

MIGRATORY DIRECTIONS OF FREE-FLYING BIRDS *VERSUS* ORIENTATION IN REGISTRATION CAGES

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Summary

Good conditions for migration may promote offshore flights in nocturnal autumn migrants at the northern border of the Mediterranean Sea, whereas unfavourable conditions may induce flights along the coast. These predictions were tested by performing orientation cage experiments and making simultaneous observations of free-flying birds using a tracking radar. The flight directions of free-flying birds were mainly towards southwest and did not differ between overcast and clear sky conditions. The caged birds, however, tended towards southwest under clear sky and showed a more scattered distribution in the southwest and southeast quadrants under overcast conditions. Similar directional scatter occurred when the cage experiments were performed late at night. In contrast, free-flying birds shifted their flight direction towards west as night progressed to avoid flights

across the sea. Flight directions observed by radar shifted slightly towards west as the season progressed owing to more frequent southeasterly winds. In orientation cages, however, directional preference was scattered towards southwest and southeast in the early migratory season and became unimodal (southwest) at the peak of the season; this change was not caused by different species composition. Consequently, there is a general coincidence of flight directions and directional preferences in orientation cages, but interpretations of results from orientation cages must allow for the possibility that experimental directions are different from migratory directions of free-flying birds, particularly under suboptimal migratory conditions.

Key words: bird, migration, orientation, orientation cage, radar.

Introduction

The flight direction of a bird during migration is genetically fixed and modified by both physiological and environmental factors (Gwinner and Wiltschko, 1978; Moore, 1984; Berthold, 1986; Åkesson, 1993; Alerstam, 1997; Bruderer and Liechti, 1998). In registration cages such as Emlen funnels, birds mainly show an endogenous directional preference (Gwinner and Wiltschko, 1978; Helbig and Wiltschko, 1987; Helbig et al., 1989; Bletz et al., 1996). This direction is influenced by physiological factors, such as energy reserves (Sandberg, 1991, 1994; Åkesson, 1993; Ehnbohm et al., 1993; Sandberg and Moore, 1996) and motivation (Rabøl, 1985), and by environmental factors, such as humidity, light conditions and cloud cover (Sauer, 1957; Sauer and Sauer, 1960; Emlen, 1980). A free-flying bird is additionally affected by wind and topography, which can have a strong influence on flight activity, direction and altitude (Richardson, 1978; Gauthreaux, 1991; Liechti, 1993; Liechti and Bruderer, 1995; Bruderer and Liechti, 1998). In nocturnally migrating passerines, good conditions for migration should favour offshore flights at the northern border of the Mediterranean during autumn migration. Flights along the coastline are expected to occur more frequently during unfavourable environmental or physiological conditions, such as overcast sky or low fuel reserves. To

determine the migration direction of a bird, researchers often use registration cage experiments (Emlen and Emlen, 1966). Despite the popularity of registration cages, comparisons between directional preferences in registration cages and the actual flight directions of free-flying birds observed by radar have, as far as we know, never been made. In this study, we investigated the influence of weather, time and season on the directional preference of nocturnally migrating songbirds in Emlen funnels and compared these directions with radar observations.

Materials and methods

Birds were tested in orientation cages, so-called Emlen funnels (Emlen and Emlen, 1966), and radar observations took place at the southern coast of Spain (25 km east of Malaga) from 11 August until 24 October 1996. All individuals were tested during the first hour after sunset (evening tests), and approximately half of them (234) were tested again during the last dark hour of the night (late night tests, 05:00–06:00 h). The experimental birds were caught in mist nets in a resting habitat 2–14 h before the experiments. We investigated 18 nocturnally migrating passerine species comprising 476 individual birds

