

RESEARCH

Open Access



Migratory movements of bats are shaped by barrier effects, sex-biased timing and the adaptive use of winds

Sander Lagerveld^{1*} , Pepijn de Vries¹ , Jane Harris^{2,3}, Sue Parsons³, Elisabeth Debusschere⁴ , Ommo Hüppop^{5^A} , Vera Brust⁵  and Heiko Schmaljohann⁶ 

Abstract

Background Migratory bats perform seasonal movements between their summer and winter areas. When crossing ecological barriers, like the open sea, they are exposed to an increased mortality risk due to energetically demanding long-distance flights and unexpected inclement weather events. How such barriers affect bat migratory movements is still poorly known.

Methods To study bat migration patterns in response to an ecological barrier, we tagged 44 *Nathusius'* pipistrelles *Pipistrellus nathusii* with radio-transmitters on the East coast of the United Kingdom (UK) in spring 2021 and 2022. Subsequently, we assessed their movements to continental Europe using the MOTUS Wildlife Tracking System. We investigated route selection, timing of migration, overall migration speed and the influence of wind on airspeed, groundspeed and flight altitude during migratory overseas flights.

Results Barrier effects cause migratory movements along the coast, and crossings over sea are shortened by deviating from the general migration direction. Males depart from the UK later in the season compared to females. The overall migration speed of females was 61 km/day and 88 km/day after their last detection in the UK. Our estimated airspeeds during oversea flights correspond well with airspeeds measured in a wind tunnel. Bats use wind adaptively to reduce airspeed when flying under tailwind and increase airspeed when flying under crosswind conditions. Departures over sea coincidence with tailwinds, enabling bats to more than double their airspeed, reaching ground speeds of up to 16.8 m/s (60.5 km/h). Our analysis suggests that bats select altitudes with favourable wind conditions and that they seek altitudes of several hundred meters, possibly extending up to 2,500 m. Low-altitude migration occurs when wind conditions are less favourable.

Conclusions Our study demonstrates that bat migratory movements are highly influenced by barrier effects, sex-biased timing of migration and the adaptive use of winds. The results of our study contribute to a more comprehensive understanding of the decision-making process and adaptations bats employ during their migration.

^ADeceased.

*Correspondence:
Sander Lagerveld
sander.lagerveld@wur.nl

Full list of author information is available at the end of the article



© The Author(s) 2024. **Open Access** This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

Elucidating bat migration patterns will enable us to develop effective conservation measures, for example in relation to the development and operation of coastal and offshore wind farms.

Keywords Bat migration, Nathusius' pipistrelle, North Sea, Wind farms, Flight elevation, Migration speed, Wind selectivity, MOTUS wildlife tracking system

Introduction

Several bat species migrate between their summer and winter areas. During their migratory journey they may encounter ecological barriers such as the open sea. These can be risky to cross due to energetically demanding long-distance flights and unexpected inclement weather events, as feeding and roosting opportunities are reduced or absent. How such barriers affect bat migratory movements is still poorly known.

In the North Sea region Nathusius' pipistrelle is the most observed migratory bat species [1–8]. The species' main breeding areas are located in north-eastern and central Europe [9]. Populations from the Baltic states and Russia migrate over large distances, up to 2400 km [10], to wintering areas in southern and western Europe, including the UK [9]. Populations in central Europe travel shorter distances or are sedentary [11]. Ringing recoveries of individuals ringed in the UK and mainland Europe suggest a migratory movement from west-southwest to east-northeast in spring, and vice versa in autumn [12].

Late summer adult males occupy territories along the migration route and mating occurs during the autumn migration [9]. Early migrants in autumn comprise primarily females and juveniles, while adult males migrate later in the season [11, 13, 14]. It is not yet known if this sex-dependent timing of migration also exists during spring. Our knowledge on the overall speed of migration in the North Sea region is similarly limited. So far, the best estimate comes from two radio-tracked migratory bats in autumn. These individuals flew from Helgoland (Germany) to the Netherlands and Belgium and covered average distances of 103–131 km per night when migrating, at an overall migration speed of 30–44 km per night during the entire monitoring period [15].

For flying vertebrates the relation between the mechanical power to fly and the airspeed shows a U-shaped curve [16]. The curve is characterized by the minimum power velocity representing the airspeed minimizing the energy expenditure per unit of time, and the maximum range velocity referring to the airspeed minimizing the energy expenditure per distance travelled [17, 18]. Nathusius' pipistrelle characteristic airspeeds measured under controlled conditions in a wind tunnel show a minimum power velocity of 5.8 +/- 1.0 m/s and a maximum range velocity of 7.5 +/- 1.1 m/s [19]. Experimental studies in the field, including insectivorous bats [19, 20], fruit bats [21] and birds [17] have shown that the minimum power velocity is used during foraging flights, whereas

migratory or commuting flights are rather performed at the maximum range velocity.

Flight mechanical theory predicts that airspeeds exceeding the maximum range velocity can be expected with headwind and crosswind, whereas airspeeds approaching the minimum power velocity are expected in tailwinds [18, 22]. In strong winds, when the wind-speed equals or exceeds the airspeed of the migrant, the animal is overpowered by the wind and has no other option than to follow its general direction [23]. Experimental studies in the field, concerning several bird species [24, 25], straw-coloured fruit bat *Eidolon helvum* [21] and Brazilian free-tailed bat *Tadarida brasiliensis* [26] confirmed reduced airspeeds during tailwinds and increased airspeeds during headwinds and crosswinds. It is currently unknown how Nathusius' pipistrelle adjusts its airspeed in response to wind conditions, and how this subsequently affects its groundspeed, which is the motion relative to the ground.

Some studies support the idea that bat migration is a low altitude phenomenon [27, 28]. Migrating bats over the Baltic Sea have been mainly observed below 10 m above sea level (asl) [27]. Nathusius' pipistrelles have been seen migrating over the North Sea during daylight hours at altitudes between 5 and 20 m [4]. Acoustic research at an offshore wind farm (OWF) off the Belgian coast showed that the number of recordings at nacelle height (93 m) was about 10% of those made at 16 m [29]. In contrast, migrating Eastern red bats *Lasiurus borealis* were photographed higher than 200 m asl off the east coast of the United States (US) in strong supportive tailwinds up to 9–10 m/s [30]. The observed relationship between stronger tailwinds and reduced migratory bat presence over the North Sea at lower altitudes (<50 m) may indicate that Nathusius' pipistrelle also migrates at relatively high altitudes under such conditions [7]. Bats may therefore respond similarly to tailwinds as migratory birds, which are known to explore wind conditions at different altitudes to select the optimal wind support [31–33].

Currently, the major gaps in our knowledge of the movement ecology of migrating bats are route selection across ecological barriers, migration timing and overall migration speed, as well as the behavioural response to wind during migratory endurance flights, e.g. adjusting airspeed, groundspeed and flight altitude.

To fill parts of these knowledge gaps we investigated Nathusius' pipistrelle' migratory movements in

the southern North Sea region. In 2021 and 2022, we equipped 44 bats with VHF-radio transmitters on the east coast of the UK using the MOTUS Wildlife Tracking System [34] and tracked their movements during spring migration to the European mainland. With the obtained data, we assessed their migratory routes, timing of migration and overall migration speed. For long-distance flights over the North Sea, we performed airspeed and ground speed calculations and assessed the optimal flight altitude and flight path.

Material & methods

Study area & receiver network

The study area includes the southern North Sea and adjacent coastal areas in the UK, Belgium, the Netherlands and Germany (Fig. 1). Bat tagging was conducted at Minsmere along marsh edge habitats in Southwark Belts (N 52.2443 E 1.6157), as well as 40 km further south at the Landguard Bird Observatory (N 51.9378 E 1.3209).

To monitor bat migratory movements, we used the MOTUS Wildlife Tracking System [34], which consisted of about 125 operational receiver stations in the study area (Fig. 1). All receivers are equipped with two to six antennas, orientated in different directions (<https://motus.org/>).

Receivers in the Netherlands, Belgium and UK used 6-element SIRIO WY140-6 N antennas and were connected to a GPS to ensure correct timestamps of the received signals. In Germany, 6-element Vårgårda Helgoland antennas were used, and most receivers were time-synchronized by GPS.

Tagging bats with radio-transmitters

Trapping and tagging of bats was carried out under Natural England project licence 2021-55582-SCI-SCI. In 2021, 15 trapping sessions were undertaken at Minsmere between 28 March and 15 May. In 2022, tagging occurred over 13 nights between 13 April and 22 May, two at Landguard and 11 at Minsmere.

Bats were trapped with no. 2 and no. 3 Austbat harp traps (Faunatec, Australia) in conjunction with AT100 acoustic lures (Binary Acoustic Technology, United States) playing male *Nathusius'* pipistrelle advertisement calls to attract conspecifics. The traps were positioned at least 150 m apart and were checked every 20 min. Captured bats were held individually in cloth bags. Each individual bat was measured, weighted, sexed, aged (if possible), and its condition and reproductive status assessed using the criteria described by [35].

