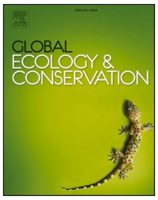
Global Ecology and Conservation 48 (2023) e02695

Contents lists available at ScienceDirect

Global Ecology and Conservation

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



Bidirectional movements of Nathusius’ pipistrelle bats (*Pipistrellus nathusii*) during autumn at a major migration corridor

Christian C. Voigt[a,*,1], Julia Kionka[a,b], Jens C. Koblitz[c], Peter C. Stilz[d], Gunārs Pētersons[e], Oliver Lindecke[f,2]

[a] *Department of Evolutionary Ecology, Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Str. 17, 10315 Berlin, Germany*
[b] *Institute of Biology, Freie Universität Berlin, Takustr. 6, 12489 Berlin, Germany*
[c] *Max-Planck Institute of Animal Behavior, Konstanz, Germany*
[d] *Freelance Biologist*
[e] *Faculty of Veterinary Medicine, Latvia University of Life Sciences and Technologies, K. Helmana street 8, LV 3004 Jelgava, Latvia*
[f] *Institute of Biology and Environmental Sciences, Carl von Ossietzky Universität Oldenburg, Oldenburg 26111, Germany*

ARTICLE INFO

Keywords:
Reverse migration
Movement ecology
Bat migration

ABSTRACT

Migration is well documented for many species throughout the animal kingdom. Although migration is also a common behaviour in bats, it is rarely studied due to the cryptic nature of the phenomenon. Recoveries of banded individuals have shown that Nathusius’ pipistrelles (*Pipistrellus nathusii*) can fly more than 2000 km between their summer and winter ranges in Europe, but further details of how and where they move between the endpoints of their seasonal journeys remain elusive. Here, we used three-dimensional acoustic tracking at a coastal migration corridor to elucidate the flight behaviour of Nathusius’ pipistrelles during late summer. Analyzing 432 recorded flight trajectories, we show that the majority of bats followed the expected southerly direction, parallel to the coastline, on all nights, and flying at the optimal speed for long-distance travel with minimal energy expenditure. However, on one day with stronger winds, about 20 % of the bats flew in the opposite, i.e. northerly, direction. The observation of a proportion of individuals flying antiparallel to the mass of migrating conspecifics within the same movement corridor highlights that individuals may follow contrasting movement strategies at the same time and place, presumably depending on environmental conditions. We argue that it is possible for Nathusius’ pipistrelles to fly back and forth (south and north) during autumn migration, spending more time on this migration corridor than required for a straight one-way flight. This highlights the urgent need to protect migration corridors along coastlines, particularly as wind energy development continues.

1. Introduction

Each year, billions of animals migrate between their breeding and wintering areas (Dingle, 2014). Travelling over long distances is risky and involves high energetic costs, imposing extreme physiological and sensory challenges on migrants, particularly when

---

* Corresponding author.
E-mail address: voigt@izw-berlin.de (C.C. Voigt).
[1] Orcid: 0000–0002-0706–3974
[2] Orcird: 0000-0002-2545-9999

https://doi.org/10.1016/j.gecco.2023.e02695
Received 6 September 2023; Received in revised form 18 October 2023; Accepted 18 October 2023

travelling at a fast pace on the wing (Alerstam and Lindström, 1990). Many migratory animals follow an optimal migratory trajectory (Alerstam and Lindström, 1990; Hedenström, 2008, 2009), which results in preferred flight corridors that are used by a species. For example, within the largest avian migration flyway, i.e., the Palaearctic-African flyway, birds concentrate in autumn at flight corridors to cross or fly around the Mediterranean Sea on their way south (Hahn et al., 2009). A comparative study confirmed that physiological constraints in combination with local topography may select for this spatial convergence of migration strategies in animals from various geographical origins (La Sorte et al., 2016).

Yet, studies also demonstrate that the realized heading directions and migration routes of individuals may be more complex than predicted based on optimality criteria. For example, some songbirds that were radio-tagged during migration outside of their normal range were observed to head in a direction away from the species-specific flyway, independent of wind drift (Thorup et al., 2012). Indeed, such vagrant behaviour has been described for many migratory bird species. In Nearctic birds, species with expanding populations seem to have more vagrant individuals than non-expanding populations (Patten and Marantz, 1996; Veit, 2000). Consistent with this notion, the occurrence of vagrancy was best explained by an increasing population and some predominant airflows at the time of migration for a North American bird species (Zawadzki et al., 2019). Vagrancy in migratory individuals often goes along with reversed migration, i.e., animals heading into the opposite direction than expected (Bruderer and Liechti, 1998). Among European passerines, both nocturnal and diurnal migratory birds regularly exhibit reverse migration. (Åkesson et al., 1996). Within the Palaearctic bird populations, reversed migration seems to be most often observed in birds from Eastern Europe or Asia compared with birds from the Mediterranean region migrating southwards (Thorup, 2004). The underlying causes for reversed migration may vary across species and populations. Likely factors include adverse weather conditions, topographic barriers, inaccuracy in navigation, and search for stopover sites depending on a migrant's physiological condition (Sandberg, 1994; Komenda-Zehnder et al., 2002).

In comparison to the vast literature on bird migration, bat migration is poorly studied, yet recent banding campaigns and technological advances have improved our understanding (Popa-Lisseanu and Voigt, 2009; Krauel and McCracken, 2013; Voigt et al., 2017a). For example, decades of banding campaigns in Europe have revealed that migratory species, such as Nathusius' pipistrelles (*Pipistrellus nathusii*), common noctules (*Nyctalus noctula*) and Leisler's noctules (*N. leisleri*) migrate between northeastern breeding areas to hibernation sites in western or southwestern Europe (Pētersons, 2004; Steffens et al., 2004; Hutterer et al., 2005). Nathusius' pipistrelles regularly migrate several hundred to more than 2,000 km, with the longest documented distance of 2,200 km between banding sites in Latvia and Russia and the hibernation site in Northern Spain and France, respectively (Alcalde et al., 2020; Vasenkov et al., 2022). Although banding data may generate highly relevant information on general migration directions, distances covered and connectivity of winter and summer areas, this approach is severely limited for several reasons. First, only a small fraction of banded animals is recaptured and the likelihood of recaptures may vary geographically, e.g., mostly because of the density and activity of bat workers. Second, in the vast majority of cases banding data connects two geographical locations. This implies a straight, unidirectional flight between the start and endpoint of the journey. However, this is simplifying the true migratory route of bats that may follow landscape features such as coastlines and river valleys (e.g., Furmankiewicz et al., 2009, Bach et al., 2022). Recently, geographic assignments of animals based on stable isotopes have offered new insights into bat migration. For example, stable hydrogen isotope ratios indicated long-distance migration in North American bats of the genus *Lasiurus* (Cryan, 2003), in African flying foxes (Ossa et al., 2012) and in European bats (Voigt et al., 2012, Lehnert et al., 2018), yet flyways of individual bats are not resolved by this approach. Lastly, a few tracking studies have revealed landscape level movements of migratory bats, e.g., for *Lasionycteris* during the summer migration period before crossing a large water body (Taylor et al., 2011; McGuire et al., 2012) and for European common noctule bats (*Nyctalus noctula*) flying at high altitude during spring migration (Dechmann et al., 2014). Despite this recent progress, we are by and large data deficient on the movements of migratory bats.