(260 reed warblers *Acrocephalus scirpaceus*, 50 willow warblers *Phylloscopus trochilus*, 43 garden warblers *Sylvia borin*, 22 blackcaps *S. atricapilla*, 16 nightingales *Luscinia megarhynchos*, 12 melodious warblers *Hippolais polyglotta*, 11 robins *Erithacus rubecula*, 11 pied flycatchers *Ficedula hypoleuca* and 51 various small thrushes and warblers). Bird activity was recorded as claw marks on typewriter correction paper (Tipp-ex) attached to the sloping walls of funnel cages (Åkesson, 1993). After the experiments, the paper was divided into 24 sectors, and the scratches in each 15° sector were counted. The direction of individual birds (experimental direction) was calculated using vector addition. Inactive individuals (less than 40 scratches) and disoriented individuals (in which the individual mean direction did not reach the arbitrarily chosen 5% limit according to the Rayleigh test; Batschelet, 1981) were excluded from further analysis. As a measurement of the concentration of scratches, we used the length of the mean vector (\mathbf{r}) divided by the expected value of \mathbf{r}_E , which corrects for the autocorrelation between \mathbf{r} and the number of scratches (n). \mathbf{r}_E is calculated according to the regression line of \mathbf{r} on the logarithm of n ($\mathbf{r}_E = -0.1691 \log n + 0.8215$, $r^2 = 0.124$, $P < 0.001$, Pearson correlation coefficient). The mean direction and the length of the mean vector for samples of birds were calculated by vector addition. To test whether the directions of a sample differ significantly from randomness, the Rayleigh test was used. Since no species-specific differences in orientation behaviour were found ($P > 0.05$, Mardia–Watson–Wheeler multivariate test), we pooled the data for the analysis.

In parallel with the funnel experiments, we recorded 250–300 tracks of free-flying nocturnal migrants each night using tracking radar (for technical details, see Bruderer, 1997). The headings of the birds were calculated by subtracting the wind vector from the flight vector. Wind profiles were collected every 4 h by tracking a pilot balloon up to an altitude of 4 km. For this study, tracks of small passerines were selected, limiting the sample to birds with intermittent wingbeat pattern and a wingbeat frequency of no less than 12 Hz. For comparison with the funnel data, we selected radar tracks between 20:30 and 22:00 h and from 05:00 to 06:00 h. Because of the small number of tracks of small passerines under overcast conditions in the evening, we selected for this specific case tracks of all species except those of swifts.

To compare different samples, we first used the nonparametric Mardia–Watson–Wheeler test (Batschelet, 1981). When there were significant differences, we used the following tests to decide whether the difference was in mean direction or in concentration: the nonparametric test for dispersion (Batschelet, 1981, p. 124) testing for significance by calculating the z -value according to Siegel (1985) and, for uniformly distributed samples only, the parametric Watson–Williams test (Batschelet, 1981) to compare mean directions. Unfortunately, high scatter prevents the use of parametric tests based on von Mises distributions to test for differences in the mean alone (Batschelet, 1981) and for bimodal distributions (Fisher, 1993).

Half the Emlen funnel experiments were performed under simulated overcast conditions, whereas the other birds were able to see approximately 160° of the open sky limited by the artificial horizon of the screen of the Emlen funnel. The results of experiments performed under natural overcast (7/8–8/8 cloud cover) and simulated overcast conditions were not significantly different ($P > 0.05$, Mardia–Watson–Wheeler test) and were therefore pooled.

Results

The preferred directions in the Emlen funnels are more scattered than the directions of the tracks and headings of free-flying birds observed by radar ($P < 0.001$ for each corresponding pair of samples, nonparametric test for dispersion). The high scatter in experimental direction in most samples, linked with the tendency to bimodality, does not allow a statistical comparison of the mean directions between experimental and free-flying birds using the tools commonly available (Batschelet, 1981).

Evening tests under clear sky conditions

In open Emlen funnels under clear sky conditions, the experimental birds preferred directions in the westsouthwest sector during the first hour after sunset (Fig. 1A). This direction did not change when individuals with low concentrations of registrations ($\mathbf{r}/\mathbf{r}_E < 1$) were excluded, although the scatter in the southeast sector was reduced. Flight directions of free-flying small passerines on clear nights at the same time were directed significantly ($P < 0.001$, Watson–Williams test) more to the south (Fig. 1B). The headings were oriented significantly ($P < 0.001$, Watson–Williams test) more to the west than the flight directions due to prevailing winds from the west. The mean experimental direction did not differ from the headings measured using radar ($P = 0.51$, Watson–Williams test). In each pair of samples, the scatter of directions differed significantly ($P < 0.001$, nonparametric test for dispersion).