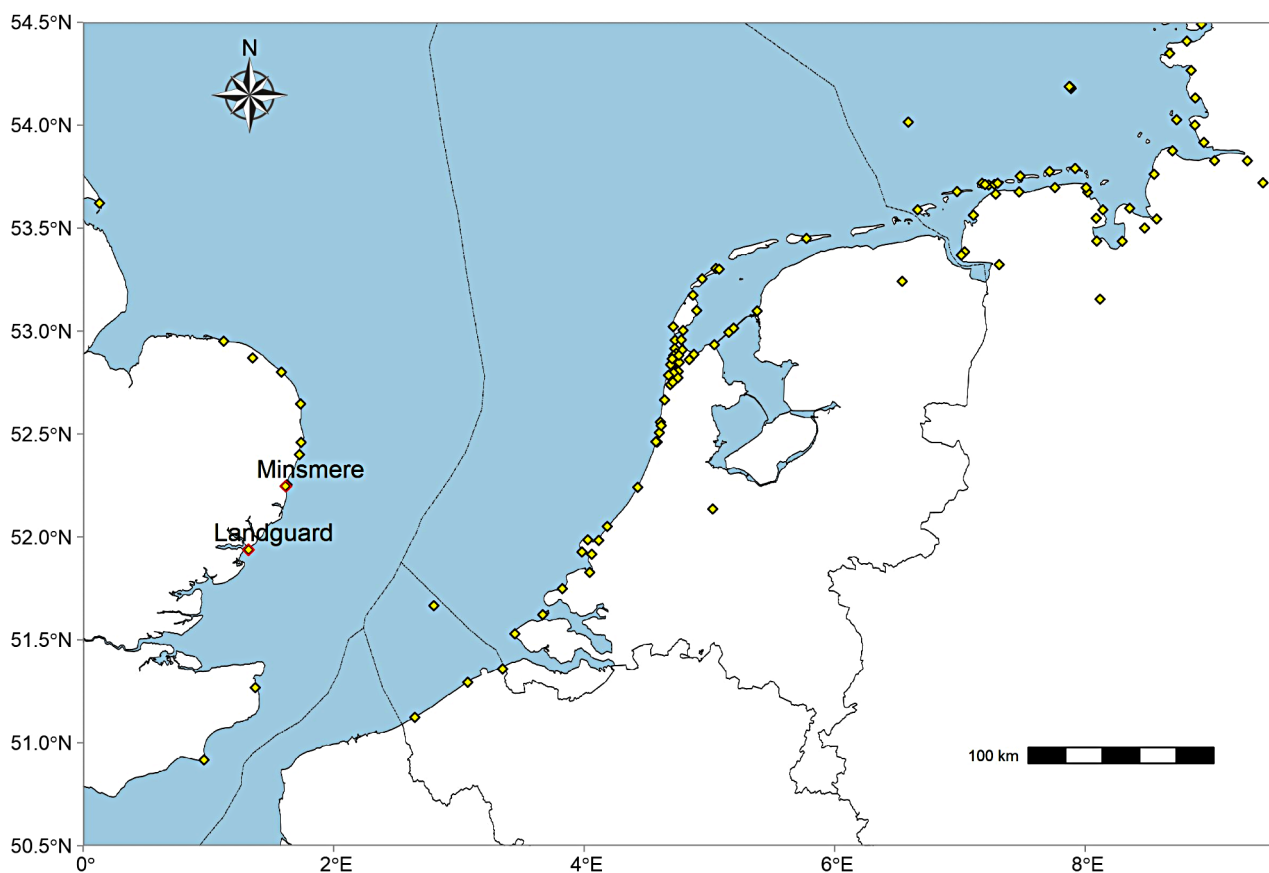


Fig. 1 Study area with the MOTUS telemetry network at the time of the study and the tagging locations at Minsmere and Landguard. Receivers are indicated in yellow, tagging locations circled in red

Nathusius' pipistrelles (males and females), considered to be in suitable condition (no visible injuries, few parasites, healthy wing membranes and fur) were tagged. Heavily pregnant females, judged to be 2 weeks or closer to parturition, and individuals in unsuitable condition were released immediately. In accordance with Natural England guidance for the capture and marking of bats (guidance note WML-G39), a minimum weight of 6 g was employed to ensure that the combined weight of the radio-transmitter and adhesive did not exceed 5% of the individual's body weight. Fur was lightly clipped between the shoulder blades to create a small pocket (8 mm x 4 mm) for the radio-transmitter which was attached with medical adhesive (Torbot Group, United States). Tagged bats were held in cloth bags on heat pads and released as soon as the adhesive was set (after about 10 min).

We used 0.26 g NTQB2-1 2 radio-transmitters (LOTEK Wireless, Canada) with burst intervals between 6.7 and 7.3 s and an expected lifespan of 51–61 days. Each transmitter broadcasts a uniquely coded signal at 150.1 MHz, allowing the identification of individually tagged animals on the same frequency.

Data curation

All calculations were performed in R, version 4.1.1 [36]. The Motus R package [37] was used to download the radio transmitter detections and metadata from www.motus.org (retrieved 2022-08-07). This yielded 923,898 recorded detections. To avoid false positives, we filtered out detections with run lengths of 3 or less (run length equals the number of consecutively detected signals), in accordance with the MOTUS R Book [37]. Furthermore, detections at specific receivers were filtered out manually as being deemed unlikely, for example at locations with lots of radio noise (see Additional file 1 for details). After this data curation, 96% of the original records remained.

The location of the station receiving the signal of a radio transmitter was used as a proxy for the current location of the bat. When there were detections adjacent in time (<30 s) on different nearby receivers (<10 km), we used the receiver at which the strongest signal was received. When a bat moved from one receiver to the next, we assigned a departure and arrival time stamp for the flightpath between the two receivers, using the timestamps when the strongest signals were received. The error in position fixes is estimated to be max. 2500 m based on the signal strengths received in the present study, in combination with the measurements of [38].

Route selection

To examine the movements, we used the package SF [39] to calculate the shortest distance between subsequent locations as well as the bearing for each flightpath. We excluded movements within 6.5 km from the tagging

location (the maximum foraging range of Nathusius' pipistrelle [40]). Flightpaths of each individual were plotted, using the package ggplot2 [41].

Timing of migration

For each individual, we determined the timestamp and geographic location of the last detection in the UK, and -if applicable- the timestamp and geographic location of the first and the last detection on the European mainland. We compared the date of last detection in the UK with the arrival date at the east coast of the southern North Sea (in Belgium and the Netherlands), as well as with the arrival date in northern Germany. Subsequently, we compared the date of last detection in the UK between the sexes, using a two-sample t-test.

Overall migration speed

For individuals detected over 400 km from the UK, we calculated an overall migration speed using the shortest distance between the tagging location and the geographical location of the last detection on the European mainland, divided by the time between tagging and the last detection. We also calculated the overall migration speed excluding the time spent in the UK, using the shortest distance between the geographical location of last detection in the UK and the last detection on the mainland divided by the time in between. We excluded one bat tagged late March which stayed until early May, and may have used the tagging area to overwinter.

Airspeed and groundspeed of migratory flights

To obtain accurate speed estimates, we restricted the analysis to single night flight paths of at least 100 km, in accordance with the MOTUS R Book [37]. This resulted in a dataset of five overseas flights from the east coast of the UK to the west coast of the Netherlands. From each flight, we assessed the potential flight paths at various altitudes assuming that the bat used a fixed heading (compass direction) and did not compensate for wind drift during the nocturnal crossing over sea (cf [42]). Furthermore, we assumed a constant airspeed and constant flight altitude.

Wind conditions at different altitudes were obtained from the ERA5 hourly data on pressure levels, where wind vectors are reported from 200 hPa up to 1000 hPa separated into 37 different barometric layers [43]. Wind data was provided at an hourly interval at a spatial resolution of 0.25×0.5 degrees. The barometric layers were converted to altitudes (in meters) by applying the rearranged barometric formula [44]:

$$h = \frac{T_b}{L_b} \left[\left[\frac{P}{P_b} \right]^{-\frac{R^* L_b}{g_0 M}} - 1 \right] - h_b \quad (1)$$

where R^* is the universal gas constant (8.3144598 J/(mol·K)); g_0 is the gravitational acceleration (9.80665 m/s²); M is the average molar mass of air (0.0289644 kg/mol); P is the air pressure (Pa) of the barometric layer; P_b is the air pressure at sea level (taken from [45]); h_b is the reference altitude (0 m per definition); T_b is the temperature at sea level (approximated by the temperature at 2m altitude taken from [45]); L_b is the temperature lapse rate (-0.0065 K/m [43]).

The wind vectors were interpolated from the barometric layers to a set of specific fixed altitudes using linear interpolation. The fixed altitudes were chosen to correspond well with the available barometric layers in the original wind data. The selected altitudes were: 10, 200, 400, 600, 800, 1000, 1200, 1400, 1600, 1800, 2000, 2500, and 3000 m. The windspeed was extracted from the collected wind data by taking the vector from the data at the simulated altitude that was closest in both space and time.

