesis birds use the stars as a time-independent celestial compass. The birds deduce north from the geometrical configurations of the stars independently of current stellar rotation. For detailed descriptions of hypotheses 2 and 3, see Emlen (1975).

Sauer (Sauer, 1957; Sauer and Sauer, 1960) claimed that his experiments supported a true star navigation hypothesis (Hypothesis 1a–1c). Gwinner and Wiltschko, however, pointed out that his data could equally well be explained as effects of an endogenous circannual clock (Gwinner and Wiltschko, 1978). Emlen's thorough investigations of how indigo buntings use stars for migratory orientation (Emlen, 1967b, 1970, 1972) strongly suggested that indigo buntings do not make use of the rotational phase (also called the hour angle) of the starry sky, neither to identify geographical position (Hypotheses 1a, 1b and 1c) nor as part of a time-compensated star compass (Hypothesis 2) like the sun compass (e.g. Schmidt-Koenig et

al., 1991). Instead, indigo buntings seemed to use only the location of the rotational point to define north. Learned geometrical knowledge of star patterns seemed to be used by the birds to pinpoint the rotational point of the starry sky. Thus, Emlen's studies strongly supported Hypothesis 3. Emlen's conclusions have been widely accepted. However, to our knowledge, his experiments have never been replicated, despite the facts that his sample size was only six birds in the crucial clock-shift experiments and he only tested one species.

Further evidence in favour of a time-independent star compass came when Wiltschko and coworkers hand-raised groups of garden warblers in four different parts of the same room, in which an artificial 'starry sky' of small back-lit holes rotated around the centre of the ceiling (Wiltschko et al., 1987). Each group of birds experienced the centre of rotation to be located at one of four different points of the compass. As adults, when tested in Emlen funnels during the migratory season under the same, but now stationary, artificial sky, the groups oriented in different directions all pointing away from the artificial sky's former centre of rotation (Wiltschko et al., 1987). The fact that the birds were able to orient under a stationary sky as adults strongly suggested that they had learned the geometrical configuration of the 'stars' (back-lit holes) relative to the location of the rotational centre during the pre-migratory period. These results also suggested that the birds are able to locate celestial north without having to observe celestial rotation in the migratory period.

In addition, Able and Able (1990) showed that young savannah sparrows *Passerculus sandwichensis*, raised under an artificial starry sky identical to that used by Wiltschko et al. (1987), calibrate their magnetic compass relative to the artificial sky's centre of rotation when tested with no visual cues available during migration.

Finally, however, using a planetarium, Rabøl subjected pied flycatchers and redstarts to star patterns from different locations on the globe (Rabøl, 1998). His data suggested that the birds corrected for the simulated displacements.

By exploiting the time-resolution of the computer-controlled funnels, it is possible to design a single experiment that distinguishes between the above-mentioned five hypotheses. This was achieved by recording the directional choices of young pied flycatchers and blackcaps tested in Emlen funnels for 11 h of the night while they could observe a stationary planetarium sky. This planetarium sky mimicked the star patterns found locally at 02:35 h (i.e. 7 h into the night). Using this experimental design, as shown in Fig. 1B, the bird's directional choices as a function of time according to the five different star orientation hypotheses outlined above can be predicted.

If Hypothesis 1a is correct, the birds should experience a virtual displacement from Siberia to North America *via* Europe over the course of one night. In Fig. 1A, the mean simulated location during each 1 h period of the night is shown along with the directions the birds are expected to orient in at different times of the night if they can deduce their geographical position from the stars and correct towards a goal on the Iberian Peninsula (black arrows, Fig. 1A). In Fig. 1B, these directions

are converted into expected directional choices as a function of time relative to the average expected direction seen over the entire night. (Note that north corresponds to 0° , east to 90° , south to 180° and west to 270°). In other words, the expected average migration directions for each 1 h period during the night according to Hypothesis 1a are: 257° , 255° , 252° , 249° , 245° , 238° , 227° , 209° , 181° , 153° and 135° , respectively. The average direction expected over the entire night is found by vector addition to be 222° . Consequently, when 222° are subtracted from each expected direction this gives for each hour the following expected deviations from the average migration direction: 35° , 33° , 30° , 27° , 23° , 16° , 5° , -13° , -41° , -69° and -87° . These values are depicted in Fig. 1B as the dashed black curve, i.e. early in the night, the directional choices are expected to be west of the average migration direction (the birds are seemingly displaced to Siberia), while late in the night the hypothesis predicts directional choices to the east of the average migratory direction (the birds are seemingly displaced to North America).

If Hypothesis 1b is correct, the birds should also experience a virtual displacement from Siberia to North America *via* Europe over the course of one night. The only difference from Hypothesis 1a is that they choose the orthodrome (great circle) heading which would lead them to the goal on the Iberian Peninsula. The expected directions from this hypothesis relative to the whole-night average direction are depicted on Fig. 1B as a dash-dotted black curve.

If Hypothesis 1c is correct, the birds should head towards west before 02:35 h and towards east after 02:35 h. This is indicated by the blue arrows in Fig. 1A and the blue curve in Fig. 1B. The reason that the blue curve in Fig. 1B is not symmetrical around 0 is that there are six 1 h periods of testing before 02:35 h and only four 1 h periods after 02:35 h, so that the expected average direction over the entire night should be close to the true direction from Aarhus to the Iberian Peninsula, since the orientation in opposite directions before and after 02:35 h should more or less cancel out. However, it should on average be skewed slightly towards the west due to the longer time of testing before 02:35 h than after 02:35 h. The exact position of the blue curve would move up and down the y-axis depending on the activity shown by any individual bird before and after 02:35 h. The important point, however, is that the orientation of the birds is expected to change by 180° at 02:35 h, i.e. their orientations should be described by a step-function in the heading-by-time diagram (Fig. 1B).

