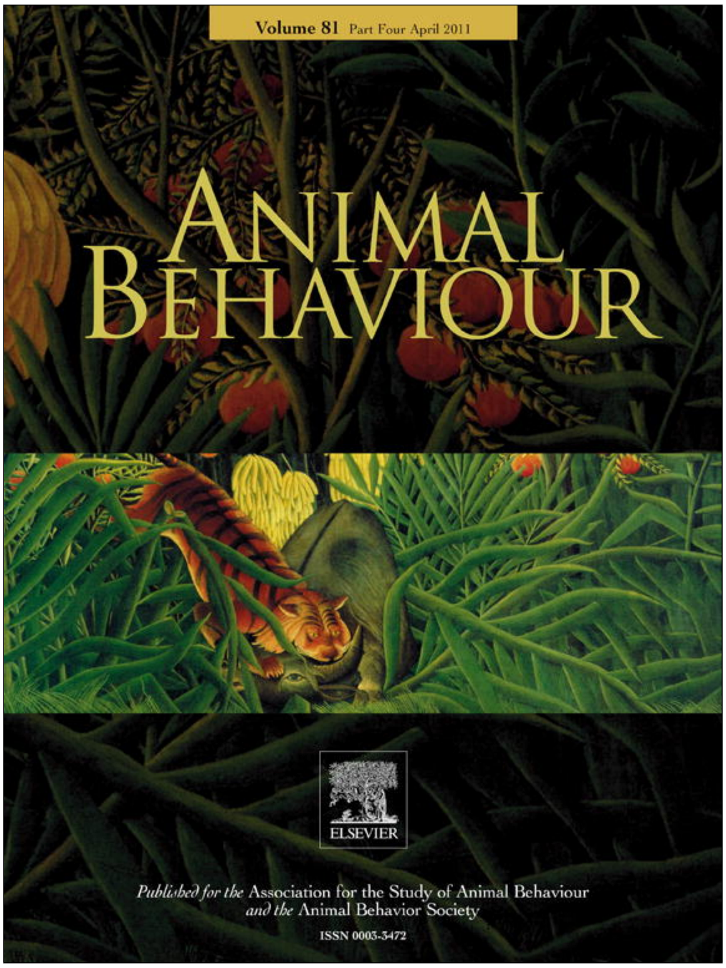
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Atmospheric conditions facilitate mass migration events across the North Sea

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Crossing large bodies of water can be extremely risky for terrestrial migrants and yet such migrants have been observed to cross hundreds and even thousands of kilometres of water. However, the mechanisms that enable nocturnal migrants to cross large bodies of water successfully remain unclear. In the north of the Netherlands, autumn migration of birds occurs mainly along a southwesterly axis and can be predicted very successfully. However, on rare occasions, intense and unexpected migration events occur with a significantly different track direction. We hypothesized that these events represent birds arriving from Norway and other Scandinavian countries after crossing the North Sea barrier. We implemented a back-trajectory model calibrated with radar data from autumn 2006–2008 to test our hypothesis, assuming that birds maintain a constant heading and airspeed during flight. A total of 14 events were identified. In some cases measured mean ground speeds were twice as high as mean airspeeds. Model results demonstrated that birds took advantage of atmospheric conditions to cross the North Sea quickly. In the majority of cases, birds could be tracked to Norway, Denmark or Sweden when maintaining a constant airspeed and heading en route, but not in all cases. Thus migrants must be flexible in their reaction to wind to take advantage of dynamic and heterogeneous atmospheric conditions experienced en route. The integration of measurements with simulation modelling provides a powerful framework to improve our understanding of how animals move through a dynamic environment and the consequences of their behaviour.

Flying across large bodies of water during migration can be extremely risky for terrestrial invertebrates and vertebrates (e.g. Dingle 1996). Nevertheless, terrestrial birds are known regularly to cross large expanses of water such as the Mediterranean Sea (e.g. Casement 1966; Bruderer & Liechti 1998; Fortin et al. 1999), the North Sea (e.g. Lack 1963; Myres 1964; Buurma 1987; Hüppop et al. 2006), the Gulf of Mexico (e.g. Moore & Kerlinger 1987; Gauthreaux et al. 2006; Stutchbury et al. 2009) and the North Atlantic (e.g. Stoddard et al. 1983; Williams & Williams 1990; Nisbet et al. 1995). Perhaps the most striking nonstop avian flight across water is that of the bar-tailed godwits, *Limosa lapponica*, crossing over 10 000 km of the Pacific Ocean (Gill et al. 2009). Crossing large expanses of water, whether several thousand or several hundred kilometres, is often associated with a potential risk of exhaustion for land birds, especially if birds encounter unfavourable atmospheric conditions en route. To avoid potential risks, some studies have shown that birds may time sea crossings with favourable winds, reducing the risk of running into adverse weather and running out of fuel en route (e.g. Williams & Williams 1990; Gill et al. 2009). Birds have also been known to conduct reverse migration (returning to the direction of departure) after initiating a sea crossing, particularly late at night (e.g. Bruderer & Liechti 1998; Fortin et al. 1999; Hüppop et al. 2006), when the risk is apparently too high to cross the sea successfully.

Wind has a strong influence on avian decisions during migration and resulting migratory patterns (e.g. Alerstam 1979; Richardson 1990; Liechti 2006) and dynamic concept-driven models that follow the Lagrangian approach (Turchin 1998) are particularly useful in quantifying the effect wind may have on migrants during flight (e.g. Erni et al. 2005; Vrugt et al. 2007; Shamoun-Baranes et al. 2010a). For example, Stoddard et al. (1983) simulated flights of migrating passerines and shorebirds over the western North Atlantic Ocean from different sites along the coast of North America to sites in the Caribbean, incorporating dynamic wind conditions en route. Their study showed that under appropriate wind conditions, birds could successfully reach known stopover sites while maintaining a constant heading and airspeed set at departure and allowing for drift (the displacement of birds by wind) while crossing the ocean.

In the Netherlands, migration has been systematically monitored with military long-range surveillance radar to provide the

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Netherlands and NATO air forces with bird migration warnings to reduce the risk of bird–aircraft collisions (Buurma 1995; van Belle et al. 2007; Shamoun-Baranes et al. 2008). Several migratory axes are observed crossing the Netherlands, the most prominent flyway in terms of numbers and frequency of occurrence being the southwest–northeast broad front flyway between Western Europe and Scandinavia (Buurma 1995; van Belle et al. 2007). On several occasions each autumn, mass migration in southerly directions is detected over the North Sea, north of the Dutch Wadden Sea Islands (Fig. 1). However, these mass migration events have been difficult to predict in an operational setting (van Belle et al. 2007). Several hypotheses have been proposed to explain the migratory patterns observed over the North Sea (e.g. Myres 1964; Bourne 1980; Buurma 1987). For example, Buurma (1987) suggested that these events represent birds departing predominantly from Norway and migrating to wintering areas in the United Kingdom in two steps, requiring an initial sea crossing of approximately 500 km, which is comparable to crossing the Mediterranean Sea in many areas.

In this study we developed a back-trajectory model incorporating actual wind conditions, to simulate nocturnal migration over the North Sea and parameterized the model with airspeeds and headings measured off the northern coast of the Netherlands. As supported by other studies, our model assumes that birds calibrate their compass at dusk (and dawn; e.g. Cochran et al. 2004; Muheim et al. 2006, 2009) and set an airspeed and heading at the onset of migration, which they maintain over sea throughout the night (e.g. Stoddard et al. 1983; Liechti 1995; Green & Alerstam 2002). Thus their trajectory over the course of the night is determined in part by drift. We used the combination of radar measurements and simulation modelling to address two aims. We investigated the hypothesis that migrants with southerly headings observed off the northern North Sea coast of the Netherlands had predominantly departed from Norway and other Scandinavian countries several hours before, crossing the North Sea. Our expectation was that these events occur when preferential winds exist along the route. The other aim was to assess the consequences of simple behavioural rules under dynamic environmental conditions to determine whether maintaining a constant airspeed and heading during the course of the night is a viable strategy when crossing the North Sea. We discuss the broader implications of integrating measurements and simulations models following the Lagrangian approach to gain insight into the movement ecology (Nathan et al. 2008) of animals.

METHODS

Medium Power Radar

We used a Thomson CSF stacked beam Medium Power Radar (MPR, Thomson ARES, Thomson ICF, Bagneux, France) from the Royal Netherlands Air Force for bird detection. The radar is located in the north of the Netherlands (53.15°N, 5.37°E; Fig. 1). General characteristics of long-range surveillance radars are their high power and detailed resolution, which make them excellent sensors for detecting individual bird echoes even at long ranges. The lower

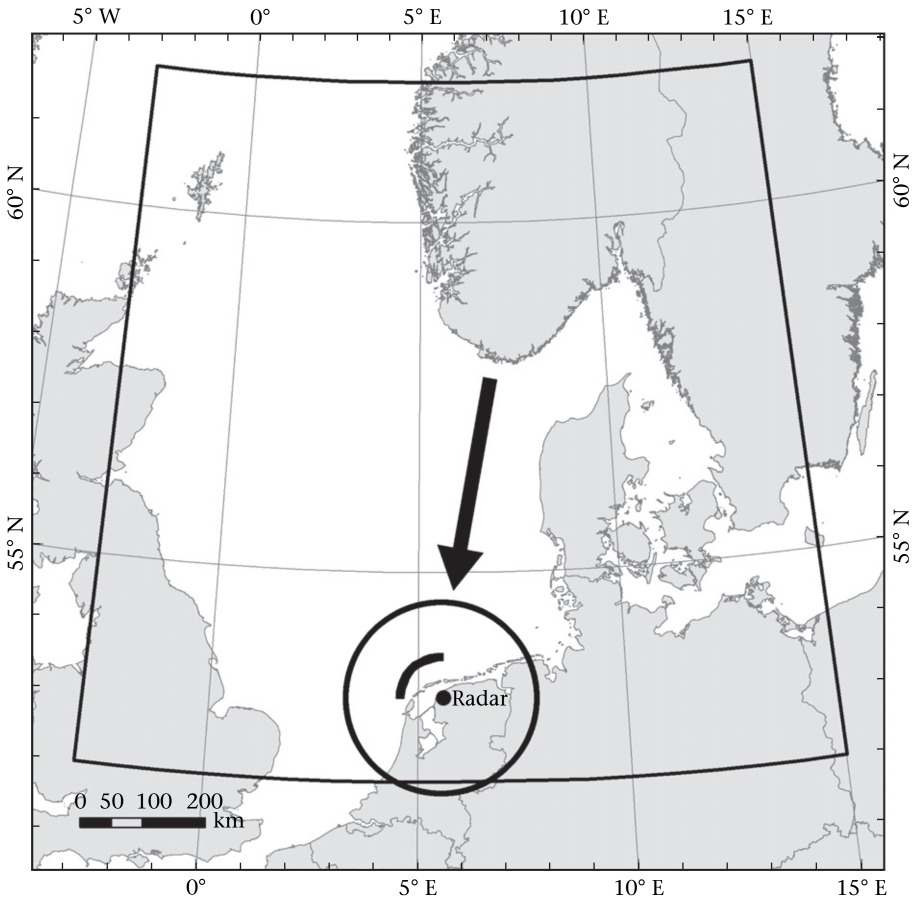

Figure 1. Map of the North Sea study area. The location of the radar in the north of The Netherlands is indicated as well as the 150 km range radar coverage (circle). Within the radar range, the standard measurement window is indicated as a black area northwest of the radar. All tracks 10 km north of the coast of the Wadden Sea Islands were used for the back-trajectory model. The extent of the back-trajectory model was constrained by the rectangle 52°–62°N, 3°W–15°E. The shortest route between Norway and the radar location is 540 km following a 190° track direction (shown by arrow).

two beams (beam width 1.2°) of the radar were used, covering the altitude layer of about 100 m up to at least 6 km. At close range even birds at 50 m altitude were detected. Nevertheless, arriving birds could fly below the radar horizon.