Evening tests under naturally or simulated overcast conditions

Under natural or simulated overcast conditions, experimental directions and flight directions were more scattered than under clear sky conditions ($P = 0.012$ and $P < 0.001$ respectively, nonparametric test for dispersion), whereas the headings were not ($P > 0.05$, nonparametric test for dispersion, Fig. 2A,B). The experimental directions showed a distribution with directional preferences for westsouthwest and southsoutheast. A χ^2 -test of the numbers of scratches in each of the four quadrants (1–90°, 91–180°, 181–270° and 271–360°) demonstrated a significant difference between clear and overcast conditions for the proportions between the southwest and southeast quadrants ($\chi^2 = 6.22$, $P < 0.05$), but not between the northwest and northeast quadrants ($\chi^2 = 0.38$, $P > 0.5$). If poorly concentrated individuals were excluded, the directional distribution

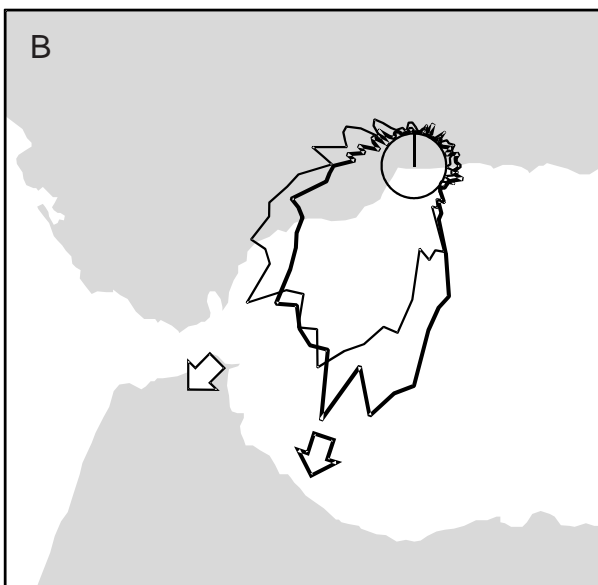
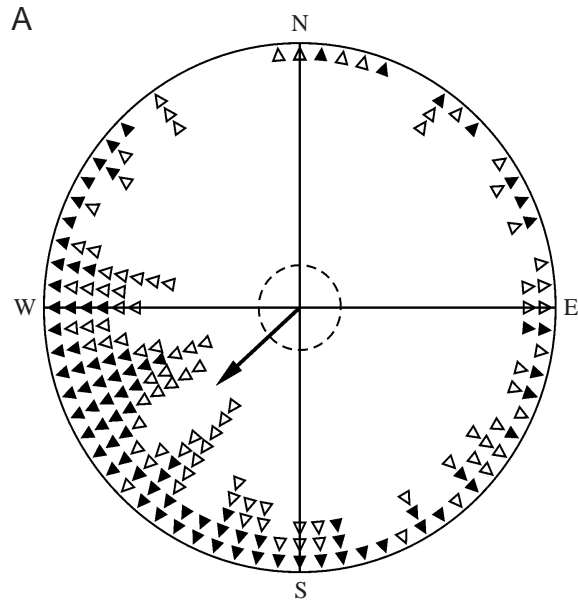


Fig. 1. (A) Preferred directions of songbirds in Emlen funnel experiments under clear sky in the first hour after sunset (mean direction 228° , $r=0.44$, $N=179$, $P<0.001$; Rayleigh test). Open triangles, individuals with $r/r_E<1$; filled triangles, individuals with $r/r_E>1$; arrow, mean vector; inner circle, 1% significance limit of mean vector (Rayleigh test). (B) Headings (thin outline, mean direction 225° , $r=0.73$, $P<0.001$; Rayleigh test) and flight directions (bold outline, mean direction 208° , $r=0.79$, $P<0.001$; Rayleigh test) of small songbirds observed using radar on clear nights between 20:30 and 22:00 h ($N=722$). Vertical line indicates north.

appeared to be bimodal, with preferences for southwest and east-southeast (Fig. 2A).

