Animal Behaviour 104 (2015) 59–68

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Weather and fuel reserves determine departure and flight decisions in passerines migrating across the Baltic Sea

Sissel Sjöberg [a,*], Thomas Alerstam [a], Susanne Åkesson [a], Axel Schulz [b], Alexander Weidauer [b], Timothy Coppack [b], Rachel Muheim [a]

[a] Department of Biology, Lund University, Lund, Sweden
[b] Institute of Applied Ecology (IfAÖ), Rostock, Germany

ARTICLE INFO

Article history:
Received 14 October 2014
Initial acceptance 25 November 2014
Final acceptance 6 February 2015
Available online 9 April 2015
MS. number: 14-00820R

Keywords:
autumn migration
bird migration
departure decision
flight duration
passerine
radiotelemetry
route choice
stopover

Departure decisions of how and when to leave a stopover site may be of critical importance for the migration performance of birds. We used an automated radiotelemetry system at Falsterbo peninsula, Sweden, to study stopover behaviour and route choice in free-flying passerines departing on flights across the Baltic Sea during autumn migration. In addition, we had an offshore receiver station (FINO 2) located about 50 km southeast from Falsterbo. Of 91 birds equipped with radiotransmitters, 19 passed FINO 2. The probability that a departing migrant passed near FINO 2 was primarily affected by winds and timing of departure. Probably, the migrants were subjected to drift by westerly winds, leading to southeasterly flight paths and an enhanced probability of passing FINO 2. Most birds passing the offshore station departed early in the night, which indicates that southward departures across the Baltic Sea usually take place during this time window. Wind condition was the dominant factor explaining the variation in flight duration between Falsterbo and FINO 2. After considering wind influence, we found additional effects of fat score and cloud cover. Birds with a higher fat score performed the flight faster than leaner individuals, as did birds that departed under clear skies compared to birds departing during overcast skies. These effects may reflect a difference in migratory motivation and airspeed between lean and fat birds together with difficulties in controlling orientation in overcast situations on oversea flights when celestial cues are unavailable. Thus, winds, clouds and fuel reserves were the primary factors determining departure and flight decisions in passerine migrants at Falsterbo in autumn.

Migrating songbirds accomplish their journeys by intermittent flights with stopovers for resting and refuelling (e.g. Schaub & Jenni, 2001). Most time and energy are spent at stopover sites (Hedenström & Alerstam, 1997; Wikelski et al., 2003). Decisions about when and how to leave a stopover site may affect the overall success of migration (Alerstam & Hedenström, 1998; Alerstam & Lindström, 1990; Newton, 2006), especially at coastal stopover sites where competition and risk of predation are expected to be high (Newton, 2008; Woodworth, Francis, & Taylor, 2014). It is highly relevant to analyse departure decisions of individual songbird migrants facing ecological barriers, such as deserts, large ice caps or extended bodies of water. In particular, it is important to understand how migrants establish their orientation and flight schedule under variable wind and weather conditions in environments that lack perceivable landmarks and predictable stopover possibilities. During stopover ahead of a barrier the risk associated with a direct flight needs to be balanced against the cost in terms of the time and energy that a detour around the barrier would incur. Passerine migrants have been shown to be highly variable in their strategies when facing a barrier. Straight barrier crossings and longer detours are regularly observed in migratory birds (e.g. Åkesson, Klaassen, Holmgren, Fox, & Hedenström, 2012; Alerstam, 2001; Stutchbury et al., 2009). Furthermore, reverse migratory directions away from the barrier (Åkesson, Karlsson, Walinder, & Alerstam, 1996; Alerstam, 1978; Woodworth et al., 2014) and postponement of the departure for more favourable weather conditions (Åkesson & Hedenström, 2000) have been observed, indicating that the decisions made at stopovers before flights over unfavourable habitats play an essential part in their migratory schedules.

Here, we investigated departure decisions and flight behaviours in free-flying migratory passerines crossing the Baltic Sea during autumn migration. We used an automatic radiotelemetry system

* Correspondence: S. Sjöberg, Department of Biology, Lund University, Biology Building, Sölvegatan 35, 223 62 Lund, Sweden.
E-mail address: Sissel.Sjoberg@biol.lu.se (S. Sjöberg).

http://dx.doi.org/10.1016/j.anbehav.2015.02.015

covering the coastal region at Falsterbo, Sweden, and an additional receiver station on the remote offshore platform FINO 2 about 50 km off the Swedish coast towards the southeast (Fig. 1). The crossing of the Baltic Sea from Falsterbo is associated with a flight of 23–100 km over open sea. This may not be comparable with a crossing of a larger ecological barrier, such as the Saharan desert, but may nevertheless be sufficiently large to make birds hesitate before the sea crossing. Furthermore, it has been described earlier that birds more often perform reverse migration in this area than at an inland site (Åkesson, 1999). A route southwest from Falsterbo is associated with a sea crossing of 23–50 km. On the other hand, one towards the southeast from Falsterbo, involving a passage of the offshore receiver station at FINO 2, requires a sea crossing of at least 80 km (Fig. 1c).

The Falsterbo peninsula, located at the southwestern tip of Scandinavia, is one of the focal sites for migratory birds during autumn migration, and large numbers of migrants concentrate in this area. We know much about the pattern of migration, species composition, phenology and the condition of birds migrating through Falsterbo from ringing and bird migration counts at Falsterbo Bird Observatory (Karlsson, 2009; Zehnder, Akesson, Liechti, & Bruderer, 2001). However, far less is known about the birds' flight and stopover decisions at the individual level when they are confronted with the sea after long migratory flights over land (cf. Åkesson, Alerstam, et al., 1996; Åkesson, Karlsson, et al., 1996). Radiotelemetry is ideally suited for following avian migrants during stopover in this area, since the peninsula has a flat topography, is fairly small and is to a large extent surrounded by water.

We focused our study on two main questions: which factors (1) lead to longer than necessary sea crossings across the Baltic Sea and (2) affect the flight duration for a specific flight distance?

(1) Environmental conditions, e.g. winds and weather, are hypothesized to affect the flight route of migrating birds. The prevailing wind situation has been shown to play a prominent role in determining the patterns and speed of bird migration (Alerstam, 1979; Liechti & Bruderer, 1998; Richardson, 1990). Reed warblers, *Acrocephalus scirpaceus*, have been observed to be more scattered in their departure directions in overcast weather (Åkesson, Walinder, Karlsson, & Ehnbom, 2001). Individual characteristics and differences in behaviour (departure timing and directions) are also hypothesized to be important for route choice. Adult individuals and individuals with larger fuel reserves have been shown to be less likely to perform a detour around an area of unfavourable habitat (e.g. Sandberg, Pettersson, & Persson, 1991; Schmaljohann & Naef-Daenzer, 2011; Smolinsky et al., 2013). There are also indications that true migratory departures in the preferred migratory directions mainly occur shortly after evening civil twilight (Åkesson, Alerstam, et al., 1996; Åkesson, Karlsson, et al., 1996; Åkesson, Walinder, Karlsson, & Ehnbom, 2002; Mills, Thurber, & Mackenzie, 2011), which made us hypothesize that departure time could also be related to route choice.

From these hypotheses and earlier tests and studies related to them we predicted that: (1) southeasterly departures leading the birds on the longer flight across the Baltic would primarily occur in crosswinds from the west, promoting a certain degree of wind drift from the main migratory course to the southeast; (2) overcast skies and low visibility would increase the likelihood of a longer sea crossing; (3) adult individuals and individuals with larger fuel stores would be more likely to perform this longer sea crossing; (4) early night-time departures would have a higher probability of being true migratory departures and have a longer sea crossing; (5) birds orienting and departing from Falsterbo in southeasterly directions would more often take the longer sea crossing and fly via FINO 2, assuming that they keep a straight flight path after take-off.