Bird echoes are detected and processed by a customized system called the ROBIN system (developed by TNO Defense, Security and Safety, The Hague, The Netherlands). The ROBIN system received the radar signal directly from the antenna output of each beam separately. Dedicated acquisition electronics processed the signal; processing was optimized for bird detection by subtracting the sensitivity time control (which performs a signal-to-range correction caused by ground clutter targets at close range) and false alarm rate (or the radar's own system noise, measured at 500 km range). These dynamic processes resulted in a clean picture just above the radar's noise level. The signal on top of this noise level was sampled and cleared of ground and rain clutter. Bird echoes were detected in the remaining signal. Ten successive high-resolution radar images were processed to extract location, ground speed and track direction of individual bird tracks (Fig. 2). Bird densities were calculated in a standardized measurement window, located perpendicular to the main migration direction at 50–60 km range, between 270 and 360 degrees azimuth, 7–32 km off the continent; at this range an altitude band of approximately 200–2600 m was measured. These images were sampled every half hour for both beams 24 h a day, 7 days a week, during 2006–2008. Only monthly maintenance periods of 55 h interrupted the continuous measurements.

ECMWF Weather Data

Gridded wind data from the European Centre for Medium-Range Weather Forecasts (ECMWF) deterministic forecast model were obtained from the 1000 hPa, 925 hPa, 850 hPa and 700 hPa pressure levels at 3 h intervals. These data, at a spatial interval of 0.25°, describe wind conditions by two components (*u* and *v*, zonal and meridional, respectively). The *u*-component describes the wind in the west/east direction (wind component blowing to the east being positive); the *v*-component describes the wind in the south/north direction (wind component blowing to the north being positive). These data were used to calculate the airspeed and heading of the birds, described in more detail below. The data were linearly interpolated in space and time to fit the exact tracks. Throughout this paper, wind directions correspond to the direction wind is blowing.

Data Selection

Nights were selected for analysis in the period 1 August–30 November, in 2006–2008, if the mean track direction was between 135° and 210° (southeast to south-southwest) and the bird density in the standardized measurement window was higher than 0.5 echoes/km^2, which is approximately 400 tracks, during at least 2 h at night.

Once the nights were selected for analysis, we used all bird tracks within the entire radar range and at least 10 km off the North Sea and Wadden Sea coast (Fig. 1), from sunset up to and including 1 h before sunrise, to parameterize each modelled trajectory. Sunrise and sunset were calculated at 53°30′N, 5°E, which is approximately the centre of the standardized measurement window (Fig. 1). Taking the inland location of the radar into account and the maximum range of detection, we could measure birds 10–120 km off the Dutch coast. The time frame and spatial extent were selected to follow compass calibration at dusk and precede potential compass recalibration at arrival at dawn.

The heading and airspeed of each track selected for further analysis were calculated by vector summation (Shamoun-Baranes et al. 2007). For each night, the mean ± SD (or angular deviation for directions) airspeed, ground speed, heading and track direction and mean vector length *r* were calculated (Batschelet 1981); values for *r* range between 0 and 1, where 1 reflects no dispersion in directions. We used the Rayleigh test to test for nonuniformity in heading, track and wind directions per night and the Watson–Williams test to test for equal means between heading, track and wind directions per night (Batschelet 1981).

Model description

A back-trajectory model was developed to simulate nocturnal migration. The model was implemented by a fixed 30 min time step, backward-integration scheme. The model was run for each individual radar track selected for analysis. The airspeed, heading, time and location extracted from each individual radar track were used to initialize each simulated trajectory. Airspeed, heading and pressure level were then kept constant within each trajectory. We adopted the following temporal and spatial constraints: (1) the model was run backwards in time until sunset (at 53°30′N, 5°E) when nocturnal migration normally starts and (2) the model extent was constrained to 52.00°N, 3.00°W and 62.00°N, 15.00°E (see Fig. 1); thus trajectories were not extended beyond these spatial boundaries. At each time step, the ground speed and track direction were calculated given the bird's heading and airspeed and the interpolated wind conditions at that

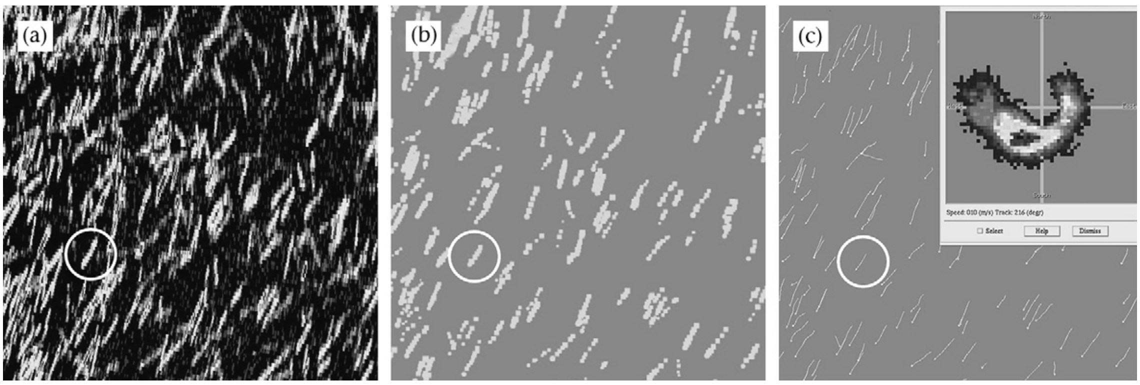

Figure 2. Result of data processing of 10 successive radar images. (a) Composite image of 10 successive high-resolution radar images processed by the ROBIN system, (b) echoes identified as birds, (c) bird echoes processed into bird tracks. The data processing of a single bird track is circled in the three images. The ground speed (distance from centre of the polar diagram) and track (azimuth direction) of each individual bird track are presented in the polar diagram inset in (c). The mean ground speed and track direction for this image are 10 m/s and 216°, respectively.

specific point in space and time. Ground speed and track direction were calculated by adding the wind components to the airspeed and heading using vector summation (for details see Shamoun-Baranes et al. 2007). The ground speed and track direction were then used to calculate the new latitude and longitude 30 min earlier, including a correction for spherical earth. This procedure was iterated backwards as long as the spatial extent and time constraints mentioned above were met. The model was run at all four pressure levels. An additional scenario was tested in which the airspeed, heading or both were increased by 20% and the model was then run at the different pressure levels. We present one example in the Results. The model was implemented in MatLab 7.5, including the circstat (Berens 2009), air_sea and geodetic toolboxes (www.mathworks.com/matlabcentral). The MatLab model code is available upon request.

Once a trajectory analysis was completed, we classified the back trajectories as follows: trajectories tracked back to Norway ('Norway'), trajectories tracked back to Sweden, including those birds that first crossed Denmark ('Sweden'), trajectories tracked back to Denmark ('Denmark'), trajectories tracked back to the European continent ('Continent'), trajectories over the North Sea and thus with unknown potential origin ('Unknown') and a special class of trajectories tracked north of 58°N (southern point of Norway), but still at sea ('Norway sea'). We considered a backwards trajectory successful when trajectories could be tracked back to land ('Norway', 'Sweden', 'Denmark' and 'Continent'). A special class, which is described in more detail in the Results, was the 'Norway sea' trajectories.

As most migration occurred below 1200 m (Table 1), we expected wind at 925 hPa to fit the conditions experienced by the birds most closely. Thus we focus the description of the results on the simulations conducted at the 925 hPa pressure level. A summary of simulation results for all pressure levels is provided in Appendix Table A1. Although the results of the trajectory analysis differed depending on the pressure level being considered, the proportion of trajectories assigned to the different classes were very similar between pressure levels within a night.

RESULTS

Description of Migration Nights

A total of 14 nights were identified with southerly oriented migration across the North Sea; 4 in 2006, 5 in 2007 and 5 in 2008 (Table 1). Migration intensity as well as airspeed, heading, ground speed and track direction varied between (Table 1) and sometimes within nights (Fig. 3). Migration intensity was lower at the beginning of the night and then increased approximately 6 h after sunset. Migration continued during the early morning on 10 of 14 nights. Although heading and track direction varied within a night, heading, track direction and wind direction were nonuniformly distributed within a night, with a high mean vector length r indicating very little dispersion in directions (Table 1, Fig. 4). Mean airspeeds were always significantly lower than mean ground speeds and mean headings, track and wind direction all differed significantly from each other (Watson–Williams test: $P < 0.001$; Table 1). Migration intensity was highest in the lowest radar beam; thus most of the migration was concentrated below 1200 m (Table 1), generally corresponding to the 925 hPa pressure level (766 m above mean sea level at standard atmospheric conditions, Anonymous 1976).

Wind conditions during the entire study period (1 August–30 November 2006–2008) were nonuniformly distributed with a mean direction to the east (88°, Rayleigh test: $r = 0.40$, $N = 35\,754$, $P < 0.001$). During the 14 nights included in the analysis wind directions were nonuniformly distributed and generally blowing to the south-southeast (153°, Rayleigh test: $r = 0.76$, $N = 1430$, $P < 0.001$), and were significantly different from the mean wind direction on all nights (Watson–Williams test: $F = 1409.73$, $P < 0.001$). The mean wind speed per night was between 3.3 and 26.7 m/s (Table 1). The mean track direction over all 14 nights included in the analysis was south-southwest (190°, Rayleigh test: $r = 0.86$, $N = 14$, $P < 0.001$) with a mean ground speed of 20.4 m/s. The mean heading was 225° (Rayleigh test: $r = 0.95$, $N = 14$, $P < 0.001$) and airspeed was 13.9 m/s. The mean heading corresponds to the endogenous direction found in other studies in this part of Europe (e.g. Bruderer & Liechti 1998; Zehnder et al. 2001; van Belle et al. 2007).