Headings and flight directions did not differ significantly from each other under overcast conditions ($P>0.05$, Mardia-Watson-Wheeler).

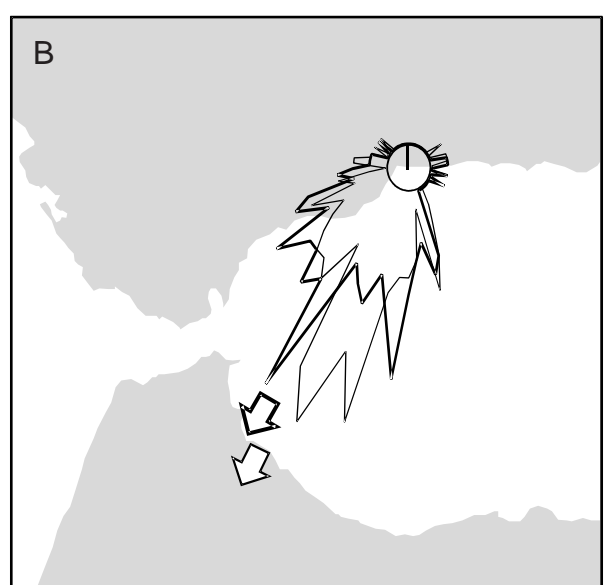
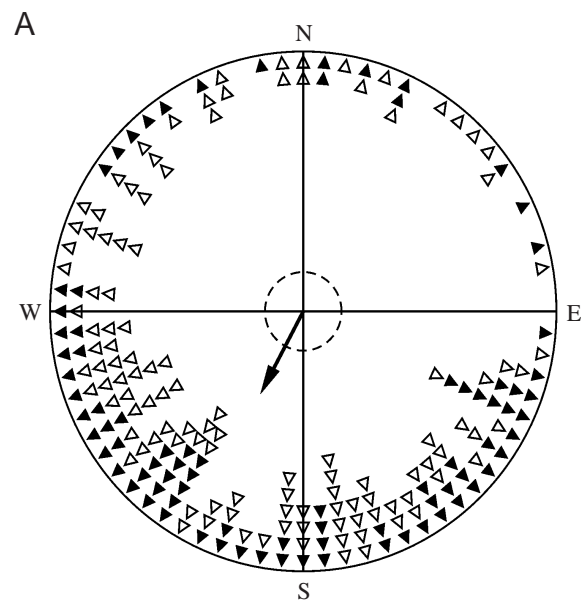


Fig. 2. (A) Preferred directions of songbirds in Emlen funnel experiments under natural or simulated overcast conditions in the first hour after sunset (mean direction 208° , $r=0.36$, $N=202$, $P<0.001$; Rayleigh test). Open triangles, individuals with $r/r_E<1$; filled triangles, individuals with $r/r_E>1$; arrow, mean vector; inner circle, 1% significance limit of mean vector (Rayleigh test). (B) Headings (thin outline, mean direction 207° , $r=0.8$, $P<0.001$; Rayleigh test) and flight directions (bold outline, mean direction 211° , $r=0.8$, $P<0.001$; Rayleigh test) of nocturnal migrants observed using radar on overcast nights between 20:30 and 22:00 h ($N=142$). Vertical line indicates north.