If Hypothesis 2 is correct, the birds should not experience any virtual displacement. However, their orientation is expected to change approximately 15°h^{-1} , if a time-compensated star compass is based on a star or star pattern near the celestial equator. The green line in Fig. 1B indicates this prediction. Stars located in other parts of the sky move at different speeds and they could be used for orientation. However, stars away from the celestial equator are less well suited as reliable orientation cues, since their apparent motion over time seen from the bird's point of view is of a much more irregular nature.

If Hypothesis 3 is correct, the birds should not experience

any virtual displacement. Since celestial rotation is used neither to establish a current geographical position nor for establishing a compass direction, the birds should orient in the same direction during the entire night. The centre of rotation (north) can be found from the geometrical constellations of the stars alone and they, of course, remain stationary throughout the night. The red arrows in Fig. 1A and the red line in Fig. 1B indicate the predictions of Hypothesis 3.

Materials and methods

Computer-controlled Emlen funnels

Traditional Emlen funnels (Emlen and Emlen, 1966) as used by Mouritsen (1998a) were modified during 1995–1997. These Emlen funnels are circular orientation cages with top diameter 300 mm, floor diameter 100 mm, 45° sloping sides, and the top opening covered by a fine-meshed plastic net allowing the birds to see the sky. Instead of covering the walls with typewriter correction paper, 24 infrared emitter/sensors (CNY70 from AEG) were fixed into $7 \text{ mm} \times 7 \text{ mm}$ holes (the sensor/emitter size is $7 \text{ mm} \times 7 \text{ mm}$) in a circle 7 cm from the floor and equally spaced by 15° (see Fig. 2). Positioning the emitter/sensors 7 cm from the floor is a compromise between, on the one hand, reducing the likelihood that the sensors are activated when a small songbird is sitting on the floor and, on the other, increasing the likelihood that the sensors are activated when the bird jumps. The emitters constantly emit infrared light (950 nm) and the sensors measure how much of this emitted light is reflected back. When a bird jumps up and then slides past a sensor it will cause increased reflection of the emitted infrared light and a registration results if the trigger level is set correctly. During the present measurements, a registration was scored if the measured reflection at any sensor exceeded a value 170% of the average of the last 1000 reflection measurements (this limit can be changed manually by the experimenter). By employing such a relative trigger level, the system can withstand changes in the background light intensity. A 100 MHz 486 computer controlled eight funnels simultaneously. The readings from the sensors were programmed as follows. Three sensors were always monitored simultaneously. First, sensors 1, 9 and 17 of funnel 1 were monitored, then sensors 2, 10 and 18 of funnel 1 and so on until sensors 8, 16 and 24 of funnel 1 were monitored, then the same procedure was run for funnel 2, then funnel 3 and so on. When all sensors of funnel 8 had been monitored, the monitoring restarted in funnel 1. Using this particular computer any given sensor was monitored once every 74 ms, giving a monitoring frequency of 13.5 Hz (in other words, a total of 2595 sensor outputs were read per second). This frequency is sufficiently high to record any bird sliding past the sensors.

Since the emitter/sensors are driven by electrical current, it was important to test whether the earth's magnetic field inside the funnels was critically affected when the infrared emitter-sensors were running. We measured the field using a Flux-Gate Magnetometer (Fluxmaster-X, Mayer Messgeräte; absolute accuracy 0.5% relative to the measured value, smallest detectable change approx. 0.01%, resolution 1 nT, where

