Nocturnal migratory flight initiation in reed warblers *Acrocephalus scirpaceus*: effect of wind on orientation and timing of migration

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We used radio-telemetry to study autumn migratory flight initiation and orientation in relation to wind and air pressure in a nocturnal passerine migrant, the reed warbler *Acrocephalus scirpaceus* at Falsterbo, southwest Sweden. The majority of the reed warblers departed in the expected migratory direction towards south of southwest, while a low number of the birds took off in reverse directions between north and east. Flight directions at departure correlated with wind directions. These correlations were particularly prominent at higher wind speeds but were absent at wind speeds below 4 m/s. Birds departing in the expected migratory direction compensated completely for wind drift. The reed warblers preferred to depart during nights with tailwinds and when air pressure was increasing suggesting that reed warblers are sensitive to winds and air pressure and select favourable wind conditions for their migratory flights. Since air pressure as well as velocity and direction of the wind are correlated with the passage of cyclones, a combination of these weather variables is presumably important for the birds' decision to migrate and should therefore be considered in optimal migration models.

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A large proportion of migratory songbirds migrates at night, and there might be several reasons why this migratory strategy is favourable (Alerstam 1990). For instance, birds can maximize their speed of migration by foraging in daylight and migrating at night (cf. Alerstam and Lindström 1990). Nocturnal passerine migrants mainly initiate migratory flights during the evening twilight period or shortly thereafter, with the peak departure intensity occurring 1–4 hours after local sunset (Moore 1987, Åkesson et al. 1996a, see also Bolshakov and Bulyuk 1999, Zehnder et al. 2001). However, radio-telemetry studies have shown that individual migrants may depart even in the middle of the night (Cochran et al. 1967, Åkesson et al. 1996a, 2001). The timing of nocturnal migratory flight initiation seems to vary between species, but perhaps also with latitude and time of year, and might be related to the availability of different celestial cues at dusk (Åkesson et al. 1996a, 2001, cf. Emlen 1980), and of weather conditions (Åkesson and Hedenström 2000).

It is well known that migratory birds are strongly influenced by passage of weather fronts and in particular by wind (e.g. Lack 1960, Able 1974, Alerstam 1978, 1979a, b, Richardson 1978, 1990, Zehnder et al. 2001), resulting in low migratory intensities during unfavourable weather with overcast conditions and headwinds. However, some studies have reported no or only minor effects of weather factors on the timing of migration in nocturnal passerine migrants in spring (Gauthreaux 1971, Hebrard 1971, Cochran 1987). One possible explanation is that birds are more likely to be under time pressure to reach their goal in spring and therefore be more prone to take greater risks and use more energy for flight to minimize the overall time spent on migration compared with in autumn (time-minimized migration, Alerstam and Lindström 1990). This strategy would result in flight departures under less favourable wind conditions. In autumn, individual birds have been shown to depart on migration mainly in tailwind conditions (Åkesson and Heden-

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ström 2000, but see Fransson 1998). Optimal migration theory predicts that birds should be sensitive to wind conditions when about to depart on migration (Liechti and Bruderer 1998, Weber et al. 1998, Weber and Hedenström 2000). By selecting to initiate migration in tailwind they will increase the flight distance covered by a given amount of fuel.

To investigate if a nocturnal long-distance passerine migrant, the reed warbler *Acrocephalus scirpaceus*, is sensitive to wind conditions, we used radio-telemetry to study departure times and initial migratory directions selected by individual birds. We expected birds to depart in tailwind conditions but to stay in the stopover area during periods with opposing winds. We also studied the effect of air pressure on the decision to migrate and expected migrants to depart with raising air pressure, a weather situation that is correlated with tailwind conditions at this site in autumn.

Methods

Study species

The reed warbler winters in tropical West Africa (Moreau 1972, Zink 1973) and migrates at night towards S and SW in autumn (cf. Roos 1984, Åkesson et al. 1996b). Every autumn approximately 2000 reed warblers are captured at Falsterbo Bird Observatory (55°23′N, 12°50′E). A few of these reed warblers engage in temporary reverse movements before resuming migration in the normal direction (Åkesson et al. 1996b). We captured reed warblers at one of the standard ringing sites, Flommen, a coastal reedbed area, located at the south-westernmost part of the Falsterbo peninsula in southwest Sweden. The birds were captured in the early morning hours from mid-August to the end of September in 1995–1998. At capture the birds were aged (Karlsson et al. 1988, Svensson 1992) and the amount of visible subcutaneous fat was estimated according to a 10-graded scale for visual fat classification (cf. Pettersson and Hasselquist 1985, extended with 3 grades at Falsterbo Bird Observatory). All reed warblers were first year-birds (1y), except two individuals, which were in their second (2y) and at least forth calendar year (4y +), respectively. The bird's mass was measured to the nearest 0.1 g with a 50-g Pesola spring balance. To increase the probability that the birds would depart on migration we only used individuals with fat scores 5 and above (mean = 7.5).