Each late summer, thousands of Nathusius' pipistrelles follow the coastline of the Baltic Sea in Latvia in a southern direction as documented by trapping followed by banding and various methods of movement tracking, and by acoustic monitoring, specifically at Pape Bird Ringing Station (PBRS) in southwestern Latvia (Pētersons, 2004; Hutterer et al., 2005; Steffens et al., 2004; Lindecke et al., 2015, Voigt et al., 2017, 2018; Lindecke et al., 2019a; Alcalde et al., 2020; Keišs et al., 2021; Lindecke et al., 2021). Recently, it was suggested that Nathusius' pipistrelles from Baltic countries and Finland may reach southwestern and western Europe by crossing the Baltic Sea to Sweden (Gaultier et al., 2020), from where they may continue their journeys to Denmark and beyond (Kurvits et al., 2011, Kruszynski et al., 2021). Based on acoustic recordings at the Finnish coastline, it was further deduced that Nathusius' pipistrelles may move north of their breeding range in Finland before they cross the Baltic Sea to Sweden. This northern movement contrasts with the general assumption of a southern and southwestern heading direction of Nathusius' pipistrelles during summer migration inferred from departure directions of radio-tracked bats (Lindecke et al., 2015, 2021; Bach et al., 2022), and from banding data (Pētersons, 2004; Steffens et al., 2004; Hutterer et al., 2005; Alcalde et al., 2020; Vasenkov et al., 2022).

Here, we investigated the directionality of free-flying Nathusius' pipistrelles at the coastal migration corridor in Latvia. Specifically, we explored whether migratory Nathusius' pipistrelles move in both directions simultaneously at this major European bat migration corridor. At PBRS, the migration corridor lies about 50–100 m from the waterline (Keišs et al., 2021), which follows a NW-SE direction (Šuba et al., 2012). Acoustic surveys have shown that bat activity drops by about 50 % when moving inland in eastern direction from 100 m to 150 m distance to the waterline (Voigt et al., 2018). We therefore focused on a distance of 50–100 m from the waterline in our study. We measured the flight trajectories of migrating bats at PBRS over distances of up to 30 m with a stationary T-array (one vertical, one horizontal branch) each equipped with ultrasonic microphones. Specifically, for each echolocation event we estimated the three-dimensional (3D) positions of bats passing through by quantifying the time delay at which the same echolocation call arrived at eight omnidirectional microphones positioned at known distances on the T-shaped array (e.g., Koblitz, 2018, Grodzinski et al., 2009, Götze et al., 2016). In a previous study at PBRS, this array helped us discern variations in flight speeds among Nathusius' pipistrelles, i.e., whether they were migrating or foraging (Troxell et al., 2019). Our findings revealed that migrating bats of this species travel optimally at maximum range speeds of roughly 7 m/s. In contrast, their foraging conspecifics moved at speeds less than 6 m/s, aligning closely with this species' minimum power speed (Troxell et al., 2019). If some bats were indeed heading north, at migration speed but oriented antiparallel to the majority of bats in the migration corridor, it would suggest a reversed migration pattern, potentially towards sites from which they could cross the Baltic Sea to Sweden (Gaultier et al., 2020, Kruszynski et al., 2021).

2. Material and methods

2.1. Study site and data acquisition

Field work was carried out between 16th and 29th August 2018, which coincides with the peak summer migration at Pape Bird Research Station (PBRS) adjacent to Pape lake in Latvia (56°09′57″N 21°01′02″E) (Šuba et al., 2012; Voigt et al., 2017b, 2018). Weather data (ambient temperature, rainfall, humidity, wind speed and direction) were obtained from a station (6152 Davis Vantage Pro 2 weather station; Davis Instruments, Rijswijk, the Netherlands) situated within a few meters next to the recording sites. Besides the predominant species Nathusius' pipistrelle, other bats such as (in decreasing abundance) soprano pipistrelles (*Pipistrellus pygmaeus*), parti-coloured bats (*Vespertilio murinus*), common noctules (*Nyctalus noctula*), and northern bats (*Eptesicus nilssonii*) can be encountered at this site as well (Voigt et al., 2017b, 2018).

We recorded echolocation calls with two microphone arrays on three occasions: on 17th of August 2018 between 2005 and 2117 h, on 22nd of August 2018 between 2011 and 2059 h and on 27th of August between 2122 and 2139 h. For each recording night, we chose a different spot, yet always adjacent to a pine forest on top of the dunes, about 50–80 m east of the shoreline. On each occasion, recordings started at sunset and ran until a maximum of 150 bats were documented, i.e., we did not record throughout whole nights but rather only during the first hours of a given night.

The microphone array was equipped with eight omnidirectional, ultrasonic microphones (Knowles, Model FG-23329, Ithaca, Illinois, USA). The horizontal part of the array consisted of three 1-m branches forming a T and a vertical 0.88-m branch pointed upwards. Each branch was equipped with two microphones, located on pipes of 10 cm length, fixed at a right angle to reduce echoes from the array surface. On the vertical branch, a top pipe of 10 cm and the microphone were fixed, which resulted in a final length of the vertical branch of 1 m. A coordinate system was defined whereby the centre of the array was assigned x, y and z coordinates of (0|0|0). The positive end of the x axis pointed to the East, the negative to the West. The positive end of the y axis pointed to the North and the positive end of the z axis pointed upwards representing the height above ground. Accordingly, the x, y and z coordinates of spatial positions were references to the array. The centre of the array was then mounted on a 1.3 m tripod, and positioned in the flight corridor of the migrating bats at about 50–100 m distance from the shoreline.

At sunset, we started sound recordings manually. Recordings were amplified and high-pass filtered using a custom-made amplifier and then digitised at a sampling rate of 300 kHz and a 16 bit resolution using an 8-channel A/D converter (National Instruments, Model USB-6356, Austin, Texas, USA). Recordings were visualized and data stored via a custom written program with the software MALTA 3.2 (CAE Software and Systems) on SSD discs. We documented temperature and humidity at the beginning and every half an hour within recordings, as both parameters have an impact on sound propagation.

We used a custom-made software toolbox to analyse echolocation calls, identify bat species, and to calculate the 3D positions of individuals. This program was written for MATLAB (Version R2015a, Mathworks, Natick, MA, USA) and contained a toolset of programs for acoustic localisation of animal vocalisations.

2.2. Bat species identification

Echolocation calls were assigned to *Pipistrellus nathusii* if the end frequency was within the range of 35–41 kHz (Skiba, 2009). *Pipistrellus pygmaeus* was identified by echolocation calls with an end frequency range of 51–56 kHz (Skiba, 2009). Owing to the similarity of call characteristics of *Eptesicus nilssonii, Nyctalus noctula* and *Vespertilio murinus* we lumped these species to a group called Nyctaloids (Voigt et al., 2017b). We analysed the end frequencies of the echolocation calls by visual inspection directly within our custom-made program, which displayed calls in one spectrogram per microphone. For each flight path the end frequencies of three calls, one at the beginning, one in the middle and one at the end of the track, were analysed to assign a bat species or species group unambiguously to the corresponding flight path.