Late-night tests

In the late-night experiments, only 41% of the birds were active. No differences were found between clear and overcast conditions, and the data were therefore pooled. The mean

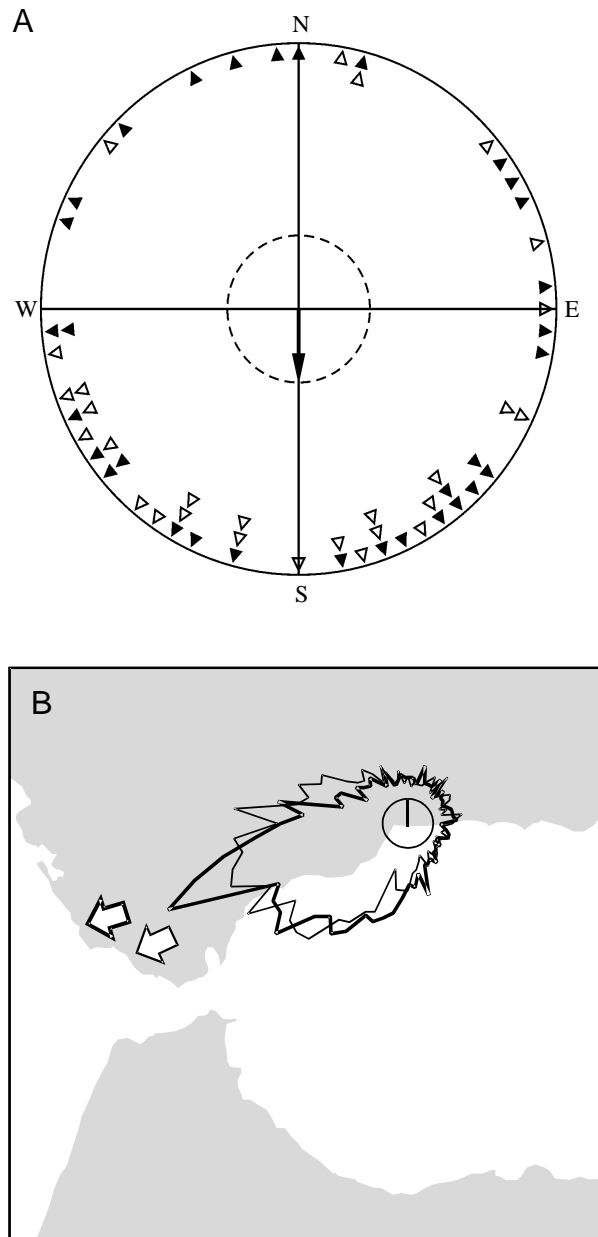


Fig. 3. (A) Preferred directions of songbirds in Emlen funnel experiments during the late night period (05:00–06:00 h) (mean direction 180° , $r=0.28$, $N=60$, $P<0.01$; Rayleigh test). Open triangles, individuals with $r/r_E<1$; filled triangles, individuals with $r/r_E>1$; arrow, mean vector; inner circle, 1% significance limit of mean vector (Rayleigh test). (B) Headings (thin outline, mean direction 253° , $r=0.62$, $P<0.001$; Rayleigh test) and flight direction (bold outline, mean direction 245° , $r=0.62$, $P<0.001$; Rayleigh test) of small songbirds observed using radar between 05:00 and 06:00 h ($N=859$). Vertical line indicates north.

experimental direction was directed towards south (Fig. 3A); however, this direction was the result of wide scatter mainly to the southwest and southeast. The majority of free-flying birds headed towards westsouthwest (Fig. 3B). Flight direction and heading did not differ from each other ($P>0.05$,

Mardia–Watson–Wheeler test), but were significantly different from the corresponding direction in the evening ($P<0.001$, Watson–Williams test). Free-flying birds shifted their flight direction significantly clockwise towards west during the night (compare Figs 2B and 3B), whereas the mean vector of the preferred directions in the registration cage shifted anticlockwise in the late night compared with the evening experiments (compare Figs 2A and 3A, $P<0.08$, Mardia–Watson–Wheeler test), because more birds headed southeast or east.

