ORIGINAL ARTICLE

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Wind selectivity of migratory flight departures in birds

Abstract Optimal migration theory predicts that birds minimizing the overall time of migration should adjust stopover duration with respect to the rate of fuel accumulation. Recent theoretical developments also take into account the wind situation and predict that there is a time window (a set of days) during which birds should depart when assisted by winds but will not do so if there are head winds. There is also a final day when birds will depart irrespective of wind conditions. Hence, the wind model of optimal migration theory predicts that birds should be sensitive to winds and that there should be a correlation between departures and winds blowing towards the intended migration direction. We tested this assumption by tracking the departures of radio-tagged passerines during autumn migration in southern Sweden. Our birds were moderately to very fat when released and therefore energetically ready for departure. There was a significant correlation between direction of departure and wind direction. We also found that during days when birds departed there was a significantly larger tail wind component than during days when birds were present but did not depart. Our results show that passerines do take the current wind situation into account when departing on migratory flights. We also briefly discuss possible clues that birds use when estimating wind direction and strength. The inclusion of wind is an important amendment to optimal migration theory of birds and should be explored further.

Key words Optimal migration theory · Stopover · Migratory departure · Winds · Birds

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Introduction

Migration is a major event in the annual routine of many birds and the energy cost of migration is substantial (Hedenström and Alerstam 1997). Different migration strategies have recently generated intensive research interest with the development of a theory of optimal migration (Alerstam and Lindström 1990; Weber and Houston 1997; reviewed by Alerstam and Hedenström 1998; Houston 1998). Depending on the ecological circumstances, migratory behaviour may be adjusted so that the birds achieve the fastest possible migration (time minimization), the cheapest possible migration (energy minimization) or the safest possible migratory journey (mortality minimization). The migration strategy might also be a compromise betweem any of these different criteria (cf. Houston 1998). In both time and energy minimization, migratory flights coincident with wind in the same direction as the intended track direction will be advantageous to the birds, as this extends the flight range on a given amount of fuel (e.g. Alerstam 1976; Richardson 1978). Typically, wind velocity and bird airspeed are of the same magnitude (Liechti and Bruderer 1998), so the range may be extended by a factor of two or reduced to only half the range in still air by tail or head winds, respectively. Some authors have even suggested that a tail wind might be a prerequisite for successful migration in certain cases (Piersma and Jukema 1990; Butler et al. 1997; but see Hedenström and Weber 1999).

The main factor determining the optimal departure fuel load in time minimization migration is the rate at which birds can store fuel for flight (Alerstam and Lindström 1990; Hedenström and Alerstam 1997). However, Weber et al. (1998) recently introduced a stochastic wind assistance factor into the basic time minimization model. They found that migrants should not be responsive to the wind situation shortly after arrival at a new stopover site, and will continue to fuel up. After a certain number of days, usually 6–8 in their calculations, birds should depart when encountering wind assistance. Hence, there is a "departure time window" when the

birds should pay attention to winds. If no favourable winds occur during this departure time window, they will then leave on some later day irrespective of wind conditions.

Previous tests of the time minimization hypothesis of bird migration have focused on the fuel deposition rate and timing of departure (Lindström and Alerstam 1992; Fransson 1998a). Fransson (1998b) analysed his data on departing whitethroats, *Sylvia communis*, with respect to wind direction, but found no correlation between departure and the tail wind component. We studied the departure behaviour in some nocturnal passerine migrants during autumn migration, using radio transmitters. Our results indicate that birds do pay attention to the wind conditions when deciding on which day to depart from a stopover site. Our findings suggest that the recent refinements of the optimal migration theory that incorporate wind are steps in the right direction.

Methods

We used small radio transmitters (0.67 g; BD-2B, Holohil Systems), glued on the bird's back, to track the movements and departure times of individual birds. The birds were captured on migration at Ottenby Bird Observatory (56°12' N, 16°24' E), situated on the southernmost point of the island of Öland (south-east Sweden) in the Baltic Sea, during the autumns of 1993 and 1994. A radio transmitter was mounted on the back of the bird immediately after capture. The bird was then kept in captivity for approximately 60 min until the glue had dried before transportation by car to release sites 2–3 km north of the capture site. The release sites were located within an area of deciduous woods and shrub that is regularly used for stopover by migrating birds. Before attaching the radio transmitters, the birds were ringed, body mass was measured to the nearest 0.1 g and a fat score was recorded from 0 (no visible subcutaneous fat) to 6 (much fat covering the tracheal pit and belly) (Pettersson and Hasselquist 1985). When there was a choice, we selected the fattest bird to release with a radio transmitter.