2.3. Acoustic tracking and flight path reconstruction

All bats passing the array were continuously analysed until a total number of 150 individuals was reached. Between the start and the end of an analysis, short time periods had to be selected to analyse the recordings bit by bit. We defined these fragments, the exact positions of the microphones, and the configuration parameters manually in *toadconfig.m*. Afterwards, the spatial positions of single or multiple bats above the array were calculated automatically using *mktoadpos.m* and *chcktoadpos.m*. Both scripts used the configurations defined in *toadconfig.m*.

We calculated 3D positions of recorded bats in our custom-made program using the time-of-arrival differences (abbreviated as TOAD). Each echolocation call reached the microphones at times depending on distances travelled between the emitting bat and microphones. TOADs were computed by cross-correlating a single echolocation call between the microphones. Each TOAD was then used to calculate the spatial position of a bat at the moment of call emission relative to the centre of the array. This calculation was affected by the speed of sound which in turn is dependent on air temperature and humidity. Both factors were measured during the recordings and included in the calculations via the script *toadconfig.m.* After running the scripts *mktoadpos.m* and *chcktoadpos.m*, the positions from consecutive calls of individual bats were assembled manually in our custom-made program. Unlikely positions, resulting in, e.g., rapid jumps within flight paths, were manually excluded from analysis as erroneous. Only individual flight paths with a minimum of four consecutive calls were considered for further analysis. In a final step, we saved a bat's consecutive positions indicated by x, y and z coordinates at a point in time in a *clicks.csv*-file for the selected period. All coordinates denoted a bat's flight altitude in relation to the array's center with the coordinates (0|0|0). Recording date, period length and track ID resulted in a unique ID for each bat. We considered individual flight paths as independent since it was highly unlikely that the same bats repeatedly passed by our study site during summer migration (Lindecke et al., 2015; Pētersons, 2004).

2.4. Parameter calculations

We used R 3.6.0 (R Foundation for Statistical Computing, Vienna, Austria) and the packages stringr (Wickham, 2019), tidyverse (Wickham & Wickham, 2017) and plotrix (Lemon, 2006) to extract relevant raw data from the *clicks.csv*-files and to calculate flight parameters (scripts: Supplementary Material). To obtain the flight altitude above ground, we added 1.3 m to the z-value, which was the height of the tripod with the microphone array on top. The average flight altitude h^{-} of each bat was computed as the mean of all altitudes received for a given bat. The movement step length between two consecutive 3D positions was calculated as the length of the vector between subsequent spatial positions.

$$a_n(n) = \sqrt{(x_{n+1} - x_n)^2 + (y_{n+1} - y_n)^2 + (z_{n+1} - z_n)^2}$$

Flight speed

Flight speed v of a bat was calculated by dividing the distance a_n of each vector by the time passed between two subsequent spatial positions.

$$v_n\left[m \quad s^{-1}\right] = \frac{a_n}{t_{n+1} - t_n}$$

The speed of an individual bat was computed as the median speed $\tilde{v}$ and the mean speed $\bar{v}$ of all vectors of the corresponding flight path.

Linearity index

We estimated the linearity of a flight path by establishing a linearity index following Suzuki et al. (2002). This index was calculated as a ratio of two velocity parameters: the curvilinear velocity *VCL* of a track consisting of n vectors divided by the straight-line velocity *VSL* which assumes a direct movement from the first to the last point of a flight path. To compute *VSL*, the direct movement from the first to the last point of a flight path was considered as a hypothetical vector with its length $a_{straight}$. This sum was then divided by the time needed from the first to the last point t^*:

$$VSL = \frac{a_{straight}}{t^*}$$

VCL was computed as the sum of all distances a_n of a flight path divided by t^*:

$$VCL = \frac{\sum_{n=1}^{n} a_n}{t^*}$$

For each individual flight path, the linearity index l was calculated as the ratio of *VSL* over *VCL*. l -values ranged between 0 and 1 with a value close to 1 indicating a high linearity typical for a migrating bat and a value close to 0 a non-linear flight trajectory typical for an insect-hunting bat (Troxell et al., 2019).

Linearity index

To calculate the cardinal direction of each flight vector, we eliminated the altitude coordinate z to analyse the flight paths in 2D. Thus, the 2D vector $(\overrightarrow{v_{2D}})_n = \langle x_{n+1} - x_n | y_{n+1} - y_n \rangle$ was defined with its length b_n. As each vector forms an angle with a hypothetical vector pointing northwards, we assumed a reference vector $\overrightarrow{v_{North}} = \langle x_{North} | y_{North} \rangle$ pointing from the centre of the array directly to the North between the points (0|0) and (0|1). Though, this vector resulted in $\overrightarrow{v_{North}} = \langle 0|1 \rangle$ with a length of 1 m, defined as c.

The angle between the vectors $(\overrightarrow{v_{2D}})_n$ and $\overrightarrow{v_{North}}$ was defined as the compass direction δ_n with 0° = N, 90° = E, 180° = S and 270° = W. The compass direction δ_n was calculated using the following formula:

$$\delta_n[^\circ] = \cos^{-1}\left(\frac{(\overrightarrow{v_{2D}})_n \bullet \overrightarrow{v_{North}}}{b_n \bullet c}\right)$$

The scalar product of $(\overrightarrow{v_{2D}})_n$ and $\overrightarrow{v_{North}}$ can be simplified as follows:

$$(\overrightarrow{v_{2D}})_n \bullet \overrightarrow{v_{North}} = (x_{n+1} - x_n) \bullet x_{North} + (y_{n+1} - y_n) \bullet y_{North}$$

$$(\overrightarrow{v_{2D}})_n \bullet \overrightarrow{v_{North}} = (x_{n+1} - x_n) \bullet 0 + (y_{n+1} - y_n) \bullet 1m$$

$$\left(\overrightarrow{v_{2D}}\right)_n \bullet \overrightarrow{v_{North}} = y_{n+1} - y_n$$

Consequently, the scalar product between both vectors was similar to $y_{n+1} - y_n$ and c was 1 m. Therefore, the formula for the compass direction δ_n was simplified to:

$$\delta_n[^\circ] = \cos^{-1}\left(\frac{y_{n+1} - y_n}{b_n}\right)$$

To calculate angles in ° within R, we used the package NISTunits (Gama 2016). As this package always computes the smallest angle between both vectors, the result ranged from 0° to 180°. For all cases with x_{n+1} - $x_n < 0$, which means a bat was flying more or less westwards, δ must be larger than 180°. Those results were subtracted from 360°.

2.5. Heading directions and circular statistics

Bats' individual flight paths consisted of vectors, each with a specific compass direction and length. We calculated the overall orientation for each bat as a weighted mean vector, which is the angular mean, weighted by the lengths of consecutive vectors. The mean vector of each bat consisted of a mean angle μ and a length r with $0^\circ = $ N, $90^\circ = $ E, $180^\circ = $ S, and $270^\circ = $ W. We assumed that bats flying at a mean angle of $\mu < 90^\circ$ or $\mu > 270^\circ$ were not migrating southwards.