Radio-telemetry and study site

We used small radio-transmitters (0.67 g; BD-2B, Holohil Systems Ltd.) glued on the back feathers of the birds to track each individual's departure direction and time of migratory flight initiation (details on attachment method are given in Åkesson et al. 2001). The mean mass of the radio-transmitter was 4.6% of the bird's mass (range: 3.9–5.4%, N = 38). The reed warblers were released in the area of capture immediately after the radio-transmitters were attached (<1 hour in captivity). We located the birds on several occasions during the day at the stopover site by using hand-held receivers, allowing the signals from a transmitter to be registered from anywhere in the reeds. The birds were very stationary during their stay in the stopover area and moved within a very restricted area of the reedbed, suggesting that presumably many of the birds captured were newly arrived. We therefore feel confident that we relocated any bird if present. After capture we tracked birds between 1 (departure the same day as the transmitter was applied) and 7 days before they departed. From well before sunset we tracked the birds' movements continuously until they departed or for at least 4 (1995) or 8 hours (1996–1998) after local sunset. We established the exact time of departure for 29 individuals and for 27 of these birds we also recorded their take-off direction. Details on the telemetry method are given in Åkesson et al. (2001). For an additional six individuals we know to within 4–7.5 hours when they left the stopover area and presumably initiated migration. In total we tracked 7 reed warblers in 1995, 8 in 1996, 17 in 1997, and 3 in 1998.

Weather observations

We used weather observations recorded every third hour (Swedish Normal Time, UTC + 1 h: 19.00, 22.00, 01.00 and 04.00 hours) at the local weather station at Falsterbo situated c. 1 km south of the reedbeds. From these we extracted data on wind direction and velocity (m/s) at 12 m above the ground (Swedish Meterological and Hydrological Institute, SMHI standard wind measure). The wind direction is given as the direction towards which the wind is blowing (i.e. opposite to the standard way of labelling wind direction). We also analysed if air pressure (hPa) influenced the time of flight departure. Cloud cover and precipitation have an effect on the timing of migratory flight departure (Åkesson et al. 2001).

Data reduction and statistical methods

The mean angle of orientation was calculated according to Batschelet (1981). Mean angle of orientation (α) is indicated by an arrow the length of which is a measure of the scatter of the circular distribution, (r; ranges between 0 and 1, being inversely related to the angular scatter). The Rayleigh test was applied to test if the

circular distribution differed significantly from random (Batschelet 1981). Difference in scatter (indicated by t) or mean orientation (F_1) between groups was analysed with Mardia's "test for homogeneity of concentration parameters" and "one-way classification test", respectively (Mardia 1972). For non-significant unimodal groups we used the Watson's U^2-test to analyse differences in orientation between groups (Batschelet 1981).

To study the effect of wind on the birds' orientation we used circular correlation to analyse whether the mean orientation differed from the wind direction at departure (Batschelet 1981). To analyse whether the birds selected to initiate migration in a typical wind condition (weather observation at 22.00 hours) we compared the wind direction during departure nights with nights when birds did not migrate but stayed in the stopover area. We also used the following method to calculate if the birds preferably selected to migrate in tailwinds. The expected forward migratory direction towards southwest (cf. Roos 1984, Åkesson et al. 1996b) was calculated based on the mean flight departure direction ($\alpha = 201°$, range: $180°–245°$, $r = 0.97$, $N = 17$, $P < 0.001$, Rayleigh test). This direction was then used to calculate the expected ground speed in the expected migratory direction as

$$\sqrt{10^2 - (\omega \cdot \sin \beta)^2} + (\omega \cdot \cos \beta),$$

where ω is the wind velocity (m/s) and β is the angular difference between the wind direction and the birds' preferred mean track direction ($201°$). The airspeed of a reed warbler was set to 10 m/s, according to radar observations of flight speeds of small passerine birds (Bloch and Bruderer 1982). Resulting track speeds below 10 m/s correspond to headwinds, while higher speeds represent tailwinds.