Model Results

On 10 of the 14 nights, more than 50% of the trajectories at 925 hPa were tracked back to land (Fig. 5). The average percentage of trajectories tracked back to land over all nights barely differed between pressure levels (Appendix Table A1). The distribution of airspeeds and headings differed between trajectory classes (e.g. Fig. 6, Appendix Table A2). The percentage of trajectories that were tracked back to 'Norway', 'Denmark' and 'Sweden' varied greatly

Table 1
Summary statistics of the measured tracks as well as the wind speed and direction corresponding to each track included in the trajectory analysis

Date	*N*	Airspeed		Heading			Ground speed		Track			Wind speed		Wind direction			Lower beam %
		Mean	SD	Mean	AD	*r*	Mean	SD	Mean	AD	*r*	Mean	SD	Mean	AD	*r*	
3 Oct 2006	3216	13.5	5.2	206	42	0.73	18.4	4.0	168	37	0.79	10.7	1.4	124	37	0.95	86.6
31 Oct 2006	6315	15.2	5.5	219	39	0.77	30.8	6.6	158	18	0.95	26.7	5.5	134	18	0.99	88.4
1 Nov 2006	8973	15.3	4.5	247	36	0.80	21.4	4.4	206	22	0.93	14.4	3.5	164	22	0.97	93.8
2 Nov 2006	15114	13.7	4.5	248	34	0.82	20.9	3.9	211	21	0.93	13.9	0.7	175	21	0.99	78.8
17 Sep 2007	4731	13.2	3.3	207	26	0.89	25.3	3.4	193	16	0.96	13.6	2.0	179	16	0.96	99.2
26 Sep 2007	11971	14.1	3.4	232	28	0.88	20.4	3.4	225	20	0.94	7.1	1.4	214	20	0.99	97.8
1 Oct 2007	8761	16.1	3.5	221	34	0.82	20.8	3.5	229	27	0.89	5.9	1.2	247	27	0.99	87.5
17 Oct 2007	4707	14.4	5.1	229	28	0.88	22.7	3.8	190	18	0.95	15.1	1.8	152	18	0.96	92.3
18 Oct 2007	8634	13.4	3.3	237	30	0.87	19.8	3.3	200	20	0.94	12.5	1.1	161	20	0.99	68.6
1 Oct 2008	1643	8.6	4.4	179	68	0.30	21.3	4.9	110	23	0.92	19.3	1.6	98	23	1.00	80.4
16 Oct 2008	4269	15.9	4.3	239	26	0.90	17.6	3.3	174	21	0.93	17.2	1.1	121	21	1.00	92.4
27 Oct 2008	1933	12.6	5.7	214	42	0.73	15.8	3.3	165	41	0.75	11.1	2.6	115	41	0.92	96.4
28 Oct 2008	11604	14.7	3.2	231	27	0.89	14.4	2.4	201	27	0.89	7.9	1.1	122	27	0.95	98.6
30 Oct 2008	8270	14.1	3.4	238	30	0.86	15.8	3.8	231	29	0.88	3.3	1.5	172	29	0.63	97.8
Mean		13.9		225			20.4		191			12.8		153			89.9

The table includes date (at sunset), number of tracks (N), mean airspeed ± SD (m/s), mean heading ± angular deviation (AD, in degrees), mean vector length r, mean ground speed ± SD (m/s), mean track direction ± AD, mean wind speed ± SD (m/s), mean wind direction ± AD and the percentage of tracks measured in the lower radar beam. Wind speeds and directions correspond to data from the 925 hPa pressure level. Mean directions (heading, track and wind) were all nonuniformly distributed (Rayleigh test: $P < 0.001$).

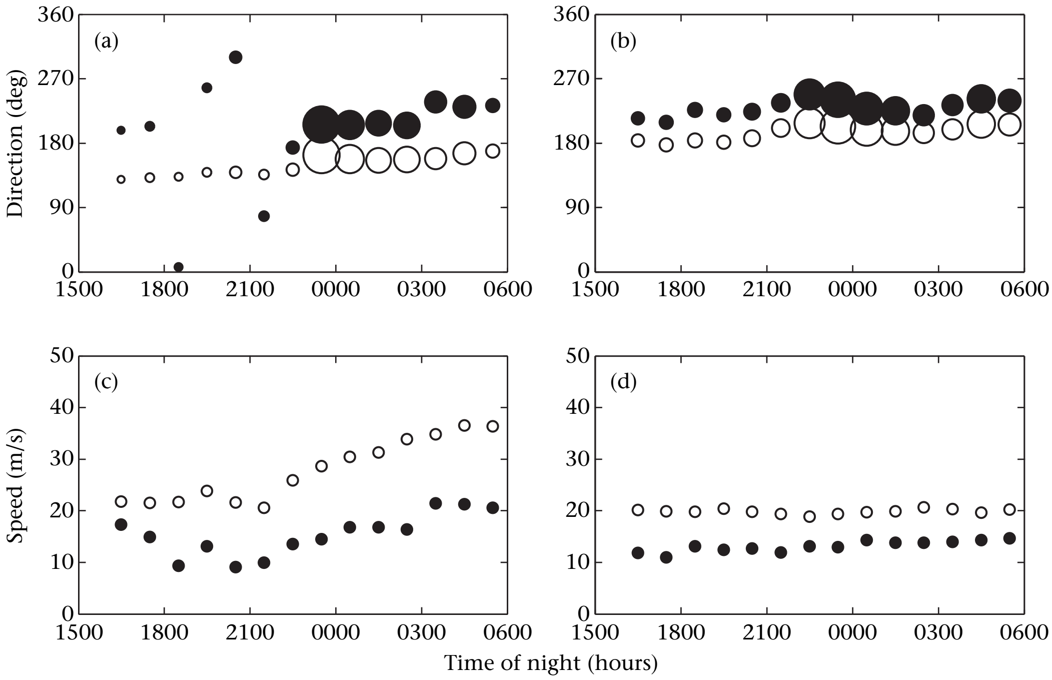

Figure 3. Examples of temporal migration pattern during the course of the night. (a, b) Mean hourly heading (closed circles) and track direction (open circles) on 31 October 2006 and 18 October 2007, respectively. Larger symbol size indicates higher relative bird density. (c, d) Mean hourly airspeed (closed circles) and ground speed (open circles) on 31 October 2006 and 18 October 2007, respectively. On 31 October 2006 (a, c) sunset was at 1604 and sunrise the next morning was at 0641 hours UTC. On 18 October 2007 (b, d) sunset was at 1633 and sunrise was at 0616 hours UTC.

within and between nights (Fig. 5, Appendix Table A3); however, on most nights a majority of the trajectories could be tracked back to those countries. On 3 nights, more than 50% of all trajectories were tracked back to 'Norway' (Fig. 5). Of the Norwegian migrants, 50% arrived off the coast of the Netherlands, on average, 10.5 h after sunset (range 8–12 h; Fig. 7, Appendix Table A3). The mean ground speed of the Norway trajectories was 21 m/s and the mean track directions were between 143° and 212° (Appendix Table A2). On several nights (e.g. 1 November 2006) there was barely any variation in track direction (<5°) while mean wind direction and heading of birds arriving from Norway did vary during the course of the night (Appendix Table A3).

On 3 nights, more than 30% of the trajectories ended just west of the coast of Norway (trajectory class 'Norway sea', Fig. 5). These trajectories were similarly oriented relative to the coast of Norway (Fig. 7). It seems very likely that most of these trajectories do represent birds that took off from Norway. When we combined both the 'Norway' and the 'Norway sea' trajectory classes, then the trajectories that potentially originated in Norway represented more than 50% of all trajectories on 7 of the nights in this study. To try to understand why the 'Norway sea' trajectories could not be tracked back to Norway, we explored them in more detail. Simulations at different flight altitudes (up to approximately 3 km above sea level) barely influenced the proportion of 'Norway sea' trajectories

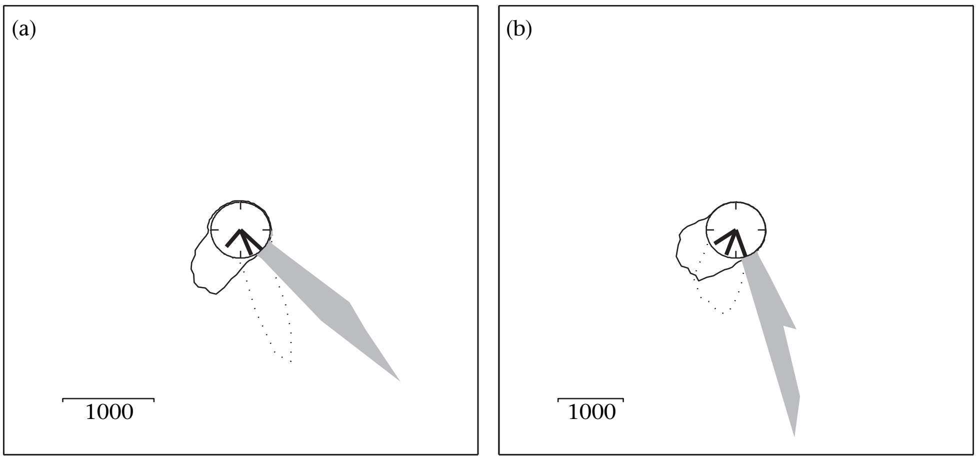

Figure 4. Circular density distribution of wind directions (shaded area), heading (solid line) and track directions (dashed line) of measured radar tracks at the 925 hPa pressure level on (a) 31 October 2006 and (b) 18 October 2007 at arrival off the Dutch coast. Mean directions are indicated by a straight line and the scale is indicated in the lower left corner. In (a) mean wind direction is 134°, mean heading is 219° and mean track direction is 158° ($N = 6315$); in (b) mean wind direction is 161°, mean heading is 237° and mean track direction is 200° ($N = 8634$).