Circular statistical tests were performed using Oriana 4.0 (Kovach Computing Services, Pentraeth, UK). Also we used Oriana 4.0 for creating circular graphics. Statistical tests were performed with R version 3.6.0 (R Foundation for Statistical Computing, Vienna, Austria). We used Moore's Modified Rayleigh test (Zar 1999) to analyse whether the cardinal directions of a flight path were uniformly distributed around the circle. A p-value less than 0.05 indicated that the cardinal directions were not uniformly distributed, and those

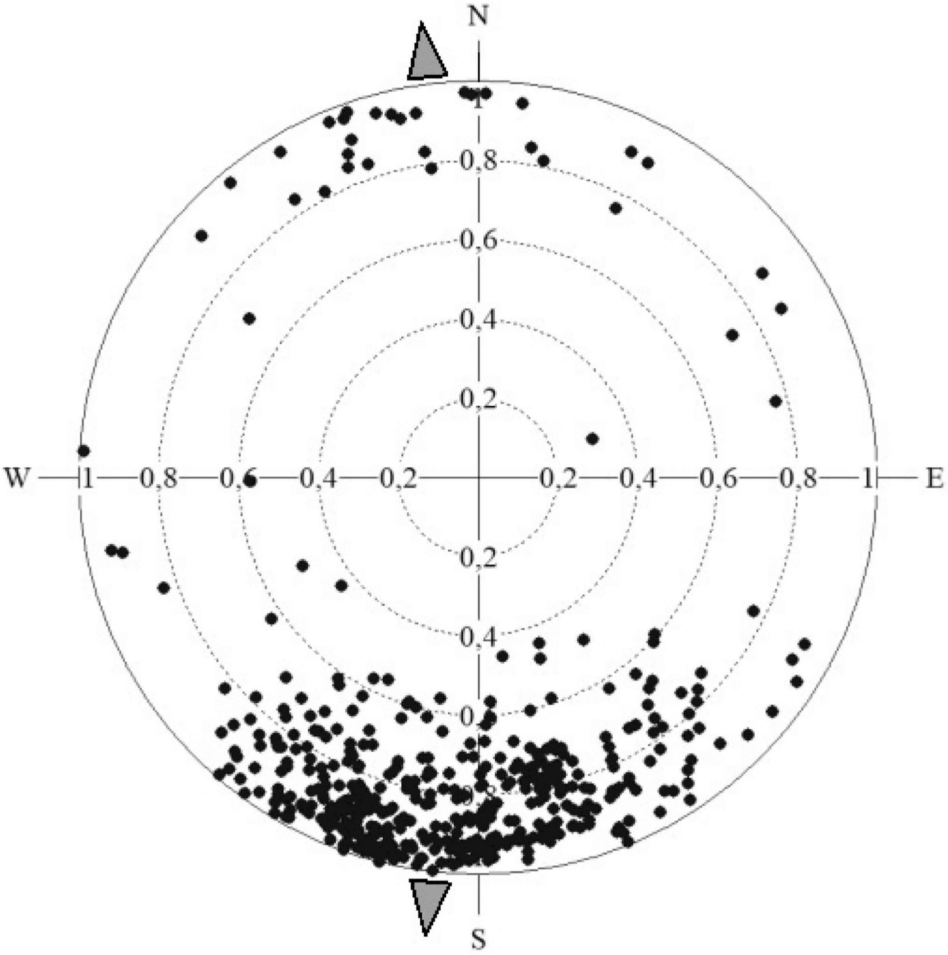


Fig. 1. Circular-linear plot of flight direction (°) and linearity index (ranging from 0 to 1 for non-linear to linear paths, respectively) of all recorded tracks from Nathusius' pipistrelles. Each point representing one out of the total of 432 individuals. Grey arrows indicate the mean flight directions of significantly northerly and southerly oriented bats.

flight paths passed the test, but those flight paths did not necessarily have a specific mean direction. The overall migration orientation of all bats per night was then computed as a mean vector. Finally, Kuiper's test was performed to compare the distribution of the weighted mean angles to the von Mises distribution.

To further examine the distribution of all bats' bearings per night, especially considering potential non-unimodal orientations, we employed a likelihood-based modelling approach as per Fitak and Johnsen (2017). This is in addition to the traditional Rayleigh test (Batschelet, 1981). This approach was implemented using the CircMLE package (R version 3.5.2), which has been developed for comparing multiple potential models of orientation behaviour in circular data. In addition to the uniform distribution of data points (random dispersion of bearings – M1), three unimodal variants (unimodal – M2A, symmetric modified M2B, and modified unimodal – M2C) and six bimodal variants (homogenous symmetric bimodal – M3A, symmetric bimodal – M3B, homogenous axial bimodal – M4A, axial bimodal – M4B, homogenous bimodal M5A, and bimodal M5B) exist (Schnute and Groot, 1992), which are considered in the modelling (Fitak and Johnsen, 2017). For each individual nightly recording session, we evaluated the generated model evaluated using the corrected Akaike information criterion (AIC_c) and the corresponding model weights (Hurvich and Tsai, 1989; Lindecke et al., 2021). We used the Mardia-Watson-Wheeler test to identify differences in orientation between all nights.

3. Results

In August 2018, we recorded flight trajectories of 450 migrating bats on three occasions (17th, 22nd and 27th of August) and at three locations in proximity of Pape Bird Ringing Station (PBRS) close to the Latvian coastline. In total, we received 6404 spatial positions from bats, or on average 14 spatial positions per flight track. On the evening of the 17th August, bat activity was highest with 12.8 bats per minute crossing the recording area of the array. On the 22nd of August, bat activity was lowest with only 3.1 individuals per minute, while on 27th of August activity was intermediate with 9.1 individuals passing by the array per minute. High migration activity coincided with low wind speeds measured next to the microphone array (0.4 m/s from SW on 17th and 0.9 m/s from SE on 27th of August) and low activity with higher wind speeds (3.1 m/s from SW on 22nd of August). However, above the canopy, winds blew similarly on all three days, with 3.7 m/s from SE on 17th, 3.4 m/s from S on 22nd, and 3.5 m/s from SE on 27th of August (GFS/NCEP/US National Weather Service via earth.nullschool.net). In total, 432 of 450 flight paths were assigned to *P. nathusii* (96 %), 8 flight paths to *P. pygmaeus* (1.8 %) and another 10 flight paths to *N. noctula* (2.2 %). In the following, we will focus only on flight paths of Nathusius' pipistrelles.

3.1. Heading directions

We distinguished between Nathusius' pipistrelles with respect to their heading direction. Since the local coastline runs along a NW-SE axis, we defined bats as 'heading south' when bearings ranged between 240° (W) and 90° (E), and as 'heading north' when bearings ranged between 240° (W) and 0° (N) or 0° (N) and 90° (E). All nights considered, but irrespective of individual linearity of flight paths, out of 432 recorded Nathusius' pipistrelles 399 bats (92.4 %) headed south and 33 north (7.6 %; Fig. 1). The heading directions of these bats averaged 185 ± 1° (SE) and 357 ± 6°, respectively. Flight speed (speed above ground) averaged 7.9 ± 1.5 m/s and flight altitude