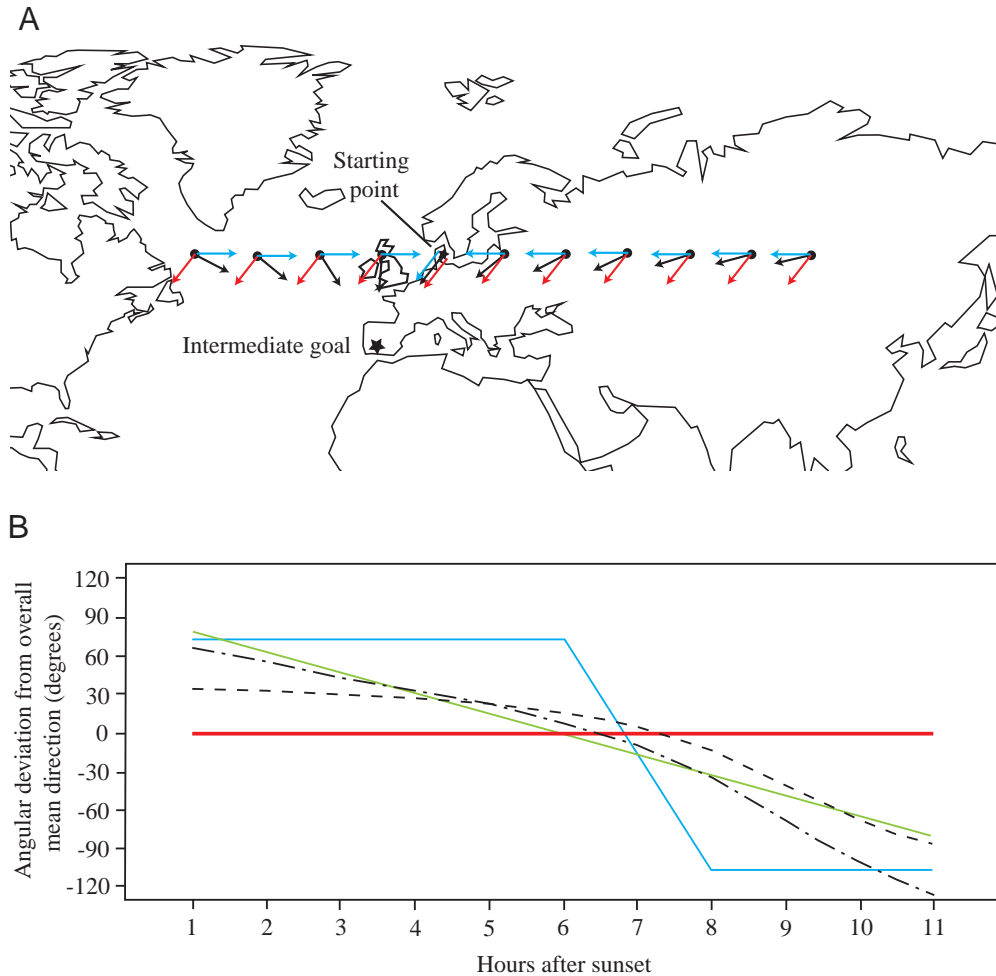


Fig. 1. (A) Map illustrating the apparent displacement that the experimental birds will experience during the night, if they use the rotational phase of the starry sky to determine geographical position. The black arrows (Hypothesis 1a) show the predicted headings for each hour of the night, if the birds (pied flycatchers) compensate for the apparent displacement by orienting towards the intermediate goal in southern Spain along a constant compass course route (loxodrome). The blue arrows (Hypothesis 1c) show the predicted headings, if birds compensate by orienting back towards their true location (the location where the birds must expect to be that night). The red arrows (Hypothesis 3) show the constant orientation in an innate migratory direction expected if birds use the stars for a time-independent compass. (B) The directional choices expected in the computer-controlled funnels as a function of time for each of the five hypotheses (H) outlined in the introduction. H1a, black dashed curve; H1b, black dash-dotted curve; H1c, blue curve; H2, green line; H3, red line. Positive ordinate values indicate directions to the west of the normal migration direction, while negative values indicate directions to the east of it. For further explanation, see text.

nT=nanotesla). The field strength changes in the north–south and east–west directions are smaller than the resolution of the magnetometer, whereas regular fluctuations between 0 and -40 nT were superimposed on the vertical field of approx. $35,000$ nT in Aarhus, Denmark. The maximum change in field strength is thus only 0.1% of the total vertical field strength, and far smaller than the natural daily fluctuations (up to ± 500 nT) in the geomagnetic field. 10 min after measuring the first field strength value, natural variations of the geomagnetic field had changed the vertical field strength more than the 40 nT maximum change imposed by the electronic funnels. In conclusion, it is very unlikely that the minute changes in the magnetic field resulting from the electrical currents running to and from the emitter/sensors had any effect on the migratory behaviour of the birds inside the funnels.

In three test trials with no birds in the eight computer-controlled funnels, three of the funnels produced one false registration each during the whole night, while the remaining 21 funnels had no false positives. This very low false registration rate will not have any measurable effect on the results. Test trials, where the authors observed the birds' migratory restlessness in the funnels, showed that virtually all jumps ($>95\%$) resulted in a corresponding directional recording.

Data collecting and analysing software

A custom-designed computer program written in Turbo Pascal (7.0 for DOS) runs the sensors. When the program is started, it first turns on the sensors and then initiates the multiplexed registration. Whenever a sensor measures an increased reflection exceeding the trigger level, an impulse is