For the analysis of wind selectivity we compared the wind assistance component in the expected migratory direction between days when birds did depart (both in forward and reverse directions) with days when our tracked birds stayed in the stopover area. We used the wind data collected at 22.00 hours for nights when birds did not depart and wind speeds within maximally 1 h 30 min of departure for birds that we recorded departing.

Analysis of drift

The bird's flight track relative to the ground is influenced by both the bird's heading and the direction and speed of the wind. For departing reed warblers we calculated the angle of compensation (γ = track minus heading direction) in relation to the wind according to the following equation:

$$\gamma = \arcsin(a \sin \beta),$$

where a = wind speed (m/s)/air speed of the bird, β is the angular difference between the wind direction and the bird's track direction. For birds departing in the expected migratory direction towards south-west we calculated the degree of drift, as the regression line (b) of track directions in relation to the angle (γ) between the track and heading directions (Alerstam 1976). For full wind-drift compensation we expected the regression line (b) to be close to 0, while full drift would result in b = 1. For this analysis we only used departure data on birds initiating migration in wind speeds > 1 m/s.

Differences in wind speed and air pressure between days with and without departures were analysed with paired t-test or ANOVA (Sokal and Rohlf 1995), using Statistica (Statsoft Inc. 1998). The significance level was set at $P < 0.05$.

Results

Effect of body condition on orientation

We found no difference in mean fat class between reed warblers departing in reverse (mean fat class = 6.8, N = 6) compared to forward directions (mean fat class = 7.5, N = 21; ANOVA, F = 2.66, df = 1,25, P = 0.11). However, the difference in mean mass of birds was almost significant between reverse (mean mass = 13.6 g, N = 6) compared to forward departures (mean mass = 14.7 g, N = 21; ANOVA F = 3.78, df = 1, 25, P = 0.063).

Orientation in relation to wind

The majority of the reed warblers departed in the expected migratory direction between south and south-west, while a limited number of birds left the stopover area in reverse directions (Fig. 1). Some of those reverse departures occurred under overcast sky
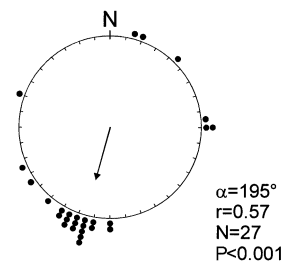

Fig. 1. Flight departure directions of migrating reed warblers tracked by radio-telemetry at Falsterbo in autumn. Mean angle of orientation (α) is indicated by the arrow and the length of the arrow is a measure of the scatter of the circular distribution, r (r ranges between 0 and 1, being inversely related to the angular scatter). Each filled symbol indicates the flight departure direction of one tracked bird. The significance level is given according to the Rayleigh test (Batschelet 1981).

Table 1. Wind velocity (m/s), calculated ground speed in the forward migratory direction (201°) caused by the wind and the bird's airspeed (m/s) as well as air pressure (hPa) for nights when birds departed on migration were compared to nights when birds did not migrate but remained in the stopover area. For all known departures we compared the values at departure with the ones recorded the same night 3 h prior to departure. For birds recorded departing in the forward direction and which did stay at least two days (i.e. the day of release and the following day) in the stopover area (N = 11) we also compared the weather conditions the night of departure (closest weather observation to departure) with the weather conditions at 22.00 hours the nights prior to migration. Weather conditions for reverse departures were also compared to departures in the expected forward migratory direction. The difference between the groups were analysed with paired t-test (t) or ANOVA (F). Degrees of freedom (df) and significance levels (P) are given for respective test.

