


## RESEARCH NOTE

# Offshore and coastline migration of radio-tagged Nathusius' pipistrelles

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## Abstract

The wind energy-bat conflict is well documented for the onshore sector, with high numbers of casualties, specifically for migratory bat species. Offshore wind turbines might be a threat to bats as well, yet offshore bat migration is poorly documented. Accordingly, potential conflicts between bat conservation and offshore wind energy production are difficult to evaluate. Here, we used automated radio-telemetry to track 50 km continuous offshore movements of two Nathusius' pipistrelles (*Pipistrellus nathusii*) within the Motus network. After crossing the marine waterbody, tagged bats traveled over several hundred kilometers along the coastline from Germany towards the Netherlands and Belgium. Our study highlights the possibility for migratory bats to collide with offshore and coastal wind turbines. Therefore, we plead for implementing pre- and post-construction surveys and adequate mitigation schemes at offshore wind turbines in sensitive areas of the North and Baltic Sea if not already practised.

## KEYWORDS

bat fatalities, conservation, migration, offshore wind power, wind energy-wildlife conflict

Names of the forth- to ninth-placed authors are listed alphabetically.

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## 1 | INTRODUCTION

Offshore wind energy production is increasing worldwide, specifically in north-western Europe (Global Wind Energy Council, 2021; Kaldellis & Kapsali, 2013). For the onshore sector, it is known that large numbers of bats die at wind turbines, with migratory species being most vulnerable (O'Shea et al., 2016; Rydell et al., 2010; Voigt et al., 2015). For the offshore sector, it was suggested that wind energy production may pose a threat to bats as well (Ahlén et al., 2009; Gaultier et al., 2020; Hüppop et al., 2019; Rydell et al., 2014), since past acoustic surveys documented the presence of bats above marine waterbodies (Ahlén et al., 2009; Brabant et al., 2019; Cryan & Brown, 2007; Gaultier et al., 2020; Hüppop & Hill, 2016; Ijäs et al., 2017; Lagerveld et al., 2021; Peterson et al., 2016; Rydell & Wickman, 2015; Rydell et al., 2014, Seebens-Hoyer et al., 2021). However, information from these surveys is usually restricted to those few locations where ultrasonic detectors can be applied in the marine environment. In addition, acoustic detectors may detect echolocating bats only over the range of a few dozen meters (Voigt et al., 2021). Lastly, these surveys do not provide information on flight directions and ground speeds. Tracking information could resolve these issues, yet application of miniaturized GPS (global positioning systems) loggers is limited by the relatively high logger weight for small and light migratory bats. The application of considerably smaller conventional radio-transmitters is hampered by the necessity of surveying vast areas above waterbodies and along coastlines. This problem is solved by the Motus Wildlife Tracking System, since automated receiver stations can be installed on a landscape scale level, and since receivers can detect individual encoded VHF (very high frequency) signals from animals carrying light-weight transmitters (McGuire et al., 2012; Taylor et al., 2017).

Understanding offshore bat migration in Europe is urgently needed because all bat species are protected by international legislation such as the EU Habitat Directive and the UN convention for the protection of migratory species of wild animals (CMS convention signed in Bonn, 1979 and UNEP/EUROBATS set up under the CMS convention, 1991). Besides, bats are also protected by national legislation in many European countries. To improve our understanding of offshore bat migration, we equipped two Nathusius' pipistrelles (*Pipistrellus nathusii*) with coded VHF radio-transmitters on the remote offshore island Helgoland in the North Sea. We then followed the movements of these bats during subsequent days by using the Motus Wildlife Tracking System. Tracking data confirmed that bats engaged in more than 1 h of continuous flight when crossing the North Sea towards