During flight, the motion relative to the ground (ground speed) was the net result of the bat's airspeed and displacement by the wind. By assuming an a priori value for airspeed (7.5 m/s) and bat heading (110°) in combination with the wind vector, the flight path was reconstructed at two-minute intervals. The calculated destination location (from the reconstructed flight path) was compared with the known arrival location (based on MOTUS data), which was the error of the simulation expressed in kilometres. By adjusting (solving) the value for airspeed and bat heading using root-finding algorithms developed by [46] this error was minimized to zero. This resulted in airspeed and bat heading estimates meeting the above-made assumptions that displacement is determined by a fixed air speed and bat heading and the wind vector. We calculated the tailwind and crosswind component of the wind vector for each two-minute interval, using Eqs. 2 and 3:

$$v_t = v_w \cdot \cos(\alpha_w - \alpha_a) \quad (2)$$

$$v_c = v_w \cdot \sin(\alpha_w - \alpha_a) \quad (3)$$

with α_w = wind heading, α_a = bat heading, v_w = windspeed, v_t = tailwind speed, v_c = crosswind speed

Positive values of tailwind indicate wind support in the direction of movement, whereas negative values indicate headwind. Crosswind refers to the wind vector perpendicular to the direction of movement. Positive values of the crosswind component indicate wind from the right and negative values indicate wind from the left. If the

windspeed equals or exceeds the airspeed, the animal can only maintain its flight path direction during tailwinds, while strong crosswind or headwind will divert it from its desired track [23]. We calculated the maximum possible angle between the estimated airspeed and the windspeed (cf [23]):

$$\alpha_{max} = \arcsin\left(\frac{v_a}{v_w}\right) \quad (4)$$

With α_{max} = maximum possible angle between wind heading and bat heading, v_a = airspeed and v_w = windspeed. Excluding angles greater than the maximum possible angle (cf [23]), resulted in a range of potential flight paths, corresponding airspeeds and flight altitudes. A flowchart of the calculation is included in Additional file 2. Next, we compared the calculated airspeeds with the minimum power velocity and the maximum range velocity measured in a controlled environment (wind tunnel experiment [19]).

Flight altitude and flight path

In the previous step, the range of potential airspeeds, corresponding flight altitudes and flight paths, were calculated for each migratory flight over sea. To assess the optimal (approximate) flight altitude and associated flight path, we identified the altitude with minimum airspeed (corresponding to the minimum energy expenditure).

Results

Route selection

44 *Nathusius'* pipistrelles were tagged; 40 at Minsmere and four at Landguard (Additional file 3). Two tags were found detached and one individual was predated by a Eurasian sparrowhawk *Accipiter nisus*. The remaining 41 individuals (four males and 37 females) were all detected at the tagging locations and 30 individuals (three males and 27 females) were also detected elsewhere (Fig. 2). Additional file 4 provides maps with the daily movements of each individual bat.

In the UK, movements of 23 individuals were observed, of which 10 moved north after tagging, three moved south and 10 performed up and down movements along the coast (Additional file 4). A total of 24 single-night movements was recorded in the UK (including 18 individuals). The average nightly distance of these movements was 36.4 km. The maximum recorded distance travelled within one night was 89.3 km (up and down along the coast).

A total of 15 bats was detected overseas, of which one individual was detected offshore at the Belwind Offshore Wind Farm in Belgian waters and three others at the coast in southern Belgium. Eight individuals made landfall on the Dutch coast. In northern Germany six bats

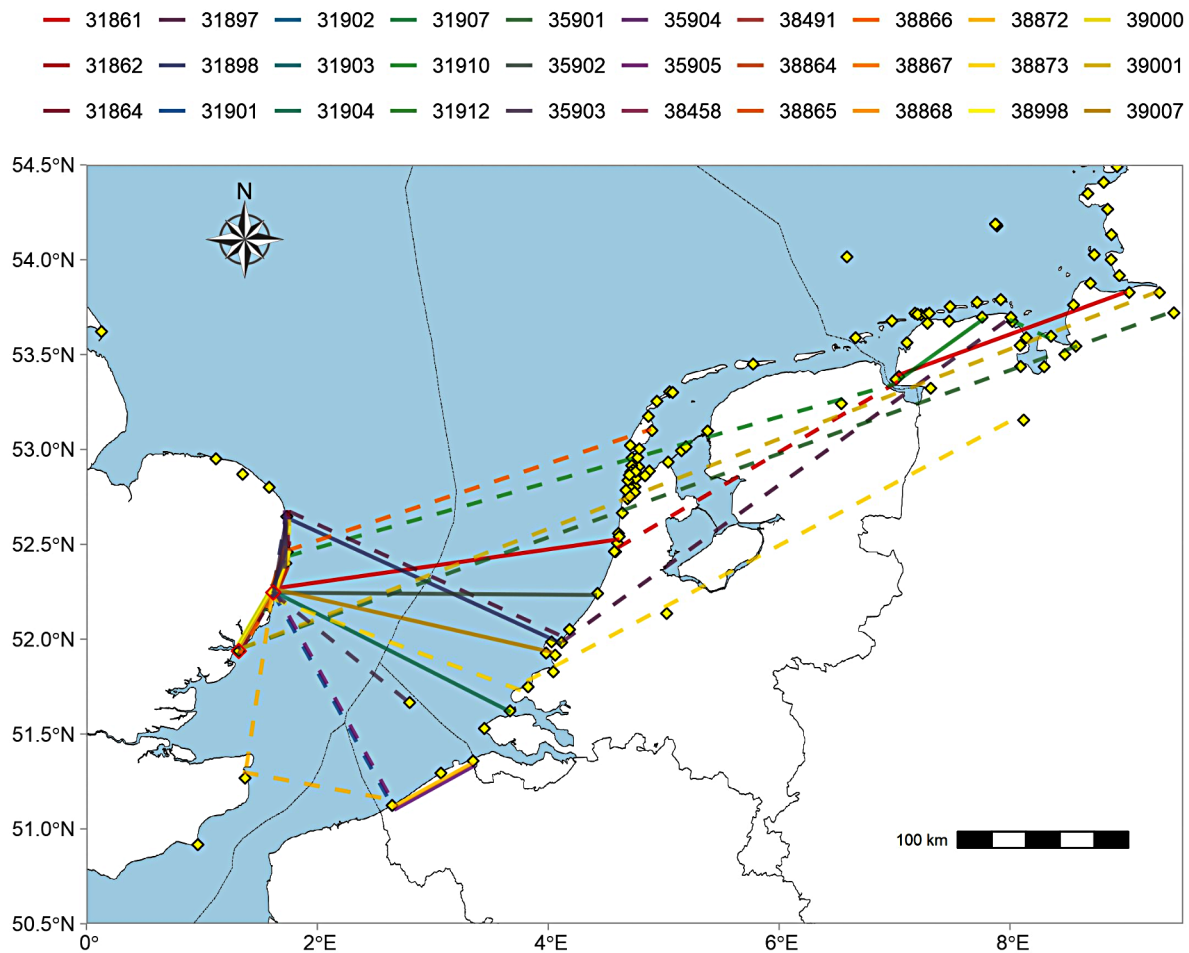


Fig. 2 Movements of *Nathusius' pipistrelles* detected away from the tagging locations ($n=30$). Receivers are indicated as yellow dots, tagging locations circled in red. Solid lines represent movements within one night whereas dotted lines indicate movements over more than one night. Note that the shortest distance between the receivers is shown, which not necessarily reflects the actual flight path between the receivers. See Additional file 4 for the day-to-day movements for each individual

were observed, three of which were detected previously on the Dutch coast (Fig. 2).

The majority of the bats detected in Belgium and the Netherlands (10 of the 12 individuals) were detected at a lower latitude than their tagging location in the UK. The five single-night overseas crossings (Fig. 2; solid lines over the North Sea) were performed in directions between 82 and 117 degrees (average 101 degrees). One individual flew south through Kent before crossing overseas. Four individuals changed their heading to the northeast after making landfall on the European mainland (Fig. 2).

Timing of migration

The last detection of females in the UK ($n=37$) occurred between 20 April and 29 May (average 10 May, $SD=9$ days). Arrivals at the east coast of the southern North Sea (in either Belgium or the Netherlands) ($n=11$) occurred between 2 and 28 May (average 13 May, $SD=9$ days) and the first occurrence in Germany ($n=6$) was observed

between 5 May and 3 June (average 16 May, $SD=10$ days). Males ($n=4$) were last detected in the UK between 24 May and 13 June (average 4 June, $SD=8$ days) of which one individual was detected offshore in Belgian waters on 25 May 2022. The difference in the date of last detection in the UK for females and males proved to be highly significant ($t = -5.2307$, $df=39$, $p\text{-value}=6.033e-06$).

Overall migration speed

For individuals tagged in April or May and subsequently detected in Germany ($n=5$, all females), the overall migration speed was 61 km/day ($SD=26$ km/day), and 88 km/day ($SD=46$ km/day) after their last detection in the UK (Table 1).