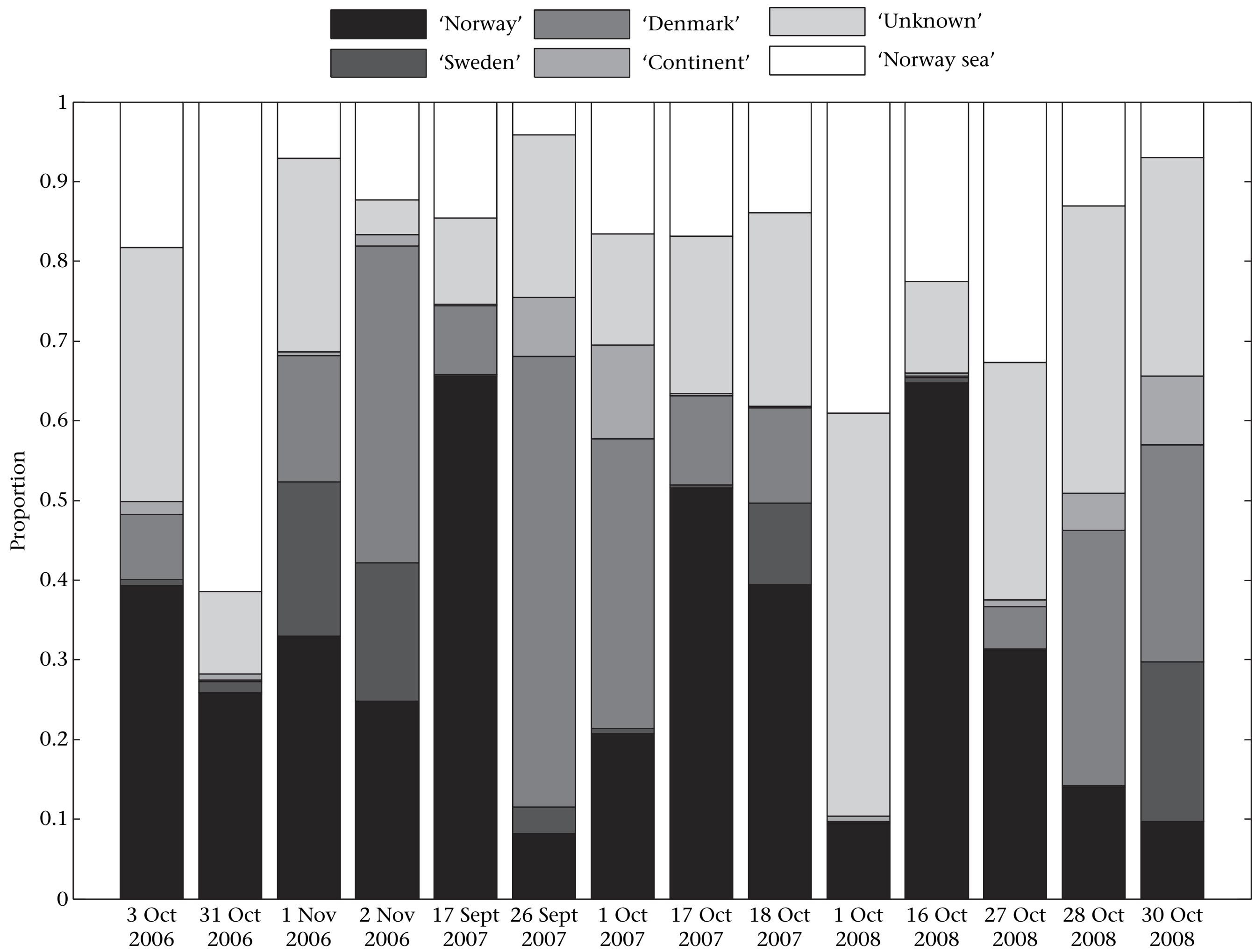

Figure 5. Summary of trajectories simulated at 925 hPa. The date at the beginning of the evening is provided on the *X* axis. The *Y* axis represents the proportion of trajectories per trajectory class ('Norway', 'Sweden', 'Denmark', 'Continent', 'Unknown' and 'Norway sea').

(Appendix Table A1). The most extreme case where the majority of trajectories were assigned to the 'Norway sea' class was 31 October 2006 (Fig. 5, Fig. 6a, c, Fig. 7a). On this night, the mean ground speed (30.8 m/s) was much higher than the airspeed (15.2 m/s; Table 1) suggesting considerable wind assistance and birds flying at these ground speeds could cross the North Sea in a direct route in less than 5 h. The mean wind speed and direction ± SD corresponding to the radar measurements were 26.6 ± 5.5 m/s and 134 ± 7°. These wind speeds fall within the Beaufort wind scale 10 and are considered 'storm' conditions (www.meteoffice.gov.uk). On 31 October 2006 at 1800 hours UTC, wind speeds were generally below 10 m/s over land in southern Scandinavia. However, during the night a storm blowing from the northwest developed over the North Sea between a high pressure system northwest of Ireland and a deep dipole low with one centre over Scandinavia which moved eastwards and another over Denmark which moved towards Poland (archived synoptic weather descriptions for the Netherlands can be accessed online http://www.knmi.nl/klimatologie/maand_en_seizoensoverzichten/weerbeschrijvingen.html). For several hours, there were strong winds to the south-southeast (>25 m/s) over the North Sea accompanied by rain showers, hail and/or lightning. Thus, wind speeds experienced over sea were approximately twice the mean airspeed of the birds, with complex atmospheric conditions in southern Scandinavia. On this night, airspeeds of successful Norway trajectories were higher and headings more to the west than those for the 'Norway sea' trajectories (17.3 m/s, 235° and 14.5 m/s, 208°, respectively; Appendix Table A2). Most of these trajectories were tracked inland, 400–600 km from the southern tip of Norway. An alternative model scenario (airspeeds and headings increased by 20% at 1000 hPa) resulted in a 40% increase in the number of birds tracked back to Norway, the lowest proportion of 'Norway sea' trajectories (18% compared to 61% in the original model run) and the lowest proportion of 'Unknown' trajectories (18%) with these model parameters.

DISCUSSION

Intense migration over the North Sea off the northern coast of the Netherlands is rare, with no more than 5 days identified per year in this study. Although the radar used in this study cannot distinguish directly between species, measured airspeeds indicate that these migration events include a variety of passerines as well as larger fast-flying migrants such as waders and waterfowl (Bruderer & Boldt 2001). Visual bird migration in the north of the Netherlands and ringing activities on the Wadden Sea Islands showed mass migration events were dominated by robin, *Erithacus rubecula*, and song thrush, *Turdus philomelos*, in September and redwing, *Turdus iliacus*, fieldfare, *Turdus pilaris*, and, in smaller numbers, blackbird, *Turdus merula*, skylark, *Alauda arvensis*, and starling, *Sturnus vulgaris*, in October (www.trektellen.nl). During an

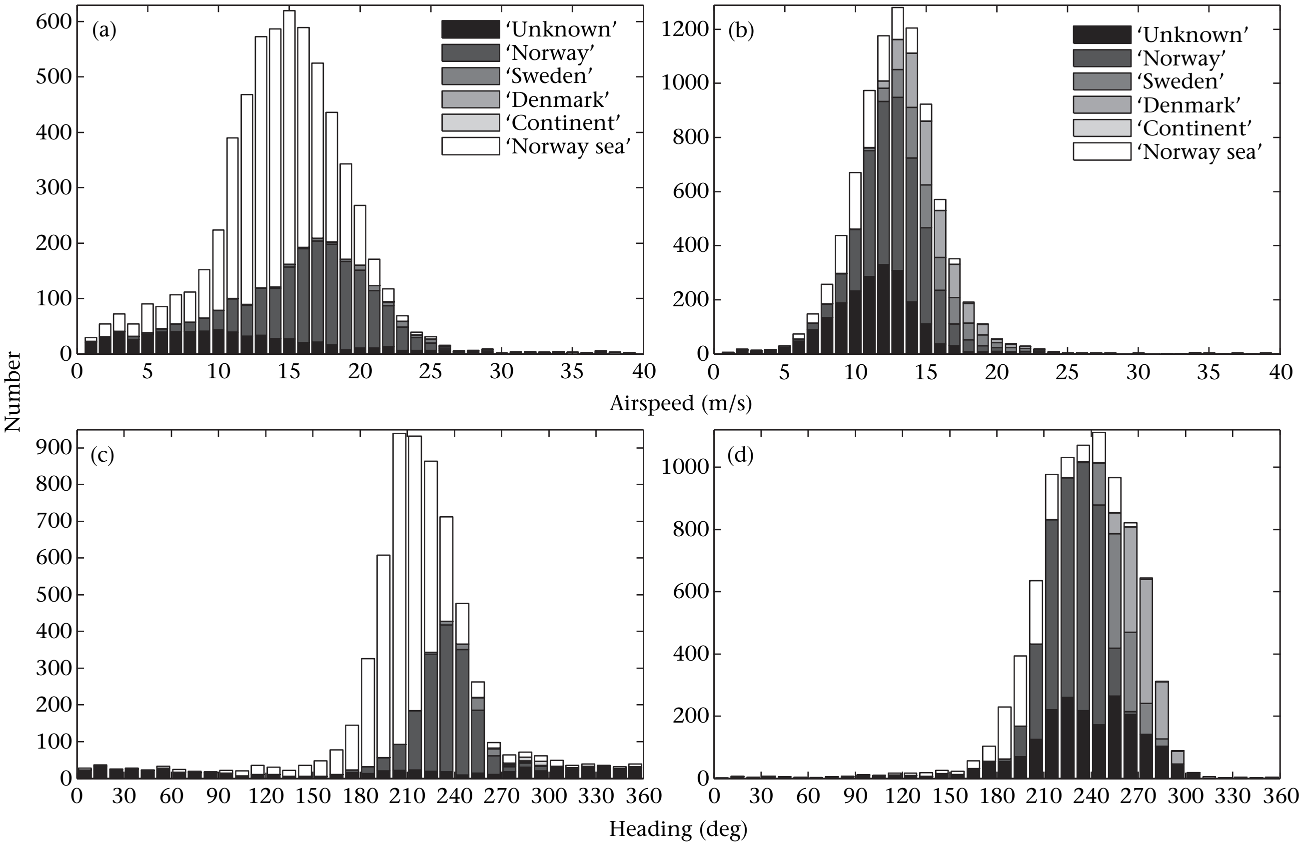

Figure 6. Density distributions of (a, b) airspeed and (c, d) heading of measured radar tracks and their associated trajectory classes based on the simulation results at 925 hPa on (a, c) 31 October 2006 and (b, d) 18 October 2007.

offshore bird migration study in the North Sea (approximately 100 km east of our study area), 70% of the registered flight calls were also from thrushes (redwing, blackbird, fieldfares and song thrushes) and around 10% from waders (Hüppop et al. 2006).