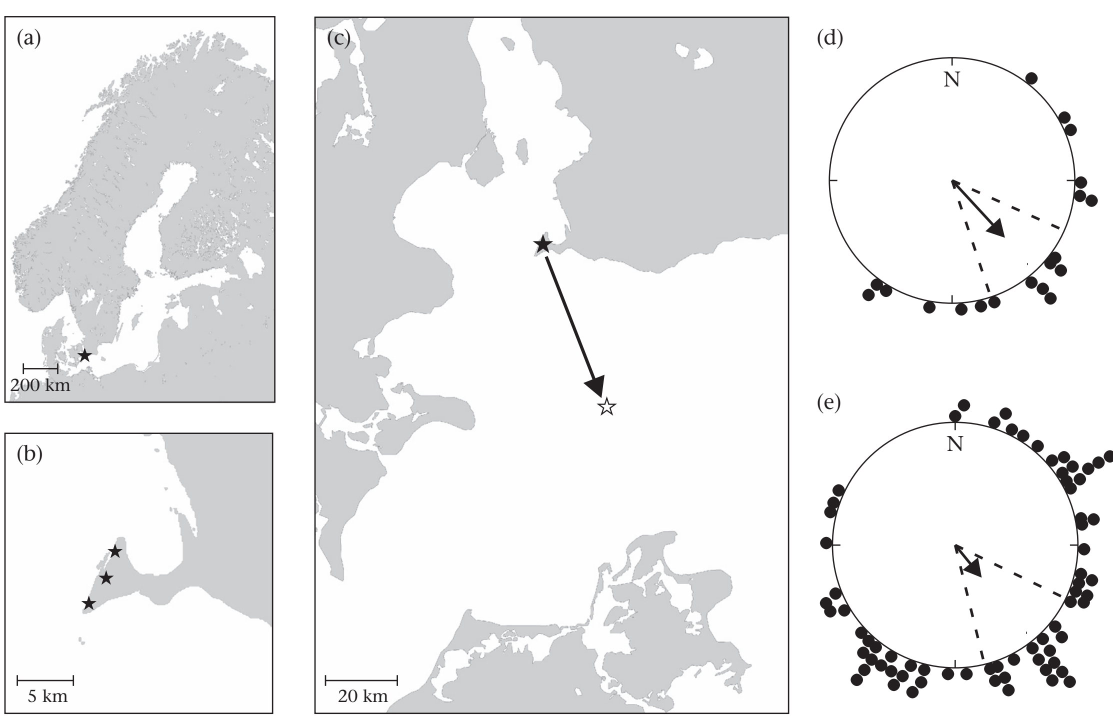

Figure 1. Maps showing the location of (a) Falsterbo in Scandinavia (black star), (b) telemetry stations at Falsterbo peninsula and (c) FINO 2 (white star). The arrow in (c) shows the direct flight route from Falsterbo to FINO 2. (d) Mean departure directions of birds that passed and (e) did not pass FINO 2. In circular plots the arrow indicates the mean direction and the length of each arrow is a measure of concentration (*r*) of the departures drawn relative to the radius of the circle. Broken lines give ±95% confidence intervals. Maps from Maptool (Seaturtle.org, 2002).

We tested these predictions by analysing the prevailing environmental conditions (wind direction, wind speed, cloudiness, visibility, time of season) during departure. We also compared critical individual characteristics (species, age, fuel reserves) and differences in the behaviour (departure timing and directions, stopover duration) between birds that did not pass FINO 2 and those that did, hence taking a longer flight than necessary over the Baltic Sea.

(2) The duration of a flight could be affected by both the actual speed and the straightness of the flight path. Several factors, including weather conditions and various individual and behavioural characteristics, are hypothesized to be involved. Ground speed is determined by the wind vector and the flight vector of the bird in relation to the surrounding air and is strongly influenced by tail or head winds (Pennycuick, 2008). White-throated sparrows, *Zonotrichia albicollis*, released under total overcast skies and tracked by radar adopted a 'zigzag'-shaped flight pattern and showed lower airspeeds than sparrows released under clear skies (Emlen & Demong, 1978). Also, several studies of free-flying songbird migrants observed more scattered departure directions under overcast conditions than under clear skies (e.g. Åkesson et al., 2001; Sandberg et al., 1991), which are hypothesized to affect the straightness of the flight path, if the birds make major adjustments of their heading en route. Similarly, young birds have been shown to be more scattered in their orientation (Moore, 1984), and birds with lower body mass and smaller fuel reserves are less prone to orient in the appropriate migratory direction (Åkesson, Alerstam, et al., 1996; Åkesson, Karlsson, et al., 1996; Deutschlander & Muheim, 2009; Sandberg & Moore, 1996; Smolinsky et al., 2013).

Based on the general hypothesis that resulting flight duration over a given distance is determined by a combination of internal and external factors affecting the speed and straightness of the flight, we predicted that: (1) the duration of the flight between Falsterbo and FINO 2 would primarily be affected by winds (assistance by tail winds or hindrance by head winds); (2) cloudy weather and weather with low visibility would prolong the duration by entailing orientation difficulties resulting in less straight flight paths; (3) the flight duration would be longer in young migrants and migrants with smaller fuel reserves because of less precise orientation and more tortuous flight paths; (4) the flight duration would be longer in birds departing from Falsterbo in a direction deviating from the direction towards the offshore receiver station.

To test these predictions we analysed the flight duration from Falsterbo to the offshore receiver station at FINO 2 in relation to environmental conditions (winds and weather), individual characteristics (age and fuel reserves) and behaviour (departure orientation). To our knowledge, this is the first study investigating the factors that determine why an individual bird flies a certain route, and how the resulting flight duration, for a medium-scale flight, is affected by environmental conditions and individual characteristics.

METHODS

Study Site and the Automatic Radiotelemetry System

The study was conducted during the autumn migration seasons of 2011 (23 August–22 October) and 2012 (21 August–20 October) at Falsterbo Bird Observatory, Falsterbo, Sweden (55°38′N, 12°82′E; Fig. 1).

The automatic receiver system consists of three terrestrial stations at Falsterbo, and one offshore station at the research platform FINO 2 (Fig. 1, Appendix Table A1). The stations at Falsterbo are located along the northeast–southwest coastline, approximately 2.9 km apart. They are mounted (1) on top of a 25 m high lighthouse surrounded by a golf course, (2) on top of a 43 m high water tower in a village on the peninsula, and (3) 5 m above ground on the roof of a farm in an area with grass/shrubby habitat and sandy beaches. Each telemetry station is equipped with a radiotelemetry receiver (SRX600; Lotek Wireless, Newmarket, ON, Canada) connected to an eight-port antenna switchbox (ASP_8, Lotek Wireless) with two to five antennas. All antennas used at the three stations at Falsterbo peninsula were custom-made six-element yagi antennas matching the frequency band of the transmitters (151.5 MHz). The farm and the lighthouse stations had four each, pointing towards 40°, 140°, 210°, 320° and 20°, 70°, 170°, 220°, respectively. The water tower station had five antennas pointing towards 0°, 72°, 144°, 216°, 288°. The offshore receiver station ('FINO 2') is located 47 km southeast of Falsterbo (Fig. 1, Table A1), with two antennas (six-element yagi antennas, Sirio WY140-6N, frequency range 140–160 MHz) mounted diametrically (90° and 270°), approximately 60 m above sea level. The receivers sequentially monitored each antenna for 3.2 s via an antenna switchbox, so that every transmitter could be logged at least once per cycle at every antenna (duration of cycle 6.4–16 s depending on the number of antennas). The receivers were active and continuously collected data throughout the study period. All receivers recorded satellite-corrected time stamps based on GPS.

Since variations in location and surroundings affected the sensitivity of the receivers at the different stations to different degrees, the gain of each receiver was adjusted separately. Usually, gain was set to 70–90 (possible scale 0–99) at the peninsula stations and to 60 at FINO 2. This resulted in a maximum detection range of at least 3 km on the Falsterbo peninsula and of at least 10 km at FINO 2.

We used ID-coded radiotransmitters (0.32 g; NTQB-2, Lotek Wireless) to enable sampling of multiple individuals simultaneously at the same frequency (151.5 MHz). Burst rates were fixed within each transmitter, but varied between 2.9 and 3.1 s to avoid interference between individual signal codes. The life span of the transmitters was guaranteed to be at least 18 days; however, we obtained several longer track records of up to 24 days.