Seasonal variation

There was a significant difference in the distribution of experimental evening directions in the early season (12 August to 9 September) compared with later in the season (10 September to 24 October) ($P<0.05$, Mardia–Watson–Wheeler test; Figs 4A, 5A). The mean experimental evening direction in the early season was 202° ($N=162$, $r=0.39$, $P<0.001$, Rayleigh test) resulting from a bimodal distribution, with the two modal directions towards southwest and southeast (Fig. 4A). Late in the season, the distribution was unimodal in a southwesterly direction (230° , $N=219$, $r=0.41$, $P<0.001$, Rayleigh test, Fig. 5A). The proportion of short-distance migrants in the early season sample was 6%, whereas in the high migration season sample it was 20%. However, long- and short-distance migrants did not differ in their directional distributions (Mardia–Watson–Wheeler test, $P>0.2$).

There was no significant difference in flight direction between early and late season during the sunset hours ($P=0.09$, Watson–Williams test), whereas headings were directed significantly more to the south early in the season than late in the season ($P<0.001$, Watson–Williams test, Figs 4B, 5B). This clockwise shift in heading as the season progressed was caused by the birds compensating for westerly winds prevailing later in the season. In contrast to free-flying migrants, birds in the Emlen funnels did not react to the actual wind direction. Moreover, we found no influence of the wind direction during the night preceding the experiment on the directional preference in the Emlen funnel.

Discussion

The directional scatter of the birds in Emlen funnel experiments was considerably higher than that of radar-tracked birds in spite of a broader variation in the species composition of free-flying birds. There could be two reasons for the experimental direction to be scattered. First, the unnatural situation of the caged birds provokes scattering in directional behaviour; second, the precision of the method itself is no more than $\pm 12^\circ$ (90% confidence interval; Nievergelt and Liechti, 1999). Studies using Emlen funnel experiments have always produced similar high levels of scatter (Helbig et al., 1989; Åkesson, 1994; Åkesson and Sandberg, 1994; Sandberg and Moore, 1996; 95% confidence intervals obtained by using Table 5.2.1 in Batschelet 1981). The most highly concentrated sample had a 95% confidence interval of $\pm 9^\circ$ in Åkesson and Sandberg's study (1994).

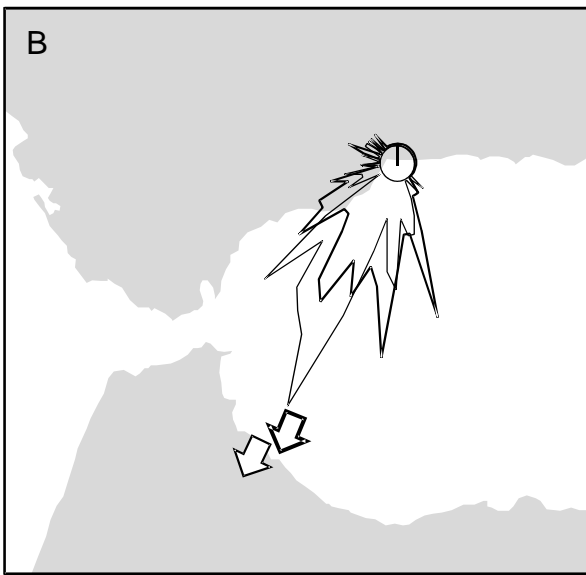
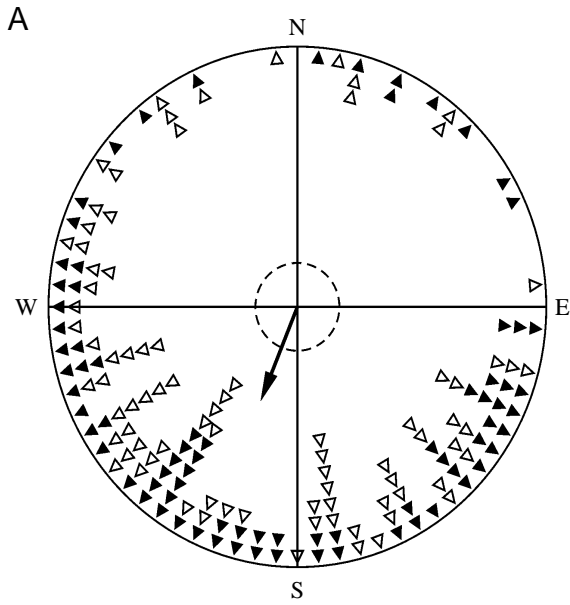