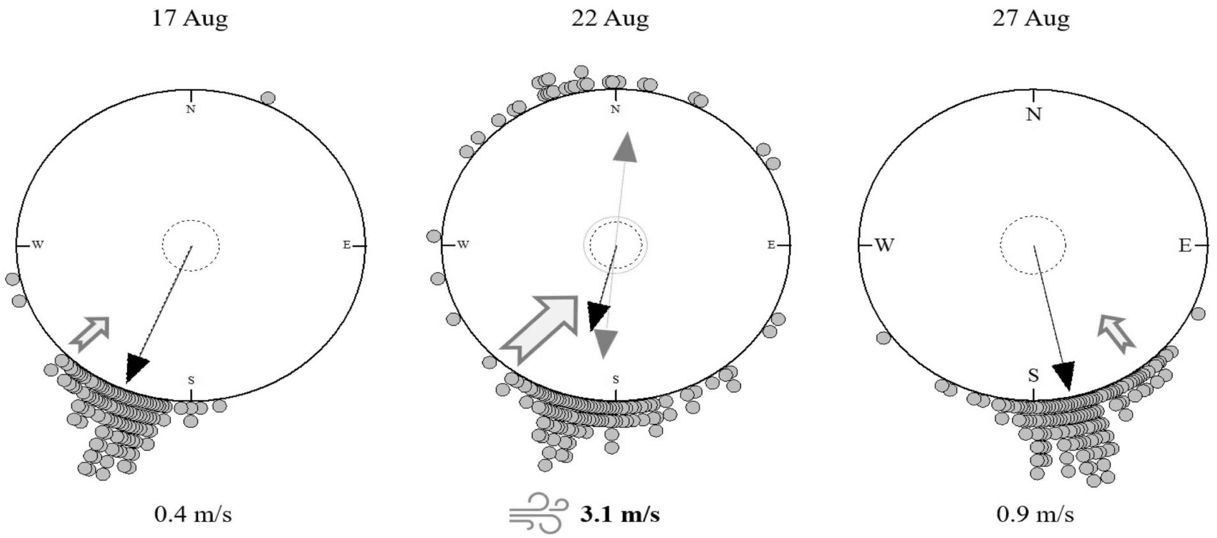


Fig. 2. Daily bat flight orientation and below-canopy wind conditions. Black vectors depict the group mean of the bat data (grey dots), the grey double-headed vector illustrates bi-directional mean orientation for the 22 Aug. In contrast to their movements on the other dates, a significant proportion of bats (21 %) on that day crossed the recording space flying northwards. Dotted circles indicate the p-value of 0.05. Grey arrows show the prevailing wind direction during a tracking session. The wind speed measured on the ground is given below each circular plot.

4.7 ± 1.8 m above ground, without any differences between north and southward flying Nathusius' pipistrelles ($p > 0.05$).

3.2. *Daily movement directions of Nathusius' pipistrelles*

On the 17 Aug, 112 Nathusius' pipistrelles (99.1 %) oriented in a seasonally expected southward direction (Fig. 2), one individual flew in the opposite direction. The mean orientation of bats was towards the south (Rayleigh's test, 17 Aug: mean vector orientation $\mu = 202^\circ \pm 1.5^\circ$ (Standard Error, SE), $r = 0.96$, $Z = 104.242$, $P < 0.001$). On the 27 Aug, under similarly low wind conditions, all 132 bats oriented southwards, too ($\mu = 168^\circ \pm 1.4$ SE, $r = 0.962$, $Z = 122.164$, $P < 0.001$). In contrast, on 22 Aug when the wind blew stronger yet from the same direction as on the other days, 30 out of 133 bats, i.e., one fifth (22.6 %) of all bats flew in a northern direction creating a circular data distribution that appears bi-directional on inspection. Indeed, based on conventional descriptive statistics the data could be described as unidirectional, as well as axial (unidirectional: $\mu = 194^\circ \pm 5.5^\circ$ SE, $r = 0.574$, $Z = 43.784$, $P < 0.001$; axial: $\mu = 185^\circ \pm 1.9^\circ$ SE, $r = 0.733$, $Z = 71.408$, $P < 0.001$), while the r-value is even greater if we assume a bi-directional (axial bimodal) pattern underlying the data.

Based on the likelihood-based modelling, data distributions of both 17 and 27 Aug are best described by unimodal orientation models (delta AICc = 0.000, AICc model weight (w) = 0.999 and w = 1.000, respectively; Table1). The modelling approach demonstrates that the circular distribution obtained for the 22 Aug were well supported by orientation models called 'modified unimodal' (w = 0.378) and 'bimodal' (w = 0.355), followed by 'axial bimodal' (w=0.245) (Schnute and Groot, 1992; Table 1).

The mean orientation of bats differed between nights (Mardia-Watson-Wheeler test, 17 Aug vs. 22 Aug: $W = 0.189$, $P = 8.61 \times 10^{-12}$; 17 Aug vs. 27 Aug: $W=167.759$, $P < 1 \times 10^{-12}$; 22 Aug vs. 27 Aug: $W=104.852$, $P < 1 \times 10^{-12}$).

4. Discussion

We measured the heading directions of bats at a major migration corridor along the coastline of the Baltic Sea in southern Latvia. Nathusius' pipistrelles represented 96 % of all bats recorded in late August at our study site. Overall, the majority of Nathusius' pipistrelles were heading in the expected southern direction. On one day with heavier head winds from southwestern direction (at the recording height), we observed about 20 % of Nathusius' pipistrelles heading in an antiparallel way, i.e., into northern direction. Overall, bats flew in straight trajectories, which is typical for migratory movements (Troxell et al., 2019). Additionally, bats were not recorded hunting when migrating, yet the horizontal detection distance of our ultrasonic array covered only a maximum of 20 m (Voigt et al., 2021) and the vertical detection distance was likely much lower because of the directionality of the bats' echolocation beam. Both factors constrained our ability to detect hunting of migrating bats (Voigt et al., 2012). Notably, travel speed was about 8 m/s, which was slightly higher than travel speeds observed before for Nathusius' pipistrelles during migration (Troxell et al., 2019; Bach et al., 2022). At this travel speed, bats may benefit from a higher efficiency in converting metabolic to mechanical power, which supports an efficient mode of transport for covering long distances at minimum costs (Currie et al., 2023). Flight height was about 5 m above ground, which is lower than the canopy height of the adjacent pine forest. Yet, we acknowledge that the vertical detection distance was limited due to the directionality of the echolocation call beams. Overall, straight flight trajectories, lack of hunting events and a relatively high travel speed are typical for Nathusius' pipistrelles when migrating at this site.

Our observation of bidirectional movements of migrating Nathusius' pipistrelles is consistent with those of past bat orientation studies. Specifically, in an early experiment, one half of the Nathusius' pipistrelles captured at PBRS departed in a northern instead of a southern direction when released from a circular release arena set up next to where we conducted the acoustic recordings (Lindecke et al., 2019a). In the same study, soprano pipistrelles (*P. pygmaeus*) flew southwards. These observations may reflect species-specific orientation responses. However, in contrast to our free-flight recordings that started shortly after sunset, the above experiments on Nathusius' and soprano pipistrelles covered the second half of the night when some bat individuals might already abandon migratory orientation in favour of stopover site searches. Nevertheless, in 2021, another bimodal take-off orientation was observed for soprano pipistrelles at the same location, which served as a control group (Schneider et al., 2023). During one week when coastal weather

Table 1

Model-based analysis of bat orientation on a given date. ΔAICc< 2 are shown in bold, w = AICc model weights. An asterisk denotes the best model to describe the data distribution, two asterisks indicate the second and third best model for the 22 Aug, the date when bi-directional flights were recorded.