Study Species and Selection of Individuals

The study species were nocturnal passerine migrants: two long-distance and two medium-distance. Garden warblers, *Sylvia borin*, and willow warblers, *Phylloscopus trochilus*, are long-distance migrants which breed throughout Scandinavia and northern Europe and winter in tropical Africa (Cramp, 1992). The Scandinavian breeding populations of European robins, *Erithacus rubecula*, and song thrushes, *Turdus philomelos*, winter in the southwestern parts of Europe and in northern Africa, and are regarded as medium-distance migrants (Cramp, 1988). All species migrate in a prevailing southwesterly direction from southern Sweden according to ringing recoveries (Fransson & Karlsson-Hall, 2008). The birds were caught as part of the regular ringing scheme at Falsterbo Bird Observatory using mist nets in the lighthouse garden and were all handled and tagged within 1 h of capture (usually within 20 min).

We selectively tagged individuals to balance juvenile and adult birds as well as individuals with different amounts of stored fat. Age was determined on the basis of plumage characteristics, wing length (maximum wing length; Svensson, 1992) was measured to the closest mm, and body mass to the closest 0.1 g with a Pesola spring balance. Fat stores were estimated on a 0–9 visual scale (based on Pettersson & Hasselquist, 1985, but adapted for Falsterbo Bird Observatory and extended with fat class 7–9; see Appendix Fig. A1). To attach the radiotransmitter we cut the feathers on a small area of the birds' backs and attached the transmitters with a small amount of glue (contact adhesive, Casco) to avoid any extra weight and to ensure that the transmitters fell off during the next moult, if not before. We attached transmitters to 108 birds in total: 43 in 2011 and 65 in 2012. Of these, 35 were willow warblers (including 20 juveniles), 29 European robins (10 juveniles), 13 garden warblers (11 juveniles) and 31 song thrushes (16 juveniles).

Weather Data

Weather data were collected every third hour by the Swedish Meteorological and Hydrological Institute (SMHI) at Falsterbo Bird Observatory. For the analysis of departure behaviours we used the weather data nearest in time to each bird's departure time. Wind speed and direction were automatically measured, whereas visibility and degree of overcast were visually estimated by human observers. North/south and east/west wind components were calculated from the observed wind direction (north/south component = cos (wind direction); east/west component = sin (wind direction)). Visibility was estimated in intervals to the nearest 100 m for the distance between 0 and 5 km, to the nearest 1 km for 6–30 km and to the nearest 5 km for visibility exceeding 30 km up to maximum visibility (>75 km). The degree of overcast was estimated by an eight-degree scale where 0/8 = clear sky and 8/8 = total overcast.

Processing of Telemetry Data

For each detected signal the receivers collected ID code (individual), date, time stamp, antenna and signal strength (nonlinear scale 30–255). The data were filtered before analysis to remove false signals by making use of the transmitters' stable burst rates. The binary files downloaded from the receivers contained the exact time of each signal (ms), which we used to calculate the specific burst interval (ms) for each transmitter (Mills et al., 2011; Taylor et al., 2011). We allowed a maximum error of ±10 ms within the interval and required at least three signals per min within the transmitter's specific interval. To calculate the departure direction we calculated a circular mean direction from all signals from a bird's last 10 min at the Falsterbo peninsula, weighing each signal by signal strength. Direction and distance to FINO 2 were calculated from the station on the Falsterbo peninsula where the last signal was received. The time of the last signal after filtering was used as the departure time of the bird and the first signal at FINO 2 was regarded as its arrival time. Departure time was both treated as a circular variable (with local time 0000–2400 hours corresponding to 0–360 degrees) and divided into three groups: daytime (0600–1800 hours), early night (1800–2200 hours) and late night (2200–0600 hours).

Statistics

The birds were grouped into two age categories: juveniles (first calendar year) on their first autumn migration and experienced adults (after first calendar year). Body mass relative to the expected size-specific fat-free body mass was calculated by relating the birds' body masses to the regression line of body weight and wing length of all birds of each species ringed at Falsterbo Bird Observatory with fat score = 0 during the last 15 years of ringing, and thus controlling for the birds' wing length (proxy for body size). To investigate which factors influenced the observed flight time to FINO 2, we calculated the expected time to FINO 2 by vector summarization of the wind vector (direction and speed of winds at departure) and the vector between Falsterbo and FINO 2 (distance and direction from the last receiver station at Falsterbo to FINO 2), and by assuming a loxodrome course and an expected airspeed. For willow warblers, garden warblers and European robins we used an expected airspeed of 10 m/s in these calculations; for song thrushes we used 13 m/s (Bruderer & Boldt, 2001). From this relationship we further calculated expected ground speed and expected heading (Appendix Table A2). The straight-line distance between positions of the bird's last signal at Falsterbo and first signal at FINO 2 may differ from the Falsterbo–FINO 2 distances (Appendix Table A1) because of the variation in the birds' positions at the detection range of the receiver stations. Hence, it is most likely that the distance of the straight-line flight paths have been somewhat overestimated (maximally by about 13 km; see detection ranges above). However, without knowledge of the birds' exact positions we are not able to correct for this possible error.

To describe the data, we performed univariate statistical tests: linear and logistic regressions, ANOVAs and chi-square tests for continuous and group variables, respectively, and Watson U^2 and Wilcoxon rank sum tests for circular variables.

A logistic regression was carried out to identify the factors that might have influenced whether or not the birds flew the longer southeast sea crossing (and thus were recorded by the receiver at FINO 2). Variables included in the original logistic regression were departure time group, departure direction from Falsterbo (deviation from the direction to FINO 2), species, age (juvenile/adult), fat score at release, degree of overcast, north/south wind component, east/west wind component and wind speed. Visibility could not be included in the model since it was correlated with the north/south wind components. We used bidirectional elimination of factors increasing the AIC criteria (Akaike, 1974) to select the most parsimonious and likely model described by the lowest AIC. A likelihood ratio chi-square test of the final logistic regression was performed to illustrate the models with P values. Subsequently, we used a general linear model (GLM) performed by bidirectional elimination of factors increasing the AIC criteria, to identify the most likely factors affecting the observed flight time to FINO 2 for the birds that flew that route (duration to FINO 2 was the dependent variable). Age (juvenile/adult), departure direction from Falsterbo (deviance from the direction to FINO 2), fat score at release, visibility, degree of overcast and expected flight time to FINO 2 (taking wind condition into account) were included as independent covariates and fixed factors in the original model.

Statistics was calculated using R.2.11.1 software (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org) using the Rcmdr package, except for the circular analyses where Oriana 4.0 (Kovach Computing Services, Anglesey, U.K.) software was used.

Ethical Note

The radiotransmitters were attached with a contact adhesive to the feathers on the bird's back (see above). We recaught a few individuals several days after attaching the transmitter and could not observe any adverse effects on the birds' skin caused by the glue. The mass of the transmitters (0.32 g) ranged between 0.4 and 4.3% of the bird's body mass (the smallest bird was a willow warbler of 7.4 g and the biggest a song thrush of 77 g), which is less than the traditionally recommended upper weight limit of 5% of body mass (Cochran, 1980). All birds were released directly after handling and tagging (usually within 20 min after capture, never more than 1 h).

The study was performed with permission from Malmö-Lund Ethical Committee, Sweden (M 27-10).

RESULTS

Of the 108 birds equipped with transmitters, 17 were excluded from the analysis. Of these, five (four willow warblers, one European robin) lost their transmitters or died at the Falsterbo peninsula. The other 12 birds (three willow warblers, six European robins, three song thrushes) passed FINO 2, but did not fly there directly from Falsterbo, spending some time elsewhere out of reach of the three receiver stations at Falsterbo (they had a time lapse of at least 1 day after departing from Falsterbo before passing FINO 2); these birds were excluded since we did not know from where and when they departed on their flights across the Baltic Sea. In total, 91 birds were included in the analyses (28 willow warblers, 22 European robins, 13 garden warblers and 28 song thrushes, of which 49 were juveniles and 42 adults). Of these, 19 individuals took the longer southeast flight route via FINO 2 (in total 21%, 21% of willow warblers, 9% of European robins, 15% of garden warblers and 32% of song thrushes; Appendix Table A2). Birds with transmitters stayed in the area for up to 24 nights before departure.