Our study clearly showed that, under appropriate atmospheric conditions, birds are able to cross the North Sea, reaching the Netherlands after several hours of flight from Norway, Denmark and Sweden. These events all occurred on nights with winds over the North Sea generally blowing southeast to south-southeast and hence favourable wind conditions supporting a long flight to the Netherlands across the North Sea (see Supplementary Material for an example of simulated trajectories and wind conditions experienced en route which can be viewed dynamically in Google Earth). Ground speeds were higher and, at times, even double the airspeed, showing that birds could derive substantial benefit from the wind conditions they experienced en route. Yet wind conditions in the region are generally unfavourable for south-southwest migration in autumn (Kemp et al. 2010). Our findings suggest that birds select nights on which wind conditions support flight to the Netherlands across the North Sea, and since these conditions are rare, they result in mass migration events. Under such conditions, the North Sea is not a barrier for migration; on the contrary, large-scale synoptic conditions result in an atmospheric 'corridor' facilitating migration. Other studies have also shown that birds take advantage of such large-scale weather systems during transoceanic flight (e.g. Williams & Williams 1990; Felicísimo et al. 2008; Gill et al. 2009). Thus, especially in autumn, when conditions are generally unfavourable for seasonal migration in northwest Europe, we expect selectivity of the appropriate atmospheric conditions to be an important adaptive strategy for numerous migrating taxa, including insects (e.g. Brattström et al. 2008; Chapman et al. 2010), birds (e.g. Alerstam 1979; Åkesson et al. 2002; Gauthreaux et al. 2005) and bats. However, the proximate cues animals use to identify these conditions are not clear and may differ between taxa.

Simulations showed that a majority of the birds could be tracked back to potential departure sites, supporting a relatively simple strategy, which assumes take-off after sunset and constant airspeed and heading en route. Birds may set an appropriate heading and airspeed to cross the North Sea successfully, thus partially compensating for wind drift at take-off (e.g. Liechti 1995; Green & Alerstam 2002). However, a proportion of trajectories could not be tracked back to land. Some of these may be attributable to local bird movements over sea (Bourne 1980; Hüppop et al. 2006), a possibility supported by the higher scatter in headings and lower airspeeds of 'Unknown' trajectories (Appendix Table A2). Others might have been successful if they had been extended further back in time, assuming birds took off before sunset. Inaccuracies in wind data may lead to some error in model results. Studies have shown that flight altitudes are influenced by wind conditions (e.g. Gauthreaux 1991; Bruderer et al. 1995; Schmaljohann et al. 2009) and uncertainties regarding flight altitude may also influence model results. However, the pressure level of the simulation had only a minor effect on the proportion of successful trajectories. Nevertheless, on several nights our model generated a large proportion of systematically unsuccessful trajectories ending off the western coast of Norway. These cases all coincided with complex atmospheric conditions over southern Scandinavia (such as on 31 October 2006) and very strong winds over the North Sea. The additional scenario tested revealed that an increase in airspeed and heading resulted in a significant increase in the proportion of

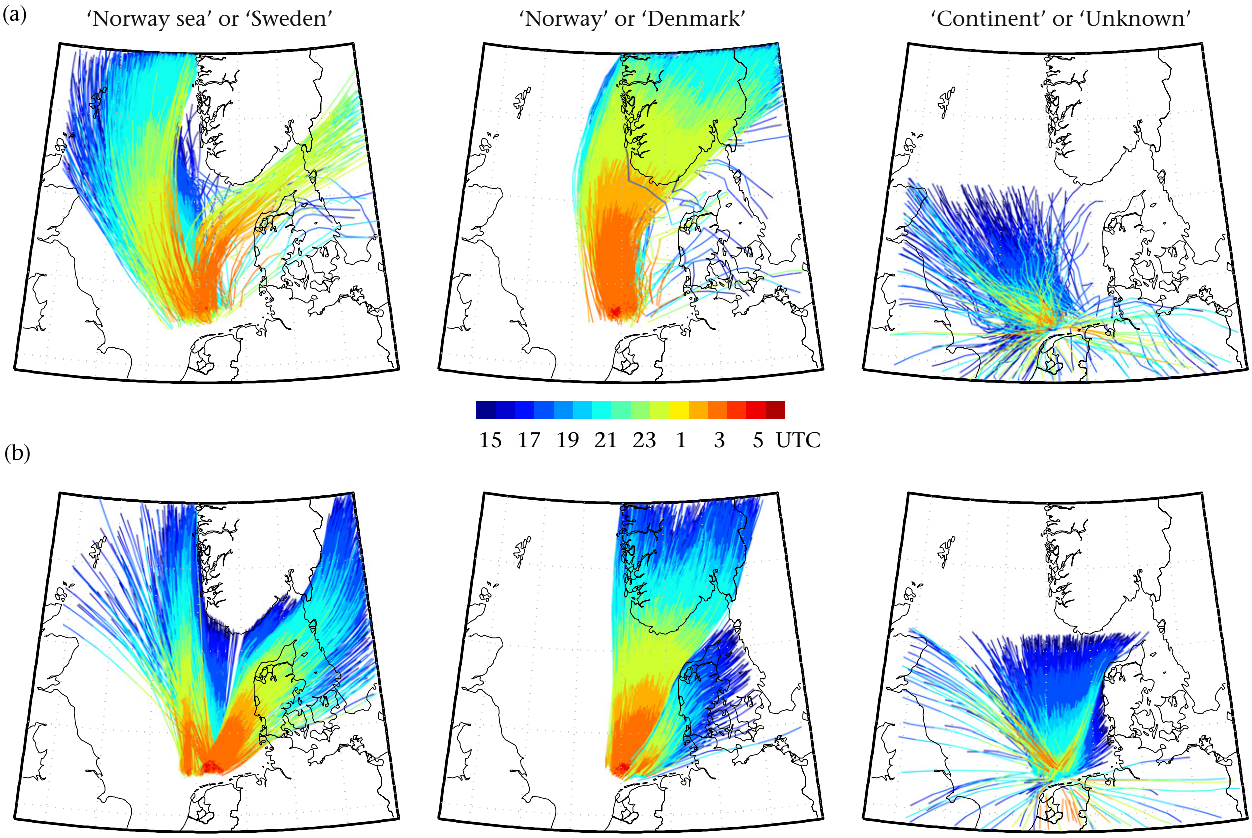

Figure 7. Simulated migration backward trajectories on (a) 31 October 2006 and (b) 18 October 2007. Colours represent successive 1 h segments of the trajectory from 1500 (dark blue) to 0600 hours (red) UTC. Trajectories were run from 1 h before sunrise back to sunset (at 53°30′N, 5°E) the previous evening; thus some trajectories seem to stop abruptly (e.g. 'Unknown' trajectories). On 31 October 2006 sunset was at 1604 and sunrise the next morning was at 0641 hours UTC. On 18 October 2007 sunset was at 1633 and sunrise was at 0616 hours UTC.

successful trajectories on these nights. Similarly, on 31 October 2006 trajectories with higher measured airspeeds and more southwest orientation could be tracked back to Norway (mean airspeed 17.3 m/s and heading 235° compared to 14.5 m/s and 208°, Appendix Table A2). These findings indicate that for some migrants, at least with complex atmospheric conditions and strong winds experienced en route, maintaining a constant heading, airspeed and altitude above sea level is not a viable strategy and a more complex strategy is required to cross the North Sea successfully. Similar conclusions were reached by Stoddard et al. (1983) following their simulation of migration over the western North Atlantic Ocean. Alternative strategies may include reorientation, alteration of airspeed or flight altitude or any combination of the above during flight, all of which would influence the flight trajectories. In the future, alternative models (e.g. Erni et al. 2005; Vrugt et al. 2007) could be implemented to study the consequences of more complex decision rules.

The mechanisms that enable birds from Norway to reach their wintering areas in the U.K. remain elusive despite several previous studies (Lack 1963; Bourne 1980; Buurma 1987; Richardson 1990). Ringing studies in the Wadden Sea Islands show recoveries of the same species in Norway, the U.K. and southwestern Europe (http://www.xs4all.nl/~holmerv/terugmeldingen.htm, http://www.vogelringschier.nl/terugmeldingen.html). Our study shows that birds with south to southwest headings can reach the Netherlands from Norway (mean headings 184°–240°) and therefore may include birds whose winter destination is the U.K. and birds migrating to southwestern Europe. Currently we cannot conclusively determine whether their proximate goal is the Netherlands or the U.K. However, the combination of headings, track directions and wind conditions strongly suggest that birds are trying to reach the Netherlands, as opposed to being blown off course when trying to reach the U.K., and from the Netherlands they will continue towards their winter destination.

Conclusions

Integrating measurements and Lagrangian models that incorporate dynamic environmental conditions, such as wind or ocean currents, provides an excellent framework to study animal movement at different spatial and temporal scales, test theories and provide new insight for a wide range of taxa (e.g. Chapman et al. 2010; Hays et al. 2010; Shamoun-Baranes et al. 2010a, b). More specifically, this study and others show how the combination of local radar measurements of migratory behaviour during flight and dynamic simulation models improves our understanding of how the movement patterns of insects (e.g. Scott & Achtemeier 1987; Chapman et al. 2010) and birds (e.g. Stoddard et al. 1983) are influenced by atmospheric dynamics and how organisms may respond to these conditions. The need for a detailed understanding of behavioural decision rules, migratory trajectories and the atmospheric conditions under which mass migration events occur is increasing especially with the rise in demand and development of large-scale wind farms, both off-shore (e.g. Desholm & Kahlert 2005; Drewitt & Langston 2006; Hüppop et al. 2006) and on-shore (e.g. Gauthreaux & Belser 2003; Barrios & Rodriguez 2004). We believe that in order to take advantage of dynamic and heterogeneous atmospheric conditions an individual migrant (bird, bat or insect) should be flexible in its reaction to wind (e.g. Nisbet 1957; Alerstam 1979; Drake & Farrow 1988; Liechti 1993; Gauthreaux et al. 2005; Chapman et al. 2010) and may adopt a simple strategy maintaining constant heading, airspeed and flight altitude or a more complex strategy, requiring an adjustment of heading, airspeed or altitude (or any combination), depending on the atmospheric conditions experienced.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at doi:10.1016/j.anbehav.2011.01.003.