Weather condition	Groups compared	Mean	±SD	N	(Paired t-test/ ANOVA)	df	P
Wind velocity (m/s)	Nights with departures vs	5.5	3.1	35	F = 0.046	1, 56	0.83
	nights at stopover without departures	5.3	3.2	23			
	Known departures vs	5.7	3.2	29	t = 2.09	28	0.046
	closest observation prior to departure	6.4	2.8	29			
	Forward departures vs	3.5	2.0	11	t = 1.24	10	0.24
	nights prior to departure #	4.5	2.2	11			
	Forward departures vs	4.2	1.9	21	F = 48.31	1, 26	≪0.001
	reverse departures	10.1	2.3	7			
Calculated ground speed (m/s)	Nights with departures vs	10.2	4.2	35	F = 0.35	1, 56	0.55
	nights at stopover without departures	9.6	3.5	23			
	Known departures vs	10.0	4.2	29	t = 0.91	28	0.37
	closest observation prior to departure	10.3	4.1	29			
	Forward departures vs	11.2	2.6	11	t = −2.07	10	0.065
	nights prior to departure #	9.8	3.2	11			
	Forward departures vs	11.2	2.4	21	F = 9.15	1, 26	0.001
	reverse departures	5.6	5.7	7			
Air pressure (hPa)	Nights with departures vs	1019.6	6.7	35	F = 7.04	1, 56	0.01
	nights at stopover without departures	1014.7	7.0	23			
	Known departures vs	1020.4	6.2	29	t = −2.82	28	0.0087
	closest observation prior to departure	1020.0	6.3	29			
	Forward departures vs	1020.0	4.3	11	t = 0.17	10	0.44
	nights prior to departure #	1020.2	5.7	11			
	Forward departures vs	1020.9	5.7	21	F = 0.58	1, 26	0.45
	reverse departures	1018.6	8.0	7			

#: Corresponding to values for birds that did stay more than one day at the stopover area.

conditions and in relatively high wind speeds (range: 4–12 m/s, N = 6, Table 1; cf. Åkesson et al. 2001).

The departure directions of reed warblers were significantly correlated with wind direction at departure (r = 0.46, N = 26, P < 0.01, circular correlation, Fig. 2). At wind speeds below 4 m/s the correlation between departure direction and wind direction was not significant (r = 0.27, N = 10, P > 0.05, circular correlation; open symbols in Fig. 2). Thus, it appears that birds migrating in low wind speeds were able to compensate for wind drift (see below). In wind speeds exceeding 4 m/s, the correlation between flight direction and wind was highly significant (r = 0.70, N = 16, P < 0.001; filled symbols in Fig. 2). The correlation between departure direction and wind direction was significant for birds initiating migration both under overcast sky conditions (7/8–8/8 sky cover; r = 0.75, N = 6, P < 0.05) and under clear skies (0–6/8; r = 0.39, N = 20, P < 0.05).

For birds departing within ± 90° of the expected migratory direction the mean track direction in side winds from the right (onhore winds) was 200° (r = 0.97, N = 15, heading: α = 222°, r = 0.96, N = 15, P < 0.001 in both conditions, Fig. 3A). In offshore winds it was 219° (r = 0.79, N = 5, P < 0.05, heading: α = 207°, r = 0.75, N = 5, P = 0.059, Fig. 3B). This difference in

mean orientation was not statistically significant (F$_{1,18}$ = 2.1, P > 0.05). The mean orientation in side-winds from the left (95% confidence interval: ± 6°, P < 0.05) or from the right (± 44°, P < 0.05) did not differ significantly from the orientation of the nearest coastline oriented 21°/201° (cf. Åkesson, 1993), which is located close to the reedbed from where the reed warblers initiated their migratory flights across the Baltic Sea. The analysis of drift for reed warblers departing in the expected migratory direction towards south-west (± 90°) resulted in a regression coefficient not significantly different from 0 (b = − 0.27; F$_{1,19}$ = 0.52, P > 0.05, linear regression) with the intercept at 209.6°, suggesting almost complete wind drift compensation (Fig. 4).

Migratory flight initiation in relation to wind

Wind speed

The mean calculated ground speed in the expected migratory direction (201°) for departure nights did not differ significantly from nights when the birds stayed in the stopover area (Table 1, Fig. 5). Wind velocity did
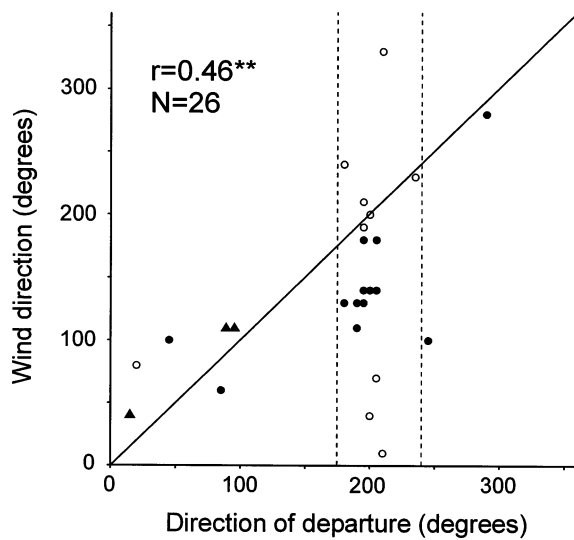
Fig. 2. Circular correlation between direction of departure and wind direction at departure for reed warblers initiating nocturnal migration flights at Falsterbo in autumn. The wind direction is given as the direction in which the wind is blowing (i.e. winds from due east corresponds to 270°). Each symbol represents the value for an individually departing bird tracked by radio-telemetry. Open symbols represent birds departing in low wind speeds (0–4 m/s), filled symbols birds departing in medium (circles: 5–8 m/s) and high wind speeds (triangles: 9–12 m/s), respectively. One bird departing in still air was excluded from this analysis. The correlation coefficient refers to a circular distribution (Batschelet 1981).