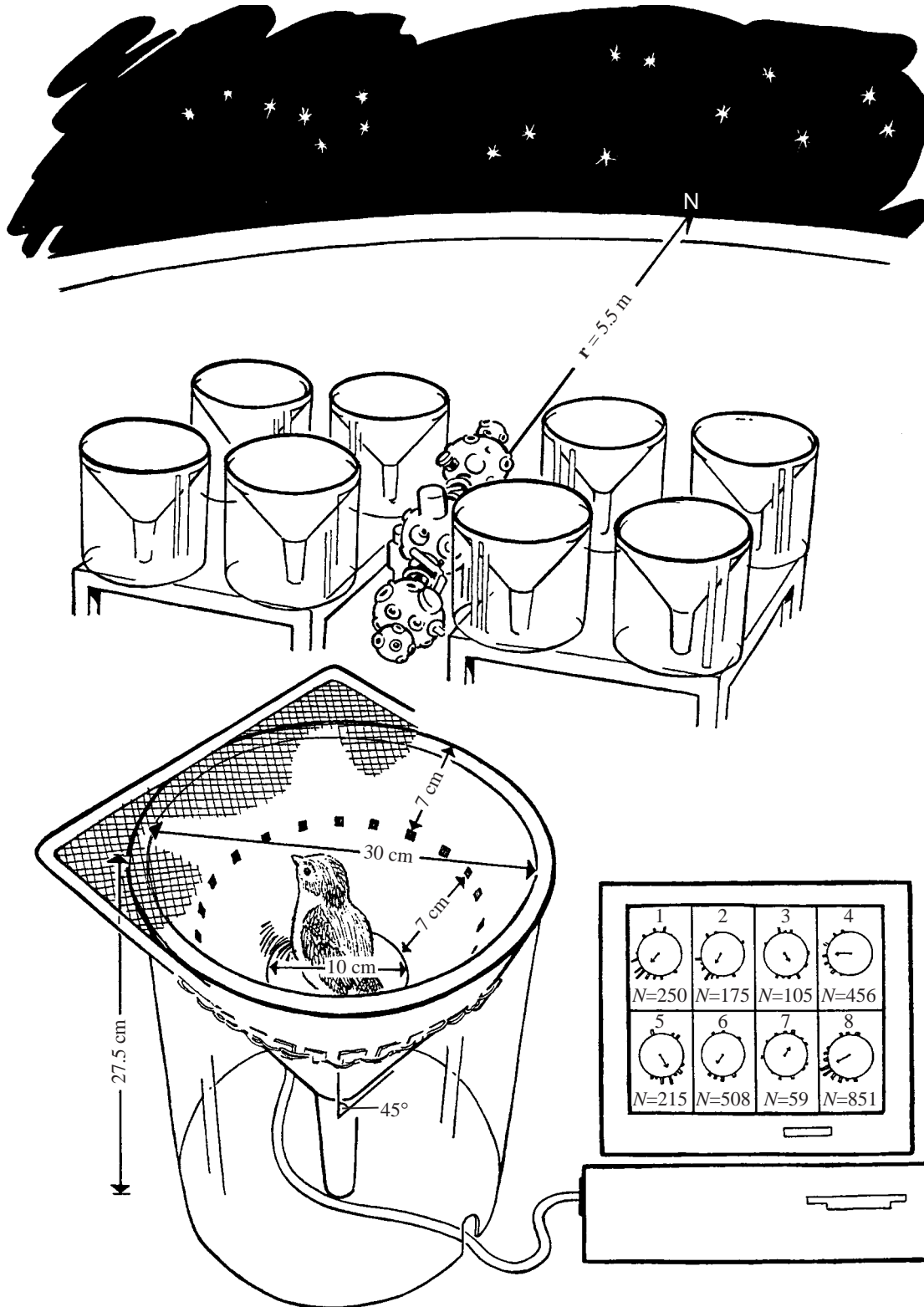


Fig. 2. Sketch of the experimental equipment and set-up in the planetarium.

sent to the computer *via* a simple A/D-converter. The program stores on a RAM-disk the identity of the activated sensor and funnel and the activation time to the nearest second. Also, it calculates the direction and length of the current cumulated

mean vector of the given funnel [i.e. the mean direction and concentration of the given bird's orientation, based on cumulated data up to the present time (Batschelet, 1981)]. During a delay of 500 ms, which helps to avoid double

registrations, the current result is updated on the computer screen. Recording is then resumed. Thus the program automates the recordings completely. If the experimenter is present, however, he can continuously monitor developing results on the screen.

When the results are saved, the program offers multiple analysing tools and possibilities. One can view the raw data, get significance values for the Rayleigh Test, view the results graphically or schematically, view how the mean direction and significance level developed with jump number and, most importantly, analyse any subset of the data separately. Thus, the program enables the experimenter to analyse any particular time interval separately. Only statistical analyses comparing differences in direction or concentration between two different birds or two different time-periods need to be done off-line with separate software.

The orientation experiments

Experimental birds and sites

In 1997, 14 first calendar-year pied flycatchers *Ficedula hypoleuca* were caught in mistnets during autumn migration on 30–31 August at Christiansø Bird Observatory (55°19'N, 15°12'E), Denmark, and 14 first calendar-year blackcaps were caught 13–16 September at Blåvand Bird Observatory (55°34'N, 8°06'E). All birds were subsequently transported to Aarhus (56°09'N, 10°13'E), Denmark, for testing. In 1998, another 20 first-year pied flycatchers and six first-year blackcaps were caught at Blåvand in September and then transported to Aarhus. All birds were kept outdoors in small cages (approx. 35 cm×35 cm×35 cm made of wood and aluminium) in the natural magnetic field with food (mealworms) and water *ad libitum*. As a result, the birds had fat indexes of 4 or higher when used for experiments [the intestine was invisible owing to fat coverage according to the 0–8 scale (Kaiser, 1993)]. Thereby, the reverse orientation often shown by lean birds was avoided (e.g. Sandberg et al., 1988; Åkesson et al., 1996).

In 1997, seven pied flycatchers were tested in the automatic funnels on 21 September and seven blackcaps were tested on 28 September. In 1998, six pied flycatchers were tested on 14 September, six other individuals on 20 September, and the final six individuals on 4 October. On 19 October, six blackcaps were tested. The tests were performed inside the planetarium at the Steno Museum, Aarhus, Denmark. The planetarium dome has a diameter of 11 m and the star projector (Zeiss Skymaster ZKP 3) projects approximately 7000 stars, which is equivalent to those that can be seen by the naked human eye under optimal conditions. Celestial north in the planetarium was identical to true geographical north. The geomagnetic field strength inside the planetarium was slightly weaker than the natural geomagnetic field (5–10% reduced) but the direction and inclination did not differ measurably from those of the natural geomagnetic field (the same Flux-Gate Magnetometer as mentioned above was used). Thus, the directional relationship between celestial and magnetic north was identical to the outdoors situation. All tests were performed in the

unaltered (natural) magnetic field of the planetarium, which simulated the natural local starry sky of Aarhus, Denmark, as it looks at 02:35 h in the morning (local daylight savings time). The 02:35 h setting was chosen because the star projector was completely out of view from all the funnels at this setting.