Airspeed and groundspeed of migratory flights

Five single-night overseas crossings (all females) were suitable for analysis. The minimum distance of over-sea crossings ranged from 157 to 205 km which took

Table 1 Spring migration speed, based on the time difference between release in the UK and last detection in Germany, as well as last detection in UK and last detection in Germany. Distances refer to the shortest distance between the tagging location and the location of the last detection

Deployment	Time between tagging and last detection UK [days]	Overall migration speed, including time spent in UK			Overall migration speed after last detection UK		
		Days	km	km/day	Days	km	km/day
31910	4	7	493	71	3	477	157
31897	9	18	457	25	9	434	47
35901	0	9	547	61	9	579	65
38873	1	9	449	50	8	450	56
39001	1	6	574	96	5	574	113
Average	3	10	504	61	7	503	88

Table 2 Timing of departure and arrival, and minimal distance of flight paths over 100 km during one night

Deployment	Departure			Arrival			Duration [min]	Min. distance [km]
	Date/Time [UTC]	Location	Time after sunset [min]	Date/Time [UTC]	Location	Time before sunrise [min]		
31861	2021-05-02 20:00	N 52.25 E 1.62	40	2021-05-02 23:57	N 52.51 E 4.60	250	237	205
31904	2021-05-17 20:41	N 52.25 E 1.63	56	2021-05-17 23:59	N 51.62 E 3.67	230	198	157
31898	2021-05-25 21:52	N 52.65 E 1.74	114	2021-05-26 01:27	N 51.98 E 4.12	129	215	178
35902	2022-05-06 20:08	N 52.25 E 1.63	41	2022-05-07 01:09	N 52.24 E 4.43	173	301	191
39007	2022-05-11 21:10	N 52.25 E 1.63	95	2022-05-12 00:00	N 51.92 E 4.06	236	170	170
Average	-	-	69	-	-	204	224	180

170–301 min to complete. Bats departed on average 69 min (range 40–114 min) after sunset and arrived on average 204 min (range 129–250 min) before sunrise (Table 2, Additional file 5).

In all but one case, the received signals at departure and arrival showed a gradually increasing and subsequently decreasing signal strength, indicating the animal was already in flight. The only exception is the departure of deployment 35,902, which shows a sharp increase and gradually decreasing signal, indicating that the animal was taking off in close proximity to the receiver (Additional file 5).

Figure 3 shows the calculated average airspeed during the overseas flights at different altitudes based on the wind conditions encountered along the way at those altitudes (Fig. 4). Excluding non-feasible angles between the airspeed and windspeed (Eq. 4), the calculated airspeeds correspond well with the minimum power velocity and maximum range velocity (Fig. 3).

During the overseas crossings windspeeds at 10 m asl ranged from 3.7 to 9.9 m/s, mostly increasing with altitude (Fig. 4). Separating the wind vector in tailwind and crosswind components showed that the wind direction differed with altitudes. Migratory flights over sea coincided with tailwinds, whereas the crosswinds components were much smaller or absent (Fig. 4). When the crosswind component is small compared to the tailwind component the calculated airspeed approaches minimum power velocity. Increasing crosswinds in relation to the

tailwinds results in calculated airspeeds in the range of the maximum range velocity (Figs. 3 and 4). Information on the bat heading, wind heading, and ground heading is presented in Additional file 6.

Ground speeds ranged from 10.7 to 16.8 m/s, and were on average a factor 2.2 (range 1.7–2.7) higher than the calculated airspeeds (Fig. 3), thus reducing the average energy expenditure by about 55% (range 41–59%) per unit of distance travelled.

Flight altitude and flight path

Unfeasible combinations of the angle between the wind-speed and airspeed (Eq. 4) limit the altitudinal range in which migratory flights can be performed (Fig. 3). In most cases, this results in a well-defined range of potential flight altitudes: deployment 31861 (1000–1800 m), deployment 31904 (400–2500 m), deployment 35902 (10–1000 m) and deployment 39007 (10–400 m). It is also possible that multiple possible altitudes are identified: deployment 31898 (10–2500 m), or that more than one optimum is present in a particular altitudinal range: deployment 31904 (600 and 2500 m).

The potential estimated flight paths for each overseas flight are shown in Fig. 5, of which the higher altitude flight paths generally increasingly resemble a straight line. Despite the different shape, the length of the estimated flight paths does not change much. A maximum difference between the shortest distance and calculated flight path of 5.4 km (2.7%) was noted in deployment 35902,

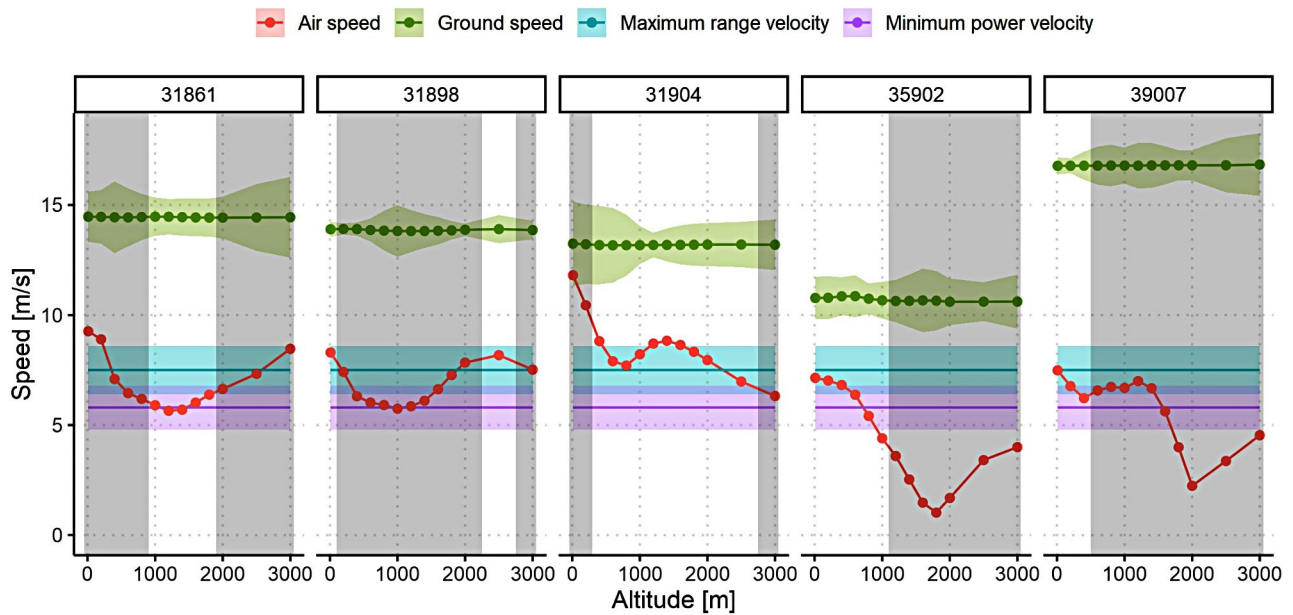


Fig. 3 Airspeed and ground speed at different altitudes. Numbers in panel titles are the tag deployments of the selected individuals. Grey areas indicate unfeasible angles between airspeed and windspeed, which means the animal is unable to actually follow this flight path (Eq. 4), although it can be calculated. Ribbons indicate the variation experienced along the track expressed as \pm their respective standard deviation. Characteristic airspeeds, measured under controlled conditions, are also shown: minimum power velocity (5.8 \pm 1.0 m/s) and maximum range velocity (7.5 \pm 1.1 m/s) (cf. [19])

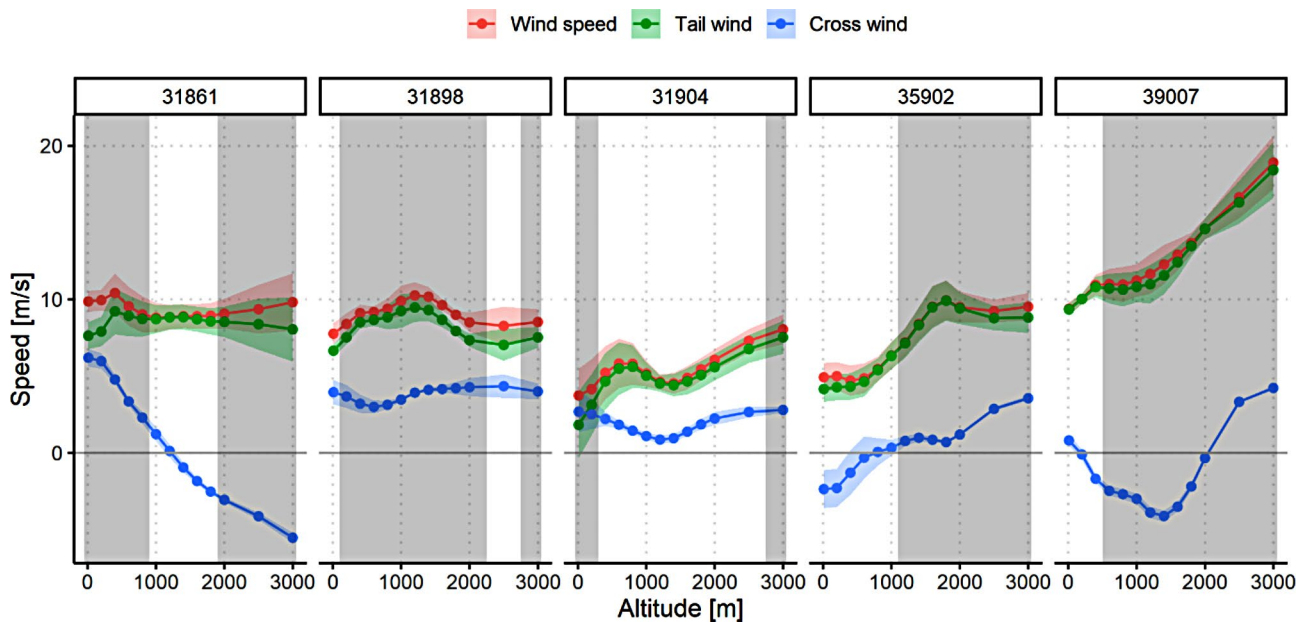


Fig. 4 Average windspeed at different altitudes, including tailwind and crosswind component. Positive values of the crosswind component indicate wind from the left of the bat, and negative values wind from the right. Numbers in panel titles are the tag deployments of the selected individuals. Grey areas indicate unfeasible angles between airspeed and windspeed, which means the animal is unable to actually follow this flight path (Eq. 4), although it can be calculated. Ribbons indicate the variation experienced along the track expressed as \pm their respective standard deviation

while the potential flight paths of the other deployments did not change more than 1.2 km (0.6%). Details can be found in Additional file 7.