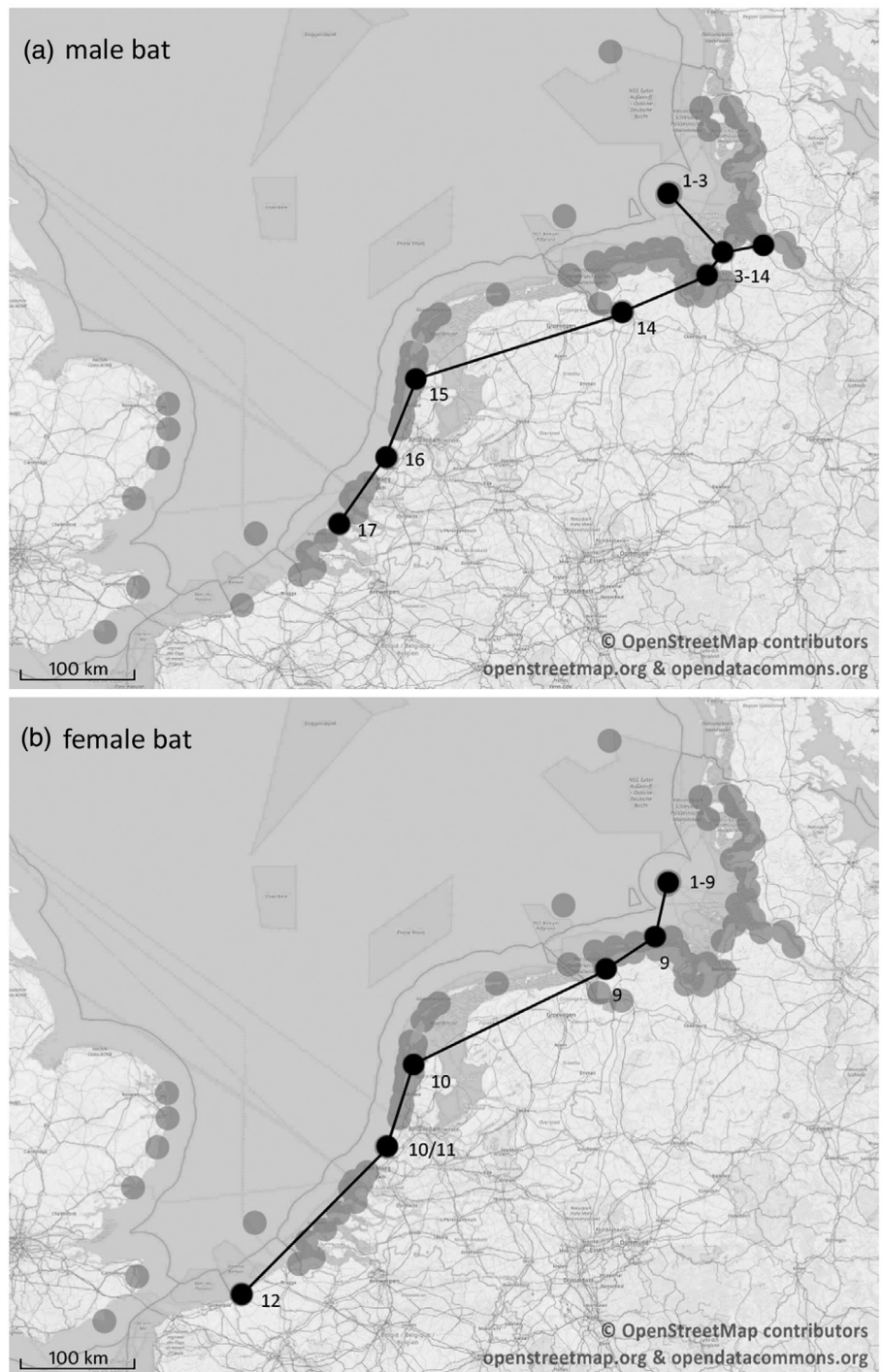
the mainland. After reaching the German coastline, bats traveled over several hundred kilometers in southwestern direction towards Belgium within multiple nights. Our study highlights the potential for migratory bats to interact and possibly collide with offshore and coastal wind turbines.