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APPENDIX

Table A1. Summary of simulated trajectories

Date	Pressure level (hPa)	*N*	% Norway	% Sweden	% Denmark	% Continent	% Unknown	% Norway sea
3 Oct 2006	700	3215	48.0	1.8	6.3	1.2	24.8	17.9
	850		49.6	0.5	5.6	1.2	27.1	16.0
	925		39.4	0.7	8.2	1.6	31.9	18.2
	1000		49.4	1.4	5.0	1.5	25.7	17.1
31 Oct 2006	700	6314	25.1	11.5	0.2	0.7	11.4	51.0
	850		17.3	12.0	0.3	0.7	10.0	59.7
	925		16.4	10.7	0.5	0.6	10.4	61.4
	1000		20.1	5.1	0.3	0.6	11.4	62.5
1 Nov 2006	700	8974	33.7	23.2	13.2	0.5	21.1	8.3
	850		30.5	23.4	13.3	0.6	23.3	8.9
	925		29.8	22.5	15.9	0.5	24.3	7.0
	1000		28.3	23.2	16.9	0.6	23.3	7.7
2 Nov 2006	700	15 115	34.4	12.9	35.3	1.0	4.0	12.5
	850		28.3	13.0	37.3	0.7	6.6	14.1
	925		24.0	17.6	40.8	1.0	4.3	12.3
	1000		24.2	13.8	41.2	1.4	4.3	15.1
17 Sep 2007	700	4731	56.6	8.0	16.2	0.1	6.2	12.9
	850		61.0	0.3	8.9	0.1	18.1	11.7
	925		65.5	0.3	8.6	0.2	10.9	14.5
	1000		65.1	0.8	9.4	0.2	7.9	16.6
26 Sep 2007	700	11 971	5.6	1.7	63.7	6.1	17.5	5.5
	850		10.1	3.9	57.4	6.7	18.9	3.0
	925		8.3	3.3	58.1	5.9	20.4	4.1
	1000		5.5	3.6	60.2	4.7	18.2	7.8
1 Oct 2007	700	8761	26.9	7.3	49.5	9.8	3.5	2.9
	850		25.6	1.4	41.9	12.1	8.4	10.5
	925		20.2	0.8	37.0	11.5	13.9	16.6
	1000		14.0	0.6	40.7	9.3	15.1	20.3
17 Oct 2007	700	4707	41.0	1.0	9.3	0.4	23.2	25.1
	850		47.2	0.9	9.1	0.3	19.9	22.5
	925		51.3	0.7	11.2	0.3	19.7	16.8
	1000		49.8	1.3	11.5	0.3	19.3	17.9
18 Oct 2007	700	8634	32.9	9.2	15.8	0.2	22.5	19.4
	850		37.6	12.8	15.3	0.2	22.4	11.8
	925		36.9	12.7	11.9	0.2	24.2	13.9
	1000		34.9	13.2	11.0	0.2	25.1	15.4
1 Oct 2008	700	1643	9.3	0.2	0.1	0.5	52.5	37.4
	850		13.0	0.5	0.2	0.6	51.2	34.5
	925		9.3	0.4	0.1	0.6	50.6	39.0
	1000		4.0	0.2	0.0	0.6	54.2	41.1
16 Oct 2008	700	4269	45.5	0.8	0.2	0.3	11.9	41.4
	850		54.3	0.8	0.3	0.3	11.5	32.7
	925		63.9	1.5	0.2	0.3	11.5	22.5
	1000		64.3	2.5	0.2	0.3	12.6	20.1
27 Oct 2008	700	1933	37.1	0.1	5.3	0.9	31.7	24.9
	850		27.2	0.1	4.2	1.0	30.7	36.9
	925		31.2	0.2	5.3	0.9	29.7	32.7
	1000		27.9	1.1	7.1	1.0	30.1	32.8
28 Oct 2008	700	11 604	3.1	1.3	45.4	0.9	35.8	13.6
	850		12.7	0.2	41.5	1.3	27.9	16.4
	925		14.0	0.1	32.5	4.3	36.1	13.0
	1000		13.9	0.5	34.1	4.2	33.7	13.6
30 Oct 2008	700	8279	5.0	8.9	23.2	9.9	43.2	9.8
	850		7.5	10.5	32.5	10.5	30.9	8.2
	925		9.3	20.5	27.2	8.6	27.4	7.0
	1000		10.8	22.7	24.3	8.9	27.5	5.7

The date at the beginning of the evening, pressure level at which the simulation was run, number of tracks (*N*) and percentage of trajectories per class are provided. The trajectory classes include trajectories tracked back to Norway ('Norway'), trajectories tracked back to Sweden ('Sweden'), trajectories tracked back to Denmark ('Denmark'), trajectories tracked back to the European continent ('Continent'), trajectories over the North Sea and thus with an unknown potential origin ('Unknown') and a special class of trajectories tracked just west of Norway, but still at sea ('Norway sea').

Table A2
Summary statistics (per night) of the measured tracks corresponding to each trajectory class resulting from simulations at the 925 hPa pressure level

Date	Trajectory class	*N*	Airspeed (m/s)		Heading (deg)			Ground speed (m/s)		Track (deg)			Wind speed (m/s)		Wind direction (deg)		
			Mean	SD	Mean	AD	*r*	Mean	SD	Mean	AD	*r*	Mean	SD	Mean	AD	*r*
3 Oct 2006	Norway	1266	14.8	1.6	208	7	0.99	20.3	1.7	176	5	1.00	10.9	1.2	130	5	1.00
	Sweden	23	19.1	1.6	226	5	1.00	20.7	1.9	195	4	1.00	10.8	0.6	129	3	1.00
	Denmark	262	15.9	3.7	235	9	0.99	16.8	3.0	198	13	0.98	10.3	1.5	131	8	0.99
	Continent	52	22.7	9.4	318	45	0.69	19.0	9.2		67	0.32	10.5	1.5	123	26	0.90
	Unknown	1027	10.0	7.1	164	63	0.40	16.0	5.1	127	48	0.65	10.3	1.7	109	26	0.90
	Norway sea	586	14.8	2.1	214	16	0.96	19.3	2.1	179	10	0.98	11.0	1.0	130	4	1.00
31 Oct 2006	Norway	1634	17.3	4.0	235	19	0.94	35.2	5.0	165	8	0.99	33.5	4.2	137	5	1.00
	Sweden	88	23.3	7.5	255	14	0.97	32.1	4.5	178	14	0.97	34.0	2.8	138	6	0.99
	Denmark	13	31.6	17.8	278	11	0.98	24.2	11.3	199	33	0.83	30.3	7.4	131	7	0.99
	Continent	45	43.3	12.3	305	24	0.91	23.9	10.9	291	52	0.58	24.3	5.6	131	10	0.98
	Unknown	655	11.2	7.1	338	72	0.22	20.7	7.1	132	27	0.89	22.1	3.3	134	14	0.97
	Norway sea	3880	14.5	3.7	208	27	0.89	30.7	4.9	158	10	0.98	24.4	3.0	133	6	0.99
1 Nov 2006	Norway	2960	15.5	3.5	223	16	0.96	22.3	3.4	193	9	0.99	11.6	2.1	153	8	0.99
	Sweden	1733	16.6	3.5	258	11	0.98	18.4	3.4	215	9	0.99	12.3	2.2	153	10	0.99
	Denmark	1420	16.3	3.4	284	15	0.96	21.0	3.5	228	11	0.98	17.8	1.3	180	4	1.00
	Continent	50	36.5	9.8	318	24	0.91	27.5	10.7	293	33	0.84	15.7	4.7	172	16	0.96
	Unknown	2179	13.4	5.0	264	43	0.72	21.8	4.9	209	26	0.90	18.0	1.8	178	6	0.99
	Norway sea	631	13.0	4.0	190	36	0.80	24.3	4.7	175	18	0.95	13.1	2.0	162	10	0.98
2 Nov 2006	Norway	3752	11.7	2.8	216	16	0.96	23.7	3.0	194	6	0.99	13.7	0.6	177	4	1.00
	Sweden	2619	13.3	2.6	262	13	0.97	19.9	3.0	218	9	0.99	13.7	0.7	177	4	1.00
	Denmark	6015	15.7	3.9	270	17	0.96	19.2	3.1	225	12	0.98	14.0	0.6	172	7	0.99
	Continent	216	24.7	10.4	311	21	0.93	19.7	8.1	273	33	0.83	13.9	1.1	180	11	0.98
	Unknown	653	13.7	8.5	258	56	0.52	19.7	6.6	194	39	0.77	14.1	0.7	173	7	0.99
	Norway sea	1859	11.0	2.6	207	34	0.82	22.9	2.8	189	15	0.97	13.8	0.5	176	3	1.00
17 Sep 2007	Norway	3104	13.4	2.9	204	15	0.97	26.3	2.5	193	9	0.99	13.7	1.9	181	9	0.99
	Sweden	11	22.0	2.7	240	7	0.99	27.2	3.1	219	7	0.99	10.8	3.4	162	23	0.92
	Denmark	405	15.2	3.5	243	11	0.98	23.4	2.7	214	7	0.99	12.8	2.3	176	18	0.95
	Continent	10	15.4	9.6	280	17	0.96	17.3	7.0	235	11	0.98	11.5	3.7	168	30	0.87
	Unknown	514	11.7	4.5	228	36	0.80	20.7	4.7	194	32	0.84	12.6	2.3	165	34	0.83
	Norway sea	687	12.0	3.0	179	31	0.86	25.1	2.7	182	16	0.96	14.3	1.7	183	10	0.99
26 Sep 2007	Norway	988	15.3	2.1	184	8	0.99	20.8	2.1	192	6	0.99	6.0	0.6	210	3	1.00
	Sweden	390	18.4	3.1	236	9	0.99	23.6	3.0	231	7	0.99	5.6	0.5	212	5	1.00
	Denmark	6770	14.2	2.9	238	15	0.96	20.8	3.2	230	11	0.98	7.0	1.3	216	6	0.99
	Continent	886	14.4	3.5	279	13	0.97	18.8	3.6	259	10	0.99	7.1	1.6	219	9	0.99
	Unknown	2444	12.5	4.1	227	30	0.86	19.6	3.9	219	18	0.95	8.1	1.3	210	9	0.99
	Norway sea	493	14.4	2.7	175	20	0.94	19.7	2.9	186	14	0.97	6.3	0.6	210	4	1.00
1 Oct 2007	Norway	1817	15.1	2.7	199	10	0.98	20.4	2.7	212	7	0.99	6.7	0.8	242	6	1.00
	Sweden	60	19.9	4.6	243	10	0.98	25.2	4.6	242	8	0.99	5.4	0.6	237	4	1.00
	Denmark	3180	17.3	3.0	240	13	0.98	22.6	2.7	242	10	0.99	5.5	1.0	250	6	1.00
	Continent	1034	16.0	4.0	280	20	0.94	20.2	3.7	273	16	0.96	4.9	1.6	251	8	0.99
	Unknown	1219	15.9	4.8	211	29	0.87	20.1	4.3	221	26	0.90	5.8	1.2	248	6	0.99
	Norway sea	1451	14.6	2.7	175	14	0.97	18.3	2.7	195	13	0.97	6.7	0.8	242	6	1.00
17 Oct 2007	Norway	2428	13.6	3.9	231	15	0.96	24.0	2.5	192	7	0.99	16.0	1.4	160	12	0.98
	Sweden	18	23.1	6.8	255	8	0.99	27.8	6.4	218	6	0.99	16.3	1.6	162	12	0.98
	Denmark	526	20.3	2.3	253	9	0.99	18.8	2.8	213	8	0.99	13.3	0.9	137	9	0.99
	Continent	15	37.0	8.9	306	24	0.92	28.8	8.9	288	34	0.83	13.6	2.4	160	10	0.98
	Unknown	928	13.5	5.6	220	41	0.75	19.5	3.6	176	25	0.90	13.4	1.0	138	10	0.99
	Norway sea	792	13.2	5.4	209	30	0.86	24.5	3.3	182	13	0.97	15.6	1.6	156	14	0.97
18 Oct 2007	Norway	3402	13.4	2.4	229	15	0.97	20.8	2.7	197	8	0.99	11.9	0.9	160	5	1.00
	Sweden	886	16.0	2.6	259	10	0.99	19.3	2.5	219	8	0.99	12.5	0.3	164	4	1.00
	Denmark	1031	16.1	2.2	273	9	0.99	17.0	2.5	226	7	0.99	13.1	0.6	163	6	1.00
	Continent	19	37.4	9.0	318	18	0.95	27.1	9.5	308	27	0.89	12.4	1.2	158	6	0.99
	Unknown	2093	11.8	3.3	236	37	0.79	18.8	3.4	193	24	0.92	13.3	0.8	159	9	0.99
	Norway sea	1203	11.7	2.5	208	27	0.89	21.0	3.0	185	15	0.97	11.9	1.1	162	5	1.00
1 Oct 2008	Norway	155	13.2	2.6	214	12	0.98	17.9	2.6	143	9	0.99	18.1	1.2	101	3	1.00
	Sweden	4	32.7	17.2		5	1.00	22.4	13.5		28	0.88	18.4	1.2		2	1.00
	Denmark	1	17.1	0.0		0	1.00	9.5	0.0		0	1.00	17.9	0.0		0	1.00
	Continent	10	24.5	11.1	303	30	0.86	16.5	8.2		54	0.55	18.9	1.4	92	3	1.00
	Unknown	832	6.9	4.3	15	70	0.25	21.1	5.8	94	16	0.96	20.0	1.6	97	3	1.00
	Norway sea	641	9.3	2.1	175	26	0.90	22.6	3.3	122	8	0.99	18.7	1.1	100	2	1.00