The properties of the flight paths coinciding with minimal airspeeds are shown in Table 3. When more than one optimum is present in a particular flight path both

options are shown. Vector representations of windspeed, airspeed and groundspeed at the departure location, half-way and at the arrival location of the flight paths (Table 3) can be found in Additional file 8.

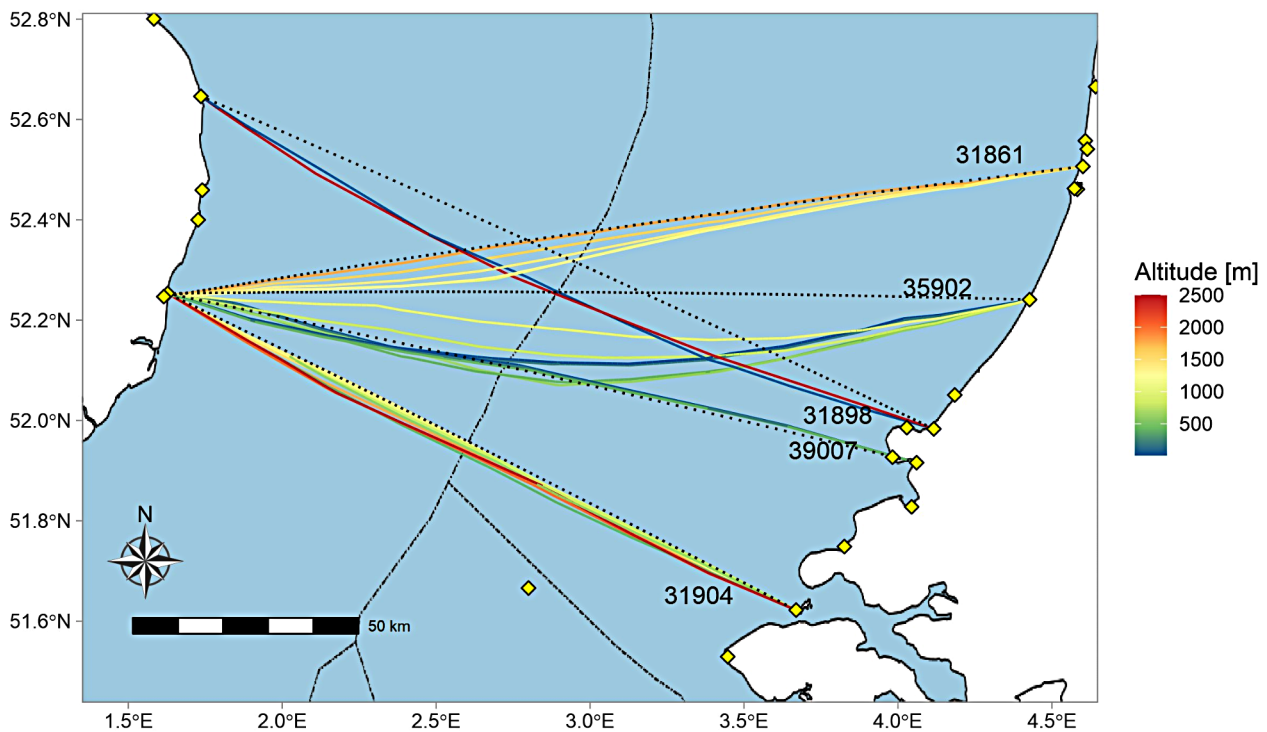


Fig. 5 Potential flight paths for different flight altitudes, indicated by different colors. The dotted tracks indicate the shortest distance between the departure and arrival locations

Table 3 Flight paths at altitudes with minimal air speeds. Values are means \pm their respective standard deviation along the flight path. Headings are indicated in degrees from North. Bat headings and airspeeds show no variation due to the applied assumption of being constant during the entire migratory flight

Deployment	Altitude [m]	Bat heading [°]	Air-speed [m/s]	Wind heading [°]	Wind speed [m/s]	Tail-wind [m/s]	Cross-wind [m/s]	Ground heading [°]	Ground-speed [m/s]
31861	1200	83	5.7	81 \pm 7	8.8 \pm 0.8	8.8 \pm 0.8	0.1 \pm 0.4	82 \pm 4	14.5 \pm 0.8
31898	10	143	8.3	83 \pm 10	7.8 \pm 0.7	6.7 \pm 0.4	4.0 \pm 0.8	114 \pm 6	13.9 \pm 0.3
	2500	147	8.2	82 \pm 8	8.3 \pm 1.2	7.0 \pm 1.0	4.3 \pm 0.8	114 \pm 6	13.9 \pm 0.6
31904	800	128	7.7	102 \pm 5	5.8 \pm 1.4	5.6 \pm 1.4	1.4 \pm 0.2	117 \pm 2	13.2 \pm 1.4
	2500	139	7.0	95 \pm 8	7.3 \pm 0.8	6.8 \pm 0.9	2.7 \pm 0.4	117 \pm 3	13.2 \pm 1.0
35902	1000	95	4.4	87 \pm 11	6.3 \pm 0.9	6.3 \pm 0.9	0.3 \pm 0.5	90 \pm 7	10.7 \pm 0.8
39007	400	87	6.2	112 \pm 4	10.9 \pm 0.7	10.8 \pm 0.7	-1.7 \pm 0.3	103 \pm 3	16.8 \pm 0.6

Discussion

Our study shows movements back and forth along the east coast of the UK, and crossings over sea are shortened by deviating from the general migration direction. Males migrate later in the spring in comparison to females, which shows that sex-biased timing of migration does not take place only in autumn.

Our analyses show that airspeeds correspond well with airspeeds measured under controlled conditions, and that free flying *Nathusius' pipistrelle* reduce airspeed under tailwind conditions and increase airspeed under crosswind conditions. Departures over sea coincided with tailwinds, enabling bats to reach ground speeds up to 16.8 m/s (60.5 km/h), more than doubling their flight range compared to windless conditions. Our analysis

suggests that bats select altitudes with favourable wind conditions and that they often seek altitudes of several hundred meters, possibly extending up to 2,500 m. Low-altitude migration occurred in less favourable wind conditions, e.g. during generally low wind speeds and in response to increasing headwinds or crosswinds at higher altitudes.

Route selection

The coastal movements in the UK were performed over relatively large distances, up to 89 km in one night back and forth along the coast (Fig. 2 & Additional file 4). As *Nathusius' pipistrelle* forages at a maximum distance of 6.5 km from its roost [40], it seems unlikely that these movements concern commuting flights between roosts

and foraging areas. Likewise, it seems improbable that these movements refer to landscape movements, which are movements within a larger stopover landscape [47]. So far, landscape movements of bats during stopovers are only known for Silver-haired Bats *Lasionycteris noctivagans*, with a mean distance of 6.7 km (max 18 km) from their tagging location [47]. As the observed movements were performed along the coast, it seems also unlikely that we observed reorientation movements, which are known from migratory birds who disperse to areas further inland to escape coastal areas with high competition for food and high predation risk [48, 49]. Therefore, it seems plausible that we observed migratory movements which are adjusted in directions perpendicular to the main migration direction aiming to avoid the open sea. Increased migratory presence along coastlines is also known from bats in other areas [8, 14, 27, 50–52], as well as from migratory birds (cf [42]). Bat migratory movements inland seem also to be affected by large water bodies, as departures along the shoreline perpendicular to the main migration direction have been observed at Lake Erie (Michigan, US) [53].

Another option to reduce the risk of crossing the open sea is to shorten the barrier crossing by diverting from the general migration direction, which is known from migratory birds [54, 55]. The single-night crossings ($n=5$) from the UK to the Dutch coast showed movements over the North Sea in directions between east and southeast. Other oversea crossings, with observed arrivals at the European coast, but with unknown departure location and time from the UK ($n=7$), showed lower latitudes on the European mainland in comparison to the location where they were tagged. One individual circumnavigated the southern North Sea by flying from Minsmere to Kent and subsequently northeast along the Belgian coast (Fig. 2 & Additional file 4). A similar circumnavigation of Delaware Bay (eastern US) by migratory bats has been observed before [56].

Therefore, our data shows that bat migratory movements are shaped by barrier effects resulting in movements along coastlines and detours taken to reduce travelling over water. Consequently, most migratory bats can be expected along the coast and most overseas crossings can be expected in southern parts of the study area.