Model	17 Aug		22 Aug		27 Aug	
	ΔAICc	w	ΔAICc	W	ΔAICc	w
M1 (uniform)	374.984	0.000	221.160	0.000	444.191	0.000
M2A (unimodal)	**0.00***	**0.999***	128.731	0.000	**0.00***	**1.00***
M2B (symmetric modified unimodal)	24.755	0.000	6.712	0.013	101.398	0.000
M2C (modified unimodal)	416.184	0.000	**0.000***	**0.378***	97.203	0.000
M3A (homogenous symmetric bimodal)	88.594	0.000	60.969	0.000	182.991	0.000
M3B (symmetric bimodal)	26.958	0.000	8.283	0.006	122.985	0.000
M4A (homogenous axial bimodal)	37.183	0.000	15.659	0.000	207.289	0.000
M4B (axial bimodal)	65.695	0.000	**0.903****	**0.245****	151.709	0.000
M5A (homogenous bimodal)	121.424	0.000	9.581	0.003	150.758	0.000
M5B (bimodal)	67.415	0.000	**0.125****	**0.355****	153.183	0.000

conditions were suboptimal for the migration of birds, bats, and insects, the study revealed that a subset of bats might opt for a reverse direction, resulting in a bimodal orientation pattern even under undisturbed conditions of the release that was conducted indoors. Interestingly, in that study, individuals subjected to a magnetic North shift in the experimental group displayed unidirectional orientation. Considering all the data from both free-flying and released bats, we now believe that simultaneous local bi-directional movements may occur at this major bat migration corridor under specific conditions. However, the factors driving these bidirectional movements remain to be elucidated. Northerly movements of a proportion of the migratory bat population are also consistent with a previous isotopic assignment study that argued for a southern origin of Nathusius' pipistrelles in their migration across the European boreal zone (Kruszynski et al., 2021).

Weather conditions are known to influence the migratory decisions of bats. For example, migratory bats integrate information on barometric pressure, wind directions and rainfall when departing from a hibernation or stopover site (Dechmann et al., 2017; Bach et al., 2022). During all our study nights, wind speed and directions (head winds) were similar above the treetop of the nearby pine forest. When, at the same time, wind speed was lower on the clearing where the recordings were made, bats were unimodally oriented in a southern, seasonally expected migratory direction (17 & 27 Aug). When, at another site, wind speed below and above canopy height were similarly strong (22 Aug), we observed instead that bats flew along the forest edge at a typical migratory speed in both directions. We therefore speculate that the strength of local head winds may cause bats to move northwards. Presumably, adverse weather conditions further in the south may have also caused bats to move northwards. During upcoming hostile weather periods, Nathusius' pipistrelles may be at risk of encountering prolonged stopovers, with unforeseen consequences for the delay of their migratory journey and their energy budget. A recent radio-tracking study found that Nathusius' pipistrelles can cover about 100 km per night (Bach et al., 2022). This suggests that bats in Latvia could potentially reach their wintering sites within just a few days using alternative routes (Gaultier et al., 2020; Kruszynski et al., 2021). Admittedly, we lack conclusive evidence for this scenario, yet future tracking studies may shed light on the specific routes of Nathusius' pipistrelles under variable weather conditions in late summer. However, previous navigation research on radio-tracked Nathusius' pipistrelles (Lindecke et al., 2015, 2021) has shown that migratory bats maintain their expected southern orientation – even after being experimentally displaced 10 km from their coastal corridor. Notably, these works have been conducted under calm and windless, i.e., optimal conditions.

A higher insect abundance at higher latitudes may be another reason for bats to move northwards (Kotila et al., 2023). Indeed, acoustic monitoring in Finland suggests that large populations of Nathusius' pipistrelles move northward before likely heading in western direction to Sweden (Ijäs et al., 2017; Blomberg et al., 2021; Kotila et al., 2023). Currently, it is unknown for Finland and the Baltic countries from where northward moving Nathusius' pipistrelles come from. Apparently, the breeding population of Nathusius' pipistrelles in Finland is too small to explain a substantial increase in the acoustic activity of bats at more northern latitudes. Instead, it is more likely that bats from Southeastern populations may move northwards to the Baltic countries and Finland (Kruszynski et al., 2021).

From a conservation point of view, it is important to recognize bidirectional movements of migratory bats along coastlines. During migration, bats are highly vulnerable at wind turbines (Rydell et al., 2010; Lehnert et al., 2014; Voigt et al., 2015), and coastlines are in high demand for wind energy production, specifically also along the coastline of the Baltic Sea (Katinas et al., 2009). High densities of wind turbines at coastlines may impair the migratory connectivity of bats (Reusch et al., 2022) and contribute to massive losses of bats when turbine operation is not curtailed at times of high bat activity (Rydell et al., 2010; Voigt et al., 2022). If during a given season migratory bats move repeatedly back and forth along coastlines, depending on weather conditions or insect abundance, the collision risk of individual bats at wind turbines might be particularly high. Therefore, it is crucial to regulate the commissioning of wind turbines at coastlines, i.e., in order to protect some ecological stepping stones for bats, and to enforce strict curtailments of wind turbines for the protection of bats when wind turbines are built in proximity to a migratory corridor.

4.1. Conclusions

Our study is consistent with the notion that during summer migration Nathusius' pipistrelles conduct bidirectional movements along the Latvian coastline, one of the most important migration corridors for bats in Europe. It is important to note, however, that we observed northward movements only in one out of three nights; not counting the single recording of a northward movement on one of the three nights. Although we have analyzed several hundred flight trajectories of bats during summer migration, only a small fraction of bats chose to fly in a northward migration. We acknowledge that our recordings covered only the onset of nights and that our sample size (number of survey days) is too small to elucidate the causal mechanisms underlying northward migration of Nathusius' pipistrelles in late summer. We speculate that bidirectional movements may be elicited by strong (head) winds or a higher insect prey density at higher latitudes. Future studies will have to look into more details about the variability of migratory movements of bats. More extensive 3D-tracking of flight paths may yield important insights into the migratory strategies of bats. Also, tracking studies with light-weighed transmitters will further improve our understanding of the migratory behaviour in Nathusius' pipistrelles and other species (Bach et al., 2022). We infer from our observations that migratory directions of bats are more complex than previously anticipated at this major migratory corridor and likely also at other places throughout Europe. Most likely, other bat species conduct similar complex migratory behaviour when moving between summer and wintering ranges.

CRediT authorship contribution statement

C.C.V. conceptualized the project, acquired funding, organized and supervised the project. J.Ko. conducted the field experiment. J. Ko, J.Ki and P.T. analysed the raw acoustic data. G.P. supported fieldwork and administration. J.Ki. and O.L. performed the data

analysis and visualization. C.C.V., J.Ki. and O.L. wrote the initial manuscript. All authors reviewed and edited the manuscript.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Christian C. Voigt reports financial support was provided by Leibniz Institute for Zoo and Wildlife Research (IZW) in the Forschungsverbund Berlin eV. Oliver Lindecke reports financial support was provided by Deutsche Forschungsgemeinschaft (SFB 1372–395940726).

Data Availability

Data will be made available on request.

Acknowledgements

We thank Oskars Keišs for supporting our work at PBRS. Christian Voigt was supported by the SAW Leibniz Association (grant no. K101/2018). Oliver Lindecke is grateful for funding to the Sonderforschungsbereich (SFB) 1372 'Magnetoreception and Navigation in Vertebrates' (project-ID395940726) by the Deutsche Forschungsgemeinschaft (DFG). Publication of this article was supported by the Open Access Fund of the Leibniz Association and the IZW, and funded by the Deutsche Forschungsgemeinschaft (DFG Projektnummer 491292795).