We used four species of nocturnal passerine migrants for the experiment: seven thrush nightingales *Luscinia luscinia*, one robin *Erithacus rubecula*, ten song thrushes *Turdus philomelos* and one blackbird *T. merula*. The thrush nightingale is a long-distance tropical migrant wintering in south-eastern Africa (Moreau 1972; Zink 1973), while the other species are short- to medium-distance migrants wintering in western and south-western Europe (Zink 1973).

We located the birds with radio transmitters in the stopover areas repeatedly during daytime to monitor possible movements, by using hand-held radio receivers. These allowed the signals from a transmitter to be registered at a range of up to 300–500 m in the woods and at distances of approximately 1 km in open country. From well before sunset we constantly tracked the birds' movements until they departed on migratory flights or for at least 3 h after sunset; the birds were then checked intermittently during the night. If a bird could not be relocated the next morning, we assumed that it had departed during the night. Of the 19 birds released with radio transmitters, 3 thrush nightingales lost their transmitters before migrating. Of the 16 remaining birds, we recorded the actual departure of 7, while in 8 cases, we recorded the approximate departure or the time interval of departure, while for 1 bird we did not obtain any reliable information.

Migration flight tracks were recorded by tracking birds and measuring the vanishing direction of transmitter signals with a hand-held compass. Birds could be tracked for up to about 30 min when departing, during which time they would cover approximately 20 km. Information on wind direction and strength were recorded every third hour at Ottenby Bird Observatory. We calculated the mean flight track direction for the seven birds tracked during departure by circular statistics (Batschelet 1981). This direction was then used to calculate the tail wind component as $V_w\cos(\varphi_T-\varphi_w)$, where V_w is the wind velocity, φ_T is the mean preferred track direction of departing birds and φ_w is the wind direction. For analyses of wind selectivity, we compared the tail wind component between days when birds departed and days when birds did not depart but were present in the area and could potentially have departed. We also compared the tail wind component between the day of departure and the day before. Five birds departed on the same day as they were released with radio transmitters and could not be used for this latter analysis. We matched the wind data of the nearest registration to the relevant time of departure of the birds or, for intervals of departures, we used the mean wind speed and direction. However, during the night, wind generally changed very little.

Cloud cover may influence departure decision since it might obscure orientation cues such as sunset direction, the skylight polarization pattern and stars (Åkesson et al. 1996). We therefore investigated if the birds time their departure with respect to cloud cover. Cloud coverage was registered by the weather observer at the same time as wind measurements on a scale from 0 (clear sky) to 8 (totally overcast).

Results

Birds released with radio transmitters remained in the area between 0 (i.e. the bird migrated on the first night after being released earlier the same day) and 11 days. When released, the overall mean fat class was 4.0 (SD=1.03, $n=16$). The thrush nightingales were very fat (mean±SD: 5.25±0.5, $n=3$), while the song thrushes were moderately fat (3.6±0.84, $n=10$, range 3–5), the blackbird was in fat class 3 and the robin in fat class 4 when released. There was a negative correlation between fat class when released and number of days before departure (Kendall $\tau=-0.33$, $P=0.072$, $n=16$), but it was not statistically significant.

The overall axial departure track direction of those birds tracked when departing was 26°/206°, which is west of south (Fig. 1; $r_2=0.61$, Rayleigh test: $P<0.08$, $n=7$). This direction was used for reducing the wind data to a tail wind component. Excluding the two thrush