not differ between the two groups of night (Table 1). For birds staying in the stopover area at least two days and departing in the expected migratory direction, the increase in calculated ground speed from the night prior to migration to the night of migratory departure was not significant (Table 1). For all known departures irrespective of their direction, there was no statistically significant difference in calculated mean ground speed
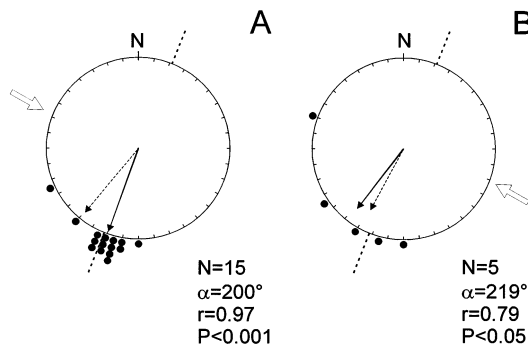

Fig. 3. Distribution of forward flight departure directions in relation to sidewinds from (A) the right (onshore) and (B) the left (offshore). Open arrows indicate the direction of the wind. The mean track (filled line of arrow) and heading (broken line of arrow) directions are given for each distribution. For further information see Figs 1 and 3.
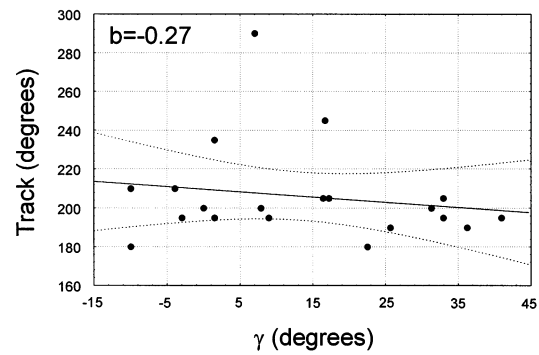

Fig. 4. Track directions in relation to the angular difference (γ) between track and heading of individual reed warblers initiating nocturnal migration from a coastal stopover site in southwest Sweden. The regression line and 95% confidence interval are given for birds departing in the expected migratory direction (b = −0.27).

between 3 h prior to departure and the time of departure (Table 1). The calculated ground speed for birds departing in forward directions was significantly differ-
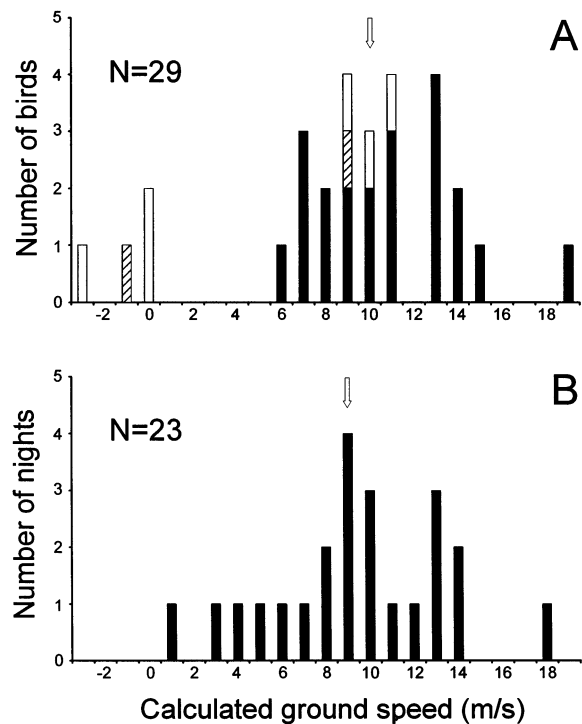
Fig. 5. Calculated ground speed (m/s) in the forward migratory direction (201°) as measured for (A) birds initiating migratory flights compared to (B) velocities birds would have attained on nights when they chose not to migrate. Velocities above 10 m/s correspond to departures with tailwind assistance, while lower values corresponds to headwinds. Open bars indicate values for birds which departed in reverse directions, while filled bars represent birds departing in the expected migratory direction towards south to west of southwest. In total 29 birds were recorded departing, two of which (hatched bars) departed in unknown directions.