Departure Conditions Associated with Passage of FINO 2

Both the north/south wind component and the circular wind direction significantly affected which of the birds flew the longer southeast route in univariate tests (Table 1). Furthermore, visibility was positively associated with the probability of passing FINO 2 (Table 1), but was not included in the logistic model due to correlations with the north/south wind component. The univariate statistics further revealed a significant effect of timing of departure, both as a grouped variable and as a circular variable (Table 1). This difference in timing between the two samples describes a difference in scatter and there was no difference in mean departure time between the birds that did (mean ± SD: 2027 ± 1 h 53 min; Fig. 2a) and did not pass FINO 2 (2036 ± 4 h 35 min; Fig. 2b). Mean departure direction was similar for both groups (birds that passed FINO 2: 138 ± 52.5°; birds that did not pass FINO 2: 141 ± 82.1°), and there was no difference in deviation from the direction to FINO 2 (Table 1). However, we found a difference in the concentration of departure directions: birds that flew the southeast route and passed near FINO 2 showed a smaller angular departure scatter than the migrants that departed on other routes (Fig. 1d, e, Table 1). Species, age (juvenile/adult), fat score at release, body mass relative to size-specific fat-free body mass, east/west wind component, wind speed and degree of overcast were not significantly correlated with the likelihood of passing FINO 2 (Table 1).

Included in the final logistic multiple regression model for factors affecting which birds flew by FINO 2 (for factors included in the original model see Methods) were departure time group, age (juvenile/adult) and the north/south wind component (Table 2). Still, it was only the departure time group and the north/south wind component that significantly affected which birds passed by FINO 2 according to the likelihood ratio chi-square test of the logistic regression (Table 2).

The birds that flew the southeast crossing over the Baltic Sea past FINO 2 left Falsterbo in more westerly winds (mean ± SD: 273 ± 62.5°; Fig. 2c) than birds that took other routes from Falsterbo (221 ± 60.8°; Fig. 2d). All except one individual flying past FINO 2 departed in the early night-time group, whereas the birds that took off on other routes departed at all hours. In addition, we found a suggestion that age may have increased the probability of a crossing of the Baltic Sea near FINO 2 with a higher proportion of adults flying this route (28.6% of the adults flew via FINO 2, 14.3% of the juveniles).

Flights Between Falsterbo and FINO 2

Observed flight durations between Falsterbo and FINO 2 varied between 33.7 and 123.3 min, with an average time of 72.7 min (SD = 21.5 min). Observed ground speeds were on average 11.9 m/s (SD = 3.8 m/s; Appendix Table A2). Expected flight time to FINO 2 was the only factor that significantly affected the observed flight time to FINO 2 in univariate statistical tests (Table 3). Species, age (juvenile/adult), fat score at release, body mass relative to size-specific fat-free body mass, deviation of the departure direction from the direction to FINO 2, visibility and degree of overcast were not significantly correlated with the observed flight time according to univariate statistic tests (Table 3).

In the GLM that best described factors affecting the observed flight time to FINO 2 according to the lowest AIC (Fig. 3, Table 4), fat score at release and degree of overcast were included in addition to the expected flight time to FINO 2; for factors included in the original model see Methods. We estimated the effect of wind by calculating the expected ground speed for each bird on the basis of surface wind conditions at departure time, and assumed that the bird flew in a constant track direction directly towards FINO 2. We found a strong agreement between this expected ground speed (and the expected duration associated with it, taking into account

Table 1
Differences in external and internal factors between birds that did (yes) or did not (no) pass FINO 2

	Mean (SD) yes	Mean (SD) no	*df*	$z/U^2/\chi^2/W$[a]	*P*	Test
Fat score at release (0–8)	3.8 (1.4)	3.4 (1.3)	90	1.22	0.22	Logistic regression
Body mass relative to size-specific fat-free body mass	1.08 (0.06)	1.06 (0.2)	89	0.43	0.67	Logistic regression
Departure direction, deviance from direction towards FINO 2 (°)	45 (29.9)	63 (41.3)	90	−1.77	0.077	Logistic regression
North/south wind component (m/s)	0.03 (0.5)	−0.4 (0.6)	90	2.83	0.005	Logistic regression
East/west wind component (m/s)	−0.6 (0.6)	−0.4 (0.6)	90	−1.12	0.26	Logistic regression
Wind speed (m/s)	6.7 (4.4)	5.7 (3.2)	90	1.059	0.29	Logistic regression
Visibility (km)	35.0 (17.9)	23.9 (19.2)	90	2.15	0.032	Logistic regression
Degree of overcast (0–8)	3.8 (2.5)	4.7 (2.7)	90	−1.19	0.24	Logistic regression
Species	–	–	3	4.24	0.24	χ^2
Age (juvenile/adult)	–	–	1	2.79	0.095	χ^2
Departure time group	–	–	2	10.15	0.006	χ^2
Wind direction, circular (°)	273 (62.5)°	221 (60.8)°	19	0.21	<0.05	Watson U^2
Departure time, circular (hours)[b]	20:27 (01:53)	20:36 (04:35)	19	0.22	<0.05	Watson U^2
Departure direction, circular (°)[b]	138 (52.5)°	141 (82.1)°	–	895	0.040	Wilcoxon rank sum[c]

[a] Test statistics differ depending on the statistical method: *z* for logistic regressions, χ^2 for chi-square tests, U^2 for Watson U^2-tests and *W* for Wilcoxon rank sum test.
[b] Significant difference in scatter but not in mean.
[c] The ranking in the Wilcoxon rank sum test is circular, see text.

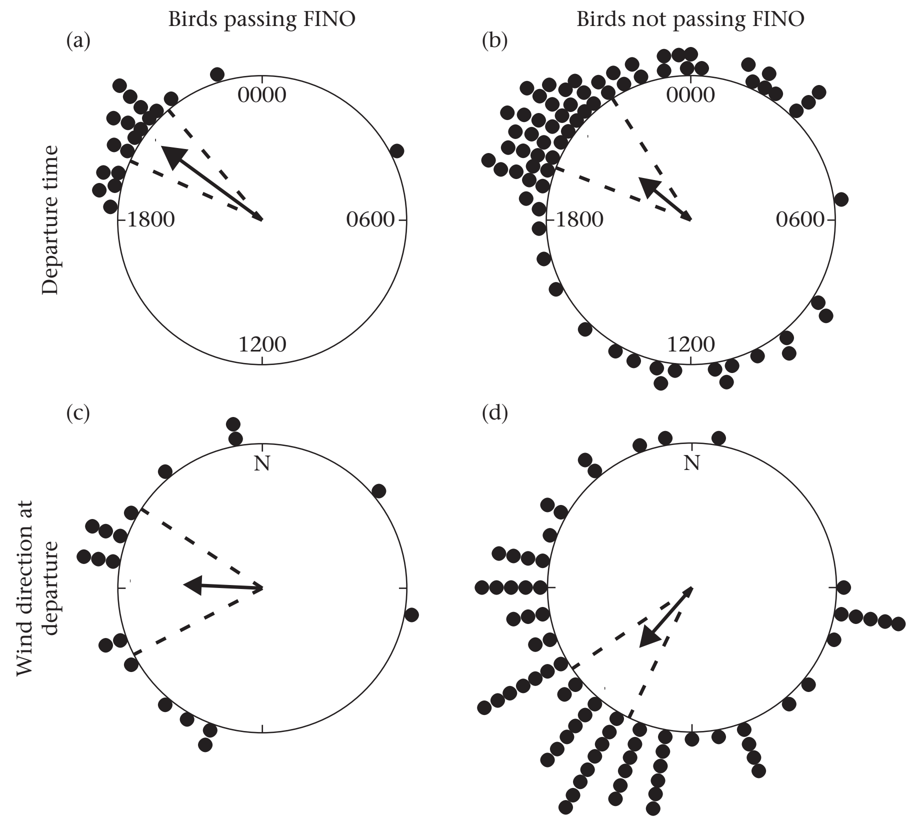

Figure 2. Departure time for birds that (a) passed and (b) did not pass FINO 2. (c) Wind direction at the time of departure for birds that later flew past FINO 2 and (d) for birds that did not fly this route. The arrow indicates the circular mean and the length of each arrow is a measure of concentration (r) drawn relative to the radius of the circle. Broken lines give ±95% confidence intervals.

the distance to FINO 2) and the observed resulting ground speed (or observed flight duration) (Table 4). This suggests that the birds were flying relatively straight and directly to FINO 2, making the expected ground speed along the track direction to FINO 2 the clearly dominating predicting variable for the duration of this flight. After taking the effect of wind into account (incorporated in the expected flight time to FINO 2), we found significant additional effects of fat score and cloud cover on flight time. Birds with a higher fat score at release flew faster from Falsterbo to FINO 2. Cloud cover had a negative effect on flight duration with longer flights under overcast conditions.