Timing of migration

In spring, bat migration over the North Sea occurs from late March until early June and peaks between mid-April and late May [3, 5]. The observed movements in this study fit well in this seasonal pattern. All oversea crossings occurred throughout May and movements over the European mainland were observed until early June.

We found males to migrate on average 25 days later than females in spring, which shows that adult males do

not only migrate later in the season in autumn (cf [11, 13, 14]). Sex-biased timing during spring migration has also been observed in silver-haired bats *Lasionycteris noctivagans* [57]. Early arrival in the breeding areas provides female bats a fitness advantage as early-born pups are more likely to survive the winter [58]. In addition, early-born female pups are more likely to reproduce already in their first year [58, 59]. For males, there is no need to arrive early in the breeding areas as they do not provide parental care and mating takes place in autumn [57].

Overall migration speed

For females we observed an average overall migration speed of 61 km/day and 88 km/day after their last detection in the UK (Table 1). In the Baltic area, a daily spring migration speed of 55 km/day was observed based on acoustic data [8]. Radio tracked Nathusius' pipistrelles in autumn ($n=2$) showed an average daily migration speed including stopover time at the tagging location of 37 km/day [15]. Ringing recoveries ($n=12$) indicate a daily autumn migration speed of about 48 km/day [14]. The observed migration speeds in spring are somewhat higher compared to autumn and therefore it may be possible that bats migrate faster in spring. Many bird species also show faster migrations in spring to ensure an early arrival in the breeding areas [60, 61].

Airspeed and ground speed of migratory flights

Our analysis shows a range of estimated airspeeds which match well with the maximum range velocity and minimum power velocity of Nathusius' pipistrelle measured under controlled conditions (cf [19]). The estimated airspeed falls in the range of the minimum power velocity during tailwinds, while relatively strong crosswinds in relation to the tailwind lead to higher airspeeds in the range of the maximum range velocity. Our results therefore not only show realistic values of the estimated airspeed (cf [19]), but also indicate responses to tailwind and crosswind similar to those of migratory birds [18, 24, 25], straw-coloured fruit bats [21] and Brazilian free-tailed bats [26].

Our results show that bats select tailwinds to cross over the North Sea from the UK, and that crosswinds, to some extent, are not avoided (Fig. 4). Departures during headwinds were not observed. Departures coincided with an average windspeed at 10 m asl of 7.1 m/s (range 3.7–9.9 m/s) with an average tailwind component at 10 m asl of 5.9 m/s (range 1.8–9.3 m/s).

During this study, we observed ground speeds between 10.7 and 16.8 m/s (38.5–60.5 km/h). These were on average a factor 2.2 (range 1.7–2.7) higher than the calculated airspeeds (Table 3), indicating a reduction of the energy expenditure by about 55% (range 41–59%) per unit of distance travelled. Like migratory birds [62], bats are

therefore able to extend their flight range significantly by using tailwinds.

In autumn, migrating bats are known to regularly interrupt their directed flight to forage [50]. At sea, insects frequently accumulate at offshore structures and foraging at offshore platforms and wind turbines has been documented in the Baltic Sea [27] and the North Sea [3, 7, 29]. The relatively low ground speeds of two radio tracked *Nathusius'* pipistrelles from Helgoland to the German mainland of 4.5–5.7 m/s and 5.8–7.9 m/s during autumn [15], may also indicate foraging along the way. Our results show that the calculated airspeeds (Fig. 3) correspond well with the characteristic airspeeds (cf [19]). Therefore, it seems unlikely that time was spent foraging en route, or that stopovers were made at offshore structures (cf [7]). Migratory *Nathusius'* pipistrelles departing from the east coast of the UK are therefore able to cross the North Sea to the Netherlands in a non-stop flight of 3–5 h, covering a minimal distance of 170–205 km. Radio tracked migratory bats ($n=2$) from Helgoland (Germany) to the Netherlands and Belgium in autumn showed lower average travel distances of 103–131 km/night during nights when the bats migrated [15]. It may be possible that bats in spring cover more distance per night than in autumn, e.g. due to a higher overall migration speed or by prevailing westerlies which generally correspond with tailwind in spring and headwind in autumn. Other factors may also be involved like limited options for stopovers at sea.

Flight altitude and flight path

Wind conditions in combination with airspeed (Eq. 4) determine the altitudinal range in which migratory flights can be performed in a particular direction (Figs. 3 and 4). Our calculations show that at least two migratory flights over sea were performed at minimum altitudes of about 400 and 800 m (deployment 31904 and 31861: Fig. 3). Birds are known to explore wind conditions at different altitudes during migratory flights to select the optimal wind support [31, 32]. However, there is also evidence that the first optimum is chosen, even when better wind conditions prevail at higher altitudes [63]. In theory, bats are also expected to select flight altitudes to exploit optimal wind support [64]. If bats do select the optimal altitude (minimal airspeed) approximate flight altitudes of respectively 400, 800, 1200, 2500 and 2500 m (Fig. 3; Table 3) would likely be used. When selecting the first optimum this would result in flight altitudes of about 10, 400, 800, 1000 and 1200 m (Fig. 3; Table 3). That bats perform migratory flights over sea at relatively high altitudes has been shown by [29] who photographed several eastern red bats *Lasiurus borealis* off the east coast of the U.S at altitudes over 200 m during tailwinds up to 9–10 m/s. Also, in terrestrial habitats bat migration at higher altitudes has been documented. For example, radar-tracked

migratory bat movements over the Hula valley (Israel) occur mainly at altitudes between 200 and 600 m [65] and the migratory hoary bat *Lasiurus cinereus* has been recorded over 2400 m [66]. Acoustic research in the Alps mountain range in Austria and Italy revealed migratory bat activity at altitudes over 2700 m [67, 68]. Thus, high altitude migratory flight, and its consequential thinner air and lower temperatures, apparently do not seem to pose a restriction on the occurrence of migratory bats.

Bat migration also occurs at low altitudes (<10 m) over land [28] and over sea [27]. The results of our study indicate that low flight altitudes will be used when unfeasible combinations of windspeed and airspeed (Eq. 4) arise due to increasing crosswind or headwind at higher altitudes. Low-altitude migration can also be expected during generally low wind speeds [2, 4, 6, 7]. Foraging and roosting opportunities at offshore platforms (cf [7]), may also contribute to low altitude migration over sea.

Conclusion

The routing decisions of migratory bats are highly influenced by barrier effects, including avoidance of the open sea and reducing the extent of the overseas crossing. The migration timeframe depends on the sex of the animal, while the overall speed of migration may be seasonally dependent. Wind conditions affect departure decisions and determine how migratory flights are conducted.

The results of our study contribute to a more comprehensive understanding of the decision-making process and adaptations bats employ during their migration. Elucidating bat migration patterns will enable us to develop effective conservation measures, for example in relation to the development and operation of coastal and offshore wind farms.

Abbreviations

UK	United Kingdom
asl	Above sea level

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40462-024-00520-7>.

- Additional file 1: Removal of false positive detection data.
- Additional file 2: Flowchart of the flight path calculation.
- Additional file 3: Metadata tagged bats.
- Additional file 4: Individual flight paths.
- Additional file 5: Signal strength at departure and arrival of migratory flights over sea.
- Additional file 6: Bat heading, ground heading and wind heading at different altitudes of migratory flights over sea.
- Additional file 7: Extent of flight paths at different altitudes of migratory flights over sea.
- Additional file 8: Windspeed, airspeed and groundspeed during migratory flights over sea at optimal altitudes.

Acknowledgements

We sincerely thank Martijn Keur, Bart Noort, Cor Sonneveld, Hans Verdaat and Simon de Vries (Wageningen University & Research), Heinz-Hinrich Blikslager, Thomas Klinner, Thomas Mertens, Mario de Neidels and Florian Packmor (Institute of Avian Research "Vogelwarte Helgoland", Carl von Ossietzky Universität Oldenburg), Ewan Parsons (Norfolk & Norwich Bat Group), René Janssen (Bionet Nature Research), Wouter Faveyts (Zwin Natuur Park) and Robin Brabant (Royal Belgian Institute of Natural Sciences), as well as the entire team behind the Motus wildlife tracking system for their invaluable technical support. We also thank Dagmar van Nieuwpoort, Maarten Platteeuw, Marije Wassink and Henri Zomer (Dutch Ministry of Infrastructure and Water Management), Steve Geelhoed and Josien Steenbergen (Wageningen University & Research), Linda McPhee (Linda McPhee Consulting), and our anonymous reviewers for their valuable comments and suggestions to improve the manuscript.

Author contributions

Fieldwork: JH and SP. Project licence: JH. Study design and original draft: SL. Data analysis: SL and PdV. Editing and review: all authors. Funding: OH, ED, JH, HS and SL.