Test procedure

Approximately 30 min before natural sunset (approx. 19:00 h, depending on the exact date) each experimental bird was transferred from its cage *via* a dark, numbered textile bag to its funnel (see Fig. 2). At local sunset, the star projector was switched on and a program was initiated that simulated the local starry sky at 02:35 h, including the Milky Way. The moon had been turned off and neither sunset nor sunrise was simulated. After a couple of minutes, the recordings of funnel activity commenced, upon which the experimenter left the planetarium swiftly and silently. Between 07:30 h and 10:00 h, the experimenter returned to the planetarium, and the birds were caught and transferred back to their cages.

In 1998, a control experiment was conducted with the same group of 20 pied flycatchers used in the stationary sky experiment. These birds were also tested in the computer-controlled funnels under a planetarium sky simulating the local natural rotating starry sky for the first 5.5 h of the night. In the middle of the night, the star projector was turned off for 18 s and turned 180° horizontally. When the star projector was turned on again celestial north was located in geographical and magnetic south. The birds were tested under this 180°-turned sky for the last 5.5 hours of the night. The stars continued to rotate. Magnetic north was unchanged.

Data analysis and statistics

Most calculations were performed in the specially written control and analysing program described above. Some calculations were done by a custom-written Matlab programme (Matlab version 5.3). For the main stationary sky experiment, the following data analysis procedure was executed. First, the overall mean direction and directional concentration were calculated for each bird (Fig. 3, Fig. 5). Second, the mean directions during each of the night's 1 h periods were calculated for each individual bird. If less than ten jumps occurred or if the mean direction was insignificant according to the Rayleigh Test (Batchelet, 1981) within a given 1 h period, the deviation from the mean direction was excluded from these analyses. Our exclusion rules demanding 'significance' (quotation marks are used because the jumps are unlikely to be independent) and more than 10 jumps were based on analyses of control experiments where no orientation cues were changed. If we split such data into 10-jump intervals, most subsets of data reflect well the total mean direction of a given bird based on hundreds or thousands of jumps, whereas this is not the case for e.g. 5 jump intervals or intervals of any size where the mean direction is insignificant, according to the Rayleigh test. This rule, therefore, ensured exclusion of meaningless orientation results. Furthermore, a bird had to be active during at least five 1 h periods in a given night to be

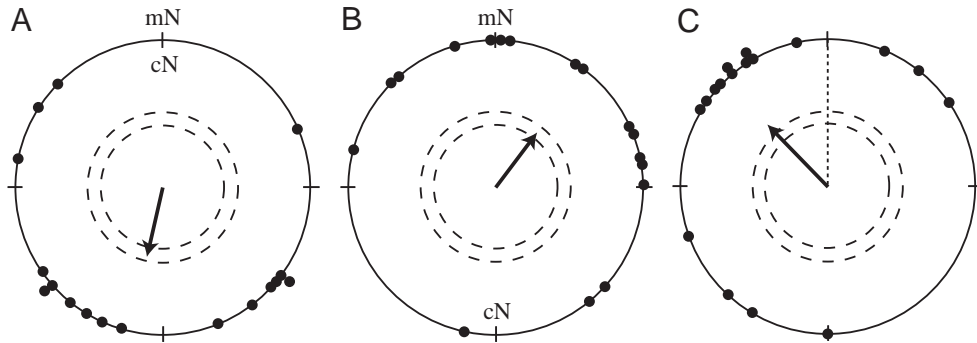


Fig. 3. Orientation of 17 pied flycatchers tested under a rotating planetarium sky, where the stars were turned 180° in the middle of the night. (A) The orientation of the birds before the turn (first 5.5 h of the night). (B) The orientation of the same birds after the celestial cues were turned 180° (last 5.5 h of the night). (C) Comparison on an individual basis of the orientation after the turn relative to the orientation before the turn of the celestial cues. Each individual bird's orientation before the turn is defined as 180° . Thus, a direction of 360° indicates a 180° turn in orientation of the individual bird, equivalent to the turn of the celestial cues. The inner and outer dashed circles indicate the radius of the group mean vector needed for significance ($P < 0.05$ and $P < 0.01$, respectively) according to the Rayleigh Test of uniformity. mN, magnetic north; cN, celestial north.

included in the analyses (i.e. to be included, a bird must have produced at least 10 registrations and the mean direction shown must be significant during at least 5 of the 11 1 h periods of the night). Thirdly, for each individual, the deviations from that individual's own total mean direction over the entire night were calculated for each 1 h period. Fourthly, group mean vectors and 95 % confidence intervals (Batschelet, 1981) for these deviations in each 1 h period were calculated and depicted as a function of time (see Fig. 4, Fig. 6). For all calculations on direction, vector addition and circular statistics were used. For testing how the mean direction chosen by the birds changes over the course of the night, we tested whether the birds' orientation during the different hours of the night