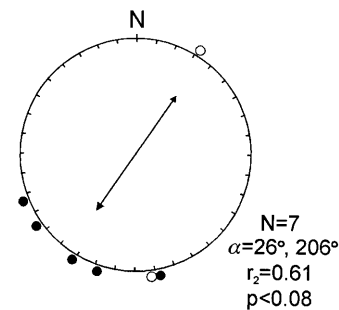**Fig. 1** Departure track directions of thrush nightingale (open *symbols*, $n=2$), song thrush (*filled symbols*, $n=4$) and blackbird (*filled symbol*, $n=1$). North (N) is assigned 0°. The *arrow* shows the axial track direction for all birds combined (26°/206°, $r_2=0.61$, $P<0.08$; Batschelet 1981). The thrushes considered alone showed a mean track direction of 212° ($r_1=0.89$, $P=0.011$, $n=5$)
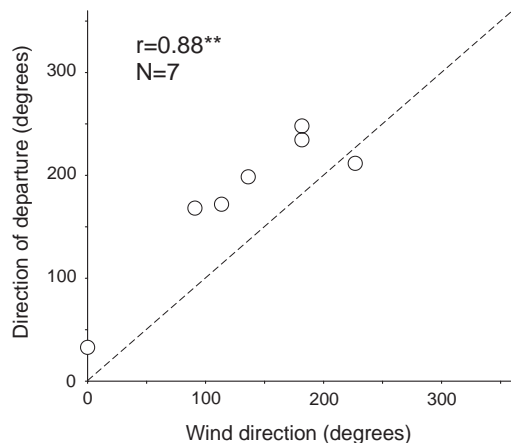
Fig. 2 The relationship between departure track direction and wind direction when departing for the birds shown in Fig. 1. The correlation coefficient refers to a circular distribution (Batschelet 1981)
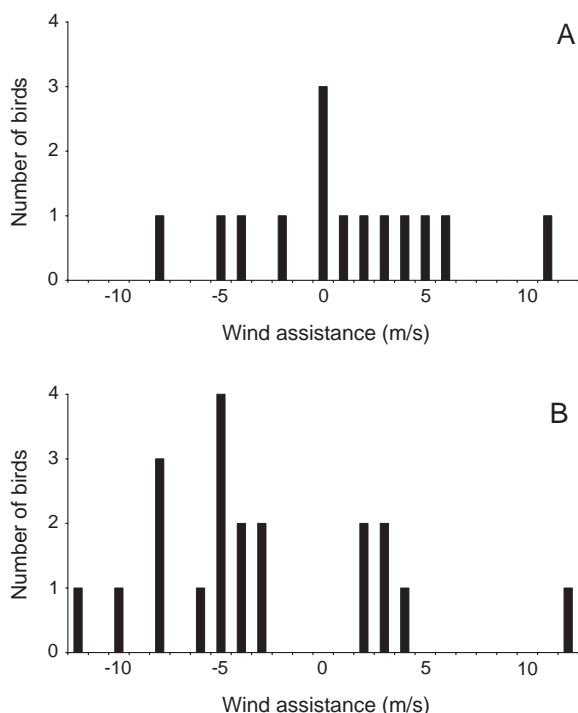

Fig. 3 Tail wind component on days when birds departed on migratory flights (**A**) and on days when birds were present but did not depart (**B**). The tail wind component was calculated as $V_w\cos(\varphi_T-\varphi_w)$, where V_w is the wind velocity, φ_T is the mean preferred track direction of departing birds and φ_w is the wind direction

nightingales (Fig. 1; open symbols) and analysing only the thrushes revealed a significant track direction of 212° (r_1=0.89, Rayleigh test: P=0.011, n=5), which was very similar to the axial direction of all birds.

We found a highly significant association between flight track directions of the birds tracked when departing and the wind direction (Fig. 2; circular correlation, r=0.88, P<0.01, n=7; Batschelet 1981). Hence, these birds departed when they encountered a tail wind. Dur-

ing August 1993 and October 1993 and 1994, study birds potentially could have left on 34 days. Birds departed on 14 of these 34 days (on one occasion, two birds departed on the same evening/night). The tail wind component on days of departure was 0.88±4.70 m/s (mean±SD) and on days without departing birds, it was –2.99±5.72 m/s, i.e. on average there was a tail wind on days of departures and a head wind on days without departures (Fig. 3). The difference between departure and non-departure days was statistically significant (ANOVA, $F_{1,32}$=4.34, P<0.05). We also compared the tail wind component on days of departure with that on the day before for those birds that stayed at least one night before departing. On nights of bird departures, the tail wind component was 0.33±5.12 and on the day before it was –1.90±4.89, a statistically significant difference (paired two-sample t-test, one-tailed, t= 2.02, P<0.05, n=11). A few birds departed with head winds (Fig. 3), two of which had encountered a run of days (4 and 10) with head winds immediately before their departure.

The cloud cover mean score on days when birds departed was 3.4 (SD=3.2, n=14) and on days with no birds departing it was 5.4 (SD=3.3, n=20), but the difference was not statistically significant (ANOVA, $F_{1,32}$=3.25, P>0.05).

The mean departure time was 68 min after sunset (SD=74 minutes, n=9, range 7 min before sunset to 234 min after sunset) for those individuals for which the departure was registered (see Åkesson et al. 1996). A further six individuals departed and escaped the notice of the observers, but their inferred earliest departure times ranged from 188 to 430 min, i.e. one bird commenced migration flight at the earliest about 7 h after sunset.