References

Åkesson, S., Karlsson, L., Walinder, G., Alerstam, T., 1996. Bimodal orientation and the occurrence of temporary reverse bird migration during autumn in south Scandinavia. Behav. Ecol. Sociobiol. 38 (5), 293–302.

Alcalde, J.T., Jiménez, M., Brila, I., Vintulis, V., Voigt, C.C., Pētersons, G. (2020). Transcontinental 2200 km migration of a Nathusius' pipistrelle (*Pipistrellus nathusii*) across Europe. Mammalia, 1(ahead-of-print).

Alerstam, T., Lindström, Å., 1990. Optimal bird migration: the relative importance of time, energy, and safety. Bird Migration. Springer, Berlin, Heidelberg, pp. 331–351.

Bach, P., Voigt, C.C., Göttsche, M., Bach, L., Brust, V., Hill, R., Seebens-Hoyer, A., 2022. Offshore and coastline migration of radio-tagged Nathusius' pipistrelles. Conserv. Sci. Pract. 4 (10) e12783.

Batschelet, E., 1981. Circular Statistics in Biology. Academic Press, London, UK.

Blomberg, A.S., Vasko, V., Salonen, S., Pētersons, G., Lilley, T.M., 2021. First record of a Nathusius' pipistrelle (*Pipistrellus nathusii*) overwintering at a latitude above 60 N. Mammalia 85 (1), 74–78.

Bruderer, B., Liechti, F., 1998. Flight behaviour of nocturnally migrating birds in coastal areas: crossing or coasting. Journal of Avian Biology 499 (507).

Cryan, P.M., 2003. Seasonal distribution of migratory tree bats (*Lasiurus* and *Lasionycteris*) in North America. J. Mammal. 84 (2), 579–593.

Currie, S.E., Johansson, L.C., Aumont, C., Voigt, C.C., Hedenström, A., 2023. Conversion efficiency of flight power is low, but increases with flight speed in the migratory bat *Pipistrellus nathusii*. Proc. R. Soc. B 290 (1998), 20230045.

Dechmann, D.K., Wikelski, M., Ellis-Soto, D., Safi, K., O'Mara, M.T., 2017. Determinants of spring migration departure decision in a bat. Biol. Lett. 13 (9), 20170395.

Dechmann, D.K., Wikelski, M., Varga, K., Yohannes, E., Fiedler, W., Safi, K., O'Mara, M.T., 2014. Tracking post-hibernation behavior and early migration does not reveal the expected sex-differences in a "female-migrating" bat. PLoS One 9 (12) e114810.

Dingle, H., 2014. Migration: the Biology of Life on the Move. Oxford University Press, USA.

Fitak, R.R., Johnsen, S., 2017. Bringing the analysis of animal orientation data full circle: model-based approaches with maximum likelihood. J. Exp. Biol. 220, 3878–3882.

Furmankiewicz, J., Kucharska, M., 2009. Migration of bats along a large river valley in southwestern Poland. J. Mammal. 90 (6), 1310–1317.

Gaultier, S.P., Blomberg, A.S., Ijäs, A., Vasko, V., Vesterinen, E.J., Brommer, J.E., Lilley, T.M., 2020. Bats and wind farms: The role and importance of the Baltic Sea countries in the European context of power transition and biodiversity conservation. Environmental Science & Technology 54 (17), 10385–10398.

Grodzinski, U., Spiegel, O., Korine, C., Holderied, M.W., 2009. Context-dependent flight speed: evidence for energetically optimal flight speed in the bat *Pipistrellus kuhlii*? J. Anim. Ecol. 78 (3), 540–548.

Hahn, S., Bauer, S., Liechti, F., 2009. The natural link between Europe and Africa - 2.1 billion birds on migration. Oikos 118 (4), 624–626. https://doi.org/10.1111/j.1600-0706.2008.17309.x.

Hedenström, A., 2008. Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. Philos. Trans. R. Soc. B: Biol. Sci. 363 (1490), 287–299.

Hedenström, A., 2009. Optimal migration strategies in bats. J. Mammal. 90 (6), 1298–1309.

Hurvich, C.M., Tsai, C.L., 1989. Regression and time-series model selection in small samples. Biometrika 76, 297–307.

Hutterer R. (2005) Bat migrations in Europe: a review of banding data and literature (Vol 28) Federal Agency for Nature Conservation.

Ijäs, A., Kahilainen, A., Vasko, V.V., Lilley, T.M., 2017. Evidence of the migratory bat, *Pipistrellus nathusii*, aggregating to the coastlines in the Northern Baltic Sea. Acta Chiropterologica 19 (1), 127–139.

Katinas, V., Marciukaitis, M., Markevicius, A., 2009. Current situation of the wind energy use and investigation of wind resources in the coastal region of the Baltic Sea in Lithuania. Renew. Sustain. Energy Rev. 13 (1), 201–207.

Keišs, O., Spalis, D., Pētersons, G., 2021. Funnel trap as a method for capture migrating bats in Pape. Latv. Environ. Exp. Biol. 19, 7–10.

Koblitz, J., 2018. Arrayvolution: using microphone arrays to study bats in the field. Can. J. Zool. 96, 933–938.

Komenda-Zehnder, S., Liechti, F., Bruderer, B., 2002. Is reverse migration a common feature of nocturnal bird migration? – an analysis of radar data from Israel. Ardea 90 (2), 325–334.

Kotila, M., Suominen, K.M., Vasko, V.V., Blomberg, A.S., Lehikoinen, A., Andersson, T., et al., 2023. Large-scale long-term passive-acoustic monitoring reveals spatio-temporal activity patterns of boreal bats. Ecography 2023, e06617.

Krauel, J.J., McCracken, G.F., 2013. Recent advances in bat migration research. Bat Evol. Ecol. Conserv. 293–313.

Kruszynski, C., Bailey, L., Courtiol, A., Bach, L., Bach, P., Ma, G.öttsche, Mi, G.öttsche, Hill, R., Lindecke, O., Matthes, H., Pommeranz, H., Seebens-Hoyer, A., Voigt, C. C., 2021. Identifying migratory pathways of Nathusius' pipistrelles (Pipistrellus nathusii) using stable hydrogen and strontium isotopes. Rapid Commun. Mass Spectrom. 35 e9031.

Kurvits T., Nellermann C., Alfthan B., et al. (2011) Living Planet: Connected planet. preventing the end of the World's wildlife migrations through ecological networks.

La Sorte, F.A., Fink, D., Hochachka, W.M., & Kelling, S. (2016). Convergence of broad-scale migration strategies in terrestrial birds. Proceedings of the Royal Society B: Biological Sciences, 283(1823), 20152588.

Lehnert, L.S., Kramer-Schadt, S., Schönborn, S., Lindecke, O., Niermann, I., Voigt, C.C., 2014. Wind farm facilities in Germany kill noctule bats from near and far. PloS One 9 (8), e103106.

Lehnert, L.S., Kramer-Schadt, S., Teige, T., Hoffmeister, U., Popa-Lisseanu, A., Bontadina, F., Voigt, C.C., 2018. Variability and repeatability of noctule bat migration in Central Europe: evidence for partial and differential migration. Proceedings of the Royal Society B 285 (1893), 20182174.