Funding

The receiver network in the Netherlands is funded by the Dutch Ministry of Infrastructure and Water Management (Offshore wind ecological program), the Ministry of Agriculture, Nature and Food Quality (Nature inclusive energy transition program), the Wageningen University and the Groningen University. The receiver network in Belgium was funded as part of the Flemish contribution to LifeWatch ESFRI and Zwin Natuur Park, and in Germany by the German Research Foundation (SCHM 2647/3–1, SCHM 2647/4–1, SCHM 2647/7–1) and the German Federal Agency for Nature Conservation (BfN) within the Federal Ministry for the Environment, Nature Conservation and Nuclear Safety (BMUV; grants: no 351582210 A and 351986140 A). Funding of the UK receiver network was received from the Dutch Ministry of Infrastructure and Water Management, Wageningen University, UK Bird Observatories and Norfolk & Norwich Bat Group. Fieldwork and the analysis or the data were funded by the Dutch Ministry of Infrastructure and Water Management, Kepwick Ecological Services, Norfolk & Norwich Bat Group, Suffolk Bat Group and Suffolk Naturalists Society.

Data availability

The data are not publicly available yet, in due time they will be made publicly available in the datalab from the Dutch Offshore Wind Ecological Programme (WOZEP).

Declarations

Ethics approval and consent to participate

Trapping and tagging of bats was carried out under Natural England project licence 2021-55582-SCI-SCI.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

Author details

¹Wageningen University & Research, Ankerpark 27, Den Helder NL-1781 AG, The Netherlands

²Kepwick Ecological Services, Kepwick Cottage, Wymondham Road, East Carleton, Norfolk NR14 8JB, UK

³Norfolk and Norwich Bat Group, Norwich, UK

⁴Flanders Marine Institute, Jacobsenstraat 1, Oostende 8400, Belgium

⁵Institute of Avian Research, An der Vogelwarte 21, 26382 Wilhelmshaven, Germany

⁶Institute of Biology and Environmental Science, Carl von Ossietzky Universität Oldenburg, Ammerländer Heerstraße 114-118, 26129 Oldenburg, Germany

References

1. Boshamer JPC, Bekker D. 08. Nathusius' pipistrelles (*Pipistrellus nathusii*) and other species of bats on offshore platforms in the Dutch sector of the North Sea. *Lutra*. 2008;51:17–36.
2. Brabant R, Laurent Y, Jonge Poerink B, Degraer S. (2021). The Relation between Migratory Activity of *Pipistrellus* Bats at Sea and Weather Conditions Offers Possibilities to Reduce Offshore Wind Farm Effects. *Animals*. 2021; 11(12), 3457. <https://doi.org/10.3390/ani11123457>
3. Hüppop O, Hill R. Migration phenology and behaviour of bats at a research platform in the south-eastern North Sea. *Lutra*. 2016;59:5–22.
4. Lagerveld S, Jonge Poerink B, Haselager R, Verdaat H. Bats in Dutch offshore wind farms in autumn 2012. *Lutra*. 2014;57(2):61–9.
5. Lagerveld S, Gerla D, van der Wal JT, de Vries P, Brabant R, Stienen E, Deneudt K, Manshanden J, Scholl M. Spatial and temporal occurrence of bats in the southern North Sea area. (Wageningen Marine Research report; no. C090/17). Wageningen Marine Research. 2017. <https://doi.org/10.18174/426898>
6. Lagerveld S, Jonge Poerink B, Geelhoed SCV. Offshore occurrence of a migratory bat, *pipistrellus nathusii*, depends on seasonality and weather conditions. *Animals*. 2021;11(12):3442. <https://doi.org/10.3390/ani11123442>.
7. Lagerveld S, Wilkes T, van Puijenbroek MEB, Noort CE, Geelhoed SCV. Acoustic monitoring reveals spatiotemporal occurrence of *Nathusius' pipistrelle* at the southern North Sea during autumn migration. *Environ Monit Assess*. 2023;195:1016. <https://doi.org/10.1007/s10661-023-11590-2>.
8. Rydell J, Bach L, Bach P, Diaz LG, Furmankiewicz J, Hagner-Wahlsten N, Kyheröinen E-M, Lilley T, Masing M, Mayer M, Pétersons G, Suba J, Vasko V, Vintulis V, Hedenström A. Phenology of migratory bat activity across the Baltic Sea and the south-eastern North Sea. *Acta Chiropterologica*. 2014;16(1):139–47.
9. Russ J. *Nathusius's Pipistrelle Pipistrellus nathusii* (Keyserling and Blasius, 1839). In: Hackländer K, Zachos FE, editors. *Handbook of the mammals of Europe*. Handbook of the mammals of Europe. Cham: Springer; 2022. https://doi.org/10.1007/978-3-319-65038-8_68-1.
10. Vasenkov D, Desmet JF, Popov I, Sidorchuk N. Bats can migrate farther than it was previously known: a new longest migration record by *Nathusius' pipistrelle Pipistrellus nathusii* (Chiroptera: Vespertilionidae) *Mammalia*, vol. 86, no. 5, 2022, pp. 524–526. <https://doi.org/10.1515/mammalia-2021-0139>
11. Sachanowicz K, Ciechanowski M, Tryjanowski P, Kosicki JZ. Wintering range of *Pipistrellus nathusii* (Chiroptera) in Central Europe: has the species extended to the north-east using urban heat islands? *Mammalia*. 2019;83:260–71.
12. National *Nathusius' Pipistrelle* Project. 2024. Available online: <https://www.bat-s.org.uk/our-work/national-bat-monitoring-programme/surveys/national-nathusius-pipistrelle-survey> (accessed 2 July 2023).
13. Jarzembowski T. Migration of the *Nathusius' pipistrelle Pipistrellus nathusii* (Vespertilionidae) along the Vistula Split. *Acta Theriol*. 2003;48:301–8.
14. Pétersons G. Seasonal migrations of north-eastern populations of *Nathusius' bat Pipistrellus nathusii* (Chiroptera). *Myotis*. 2004;41–42:29–56.
15. Bach P, Voigt CC, Götsche M, Bach L, Brust V, Hill R, Hüppop O, Lagerveld S, Schmaljohann, Seebens-Hoyer A. Offshore and coastline migration of radio-tagged *Nathusius' pipistrelles*. *Conserv Sci Pract*. 2022;4:e12783. <https://doi.org/10.1111/csp2.12783>.
16. Pennycuik CJ. Mechanics of flight. In D. S. F., & J. R. K, editors, *Avian Biology*, Vol. 5 (Vol. Vol 5, Chap. 1:1–75). Academic Press. 1975.
17. Alerstam T, Lindström A. Optimal bird migration: the relative importance of time, energy and safety. In: Gwinner E, editor. *Bird Migration: physiology and ecophysiology*. Berlin, Germany: Springer; 1990. pp. 331–51.
18. Hedenström A, Alerstam T. Optimal flight speed of birds. *Phil Trans R Soc Lond*. 1995;B 348:471–87.
19. Troxell SA, Holderied MW, Pétersons G, Voigt CC. *Nathusius' bats optimize long-distance migration by flying at maximum range speed*. *J Exp Biol*. 2019;222(4):jeb176396. <https://doi.org/10.1242/jeb.176396>.
20. Grodzinski U, Spiegel O, Korine C, Holderied MW. Context-dependent flight speed: evidence for energetically optimal flight speed in the bat *Pipistrellus kuhlii*. *J Anim Ecol*. 2009;78:540–8.
21. Sapir N, Horvitz N, Dechmann DKN, Fahr J, Wikelski M. Commuting fruit bats beneficially modulate their flight in relation to wind. *Proc. R. Soc. B*. 2014;281: 20140018. <https://doi.org/10.1098/rspb.2014.0018>
22. Leicht F, Hedenström A, Alerstam T. Effects of Sidewinds on Optimal Flight speed of birds. *J Theor Biol*. 1994;170(2):219–25. <https://doi.org/10.1006/jtbi.1994.1181>.
23. Alerstam T. A graphical illustration of pseudodrift. *Oikos*. 1978a;30:409–12. <https://doi.org/10.2307/3543492>.