(*continued on next page*)

Table A2 (*continued*)

Date	Trajectory class	*N*	Airspeed (m/s)		Heading (deg)			Ground speed (m/s)		Track (deg)			Wind speed (m/s)		Wind direction (deg)		
			Mean	SD	Mean	AD	*r*	Mean	SD	Mean	AD	*r*	Mean	SD	Mean	AD	*r*
16 Oct 2008	Norway	2765	17.2	2.2	240	10	0.98	17.6	2.6	180	8	0.99	17.1	0.9	121	2	1.00
	Sweden	29	26.3	6.2	257	7	0.99	18.7	6.2	213	9	0.99	17.9	0.8	122	3	1.00
	Denmark	7	25.8	5.7	271	6	0.99	12.8	4.8	225	16	0.96	18.6	0.9	118	4	1.00
	Continent	16	40.1	13.4	307	28	0.88	26.3	10.2	311	48	0.65	17.5	1.6	117	4	1.00
	Unknown	492	9.7	5.6	255	68	0.29	18.7	4.9	132	32	0.84	18.0	1.6	120	3	1.00
	Norway sea	960	14.4	2.6	234	15	0.97	17.0	3.1	168	10	0.98	17.1	1.0	119	3	1.00
27 Oct 2008	Norway	603	15.5	2.7	218	12	0.98	16.4	2.2	179	14	0.97	10.9	2.2	116	18	0.95
	Sweden	3	35.7	19.9		3	1.00	27.0	17.6		11	0.98	12.1	0.8		5	1.00
	Denmark	102	21.6	2.4	248	5	1.00	14.0	2.3	219	8	0.99	12.1	1.5	106	13	0.97
	Continent	18	19.8	8.0	296	32	0.84	13.2	6.3		56	0.52	11.4	1.9	107	21	0.93
	Unknown	575	8.1	6.3	234	67	0.32	13.9	3.2	113	50	0.62	13.0	2.0	97	19	0.94
	Norway sea	632	12.1	2.8	197	21	0.93	17.3	3.1	168	17	0.96	9.4	2.3	130	17	0.95
28 Oct 2008	Norway	1625	14.2	2.3	216	7	0.99	15.3	2.1	189	7	0.99	7.1	0.7	120	12	0.98
	Sweden	17	21.1	4.4	238	6	1.00	17.3	2.5	221	8	0.99	7.0	1.0	108	12	0.98
	Denmark	3726	16.6	3.3	246	10	0.98	14.3	2.2	218	11	0.98	7.9	0.9	125	16	0.96
	Continent	538	17.7	2.4	269	12	0.98	13.0	2.4	244	19	0.95	8.3	0.9	128	13	0.97
	Unknown	4184	13.4	2.6	227	33	0.83	13.8	2.5	192	31	0.85	8.5	1.0	121	24	0.91
	Norway sea	1514	13.3	2.3	205	16	0.96	15.6	2.1	180	14	0.97	7.1	0.8	121	15	0.97
30 Oct 2008	Norway	808	14.1	2.3	199	10	0.98	15.0	2.4	193	10	0.98	1.9	0.6	137	15	0.96
	Sweden	1654	16.1	2.8	242	13	0.97	15.0	2.8	236	14	0.97	2.3	0.6	121	15	0.96
	Denmark	2251	13.7	2.7	243	15	0.97	15.4	4.5	235	15	0.96	3.5	1.4	171	50	0.62
	Continent	716	14.4	4.3	291	16	0.96	16.6	4.1	278	14	0.97	4.3	1.7	224	35	0.81
	Unknown	2266	13.1	3.8	240	28	0.88	17.0	3.7	235	24	0.91	4.5	1.2	219	22	0.92
	Norway sea	575	13.6	3.4	184	29	0.88	14.9	3.7	179	26	0.89	2.2	0.7	136	22	0.92

The table includes date (at sunset), trajectory class, number of tracks (N), mean airspeed $\pm$ SD (m/s), mean heading $\pm$ angular deviation (AD), mean vector length r, mean ground speed $\pm$ SD (m/s), mean track direction $\pm$ AD, mean vector length r, mean wind speed $\pm$ SD (m/s), mean wind direction $\pm$ AD and mean vector length r. Mean heading, track and wind directions shown were all nonuniformly distributed (Rayleigh test: $P < 0.001$). The trajectory classes include trajectories tracked back to Norway ('Norway'), trajectories tracked back to Sweden ('Sweden'), trajectories tracked back to Denmark ('Denmark'), trajectories tracked back to the European mainland ('Continent'), trajectories over the North Sea and thus with an unknown potential origin ('Unknown') and a special class of trajectories tracked just west of Norway, but still at sea ('Norway sea').

Table A3. Summary statistics, in 2 h intervals, of the measured tracks corresponding to each trajectory class resulting from simulations at the 925 hPa pressure level

Date	No. hours after sunset	N	Airspeed (m/s)	Heading (deg)	r	Ground speed (m/s)	Track (deg)	r	Wind speed (m/s)	Wind direction (deg)	r	% Norway	% Sweden	% Denmark	% Continent	% Unknown	% Norway sea
3 Oct 2006	0	292	6.4	121	0.56	15.0	81	0.86	11.0	76	0.99	0.0	0.0	0.3	3.4	96.2	0.0
	2	152	7.9	118	0.72	15.7	100	0.90	9.3	89	0.98	0.0	0.0	0.0	0.7	98.7	0.7
	4	104	9.6	151	0.75	14.8	134	0.84	7.4	113	0.97	0.0	0.0	2.9	1.9	95.2	0.0
	6	119	13.0	249	0.48	14.4	195	0.66	8.5	141	0.98	0.0	0.0	26.9	11.8	61.3	0.0
	8	372	14.8	209	0.85	19.3	181	0.93	9.2	138	1.00	54.6	0.0	10.5	1.1	18.0	15.9
	10	2177	14.9	215	0.90	19.3	177	0.93	11.3	129	1.00	48.8	1.1	8.6	1.0	16.4	24.2
31 Oct 2006	0	103	13.2	203	0.64	21.6	132	0.90	19.3	104	0.98	0.0	0.0	0.0	1.0	99.0	0.0
	2	187	11.1		0.18	22.7	136	0.84	22.6	141	1.00	0.0	0.0	0.5	5.3	92.0	2.1
	4	294	9.4		0.08	21.2	138	0.91	21.3	139	1.00	0.0	0.0	0.0	0.7	78.6	20.7
	6	1828	13.5	212	0.85	28.4	161	0.97	22.3	138	1.00	0.6	0.1	0.1	0.3	4.6	94.4
	8	1727	16.9	213	0.87	30.9	158	0.96	25.3	127	1.00	8.0	0.3	0.2	0.9	2.0	88.5
	10	1344	16.2	225	0.81	34.3	158	0.97	31.7	134	1.00	57.0	0.4	0.2	0.4	2.1	40.0
	12	832	17.1	235	0.91	36.5	167	0.98	34.7	141	1.00	86.4	9.3	0.5	0.6	0.4	2.9
1 Nov 2006	0	271	16.5	270	0.74	23.4	205	0.90	19.6	168	1.00	0.0	0.0	0.0	0.7	99.3	0.0
	2	1903	15.5	282	0.88	21.4	224	0.95	18.8	181	1.00	0.0	0.0	39.0	0.7	60.2	0.1
	4	1314	13.6	259	0.79	22.0	214	0.93	16.8	180	1.00	0.7	0.8	46.0	1.1	46.0	5.3
	6	495	13.8	228	0.76	23.2	198	0.89	14.0	173	1.00	14.5	13.5	11.1	1.6	24.2	34.9
	8	1344	18.0	222	0.93	22.2	199	0.95	9.5	148	0.98	72.2	19.5	0.1	0.7	0.3	7.2
	10	1971	15.6	232	0.88	20.7	198	0.95	11.6	152	0.99	59.3	30.8	0.7	0.2	1.0	8.0
	12	1675	14.0	243	0.86	20.2	198	0.95	14.0	157	1.00	44.1	46.9	0.2	0.0	0.9	7.9
2 Nov 2006	0	11	9.7		0.66	17.4	185	0.88	15.1	156	1.00	0.0	0.0	0.0	0.0	100.0	0.0
	2	203	20.1	273	0.92	20.4	227	0.93	15.0	160	1.00	0.0	0.0	73.9	2.0	24.1	0.0
	4	2868	18.0	272	0.97	19.8	228	0.98	14.3	167	1.00	0.2	0.1	92.9	0.6	6.0	0.1
	6	3017	14.9	246	0.82	22.0	211	0.92	13.7	174	1.00	18.2	8.4	50.7	2.2	6.8	13.6
	8	5200	12.3	238	0.80	21.6	205	0.94	13.9	179	1.00	36.4	14.9	25.3	1.8	3.2	18.4
	10	2950	11.4	244	0.85	20.2	206	0.96	13.6	177	1.00	34.5	40.0	11.2	1.1	1.0	12.1
	12	865	10.8	237	0.77	19.3	200	0.93	13.1	174	1.00	32.7	46.8	2.5	0.6	2.2	15.1
17 Sep 2007	2	47	13.3		0.34	14.5	136	0.51	10.9	92	0.94	0.0	0.0	2.1	0.0	97.9	0.0
	4	79	14.8	205	0.45	16.3	159	0.61	8.6	100	0.95	3.8	0.0	12.7	0.0	79.7	3.8
	6	2276	14.3	201	0.94	25.7	190	0.98	12.6	175	0.99	71.2	0.1	5.4	0.2	11.9	11.3
	8	1844	12.0	215	0.89	25.0	199	0.98	14.7	186	0.99	61.6	0.4	13.7	0.3	7.1	17.0
	10	485	12.3	199	0.88	26.7	194	0.98	15.3	189	1.00	71.3	0.2	4.1	0.2	0.8	23.3
26 Sep 2007	0	274	12.6	249	0.80	19.1	223	0.92	8.8	197	0.99	0.0	0.0	0.0	8.4	91.6	0.0
	2	1674	15.3	253	0.92	21.6	238	0.96	8.1	211	0.98	0.0	0.0	38.0	14.3	47.7	0.0
	4	3348	13.6	239	0.93	21.3	231	0.97	8.3	219	1.00	0.0	0.0	72.3	6.1	21.7	0.0
	6	3055	14.4	229	0.92	20.2	224	0.96	6.2	213	1.00	3.9	2.7	70.4	4.9	14.8	3.2
	8	2893	14.0	217	0.85	19.4	216	0.92	6.0	213	1.00	20.2	7.8	47.1	6.9	6.8	11.2
	10	727	14.0	211	0.81	19.3	211	0.90	6.1	210	1.00	39.2	11.3	27.5	9.5	2.8	9.8
1 Oct 2007	0	129	18.7	272	0.86	20.6	268	0.88	2.7	236	0.98	0.0	0.0	0.0	66.7	33.3	0.0
	2	498	19.1	259	0.91	21.9	257	0.93	3.3	241	0.99	0.0	0.0	35.3	45.0	19.7	0.0
	4	2585	17.1	239	0.92	22.0	242	0.95	5.3	253	1.00	0.1	0.0	66.5	14.1	19.3	0.1
	6	2285	15.7	228	0.88	21.2	234	0.93	6.3	249	1.00	11.4	0.0	47.2	11.3	21.3	8.8
	8	1475	15.7	196	0.88	20.5	211	0.93	7.1	244	1.00	49.3	0.7	8.9	4.1	3.1	33.8
	10	1789	14.3	189	0.87	18.5	204	0.92	6.3	239	1.00	46.3	2.7	4.2	2.2	2.7	41.9
17 Oct 2007	0	86	8.9	197	0.58	17.0	163	0.89	12.0	140	0.99	0.0	0.0	0.0	0.0	100.0	0.0
	2	264	11.3	214	0.73	18.7	176	0.92	12.7	144	1.00	0.0	0.0	0.4	0.0	99.6	0.0
	4	316	13.6	214	0.81	19.6	171	0.92	13.7	130	0.99	1.3	0.0	5.1	0.0	89.9	3.8
	6	1663	19.1	232	0.95	22.5	197	0.97	13.6	138	1.00	37.7	0.2	28.8	0.1	15.7	17.5
	8	188	13.4	224	0.88	24.8	189	0.94	16.0	162	1.00	72.9	0.0	2.7	2.1	2.7	19.7
	10	973	11.5	230	0.86	23.9	190	0.96	16.9	168	1.00	71.1	0.7	2.1	0.6	2.1	23.4
	12	1217	11.5	230	0.91	23.7	191	0.98	16.8	166	1.00	79.5	0.7	0.4	0.2	0.7	18.4