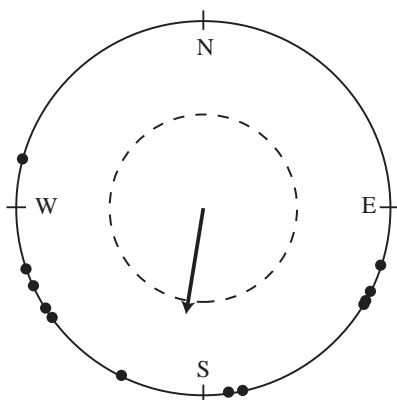


Fig. 4. Whole-night orientation of the 12 pied flycatchers that were tested under a stationary planetarium sky, and whose hourly orientations form the basis for Fig. 5. The birds oriented in a southerly direction, not significantly different from the expected autumn migratory direction. Each dot at the circle periphery indicates the mean orientation of one individual bird. The arrow indicates the group mean vector. The dashed circle indicates the radius of the group mean vector needed for significance ($P < 0.05$) according to the Rayleigh Test of uniformity.

agreed with the predictions from any of the five hypotheses outlined in the introduction.

For the control experiment in 1998, we calculated the mean direction for each individual bird during the first 5.5 h of the night, where celestial north agreed with geographic and magnetic north, and during the last 5.5 h of the night, where celestial north was turned 180° relative to magnetic and geographic north. The direction chosen by each individual after turning celestial north was also compared to the same individual's heading before the turn.

Results

In the experiment where celestial north was turned in the middle of the night, the birds oriented towards SSW ($\alpha = 192^\circ$, $r = 0.47$, $N = 17$, $P < 0.05$, 95 % confidence interval $150\text{--}234^\circ$) during the first half of the night, but towards NE ($\alpha = 37^\circ$, $r = 0.45$, $N = 17$, $P < 0.05$, 95 % confidence interval $350\text{--}84^\circ$) in the last half of the night following the 180° turn of the celestial cues, see Fig. 3A,B. The 95 % confidence intervals do not overlap, so the turn in orientation is statistically significant. Comparing the directions at an individual level before and after the 180° turn of the celestial cues revealed a significant clockwise turn of 136° ($r = 0.56$, $N = 17$, $P < 0.01$, 95 % confidence interval $100\text{--}172^\circ$), see Fig. 3C. Analysed this way, the birds turned slightly less than the expected 180° .

In the stationary sky experiment, 12 pied flycatchers were active and oriented during at least 5 h of the night. These birds showed significant southern orientation ($\alpha = 189^\circ$, $r = 0.53$, $N = 12$, $P < 0.05$) seen over the entire night, as shown in Fig. 4. The mean autumn migratory direction of Scandinavian pied flycatchers found in ringing recoveries is 212° (Mouritsen and Mouritsen, 2000). This direction is included in the 95 % confidence interval ($142\text{--}236^\circ$) (Batschelet, 1981) for the orientation of the experimental birds.

The headings as a function of time for the 12 pied flycatchers

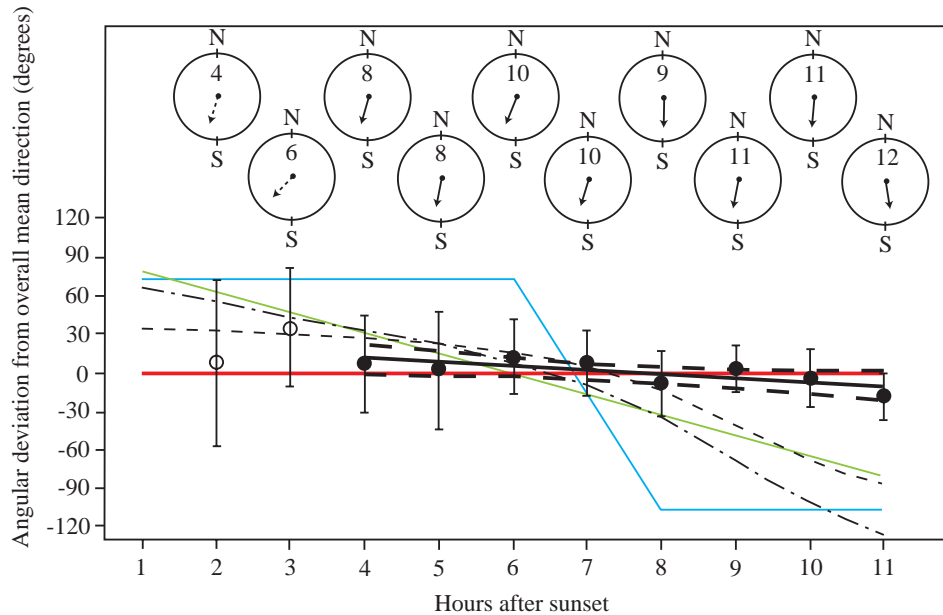


Fig. 5. Orientation of young pied flycatchers tested under a stationary planetarium sky for 11 h. The black dashed (constant compass course routes) and the black dash-dotted (great circle routes) curves represent the predicted orientations, if the birds could deduce geographical (map) information from the stars and corrected for their apparent displacement. The solid blue line represents the predicted orientations, if the birds could deduce geographical (map) information from the stars and corrected back towards the capture site. The solid green line with a -15° slope indicates the predicted orientation of the birds if they use a time-compensated star compass. The horizontal red line represents the predicted orientation of the birds if they use a time-independent star compass. The group's mean headings during each 1 h interval are shown on the circular diagrams at the top. Each diagram corresponds to the point directly below it. The numbers in these diagrams give the number of birds that were active and oriented during each 1 h period. Directly below, the headings are plotted as circles with error bars indicating 95 % confidence intervals for the groups' mean orientation, for easy comparison with the predictions of the different hypotheses. A solid circle indicates that the group-mean-vector was significant. Open circles indicate a non-significant group-mean-vector. The heavy solid black line indicates the best linear regression through the data points and the heavy black dashed line indicates the 95 % confidence interval for the regression. The data suggest that young pied flycatchers use a time-independent star compass, and that they are not able to deduce their geographical position from the rotational phase of the starry sky.