DISCUSSION

Departure Conditions Associated with Passage of FINO 2

The probability that the birds chose the longer passage across the Baltic Sea (within the receiving range of FINO 2) increased with westerly winds and with a relatively early departure time after sunset. We also found a tendency for a higher proportion of adults to fly this route compared to juveniles..

Wind direction

We found a significant influence of wind direction on the probability of nocturnal songbirds flying across the Baltic Sea in a southeasterly direction from Falsterbo, and thereby to undertake a longer sea crossing. Westerly winds probably cause the birds to drift from primary south to southwesterly to more southeasterly migratory directions, leading to a longer sea crossing. This finding stresses the fundamental importance of winds for the flight

Table 2
Final logistic regression of factors affecting the probability of birds passing FINO 2

	df	Deviance/χ^2	Residual *df*	Residual deviance	*P*
Departure time group	2	13.53	88	79.72	0.001
Age (juvenile/adult)	1	2.61	87	77.11	0.11
North/south wind component	1	6.93	86	70.18	0.009

Likelihood ratio chi-square test results for the final logistic regression model elimination performed by backward/forward elimination according to AIC criteria. AIC = 80.18, $N = 91$. Note that the test is sequential.

Table 3
Test of possible associations between different factors and the observed flight time between Falsterbo and FINO 2

	df	F/R^2 [a]	*P*	Test
Age (juvenile/adult)	1	0.48	0.45	ANOVA
Species	3	0.079	0.97	ANOVA
Fat score at release (0–8)	1, 17	0.025	0.51	Linear regression
Body mass relative to expected size-specific fat-free body mass	1, 17	0.002	0.86	Linear regression
Visibility (km)	1, 17	0.002	0.85	Linear regression
Departure direction, deviance from direction towards FINO 2 (°)	1, 17	0.015	0.62	Linear regression
Degree of overcast (0–8)	1, 17	0.20	0.058	Linear regression
Expected time to FINO 2 (min)	1, 17	0.48	0.001	Linear regression

For means ± SD see Table 2.
[a] The test statistics vary between statistical methods: F for ANOVA tests, R^2 for linear regressions.

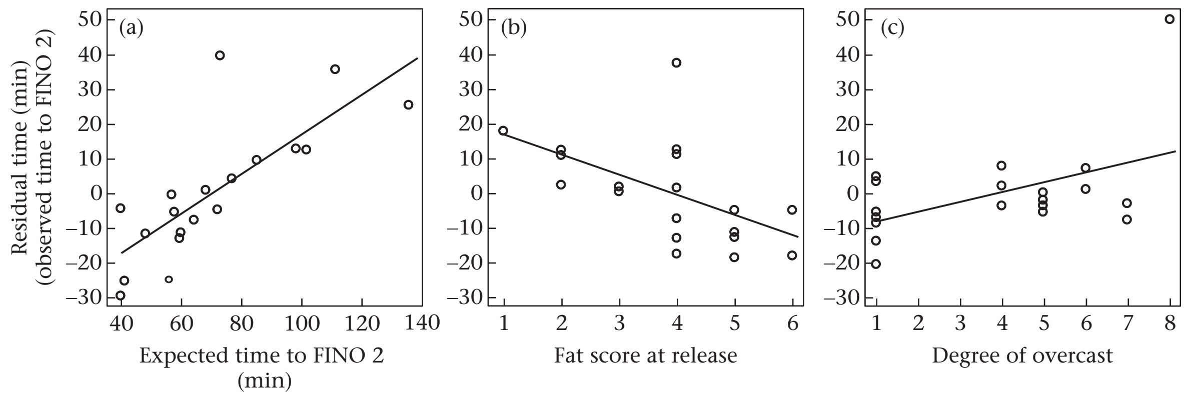

Figure 3. Relation between observed flight time to FINO 2 and (a) expected time to FINO 2 (as calculated from the surface wind situation at departure, assuming a straight flight path), (b) fat score at release (estimated on a 0–9 visual scale; Appendix Fig. A1) and (c) degree of overcast at departure (0/8 = clear sky, 8/8 = total overcast; Table 4). The plots show residual times (min) after taking into account the effects of the complementary variables.

Table 4
Final GLM of factors affecting the observed flight time between Falsterbo and FINO 2

	SE	*T*	*P*
(Intercept)	697.63	3.71	0.002
Expected time to FINO 2	0.13	4.49	<0.001
Fat score at release	2.34	−2.48	0.026
Degree of overcast	1.34	2.17	0.046

Results from the final GLM elimination performed by backward/forward elimination according to AIC criteria. AIC = 157.75, $N = 19$.

performance of migratory birds (e.g. Alerstam, 1979; Richardson, 1978, 1990).

Timing of departure

All but one of the birds flying the southeast route past FINO 2 departed from Falsterbo early in the night, i.e. after sunset but before midnight. These early departures indicate that it was not solely the westerly winds that caused the route choice; the fact that they all left early could be an indication that they were aware that a long flight was coming. Similar observations have been made in northern wheatears, *Oenanthe oenanthe*, departing from Helgoland, Germany, on their way to their breeding grounds in Greenland (Schmaljohann & Naef-Daenzer, 2011). In this study the northern wheatears that departed in directions leading to longer trans-Atlantic flights left earlier than birds heading for the closer mainland.

The concentrated departure times support the idea that birds perform different migratory behaviours at different times during the night. Departures on longer flights (across the sea) may mainly occur early in the night, while more local movements, at times directed opposite to the expected migratory direction, may be initiated later in the night (Mills et al., 2011). This also agrees well with the more accepted suggestion that movements during daytime mostly refer to searching for better feeding habitats (Newton, 2008). However, nocturnal departure timing varies considerably between species and locations, and may be influenced by timing of migration (spring and autumn), weather (visibility and winds) and body condition of the birds (Åkesson & Hedenström, 2000; Åkesson, Alerstam, et al., 1996; Åkesson, Karlsson, et al., 1996, 2001, 2002; Bolshakov et al., 2007; Bulyuk & Tsvey, 2006; Sandberg, Pettersson, & Alerstam, 1988; Schmaljohann & Naef-Daenzer, 2011).

Age

We predicted that more experienced, adult birds would fly longer distances over the open sea, and thus be more likely to pass FINO 2, while inexperienced, juvenile individuals take the shorter routes to cross unfavourable habitats as quickly as possible (Smolinsky et al., 2013). The Baltic Sea is the first major obstacle that the birds face during autumn migration in this area, thus could be expected to have a larger impact on migration decisions of inexperienced juvenile birds. However, we found only a weak trend for the more experienced adults to take the longer southeast route. Thus, our observation could not further support the findings of Smolinsky et al. (2013).

Other factors

Unexpectedly, we found no difference in initial departure direction between the groups of birds that did and did not pass FINO 2 (Fig. 1). The departure directions of the group of birds that did not fly past FINO 2, however, were more scattered and the birds faced more southerly winds, possibly leading them away from FINO 2. In a previous study at Falsterbo in which the departure directions of reed warblers were studied by radiotelemetry in autumn, the departing birds were selective in terms of departure relative to winds (preferred tail winds), and they also seemed to compensate for wind drift at their immediate departures (Åkesson et al., 2002). This suggests wind-selective departures at Falsterbo, but also that wind drift may occur during migratory flights across open water at later stages when the visual contact with the nearest land is difficult to maintain, which is the case in birds passing FINO 2 in our study. Contrary to the earlier findings that birds carrying more fuel are more prone to initiate cross-barrier flights (Schmaljohann et al., 2011; Schmaljohann & Naef-Daenzer, 2011; Smolinsky et al., 2013), we found no effect of fat score at release, or body mass relative to size-specific fat-free body mass, on the probability of a longer sea crossing. This might be because we chose not to tag very lean individuals (no individuals with fat score = 0, two individuals with fat score = 1) and most individuals in our sample were expected to have enough fuel even for the longer crossings of the Baltic Sea from Falsterbo (associated with flights over open sea for up to 100 km).