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Table A3 (*continued*)

Date	No. hours after sunset	*N*	Airspeed (m/s)	Heading (deg)	*r*	Ground speed (m/s)	Track (deg)	*r*	Wind speed (m/s)	Wind direction (deg)	*r*	% Norway	% Sweden	% Denmark	% Continent	% Unknown	% Norway sea
18 Oct 2007	0	289	11.9	218	0.83	20.3	180	0.95	13.7	150	1.00	0.0	0.0	0.0	0.0	100.0	0.0
	2	501	12.6	226	0.87	20.0	184	0.94	13.9	149	1.00	0.0	0.0	1.6	0.2	98.2	0.0
	4	1021	12.6	242	0.79	19.3	202	0.91	13.4	165	1.00	1.0	0.0	25.7	0.2	66.0	7.1
	6	2752	13.6	242	0.87	19.4	204	0.95	12.6	162	1.00	30.2	1.0	23.5	0.1	20.7	24.4
	8	1832	13.9	227	0.90	20.1	196	0.96	11.3	157	1.00	70.1	4.1	5.0	0.3	2.4	18.1
	10	1178	13.4	238	0.89	20.0	202	0.95	12.4	164	1.00	60.8	29.0	1.5	0.5	1.3	6.9
	12	1061	13.8	243	0.91	20.1	206	0.96	12.4	165	1.00	52.7	41.6	0.5	0.1	0.8	4.4
1 Oct 2008	0	40	7.5		0.16	21.3	99	0.95	19.4	95	1.00	0.0	0.0	0.0	2.5	97.5	0.0
	2	209	8.1		0.12	21.8	96	0.94	19.8	94	1.00	0.0	0.0	0.0	0.5	99.5	0.0
	4	215	6.5	20	0.39	20.8	92	0.96	19.8	97	1.00	0.0	0.0	0.0	1.4	98.1	0.5
	6	192	6.5	9	0.37	21.3	90	0.96	20.8	97	1.00	0.0	0.0	0.0	1.6	97.4	1.0
	8	159	8.1		0.15	21.4	102	0.93	21.0	98	1.00	1.3	0.0	0.0	0.0	67.3	31.4
	10	828	9.9	184	0.76	21.4	124	0.96	18.4	101	1.00	18.5	0.5	0.1	0.2	9.7	71.0
16 Oct 2008	0	48	10.7	209	0.53	18.6	142	0.84	16.9	122	1.00	0.0	0.0	0.0	4.2	95.8	0.0
	2	112	10.2	224	0.42	20.7	138	0.87	18.9	122	1.00	0.0	0.0	0.0	0.0	100.0	0.0
	4	143	10.8	241	0.46	19.3	141	0.86	18.2	122	1.00	0.0	0.0	0.0	0.0	97.9	2.1
	6	122	10.7		0.22	19.2	123	0.80	17.8	120	1.00	0.0	0.8	1.6	1.6	76.2	19.7
	8	513	16.0	239	0.85	17.5	168	0.90	17.9	116	1.00	38.0	0.4	0.6	0.2	14.8	46.0
	10	2998	16.4	240	0.98	17.1	178	0.98	17.1	121	1.00	76.4	0.6	0.0	0.3	0.7	22.1
	12	333	17.5	233	0.95	19.4	180	0.96	16.0	123	1.00	84.1	2.7	0.6	0.9	1.5	10.2
27 Oct 2008	0	39	4.9		0.26	13.7	96	0.80	12.9	95	1.00	0.0	0.0	0.0	0.0	100.0	0.0
	2	52	7.6	12	0.70	14.3	88	0.84	12.5	108	1.00	0.0	0.0	0.0	5.8	94.2	0.0
	4	237	4.8	207	0.30	14.1	88	0.94	14.3	85	0.98	0.0	0.4	0.0	1.3	97.9	0.4
	6	83	7.4		0.27	16.6	88	0.89	13.6	83	1.00	0.0	0.0	0.0	3.6	90.4	6.0
	8	506	14.9	215	0.91	15.9	168	0.92	12.6	107	0.98	45.1	0.0	6.1	0.4	14.0	34.4
	10	643	15.5	220	0.90	16.3	186	0.92	10.5	121	0.95	40.4	0.3	10.7	0.8	14.3	33.4
	12	373	11.9	207	0.93	16.1	184	0.96	7.4	143	1.00	30.8	0.0	0.5	0.5	4.6	63.5
28 Oct 2008	0	131	12.6	225	0.77	11.6	185	0.76	8.9	107	1.00	0.0	0.0	0.0	2.3	97.7	0.0
	2	723	13.4	194	0.88	14.0	154	0.86	9.6	87	1.00	0.0	0.0	0.0	2.2	97.8	0.0
	4	495	14.7	204	0.86	13.9	170	0.83	8.7	91	0.99	0.2	0.0	2.8	1.4	94.1	1.4
	6	1098	20.0	227	0.93	16.6	207	0.90	7.9	99	0.98	17.4	0.4	49.7	1.4	24.0	7.2
	8	4379	14.7	247	0.94	14.4	214	0.95	8.6	139	0.99	4.1	0.0	37.8	9.0	43.8	5.4
	10	3237	13.6	227	0.92	14.0	198	0.94	7.1	126	0.99	24.8	0.1	35.6	2.5	17.2	19.8
	12	1541	14.3	217	0.92	13.9	191	0.93	6.5	111	0.99	29.2	0.7	23.3	1.4	9.5	35.8
30 Oct 2008	0	755	14.6	257	0.89	17.0	251	0.92	3.1	223	0.99	0.0	0.0	0.1	28.2	71.7	0.0
	2	2400	13.5	255	0.91	18.1	247	0.95	5.3	226	0.99	0.0	0.0	28.1	14.6	57.3	0.0
	4	500	13.7	248	0.94	17.7	241	0.95	4.5	220	0.99	0.0	0.8	68.8	5.0	25.2	0.2
	6	287	13.8	220	0.73	16.3	220	0.78	3.1	215	0.96	5.6	4.2	33.8	11.5	29.3	15.7
	8	1816	14.9	229	0.87	14.2	220	0.87	2.6	117	0.97	9.0	35.4	36.7	2.5	5.0	11.5
	10	1969	14.1	223	0.90	14.1	216	0.90	2.0	129	0.98	24.1	37.3	21.3	1.5	1.8	14.0
	12	543	13.6	224	0.86	13.6	218	0.87	1.5	134	0.97	28.4	48.3	9.0	3.3	2.8	8.3

The table includes date (at sunset), number of hours after sunset, number of tracks (*N*), mean airspeed (m/s), mean heading, mean vector length *r*, mean ground speed, mean track direction, mean vector length *r*, mean wind speed (m/s), mean wind direction, mean vector length *r*, and percentage of trajectories per class. Mean heading, track and wind directions shown were all nonuniformly distributed (Rayleigh test: $P < 0.001$).