that showed significantly oriented activity in at least 5 1 h periods during the night is shown in Fig. 5. Linear regression of the data points yields the equation:

$$y = 22.8 - 3.0x, \quad (1)$$

where y is the deviation from the overall mean direction and x is the time of night. This is indicated by the heavy solid black line in Fig. 5. The 95 % confidence limits for the regression includes the straight line, $y=0^\circ$, predicted by Hypothesis 3. In contrast, the straight line, $y=(-15^\circ \text{h}^{-1})x+90^\circ$, predicted by Hypothesis 2, is not included by the data. No signs of any step-function as predicted by Hypothesis 1c are found in the data, nor do they follow the predictions of Hypothesis 1a and 1b.

A total of seven blackcaps were active and oriented during at least 5 h of the night under the stationary sky. These birds showed almost-significant southern orientation ($\alpha=168^\circ$, $r=0.614$, $N=7$, $P=0.07$) as shown in Fig. 6. The 95 % confidence interval for the orientation of the experimental birds is $111\text{--}225^\circ$ (Batschelet, 1981).

The headings as a function of time for the seven blackcaps that showed significantly oriented activity in at least 5 1 h

periods during the night is shown in Fig. 7. Linear regression on the data points gives the equation

$$y = -1.6 - 0.3x, \quad (2)$$

and is indicated by the heavy solid black line on Fig. 7. The 95 % confidence limits for the regression include the straight line $y=0^\circ$ predicted by Hypothesis 3. Again, the straight line $y=(-15^\circ \text{h}^{-1})x+90^\circ$ predicted by Hypothesis 2 is not included by the data, nor do they support Hypotheses 1a, 1b or 1c.

Another way to compare the data with the predictions of the five hypotheses is to count how many 95 % confidence intervals of the individual data points (hourly group mean orientations) fail to include the value predicted by each of the five hypotheses. Such an analysis is presented in Table 1. In the case of pied flycatchers, the predictions of a time-independent star compass (Hypothesis 3) are included by the confidence interval for the birds' headings during all hours of the night. For all other hypotheses, at least three data points are significantly different from the predictions. For blackcaps, the confidence intervals of the birds' headings during most hours of the night include the predictions of a time-independent star compass (Hypothesis 3). This is not the case for any of the

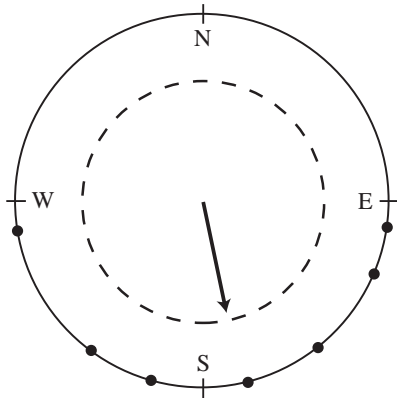


Fig. 6. Whole-night orientation of the seven young blackcaps, tested under a stationary planetarium sky, and whose hourly orientations form the basis for Fig. 7. The birds oriented in a southern direction not significantly different from the expected autumn migratory direction. For an explanation of the figure construction, see legend to Fig. 4.

other hypotheses (at least six points significantly different from predictions).

Discussion

For both pied flycatchers and blackcaps, our data obtained under the stationary sky can best be explained by Hypothesis 3. Birds use the stars as a compass only, and this compass most likely is based on geometrical recognition of star patterns learned during ontogeny, and therefore seems independent of celestial rotation and time later in life.

The pied flycatchers clearly oriented in more or less the normal migratory direction all night, even though the stars were stationary. No clear change in direction towards the end of the night, as would be expected if they had been performing

Table 1. Number of data points for which the 95 % confidence interval of a given data point does NOT include the direction predicted by a given hypothesis

| Hypothesis | Pied flycatchers | Blackcaps |
|------------|------------------|-----------|
| 1a | 3 | 6 |
| 1b | 3 | 8 |
| 1c | 7 | 10 |
| 2 | 3 | 8 |
| 3 | 0 | 2 |

true star navigation, was observed (Hypothesis 1a–c). In other words, they did not seem to perceive any longitudinal displacement during the night. Also, there was no gradual change in orientation consistent with a time-compensated star compass (Hypothesis 2).

The data on the blackcaps are less clearcut, probably because of the relatively low sample size ($N=7$). The data appear to show a turn towards the west in the middle of the night. This appearance is based mainly on one data point (the 7th hour of the night), however, and, in fact, the best linear regression is very close to $y=0^\circ$. A slight easterly turn, as predicted by the true star navigation hypotheses (Hypotheses 1a and 1b), is weakly indicated in the late night (the stars correspond to locations west of the normal migratory route). However, the data from the first half of the night are east of the orientation at midnight as opposed to the more western orientation predicted by the true star-navigation hypotheses (the stars correspond to locations east of the normal migratory route). No evidence of a time-compensated star compass mechanism was observed.