Fig. 4. (A) Preferred directions of songbirds in Emlen funnels during the early season, 12 August to 9 September 1996 (mean direction 202° , $r=0.39$, $N=162$, $P<0.001$; Rayleigh test). Open triangles, individuals with $r/r_E<1$; filled triangles, individuals with $r/r_E>1$; arrow, mean vector; inner circle, 1% significance limit of mean vector (Rayleigh test). (B) Headings (thin outline, mean direction 206° , $r=0.87$, $P<0.001$; Rayleigh test) and flight direction (bold outline, mean direction 202° , $r=0.85$, $P<0.001$; Rayleigh test) of small songbirds observed using radar between 20:30 and 22:00 h in the early season ($N=108$). Vertical line indicates north.

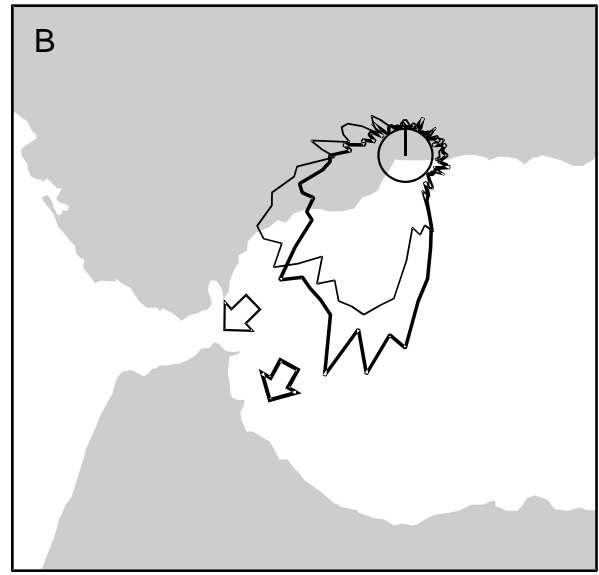
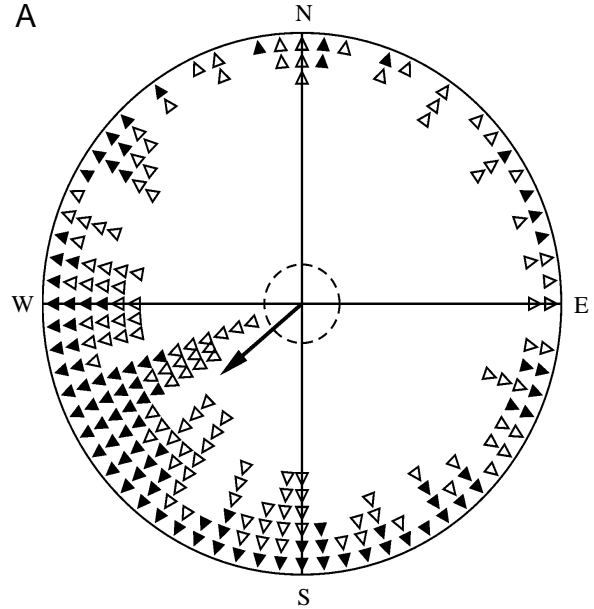


Fig. 5. (A) Preferred directions of songbirds in Emlen funnels during the late season, 10 September to 24 October 1996 (mean direction 230° , $r=0.41$, $N=219$, $P<0.001$; Rayleigh test). Open triangles, individuals with $r/r_E<1$; filled triangles, individuals with $r/r_E>1$; arrow, mean vector; inner circle, 1% significance limit of mean vector (Rayleigh test). (B) Headings (thin outline, mean direction 226° , $r=0.72$, $P<0.001$; Rayleigh test) and flight direction (bold outline, mean direction 209° , $r=0.79$, $P<0.001$; Rayleigh test) of small songbirds observed using radar between 20:30 and 22:00 h in the late season ($N=680$). Vertical line indicates north.