ent from that of birds departing in reverse directions (Table 1). For these two groups we also found significantly higher mean wind velocity at departure for reverse compared to forward departures (Table 1).

Wind direction

Including only nights with winds > 1 m/s, there was a significant difference in mean wind direction at 22.00 between nights when reed warblers initiated migration ($\alpha = 133°$, $r = 0.40$, $N = 28$, $P < 0.05$), and nights when they stayed in the stopover area ($\alpha = 293°$, $r = 0.19$, $N = 23$, $P > 0.05$; $U^2 = 0.24$, $P < 0.02$).

Effect of air pressure on migratory flight initiation

Mean air pressure was significantly higher for departure nights than nights of stopover (Table 1). The reed warblers also departed when the air pressure was increasing (Table 1). For forward migrating birds staying in the stopover area for more than one night, there was no significant difference in air pressure at departure compared to 22.00 hours the night before departure (Table 1). Furthermore, we found no difference in air pressure between reverse and forward departures (Table 1).

Discussion

Orientation in relation to wind and topography

The great majority of the reed warblers departed on nocturnal migratory flights towards south of southwest, which corresponds roughly to the expected migratory direction shown by ringing recoveries from Falsterbo (Roos 1984, Åkesson et al. 1996b). However, the radio-tracked reed warblers departed in directions slightly more towards the south, coinciding with the orientation of the nearest coastline (cf. Figs 1 and 2 in Åkesson 1993; Fig. 1). Directions from which ringing recoveries are reported might be biased slightly to the west (cf. Fig. 1 in Åkesson et al. 1996b), because of varying probabilities of receiving recoveries from different areas. For instance, particularly large numbers of reed warblers are captured on autumn migration in Belgium compared with other West European countries (Stolt et al. 1993). Birds with radio transmitters departing in onshore and offshore winds, showed no difference in orientation, neither between the two groups nor relative to the orientation of the coastline. These results suggest that the birds may have used the local topography to minimise wind drift.

The migratory flight direction of reed warblers correlated with the wind direction at departure. The correla-

tion was particularly strong for birds departing in high wind speeds (≥ 5m/s) and was absent in birds departing in low (< 4 m/s) wind speeds, suggesting at least partial wind drift compensation in the latter group. This was supported by the analysis of wind drift for birds departing in the expected migratory direction towards south-west, which demonstrated almost complete compensation in this group of birds (regression $b = -0.27$; cf. Alerstam 1976, see above).

Partial to complete wind drift compensations have been reported for a number of passerine migrants (for reviews see Alerstam 1976, 1979a, Richardson 1991). Free-flying nocturnal passerine migrants flying at low altitudes (below 100 m) along the coastlines of the Falsterbo peninsula have been shown to use the coastlines to compensate for wind drift (Åkesson 1993), while passerines migrating at higher altitudes (0.5–3 km) show partial drift in autumn in the same area (Zehnder et al. 2001). The coastal area at Falsterbo consists of long sandy beaches that might be visible to the migrants at considerable distance also at night (cf. Bingman et al. 1982, Martin 1990a, b, Åkesson 1993, Bruderer and Liechti 1998).

According to Alerstam's theory on optimal wind drift compensation (Alerstam 1979a, b), the degree of wind drift compensation should vary with the distance to the migratory goal. According to this theory, after each migratory flight the bird should minimise the remaining distance to the goal. Therefore, wind drift compensation is expected to vary among species at a particular site depending on the remaining migratory distance to the goal. Wind compensation might also differ between flight altitudes (Alerstam 1979b) and between land and sea where wind drift compensation should be more difficult over the latter due to the moving wave-scape below (cf. Alerstam and Pettersson 1976). We would expect reed warblers at Falsterbo to be sensitive to tailwind conditions at departure but to care less about wind drift compensation, since they are very far from the migratory goal in West Africa (cf. Alerstam 1979a). However, we observed close to complete wind compensation at departure, which is at variance with this expectation. How can this pattern be explained? It might be important for the departing bird to make sure that the intended migratory course is kept relative to the ground during flight, and therefore it is likely that migratory courses are selected in relation to the wind direction during departure (cf. Åkesson et al. 1996a, 2001). Very little is known about bird's ability to assess wind direction and speed. Presumably this is most easily accomplished aloft at low altitudes when migration is initiated, since the topography below should then be most clearly visible to the bird enabling the bird's movement relative to the ground to be assessed. However, detection of wind direction aloft can be accomplished by migrating birds experimentally deprived of all detailed vision (Able et al. 1982), suggest-