Received: 6 June 2024 / Accepted: 22 November 2024

Published online: 18 December 2024

24. Hedenström A, Ålerstam T, Green M, Gudmundsson GA. Adaptive variation of airspeed in relation to wind, altitude and climb rate by migrating birds in the Arctic. *Behav Ecol Sociobiol.* 2002;52:308–17. <https://doi.org/10.1007/s00265-002-0504-0>.
25. Kogure Y, Sato K, Watanuki Y, Wanless S, Daunt F. European shags optimise their flight behaviour according to wind conditions. *J Exp Biol.* 2016;219:311–8.
26. McCracken GF, Safi K, Kunz TH, Dechmann DKN, Swartz SM, Wikelski M. Airplane tracking documents the fastest flight speeds recorded for bats. *R. Soc. open sci.* 2016;13:160398. <https://doi.org/10.1098/rsos.160398>
27. Ahlén I, Baagøe HJ, Bach L. Behavior of Scandinavian bats during Migration and foraging at Sea. *J Mammal.* 2009;90:1318–23.
28. Šuba J. Migrating Nathusius's pipistrelles *Pipistrellus nathusii* (Chiroptera: Vespertilionidae) optimise flight speed and maintain acoustic contact with the ground. *Environ Exp Biol.* 2014;12:7–14.
29. Brabant R, Laurent Y, Jonge Poerink B, Degraer S. Activity and Behaviour of Nathusius' Pipistrelle *Pipistrellus nathusii* at low and high Altitude in a North Sea Offshore wind farm. *Acta Chiropterologica.* 2019;21:341–8.
30. Hatch SK, Connelly EE, Divoll TJ, Stenhouse IJ, Williams KA. Offshore Observations of Eastern Red Bats (*Lasiurus borealis*) in the Mid-atlantic United States using multiple survey methods. *PLoS ONE.* 2013;8:e83803. <https://doi.org/10.1371/journal.pone.0083803>.
31. Leichti F. Birds: blown' by the wind? *J Ornithol.* 2006;147(2):202–11.
32. Schmaljohann H, Liechti F, Bruderer B. Trans-Sahara migrants select flight altitudes to minimize energy costs rather than water loss. *Behav Ecol Sociobiol.* 2009;63:1609–19.
33. Shamoun-Baranes J, Liechti F, Vansteelant WMG. Atmospheric conditions create freeways, detours and tailbacks for migrating birds. *J Comp Physiol* 2017; a 203:509–29. <https://doi.org/10.1007/s00359-017-1181-9>
34. Taylor PD, Crewe TL, Mackenzie SA, Lepage D, Aubry Y, Crysler Z, Finney G, Francis CM, Guglielmo CG, Hamilton DJ, Holberton RL, Loring PH, Mitchell GW, Norris D, Paquet J, Ronconi RA, Smetzer J, Smith PA, Welch LJ, Woodworth BK. The Motus Wildlife Tracking System: a collaborative research network to enhance the understanding of wildlife movement. *Avian Conserv Ecol.* 2017;12(1):8. <https://doi.org/10.5751/ACE-00953-120108>.
35. Haarsma AJ. Manual for assessment of reproductive status, age and health in European Vespertilionid bats. Electronic publication, version 1, Hillegom (Holland). 2008.
36. R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. 2024 <https://www.R-project.org/>
37. Birds Canada. (2022). motus: Fetch and use data from the Motus Wildlife Tracking System. <https://motusWTS.github.io/motus>, assessed 1 June 2022.
38. Lagerveld S, Janssen R, Manshanden J, Haarsma AJ, de Vries S, Brabant R, Scholl. Telemetry for migratory bats: a feasibility study. (Wageningen Marine Research report; No. C011/17). Wageningen Marine Research. 2017. <https://doi.org/10.18174/417092>
39. Pebesma E. Simple features for R: standardized support for spatial Vector Data. *R J.* 2018;10(1):439–46. 10.32614/RJ-2018-009.
40. Dietz C, Helversen O, Nill D. Bats of Britain, Europe and Northwest Africa. A., Black C. London, UK. 2009.
41. Wickham H. ggplot2: Elegant graphics for data analysis. Springer-Verlag New York. Retrieved from <https://ggplot2.tidyverse.org>. 2016, accessed 1 Jun 2022.
42. Ålerstam T. Wind as selective agent in bird migration. *Ornis Scand.* 1979;10(1):76–93. <https://doi.org/10.2307/3676347>.
43. Hersbach H, Bell B, Berrisford P, Biavati G, Horányi A, Muñoz Sabater J, Nicolas J, Peubey C, Radu R, Rozum I, Schepers D, Simmons A, Soci C, Dee D, Thépaut JN, (CDS). ERA5 hourly data on pressure levels from 1959 to present. Copernicus Climate Change Service (C3S) Climate Data Store. 2018. (Accessed on 09-September-2022), <https://doi.org/10.24381/cds.bd0915c6>
44. NASA. (1976) <https://ntrs.nasa.gov/api/citations/19770009539/downloads/19770009539.pdf>
45. Hersbach H, Bell B, Berrisford P, Biavati G, Horányi A, Muñoz Sabater J, Nicolas J, Peubey C, Radu R, Rozum I, Schepers D, Simmons A, Soci C, Dee D, Thépaut JN, (CDS). ERA5 hourly data on pressure levels from 1959 to present. Copernicus Climate Change Service (C3S) Climate Data Store. 2018. (Accessed on 09-September-2022), <https://doi.org/10.24381/cds.adbb2d47>
46. Brent RP. An Algorithm with Guaranteed Convergence for Finding a Zero of a Function. Algorithms for Minimization without Derivatives, Englewood Cliffs, NJ: Prentice-Hall, ISBN 0-13-022335-2. 1973.
47. Taylor PD, Mackenzie SA, Thurber BG, Calvert AM, Mills AM, McGuire LP. Landscape Movements of Migratory Birds and bats reveal an expanded scale of stopover. *PLoS ONE.* 2011;6(11):e27054. <https://doi.org/10.1371/journal.pone.0027054>.
48. Ålerstam T. Reoriented bird migration in coastal areas: dispersal to suitable resting grounds? *Oikos* 1978; 30:405–8.
49. Åkesson S, Karlsson L, Walinder G, Ålerstam T. 1996. Bimodal orientation and the occurrence of temporary reverse bird migration during autumn in south Scandinavia. *Behav. Ecol. Sociobiol.* 1996; 38 (5):293–302.
50. Ijäs A, Kahilainen A, Vasko VV, Lilley TM. Evidence of the migratory bat, *Pipistrellus nathusii*, aggregating to the coastlines in the northern Baltic Sea. *Acta Chiropterologica.* 2017;19(1):127.
51. Šuba J, Petersons G, Rydell J. Fly-and-forage strategy in the bat *Pipistrellus nathusii* during autumn migration. *Acta Chiropterologica.* 2012;14(2):379–85.
52. Voigt CC, Kionka J, Koblitz JC, Stitz PC, Petersons G, Lindecke O. Bidirectional movements of Nathusius' pipistrelle bats (*Pipistrellus nathusii*) during autumn at a major migration corridor. *Global Ecol Conserv.* 2023;48:e02695640.
53. McGuire LP, Guglielmo CG, Mackenzie SA, Taylor PD. Migratory stopover in the long-distance migrant silver-haired bat, *Lasionycteris noctivagans*. *J Anim Ecol.* 2012;81(2):377–85. <https://doi.org/10.1111/j.1365-2656.2011.01912.x>. Epub 2011 Sep 28. PMID: 21954938.
54. Ålerstam T. Detours in bird migration. *J Theor Biol.* 2001;209(3):319–31. <https://doi.org/10.1006/jtbi.2001.2266>. PMID: 11312592.
55. Woodworth BK, Mitchell GW, Norris DR, Francis CM, Taylor PD. Patterns and correlates of songbird movements at an ecological barrier during autumn migration assessed using landscape- and regional-scale automated radiotelemetry. *Ibis.* 2015;157(2):326–39. <https://doi.org/10.1111/ibi.12228>.
56. True MC, Gorman KM, Taylor H, et al. Fall migration, oceanic movement, and site residency patterns of eastern red bats (*Lasiurus borealis*) on the Mid-atlantic Coast. *Mov Ecol.* 2023;11:35. <https://doi.org/10.1186/s40462-023-00398-x>.
57. Jonasson KA, Guglielmo CG. Sex differences in spring migration timing and body composition of silver-haired bats *Lasionycteris noctivagans*. *J Mammal.* 2016;97(6):1535–42. <https://doi.org/10.1093/jmamm>.
58. Frick WF, Reynolds DS, Kunz TH. Influence of climate and reproductive timing on demography of little brown myotis *Myotis lucifugus*. *J Anim Ecol.* 2010;79:128–36.
59. Barclay RM. Variable variation: annual and seasonal changes in offspring sex ratio in a bat. *PLoS ONE.* 2012;7:e36344.
60. Nilsson C, Klaassen RHG, Ålerstam T. Differences in speed and duration of Bird Migration between Spring and Autumn. *Am Nat.* 2013;181. <https://doi.org/10.1086/670335>. 837–45.
61. Schmaljohann H. Proximate mechanisms affecting seasonal differences in migration speed of avian species. *Sci Rep.* 2018;8:4106. <https://doi.org/10.1038/s41598-018-22421-7>.
62. Liechti F, Bruderer B. The relevance of wind for optimal migration theory. – *J Avian Biol.* 1998;29:561–8.
63. Mateos-Rodríguez M, Liechti F. How do diurnal long-distance migrants select flight altitude in relation to wind? *Behav Ecol.* 2012;23(2):403–9. <https://doi.org/10.1093/beheco/arr204>.
64. Hedenström A. Optimal migration strategies in bats. *J Mammal.* 2009;90:1298–309. <https://doi.org/10.1644/09-MAMM-S-075R2.1>.
65. Werber Y, Sextin H, Yovel Y, Sapir N. BATScan: a radar classification tool reveals large-scale bat migration patterns. *Methods Ecol Evol.* 2023. <https://doi.org/10.1111/2041-210X.14125>.
66. Peurach SC. High-altitude collision between an airplane and a hoary bat, *Lasiurus cinereus*. *Bat Res News.* 2003;44:2–3.
67. Widerin K, Reiter G. Bat Activity at High Altitudes in the Central Alps, Europe. *Acta Chiropterologica.* 2017;19(2):379–87. <https://doi.org/10.3161/15081109ACC2017.19.2.014>.
68. Caprio E, Patriarca E, Debernardi P. Bat activity and evidence of bat migration at two high elevation passes in the Western Alps. *Eur J Wildl Res.* 2020;66(4). <https://doi.org/10.1007/s10344-020-01402-0>.

Publisher's note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.