The distribution of the experimental directions is strikingly scattered in particular situations, such as natural or simulated overcast conditions, late at night and early in the season (Figs 2A, 3A, 4A). Age did not affect directional preference, whereas bimodality decreased with increasing pectoral muscle mass, but not with fat class (F. Nievergelt, F. Liechti and B.

Bruderer, unpublished data). The scattered orientation in Emlen funnels under natural or simulated overcast indicates the importance of visual cues for orientation. This is supported by the lower directional concentration of individuals tested under overcast conditions. More scattered directional preferences in orientation cages under overcast than under clear sky

conditions has also been found in robins *Erithacus rubecula* (Sandberg et al., 1988; Ehnbohm et al., 1993) and in other nocturnally migrating passerines (Evans, 1968; Sandberg et al., 1991; Rabøl, 1993; Åkesson, 1993, 1994).

Towards the end of the night, free-flying birds shifted their flight direction westward along the coast. Simultaneously, their flight altitude decreased (Bruderer and Liechti, 1998). This decreasing tendency to cross the open sea in the second half of the night may indicate decreasing motivation to cross ecological barriers towards the end of the night. Low motivation during the second half of the night expressed by low activity in Emlen funnel experiments has also been demonstrated by Åkesson and Sandberg (1994). In contrast to the radar observations, the directional preference in Emlen funnels became more scattered late at night.

The tendency for bimodality occurred during the early season, whereas later in the season the majority was uniformly scattered around westsouthwest (Figs 4A, 5A). Since the migration season on the Iberian Peninsula continues until November (Hilgerloh, 1985), we consider the second part of our observation period as 'peak migration season', whereas the first part of the observation period is considered as 'early migration season'. In August, we may have tested birds that were not yet fully motivated to migrate. This assumption is supported by the lower ratio of active birds among the early season sample (73 %) compared with the peak season sample (83 % active individuals). Therefore, low average migration motivation in the early season may have caused the scattered orientation in Emlen funnels. Directional preferences in registration cages deviating 90° from the expected migratory direction occur often and were emphasised by Rabøl (1993, 1994, 1995). He assumed that these directions were integrated components of the orientation system, the so-called 'cross-axis system'. The southeast preference could therefore be an alternative endogenously determined component of the migratory direction, which is not expressed by free-flying birds over the southern coast of Spain, but is shown by caged birds in response to the experimental situation. The southeast preference never exceeded 50 % of the birds from one sample, and we were unable to find any variable that separated the southeast- from the southwest-preferring individuals. In the bimodal samples, the birds appeared to prefer randomly either southeast or southwest (Figs 2A, 3A, 4A). Therefore, the southeast direction might not be an alternative direction of migration, but an error in the orientation system occurring in somehow disturbed situations. Thus, the southeast preference would not have a biological function (for an explanation, see below), but may provide important indications about the mechanism of the orientation system. For example, it is known that birds perceive the angle of inclination of the Earth's magnetic field, but it is still not known how they do this (Wiltschko and Wiltschko, 1999). A reflection of the migratory direction relative to the north-south axis changes the angle of projection of the inclination from pointing towards right to pointing towards left, whereas the size of angle remains constant. A shift in flight direction from southwest to southeast

could then be caused only by confusing left from right. Our data do not allow a decision between the two alternatives, the cross-axis system suggested by Rabøl (1993, 1994, 1995) and our idea of an orientation error. Situations in which a 90° shift in migratory direction may be meaningful under natural conditions are described by Buurma (1987), who suggested that many Scandinavian migrants possess an innate mechanism allowing them to alternate between two directional preferences differing by 90°. One of the earliest examples of such directional shifts was for Scandinavian thrushes shifting direction when over the North Sea at dawn (Myres, 1964). Alerstam (1975) showed that redwings *Turdus iliacus* may leave southern Sweden towards the southeast or southwest according to prevailing winds, but not in a southerly direction.

We have shown that, under several conditions, directional preferences in Emlen funnel experiments do not correspond to those observed in free-flying birds. These differences occur mainly when the experimental birds are in low motivational states and/or when orientational cues are restricted.

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