Discussion

Wind is probably the single most important factor affecting migratory birds during flight (e.g. Evans 1966; Alerstam 1976). Generally, the intensity of nocturnal migration is strongly correlated with the synoptic weather situation and wind velocity and direction so that most birds migrate in light or following winds (Richardson 1978, 1990). When aloft, birds even seem capable of locating those altitudes where they find the most favourable wind strata (Alerstam 1981; Bruderer et al. 1995). Our data indicate that wind direction also affects the decision to depart in nocturnally migrating passerines. Birds choose days (or, rather, nights) for departure when they experienced significantly more tail wind assistance than on days when no birds departed. The fact that the birds were already moderately to very fat when released could explain why we did not find a significant correlation between initial fuel load and stopover duration, as would be expected from optimal stopover theory (cf. Alerstam and Lindström 1990). Some birds departed on their first day in the field with a radio transmitter, indicating that their fuel loads were already sufficient and that they had entered the "departure time window"(sensu

Weber et al. 1998). Most birds departed at or shortly after dusk, but some delayed their time of departure until several hours after dusk. A few birds even departed in the middle of the night. The reason is unknown, but these birds may have been waiting for improved wind conditions. Alternatively, late-departing birds may have waited for reliable orientation cues to become available (Åkesson et al. 1996). Cloud cover did not differ significantly between departure and non-departure days. On three occasions, birds departed when the sky was totally overcast, indicating that failure to see at least part of the sky does not prevent birds from leaving on migratory flights (cf. Cochran and Kjos 1985).

A potential bias in our analysis could be the migration direction used for calculating tail wind components, obtained directly from our radio-tagged birds' departures. We found a rather homogenous migration direction towards west-south-west (206°), even for the thrush nightingale, a species known to winter in south-east Africa (Moreau 1972). However, the mean initial flight direction of four thrush nightingales ringed at Ottenby Bird Observatory showed a mean direction of 188° (r=0.82, n=4, Swedish Ringing Center, unpublished data), i.e. very similar to the mean flight direction we found in our sample. Therefore, our calculated tail wind components would have been insignificantly affected had we instead used species-specific migration directions from ringing recoveries. Our sample was rather small and with only a few different species, although all are nocturnal migrants and should therefore show similar behavioural responses to common factors. Nevertheless, since a wind-related departure pattern emerged in this small sample of different species, this should represent a general phenomenon.

What cues do birds use to determine wind direction? One previous suggestion is that they actually take off to sample the wind aloft and then make a decision whether or not to commence a migratory flight (Richardson 1990). However, we did not observe this behaviour. The decision to depart was made on the ground. One possibility is that birds use the movements of clouds (which are visible to the human eye even during late autumn nights) in relation to their intended flight direction. There are also indications that birds may sense the direction of wind without visual cues (Demong and Emlen 1978). Winds tend to remain the same for some time, so it is possible that wind direction and velocity are determined by the bird while it is still light (afternoon or dusk). The late-night departures would then mainly be explained by orientation constraints rather than changes of wind. It has been shown that pigeons, *Columba livia*, can sense changes in air pressure (Kreithen and Keeton 1974). If migrating birds have the same sensory abilities as pigeons, they might gauge changes in air pressure which are correlated with changes in wind direction and strength.

When the wind had been unfavourable for a number of consecutive days, birds eventually departed even if there was a head wind. This is expected in time-minimizing migration if there has been a period of unfavourable winds and the bird has reached the terminal day of its "departure window" (Weber et al. 1998). Otherwise, after a run of days with head winds, birds should depart with the first tail wind where winds are asymmetrically correlated, as in southern Sweden (T.P. Weber and A. Hedenström, unpublished data). Analysing auto-correlations of winds between days at two sites in southern Sweden (one of them Ottenby), Weber and Hedenström (unpublished data) found that runs of days with unfavourable wind conditions tend to be longer than runs of days with favourable winds. Hence, days of tail wind in the preferred migratory direction occur only intermittently among periods of head wind. However, in some regions, such as central Europe, days with negative tail wind components predominate during the autumn migration season, and there, days with just a light head wind may count as a favourable take-off situation (Liechti and Bruderer 1998).

The few existing tests of the time minimization hypothesis of bird migration have focused on the rate of fuel deposition and departure fuel loads (Lindström and Alerstam 1992; Fransson 1998a), since these factors were considered most important in the models (Alerstam and Lindström 1990; Hedenström and Alerstam 1997; Weber and Houston 1997). Recent theoretical developments have incorporated the wind into the model framework of optimal migration (Liechti and Bruderer 1998; Weber et al. 1998; T.P. Weber and A. Hedenström, unpublished data). Our findings indicate that wind really is important to birds' departure decisions and that the new model generation is worthwhile. The next challenge will be to investigate how fuel economy, wind condition and orientation cues interact for decisions about departure in migratory birds. We believe that a combination of our approach using radio transmitters and the use of remote-controlled balances for monitoring fuelling (sensu Lindström and Alerstam 1992; Fransson 1998a) could be a fruitful approach.

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