ing that accurate vision is not necessary for detection of wind direction. The detection mechanism of wind direction used by birds, however, remains unknown.

The reed warblers in our study departed towards the sea, where wind compensation should be most difficult (cf. Alerstam and Pettersson 1976). A possible explanation is that they used the local topography of the Falsterbo peninsula in combination with intermediate and more distant topographical features, such as lights on the Danish island of Sealand to the west of Falsterbo (closest distance approximately 24 km WSW of Falsterbo) to compensate for wind drift.

A very limited number of the reed warblers departed in reverse directions (N-NE), nearly opposite to the expected migratory direction (cf. Åkesson et al. 1996b). Some of these flights were initiated under overcast conditions (Åkesson et al. 2001) and in high wind speeds (Fig. 5). Some of these birds clearly had no chance to keep an intended track towards south-west in these strong winds, but nonetheless selected to depart from the stopover area. These reed warblers presumably engaged in temporary reverse migration, which has been shown to occur in reed warblers as well as in a large number of other passerine migrants captured at Falsterbo in autumn (Lindström and Alerstam 1986, Sandberg et al. 1988, Åkesson et al. 1996b). Temporary reverse migration presumably is performed by grounded birds confronted with the sea in order to find more suitable stopover sites further inland before migration in the forward migratory direction is resumed (Alerstam 1978, Lindström and Alerstam 1986, Åkesson et al. 1996b). Reed warblers reported from reverse directions within ten days of capture carried smaller fat reserves than those birds that continued migration in the expected direction within the same time period (Åkesson et al. 1996b). In this study we used reed warblers with high fat levels for radio-telemetry. However, there was a tendency that the reverse migrants carried smaller fat reserves and had lower mass than reed warblers departing in forward directions.

Flight departure in relation to wind and air pressure

We found no differences in expected ground speed in the forward direction between departure and stopover nights. Wind directions varied more on stopover nights compared to nights when birds initiated migration. Wind direction and speed differed greatly between occasions with reverse migration and departures in the expected migratory direction. We hypothesised that the wind assistance in the forward migratory direction should be more favourable during departure nights than during stopover nights prior to migration. However, the increase in forward assistance between nights

prior to the departure and departure nights for these forward migrants was just not significant, suggesting factors other than wind measured at ground level might have been of importance for the decision to depart (cf. Liechti and Bruderer 1998, Weber et al. 1998, Åkesson and Hedenström 2000).

The reed warblers initiated migration when the air pressure was increasing, or was relatively high compared to stopover nights. High or increasing air pressure typically occurs after the passage of cyclones, which usually arrive from the west in this part of Europe, and usually results in good migratory flight conditions (tail winds and decreasing cloud cover) for birds heading for wintering areas further south (Richardson 1982, Alerstam 1990). High intensities of migration at Falsterbo have been confirmed in such weather situations both for diurnal (Alerstam 1990) and nocturnal migrants (Zehnder et al. 2001). Birds are very vulnerable to adverse weather on migration, in particular when crossing ecological barriers, such as seas. However, at least some passerine species confronted with a sea crossing seem to be capable of selecting wind conditions favourable for migration (e.g. Williams and Williams 1990, Åkesson and Hedenström 2000, but see Fransson 1998).

How can a bird predict favourable wind conditions for migratory flights? Birds have been shown to be able to detect small differences in air pressure (Kreithen and Keeton 1974), and presumably air pressure changes can be used by the birds to predict favourable flight conditions for migration (Richardson 1982, Alerstam 1990). The possibility that sensitivity to wind drift may vary between species or migration periods is interesting, and therefore more empirical data on wind drift compensation along the migration route would be most valuable. Field data of the type presented here on migratory flight initiation should be important to consider in optimal migration models.

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