Flights Between Falsterbo and FINO 2

The flight duration from Falsterbo to FINO 2 was, as expected, highly correlated with the expected flight duration (as based on the calculated expected ground speed). The expected flight duration is a factor combining the effect of body size on speed (being calculated by assuming higher airspeeds for the larger species; Bruderer & Boldt, 2001) and the much larger wind effect. Interestingly, after we took the expected flight duration into account, our results revealed a negative effect of fat score at release and a positive effect of overcast conditions on the flight time to FINO 2. The strong correlation between the observed and the expected flight times (calculated using a straight loxodrome course) between Falsterbo and FINO 2 suggests that the birds flew a relatively straight flight path. It further indicates that the possible errors in flight distance (since not all birds flew the same path) were probably small.

Wind Support

Since the variation in expected ground speed is mostly determined by changing wind conditions, the observed effect of expected flight time on the observed flight time is equivalent to concluding that wind conditions were of greatest importance for the flight duration to FINO 2. This effect of wind support on ground speed is expected with straight and direct flights (Liechti & Bruderer, 1998), and clearly illustrates the impact of winds on avian migration.

Fat score

Birds that had more stored fat at release flew faster to FINO 2, which supports our expectations, and agrees with earlier field and experimental studies showing that fat birds are more motivated to depart in the migratory direction (Deutschlander & Muheim, 2009; Sandberg & Moore, 1996; Schmaljohann et al., 2011; Schmaljohann & Naef-Daenzer, 2011; Smolinsky et al., 2013). However, to our knowledge, this is the first study observing the effect of fat on flight speed in free-flying songbirds. The result supports earlier findings on brent geese, *Branta b. bernicla*, that migrated at higher airspeeds during spring than autumn migration, possibly as a result of their substantially higher body mass during spring (Green & Alerstam, 2000). Fat score, like fat mass, is known to be related to body mass (Pettersson & Hasselquist, 1985; Wojciechowski, Yosef, & Pinshow, 2014). The observed increase in speed relative to the amount of stored fat could partly be explained by aerodynamic theory, with heavier birds flying at a slightly higher airspeed (Karlsson, Nilsson, Bäckman, & Alerstam, 2012; Pennycuick, 2008). An increase in body mass of approximately 10% per fat score (Pettersson & Hasselquist, 1985) is expected to lead to an increase in speed of approximately 3% per fat score (Karlsson et al., 2012). This would result in a reduction in flight duration between Falsterbo and FINO 2 of about 2.6 min per unit of fat score for European robins, willow warblers and garden warblers with an expected flight speed of 10 m/s and a reduction in flight duration of 2.0 min per unit of fat score for song thrushes with the expected flight speed of 13 m/s. However, we observed a much larger reduction in flight duration in relation to increasing fat score, about 5.4 min per unit of fat score (based on the slope of the linear regression in Fig. 3b). Hence, it is likely that additional behavioural differences between lean and fat individuals, apart from the mass-dependent difference in airspeed, explain the observed pattern of flight durations in our study. Birds with the largest fuel reserves may be more risk-prone and depart straight and directly across the Baltic Sea, while birds with smaller fuel reserves may be more reluctant to leave the vicinity of land, which will lead to a longer flight duration to reach 50 km offshore. This is further supported by the fact that body mass relative to size-specific fat-free body mass neither improved the model nor showed a significant relationship with flight duration, if used to replace fat score (model including relative body mass: AIC = 164.24; model including fat score: AIC = 157.75). In addition, birds with more fat might have, for some reason, migrated at higher altitudes. A higher flight altitude would provide flying birds with air of lower density, causing them to fly at a slightly higher airspeed to maintain height (Pennycuick, 2008). Furthermore, birds have been shown to be selective for favourable wind conditions once aloft (Bruderer, Underhill, & Liechti, 1995); thus the reason for a higher flight altitude may be more favourable wind conditions. However, fat score at release as a measure of stored energy at departure is not ideal, since it is expected to change before departure. Thus, it would be interesting to further explore this difference in flight speed between lean and fat birds with a more accurate measure of fuel stores at departure. Still, most of our birds left Falsterbo the first or second night after release (10 and three, respectively, of the 19 individuals); thus their fuel stores and body mass probably did not change significantly during their stay in Falsterbo.

Overcast

The observed effect of cloud cover leading to longer flight times agrees well with observations in white-throated sparrows tracked by radar that found a reduction in airspeed and less straight flight under overcast skies (Emlen & Demong, 1978). However, it is difficult to determine the reason for this behavioural change under overcast weather situations, i.e. whether it is caused by low motivation to fly in the migratory direction when the weather is not ideal, or whether it is due to difficulties in adjusting the flight heading under unfavourable conditions for orientation and problems in keeping a fixed heading.

Conclusion

As predicted, we found that environmental conditions had a significant effect on the probability that birds performed a longer flight over the Baltic Sea than necessary. Westerly winds drifted the birds and led them on the longer southeast route over the Baltic Sea. Furthermore, we found a difference in departure time, with the birds passing the offshore station departing on average earlier than birds following other routes, indicating that they were aware that they departed on a long flight. Contrary to our predictions, we did not find any significant effects of individual characteristics, even though there was a tendency for an age effect in the most parsimonious model describing which birds took the route via FINO 2.

The flight duration between Falsterbo and the offshore receiver station at FINO 2 was, as predicted, primarily affected by winds, with tail winds clearly reducing flight duration. Additionally, we found an effect of fat score at release and on the degree of overcast. Birds with larger fuel reserves and birds that departed under clear skies flew faster from Falsterbo to FINO 2, possibly as a result of lean birds hesitating, and overcast skies causing difficulties in maintaining a constant heading, resulting in winding flight paths.

Acknowledgments

We are grateful for the help and valuable input from Falsterbo Bird Observatory and for the technical support from Johan Bäckman and Arne Andersson from the Center of Animal Movement Research (CAnMove). We thank Phil Taylor for help and advice concerning analyses of the radiotelemetry data and Tom Evans for comments on the manuscript. We also thank Kai Brosda, Christoph Kulemeyer, Konrad Schleicher, the team at DNV GL 'and ham radio operator Peter Neumann (DL1NRC)' for technical support during installation of the receiver equipment on FINO 2. This work was financially supported by grants from the Swedish Research Council (2007-5700 to R.M., 621-2010-5584 & 621-2013-4361 to S.Å. & 2009-3589 to T.A.), from the Royal Physiographical Society in Lund, The Crafoord Society (20110945) and from Lunds djurskyddsfond. The project received financial support from a Linnaeus grant (no. 349-2007-8690) to the Centre of Animal Movement Research from the Swedish Research Council and Lund University. Research on

FINO 2 was funded by the German Federal Ministry for the Environment, Nature Conservation, Building and Nuclear Safety (BMUB) until 2013 and by the Federal Ministry for Economic Affairs and Energy (BMWi) thereafter. This is report number 295 from Falsterbo Bird Observatory.

References

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control, 19*, 716–723.

Åkesson, S. (1999). Do passerine migrants captured at an inland site perform temporary reverse migration in autumn? *Ardea, 87*, 129–138.

Åkesson, S., Alerstam, T., & Hedenström, A. (1996). Flight initiation of nocturnal passerine migrants in relation to celestial orientation conditions at twilight. *Journal of Avian Biology, 27*(2), 95–102. http://www.jstor.org/stable/10.2307/3677138.

Åkesson, S., & Hedenström, A. (2000). Wind selectivity of migratory flight departures in birds. *Behavioral Ecology and Sociobiology, 47*(3), 140–144. http://dx.doi.org/10.1007/s002650050004.