During our experiments, the magnetic field in the planetarium was unaltered and identical to the geomagnetic field with respect to direction and inclination, but the intensity was reduced by 5–10%. Why did we not neutralize the geomagnetic field?

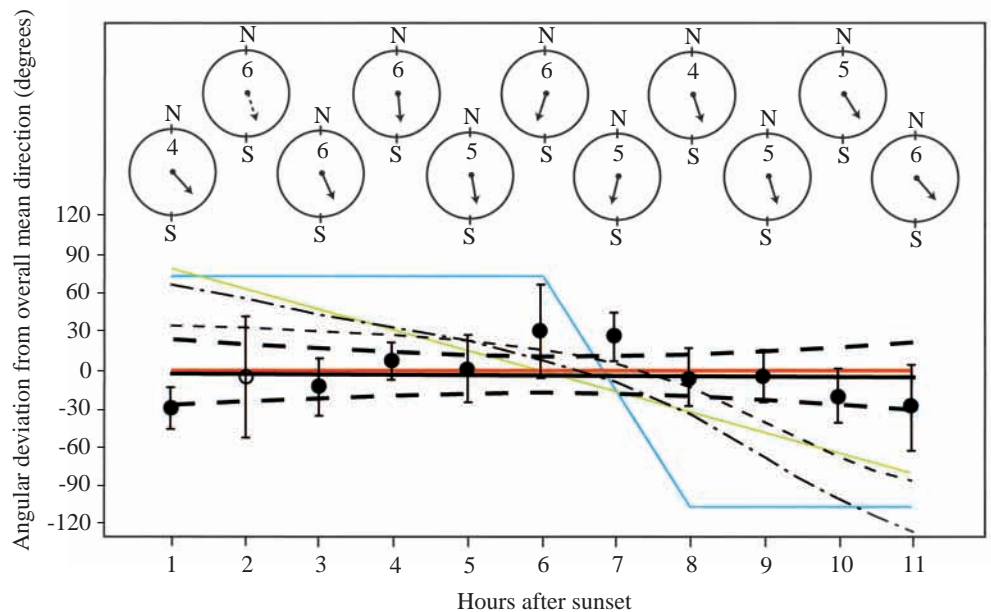


Fig. 7. Orientation of young blackcaps tested under a stationary planetarium sky for 11 h. The data suggest that young blackcaps use a time-independent star compass, and that they are not able to deduce their geographical position from the rotational phase of the starry sky. For an explanation of the figure construction, see legend to Fig. 5.

We did not neutralize the geomagnetic field because its presence provided for the most realistic test of Hypotheses 1a–1c against Hypothesis 3. Under natural conditions, the geomagnetic field is always present and its inclination remains virtually constant at a given latitude (Wiltschko and Wiltschko, 1995a). Thus, in a real displacement identical to our simulated celestial displacement, the geomagnetic field would always be present and its inclination would remain virtually constant, since the displacement occurred along a constant latitude of approx. 55°N. Therefore, we did not neutralize it. If birds are able to deduce their geographical longitude from the rotational phase of the starry sky (Hypotheses 1a–1c), they should be able to do so in the presence of an unchanged magnetic field. Similarly, an unchanged geomagnetic field is the most realistic condition for testing Hypothesis 3. Only if the birds were using a time-compensated star compass (Hypothesis 2) would a cue-conflict situation occur. In that case, the birds' reactions in the parallel experiment where we turned celestial north in the middle of the night (see Fig. 3) suggest that the birds would orient according to their star compass and not to their magnetic compass, since the same group of birds prioritised their celestial compass over their magnetic compass for orientation when tested in a cue-conflict situation.

Celestial compass domination may have been further aided by the fact that we kept the light level in the planetarium low and equivalent to the starlight intensity found in the wild. The low, but realistic, light level could have facilitated star compass orientation, since magnetic compass orientation seems to be light-driven in passerines (Wiltschko et al., 1993; Wiltschko and Wiltschko, 1995b).

In conclusion, our results suggest that pied flycatchers and probably also blackcaps use the stars only as a time-independent celestial compass. This result is in agreement with the data and conclusions of Emlen's studies of indigo buntings (Emlen, 1967a,b, 1970, 1972, 1975) and Wiltschko et al.'s study (Wiltschko et al., 1987) of celestial compass learning in garden warblers. Our results conflict with those of Sauer (1957) and Rabøl (1998), since our birds did not show any directional changes in accordance with those predicted by the simulated stellar displacements. Our results support the theory that young birds on their first autumn migration use a simple clock-and-compass/vector navigation strategy to find their first wintering quarter (Berthold, 1991; Gwinner, 1996; Berthold, 1998; Mouritsen, 1998b, 1998c, 1999; Mouritsen and Larsen, 1998; Mouritsen and Mouritsen, 2000).

Based on our data on pied flycatchers and blackcaps and on the data of Emlen (Emlen, 1967a,b, 1970, 1972, 1975) and Wiltschko et al. (1987) on indigo buntings and garden warblers, it seems clear that some, if not all, night-migrating songbirds are unable to deduce their longitudinal (east–west) geographical position from the stars. Consequently, it is difficult to imagine how a bird could detect its longitudinal position unless it makes use of two clocks, one of which should be very accurately fixed on home-time. It is well known that birds have an internal clock that quickly adapts to local time (e.g. Gwinner, 1996; Gwinner et al., 1997); however, no

evidence of a fixed-time internal clock has been found in any bird species.

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