Lemon, J. (2006). Plotrix: a package in the red light district of R. R-news, 6(4), 8-12.

Lindecke, O., Voigt, C.C., Pētersons, G., Holland, R.A., 2015. Polarized skylight does not calibrate the compass system of a migratory bat. Biol. Lett. 11 (9), 20150525.

Lindecke, O., Holland, R.A., Pētersons, G., Voigt, C.C., 2021. Corneal sensitivity is required for orientation in free-flying migratory bats. Commun. Biol. 4, 522.

Lindecke, O., Elksne, A., Holland, R.A., Pētersons, G., Voigt, C.C., 2019a. Orientation and flight behaviour identify the Soprano pipistrelle as a migratory bat species at the Baltic Sea coast. J. Zool. 308 (1), 56–65.

McGuire, L.P., Guglielmo, C.G., Mackenzie, S.A., Taylor, P.D., 2012. Migratory stopover in the long-distance migrant silver-haired bat, *Lasionycteris noctivagans*. J. Anim. Ecol. 81 (2), 377–385.

Ossa, G., Kramer-Schadt, S., Peel, A.J., Scharf, A.K., Voigt, C.C., 2012. The movement ecology of the straw-colored fruit bat. Eidolon helvum sub-Sahar. Afr. Assess. stable Isot. Ratios.

Patten, M.A., Marantz, C.A., 1996. Implications of vagrant southeastern vireos and warblers in California. Auk 113 (4), 911–923.

Pētersons, G., 2004. Seasonal migrations of north-eastern populations of Nathusius' bat Pipistrellus nathusii (Chiroptera) Myotis 41, 29–56.

Popa-Lisseanu, A.G., Voigt, C.C., 2009. Bats on the move. J. Mammal. 90 (6), 1283–1289.

Reusch, C., Lozar, M., Kramer-Schadt, S., Voigt, C.C., 2022. Coastal onshore wind turbines lead to habitat loss for bats in Northern Germany. J. Environ. Manag. 310, 114715.

Rydell, J., Bach, L., Dubourg-Savage, M.J., Green, M., Rodrigues, L., Hedenström, A., 2010. Bat mortality at wind turbines in northwestern Europe. Acta Chiropterologica 12 (2), 261–274.

Sandberg, R., 1994. Interaction of body condition and magnetic orientation in autumn migrating Robins, Erithacus rubecula. Anim. Behav. 47, 679–686.

Schneider W.T., Holland R.A., Keišs O., Lindecke O. (2023) Migratory bats are sensitive to magnetic inclination during compass calibration. bioRxiv 2023.05.03.539149; doi: https://doi.org/10.1101/2023.05.03.539149.

Schnute, J.T., Groot, K., 1992. Statistical analysis of animal orientation data. Anim. Behav. 43, 15–33.

Skiba, R., 2009. Europäische Fledermäuse. Die neue Brehm-Bücherei. Westarp Wissenschaften, Hohenwarsleben.

Steffens R., Zöphel U., Brockmann D. (2004) 40th anniversary Bat Marking Centre Dresden—evaluation of methods and overview of results Dresden, Germany: Sächsisches Landesamt für Umwelt und Geologie.

Šuba, J., Petersons, G., Rydell, J., 2012. Fly-and-forage strategy in the bat *Pipistrellus nathusii* during autumn migration. Acta Chiropterologica 14 (2), 379–385.

Suzuki, T., Shibahara, H., Tsunoda, H., Hirano, Y., Taneichi, A., Obara, H., Sato, I., 2002. Comparison of the Sperm Quality Analyzer IIC variables with the computer-aided sperm analysis estimates. International Journal of Andrology 25 (1), 49–54.

Taylor, P.D., Mackenzie, S.A., Thurber, B.G., Calvert, A.M., Mills, A.M., McGuire, L.P., Guglielmo, C.G., 2011. Landscape movements of migratory birds and bats reveal an expanded scale of stopover. PLoS One 6 (11), e27054.

Thorup, K., 2004. Reverse migration as a cause of vagrancy. Bird Study 51 (3), 228–238.

Thorup, K., Ortvad, T.E., Holland, R.A., Rabøl, J., Kristensen, M.W., Wikelski, M., 2012. Orientation of vagrant birds on the Faroe Islands in the Atlantic Ocean. J. Ornithol. 153 (4), 1261–1265.

Troxell, S.A., Holderied, M.W., Pētersons, G., Voigt, C.C., 2019. Nathusius' bats optimize long-distance migration by flying at maximum range speed. J. Exp. Biol. 222, 4.

Vasenkov, D., Desmet, J.F., Popov, I., Sidorchuk, N., 2022. Bats can migrate farther than it was previously known: a new longest migration record by Nathusius' pipistrelle *Pipistrellus nathusii* (Chiroptera: Vespertilionidae). Mammalia 86 (5), 524–526.

Veit, R.R., 2000. Vagrants as the expanding fringe of a growing population. Auk 117 (1), 242–246.

Voigt, C.C., Rehnig, K., Lindecke, O., Pētersons, G., 2018. Migratory bats are attracted by red light but not by warm-white light: Implications for the protection of nocturnal migrants. Ecol. Evol. 8 (18), 9353–9361.

Voigt, C.C., Russo, D., Runkel, V., Goerlitz, H.R., 2021. Limitations of acoustic monitoring at wind turbines to evaluate fatality risk of bats. Mammal. Rev. 51 (4), 559–570.

Voigt, C.C., Sörgel, K., Šuba, J., Keišs, O., Pētersons, G., 2012. The insectivorous bat *Pipistrellus nathusii* uses a mixed-fuel strategy to power autumn migration. Proc. R. Soc. Lond. B: Biol. Sci. rspb2 0120902.

Voigt, C.C., Lehnert, L.S., Petersons, G., Adorf, F., Bach, L., 2015. Wildlife and renewable energy: German politics cross migratory bats. Eur. J. Wildl. Res. 61, 213–219.

Voigt, C.C., Roeleke, M., Marggraf, L., Pētersons, G., Voigt-Heucke, S.L., 2017b. Migratory bats respond to artificial green light with positive phototaxis. PLoS One 12 (5), e0177748.

Voigt, C.C., Kaiser, K., Look, S., Scharnweber, K., Scholz, C., 2022. Wind turbines without curtailment produce large numbers of bat fatalities throughout their lifetime: a call against ignorance and neglect. Glob. Ecol. Conserv. 37, e02149.

Voigt, C.C., Frick, W.F., Holderied, M.W., Holland, R., Kerth, G., Mello, M.A., Yovel, Y., 2017a. Principles and patterns of bat movements: from aerodynamics to ecology. Q. Rev. Biol. 92, 267–287.

Wickham, H. (2019). stringr: simple, consistent wrappers for common string operations. R package version 1.4. 0.

Wickham, H., & Wickham, M. H. (2017). Package tidyverse. Easily install and load the 'Tidyverse.

Zar, J. H. (1999). Biostatistical analysis. Pearson Education India.

Zawadzki, L.C., Veit, R.R., Manne, L.L., 2019. The influence of population growth and wind on vagrancy in a North American passerine. Ardea 107 (2), 131–147.