Åkesson, S., Karlsson, L., Walinder, G., & Alerstam, T. (1996). Bimodal orientation and the occurrence of temporary reverse bird migration during autumn in south Scandinavia. *Behavioral Ecology and Sociobiology, 38*(5), 293–302. http://dx.doi.org/10.1007/s002650050245.

Åkesson, S., Klaassen, R., Holmgren, J., Fox, J. W., & Hedenström, A. (2012). Migration routes and strategies in a highly aerial migrant, the common swift *Apus apus*, revealed by light-level geolocators. *PloS One, 7*(7), e41195. http://dx.doi.org/10.1371/journal.pone.0041195.

Åkesson, S., Walinder, G., Karlsson, L., & Ehnbom, S. (2001). Reed warbler orientation: initiation of nocturnal migratory flights in relation to visibility of celestial cues at dusk. *Animal Behaviour, 61*(1), 181–189. http://dx.doi.org/10.1006/anbe.2000.1562.

Åkesson, S., Walinder, G., Karlsson, L., & Ehnbom, S. (2002). Nocturnal migratory flight initiation in reed warblers *Acrocephalus scirpaceus*: effect of wind on orientation and timing of migration. *Journal of Avian Biology, 33*(4), 349–357. http://dx.doi.org/10.1034/j.1600-048X.2002.02951.x.

Alerstam, T. (1978). Reoriented bird migration in coastal areas: dispersal to suitable resting grounds? *Oikos, 30*(2), 405–408. http://www.jstor.org/stable/10.2307/3543491.

Alerstam, T. (1979). Wind as selective agent in bird migration. *Ornis Scandinavica, 10*(1), 76–93. http://www.jstor.org/stable/3676347.

Alerstam, T. (2001). Detours in bird migration. *Journal of Theoretical Biology, 209*(3), 319–331. http://dx.doi.org/10.1006/jtbi.2001.2266.

Alerstam, T., & Hedenström, A. (1998). The development of bird migration theory. *Journal of Avian Biology, 29*(4), 343–369. http://www.jstor.org/stable/10.2307/3677155.

Alerstam, T., & Lindström, Å. (1990). Optimal bird migration: the relative importance of time, energy and safety. In E. Gwinner (Ed.), *Bird migration: Physiology and ecophysiology* (pp. 331–351). Berlin, Germany: Springer.

Bolshakov, C. V., Chernetsov, N., Mukhin, A., Bulyuk, V. N., Kosarev, V., Ktitorov, P., et al. (2007). Time of nocturnal departures in European robins, *Erithacus rubecula*, in relation to celestial cues, season, stopover duration and fat stores. *Animal Behaviour, 74*(4), 855–865. http://dx.doi.org/10.1016/j.anbehav.2006.10.024.

Bruderer, B., & Boldt, A. (2001). Flight characteristics of birds: I. radar measurements of speeds. *Ibis, 143*, 178–204.

Bruderer, B., Underhill, L., & Liechti, F. (1995). Altitude choice by night migrants in a desert area predicted by meteorological factors. *Ibis*, 44–55. http://onlinelibrary.wiley.com/doi/10.1111/j.1474-919X.1995.tb03218.x/full.

Bulyuk, V. N., & Tsvey, A. (2006). Timing of nocturnal autumn migratory departures in juvenile European robins (*Erithacus rubecula*) and endogenous and external factors. *Journal of Ornithology, 147*(2), 298–309. http://dx.doi.org/10.1007/s10336-005-0046-0.

Cochran, W. W. (1980). Wildlife telemetry. In S. D. Schemnitz (Ed.), *Wildlife management techniques manual* (pp. 507–520). Washington DC: The Wildlife Society.

Cramp, S. (Ed.). (1988). *Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic: Tyrant flycatchers to thrushes* (Vol. 5). Oxford, U.K: Oxford University Press.

Cramp, S. (Ed.). (1992). *Handbook of the birds of Europe, the Middle East and North Africa: The birds of Western Palearctic: Warblers* (Vol. 6). Oxford, U.K: Oxford University Press.

Deutschlander, M. E., & Muheim, R. (2009). Fuel reserves affect migratory orientation of thrushes and sparrows both before and after crossing an ecological barrier near their breeding grounds. *Journal of Avian Biology, 40*(1), 85–89. http://dx.doi.org/10.1111/j.1600-048X.2008.04343.x.

Emlen, S. T., & Demong, N. J. (1978). Orientation strategies used by free-flying bird migrants: a radar tracking study. In K. Schmidt-Koenig, & W. T. Keeton (Eds.), *Animal migration, navigation and homing* (pp. 283–293). Heidelberg, Germany: Springer-Verlag.

Fransson, T., & Karlsson-Hall, S. (2008). *Svensk Ringmärkningsatlas. Tättingar* (Vol. 3). Stockholm, Sweden: SOF förlag.

Green, M., & Alerstam, T. (2000). Flight speeds and climb rates of Brent geese: mass-dependent differences between spring and autumn migration. *Journal of Avian Biology, 2*(ii), 215–225. http://onlinelibrary.wiley.com/doi/10.1034/j.1600-048X.2000.310213.x/full.

Hedenström, A., & Alerstam, T. (1997). Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. *Journal of Theoretical Biology, 189*(3), 227–234. http://dx.doi.org/10.1006/jtbi.1997.0505.

Karlsson, L. (2009). *Wings over Falsterbo* (2nd ed.). Falsterbo, Sweden: Falsterbo Bird Observatory.

Karlsson, H., Nilsson, C., Bäckman, J., & Alerstam, T. (2012). Nocturnal passerine migrants fly faster in spring than in autumn: a test of the time minimization hypothesis. *Animal Behaviour, 83*(1), 87–93. http://dx.doi.org/10.1016/j.anbehav.2011.10.009.

Liechti, F., & Bruderer, B. (1998). The relevance of wind for optimal migration theory. *Journal of Avian Biology, 29*(4), 561–568. http://www.jstor.org/stable/10.2307/3677176.

Mills, A. M., Thurber, B. G., Mackenzie, S. A., & Taylor, P. D. (2011). Passerines use nocturnal flights for landscape-scale movements during migration stopover. *Condor, 113*(3), 597–607. http://dx.doi.org/10.1525/cond.2011.100186.

Moore, F. (1984). Age-dependent variability in the migratory orientation of the Savannah Sparrow (*Passerculus sandwichensis*). *The Auk, 101*(4), 875–880. http://www.jstor.org/stable/4086916.

Newton, I. (2006). Can conditions experienced during migration limit the population levels of birds? *Journal of Ornithology, 147*(2), 146–166. http://dx.doi.org/10.1007/s10336-006-0058-4.

Newton, I. (2008). *The migration ecology of birds* (1st ed.). London, U.K: Academic Press.

Pennycuick, C. J. (2008). *Modelling the flying bird* (1st ed.). Amsterdam, Netherlands: Academic Press.

Pettersson, J., & Hasselquist, D. (1985). Fat deposition and migration capacity of robins *Erithacus rebecula* and goldcrests *Regulus regulus* at ottenby, Sweden. *Ringing & Migration, 6*(2), 66–76. http://dx.doi.org/10.1080/03078698.1985.9673859.

Richardson, W. (1978). Timing and amount of bird migration in relation to weather: a review. *Oikos, 30*(2), 224–272. http://www.jstor.org/stable/10.2307/3543482.

Richardson, W. (1990). Wind and orientation of migrating birds: a review. *Experientia, 46*, 416–425. http://link.springer.com/article/10.1007/BF01952175.

Sandberg, R., & Moore, F. (1996). Migratory orientation of red-eyed vireos, *Vireo olivaceus*, in relation to energetic condition and ecological context. *Behavioral Ecology and Sociobiology, 39*(1), 1–10. http://www.springerlink.com/index/KUB3G6WH1WWMR7CW.pdf.

Sandberg, R., Pettersson, J., & Alerstam, T. (1988). Why do migrating robins, *Erithacus rubecula*, captured at two nearby stop-over sites orient differently? *Animal Behaviour, 36*, 865–876. http://www.sciencedirect.com/science/article/pii/S0003347288801696.

Sandberg, R., Pettersson, J., & Persson, K. (1991). Migratory orientation of free-flying robins *Erithacus rubecula* and pied flycatchers *Ficedula hypoleuca*: release experiments. *Ornis Scandinavica, 22*(1), 1–11. http://www.jstor.org/stable/3676615.

Schaub, M., & Jenni, L. (2001). Variation of fuelling rates among sites, days and individuals in migrating passerine birds. *Functional Ecology, 15*(5), 584–594. http://dx.doi.org/10.1046/j.0269-8463.2001.00568.x.

Schmaljohann, H., Becker, P. J. J., Karaardic, H., Liechti, F., Naef-Daenzer, B., & Grande, C. (2011). Nocturnal exploratory flights, departure time, and direction in a migratory songbird. *Journal of Ornithology, 152*(2), 439–452. http://dx.doi.org/10.1007/s10336-010-0604-y.

Schmaljohann, H., & Naef-Daenzer, B. (2011). Body condition and wind support initiate the shift of migratory direction and timing of nocturnal departure in a songbird. *Journal of Animal Ecology, 80*(6), 1115–1122. http://dx.doi.org/10.1111/j.1365-2656.2011.01867.x.

Smolinsky, J. A., Diehl, R. H., Radzio, T. A., Delaney, D. K., & Moore, F. R. (2013). Factors influencing the movement biology of migrant songbirds confronted with an ecological barrier. *Behavioral Ecology and Sociobiology, 67*(12), 2041–2051. http://dx.doi.org/10.1007/s00265-013-1614-6.

Stutchbury, B. J. M., Tarof, S. A., Done, T., Gow, E., Kramer, P. M., Tautin, J., et al. (2009). Tracking long-distance songbird migration by using geolocators. *Science (New York, N.Y.), 323*(5916), 896. http://dx.doi.org/10.1126/science.1166664.

Svensson, L. (1992). *Identification guide to European Passerines* (4th ed.). Södertälje, Sweden: Fingraf AB.

Taylor, P. D., Mackenzie, S. A., Thurber, B. G., Calvert, A. M., Mills, A. M., McGuire, L. P., et al. (2011). Landscape movements of migratory birds and bats reveal an expanded scale of stopover. *PloS One, 6*(11), e27054. http://dx.doi.org/10.1371/journal.pone.0027054.

Wikelski, M., Tarlow, E. M., Raim, A., Diehl, R. H., Larkin, R. P., & Visser, G. H. (2003). Costs of migration in free-flying songbirds. *Nature, 423*, 704.

Wojciechowski, M. S., Yosef, R., & Pinshow, B. (2014). Body composition of north and southbound migratory blackcaps is influenced by the lay-of-the-land ahead. *Journal of Avian Biology, 45*(3), 264–272. http://dx.doi.org/10.1111/j.1600-048X.2013.00345.x.

Woodworth, B. K., Francis, C. M., & Taylor, P. D. (2014). Inland flights of young red-eyed vireos *Vireo olivaceus* in relation to survival and habitat in a coastal stopover landscape. *Journal of Avian Biology, 45*(4), 387–395. http://dx.doi.org/10.1111/jav.00276.

Zehnder, S., Åkesson, S., Liechti, F., & Bruderer, B. (2001). Nocturnal autumn bird migration at Falsterbo, South Sweden. *Journal of Avian Biology, 32*(3), 239–248. http://dx.doi.org/10.1111/j.0908-8857.2001.320306.

Appendix

Table A1
Positions of the radiotelemetry towers, including distance and direction to the station at FINO 2

Radiotelemetry station	Latitude (°)	Longitude (°)	Distance to FINO 2 (km)	Direction to FINO 2 (°)
Lighthouse, Falsterbo	55.384	12.817	47	153
Water tower, Falsterbo/Skanör	55.404	12.845	48	156
Farm, Falsterbo/ Skanör	55.429	12.852	51	158
FINO 2, the Baltic Sea	55.007	13.154	–	–

Distances and directions to FINO 2 are calculated using a loxodrome course.

Table A2
Observed and calculated flight behaviours for individuals that were recorded flying between Falsterbo and FINO 2.

Species	Age (calendar year)	Observed			Calculated		
		Departure direction (°)	Observed time to FINO 2 (min)	Observed ground speed[a] (m/s)	Expected time to FINO 2 (min)	Expected ground speed (m/s)	Expected heading (°)
European robin	3+	142	93.5	9.1	98.3	8.6	167
European robin	2	131	62.1	12.6	59.3	13.2	229
Garden warbler	1	161	75.9	10.3	101.6	7.7	163
Garden warbler	1	98	79.2	9.9	77.0	10.2	147
Song thrush	2	39	64.3	12.2	67.9	11.5	165
Song thrush	1	68	33.7	23.2	40.0	19.6	170
Song thrush	1	177	123.3	6.4	72.7	10.8	168
Song thrush	1	62	69.3	11.3	48.1	16.3	209
Song thrush	3+	98	100.4	8.0	135.4	5.9	215
Song thrush	2	140	56.0	15.2	56.1	15.2	199
Song thrush	2	190	61.5	12.7	41.1	19.1	228
Song thrush	2	129	58.9	13.3	39.7	19.7	167
Song thrush	3+	167	70.4	11.1	64.4	12.2	172
Willow warbler	2	140	53.1	16.0	72.1	11.8	180
Willow warbler	1	211	99.1	8.1	85.0	9.4	151
Willow warbler	2	216	60.8	13.2	59.8	13.4	217
Willow warbler	1	127	60.2	13.0	56.9	13.8	146
Willow warbler	2	216	60.9	13.1	57.8	13.8	150
Willow warbler	2	92	99.1	7.9	111.1	7.1	202

The calculated values depend on the wind situation when the birds were leaving Falsterbo, taking into account the distance and direction to FINO 2 from the last radiotelemetry station in Falsterbo that was in contact with the bird, and assuming a straight loxodrome course as track direction for the flight between Falsterbo and FINO 2.
[a] Observed ground speed is the distance to FINO 2 (Table 1) divided by the flight time to FINO 2.

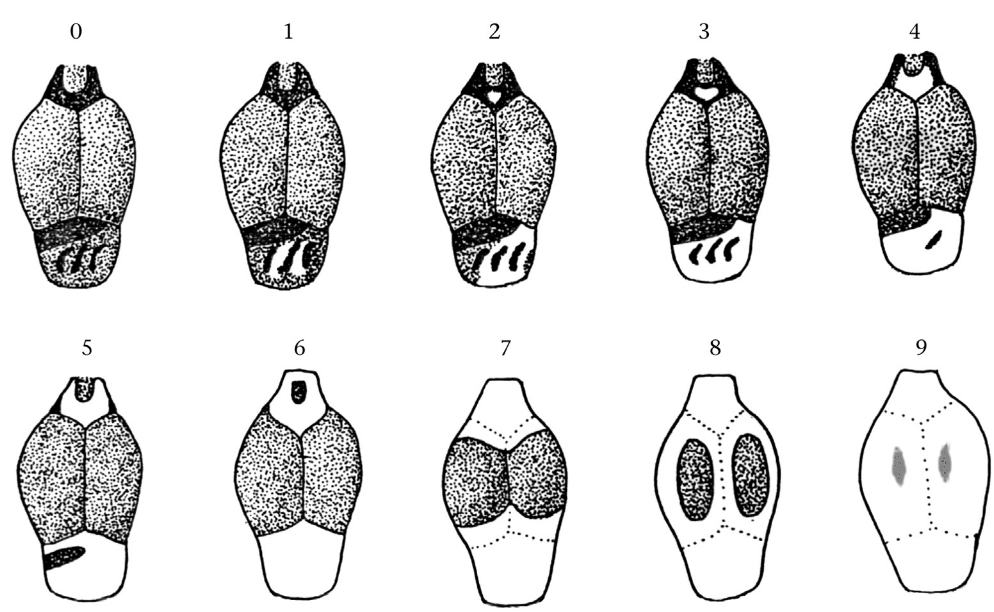

Figure A1. Illustration of the extended fat scale used at Falsterbo Bird Observatory. View from below; white areas represent fat deposits, dotted areas muscles and blackish areas digestive and other organs. Drawing by Susanne Åkesson & Falsterbo Bird Observatory.