## 2 | METHODS

On 4th and 6th September 2020, we captured a male and a female Nathusius' pipistrelle (*Pipistrellus nathusii*), respectively, with mistnets on Helgoland (54°11'N, 7°8'E; Figure 1), an island about 50 km off the mainland. Both had calcified and knobby epiphyseal plates and were determined as adults, the forearm length was 33.7 mm in the male and 33.6 mm in the female. We attached a radio-transmitter (Nanotag NTQB-2, 0.29 g; Lotek Wireless Inc., Newmarket, ON, Canada) on the back of each bat using medical skin glue (Manfred Sauer GmbH, Lobbach, Germany), after which the bats were released. The male and female weighed 6.9 and 6.3 g, respectively. Accordingly tags made up 4.2% and 4.6% of the bats' body masses (Aldridge & Brigham, 1988). Tags emitted individual encoded VHF signals, which were recorded when bats flew in proximity to antennas/receiver stations (stations hereafter) of the Motus system (Taylor et al., 2017). An array of Motus stations was recently established along the coastline, islands and some offshore sites in the North Sea region (Brust et al., 2019; Lagerveld et al., 2017; Müller, Eikenaar, et al., 2018; Müller, Rüppel, & Schmaljohann, 2018; Packmor et al., 2020). The filtered signals of the tagged bats were downloaded via the Motus R package version 4.0.5 (Brzustowski & LePage, 2021).

On the island of Helgoland and in some areas on the mainland, stations were located in close proximity so that signals of tagged bats were sometimes picked up simultaneously by several stations. On Helgoland, we defined the departure time of a tagged bat as the time when the amplitude of its radio signal dropped suddenly after several antennas received an uninterrupted sequence of high amplitude signals for half an hour. This constant signal amplitude indicated that the VHF signal was not attenuated by topography when bats flew high above ground. We considered the arrival time on the mainland not to be represented by the time of first contact by mainland stations. Instead, we defined arrival time by the time point at which we received a sequence of continuously high amplitude signals for several minutes. The flight direction refers to the cardinal direction represented by an air-line between the station from which the departure was recorded on Helgoland and the mainland station where the signal was first recorded.

**FIGURE 1** The flight of the male (a) and female (b), black dots represent stations or station clusters with detections, gray ones stations without detections. Stations or station clusters that bats passed subsequently are connected by a solid black line. Numbers indicate nights since the night of capture.



The detection ranges of stations are usually variable owing to the specification of the transmitters, antennas and receivers, the height of the antennas, the orientation and flight height of the animal relative to the antennas, landscape structure, topography, and weather conditions (Crewe et al., 2019; Kays et al., 2011; Lagerveld et al., 2017). Accordingly, it was not possible to extract information on the flight distance on a small scale, such as between Helgoland and the first receiving station on the mainland accurately. Therefore, we were

unable to determine an exact ground speed for the off-shore section.

We defined the total minimum flight distance of the respective bat as the sum of straight lines drawn between clustered stations. A cluster of stations was defined as stations within a radius of 30 km and which were visited by the tagged bats within 30 min (see Bégin-Marchand et al., 2021). We once derivated from this, when one of the bats flew back and forth between neighboring clusters 36 km from each other (against migration direction

and back). This section was not included in the migration flight distance.

Migration in temperate zone bats such as *Nathusius'* pipistrelles is generally defined as seasonal two-way movement between the summer and hibernation area (Fleming & Eby, 2003; Petersons, 2004). In the study area *Nathusius'* pipistrelles are expected to fly south-westerly in autumn (Hutterer, Ivanova & Meyer-Cords, 2005). We therefore classify a bat to migrate if it flies in the presumed migration direction and does not turn back to any station.

### 3 | RESULTS

After tagging, the male remained on the island for two subsequent nights before it left in southeastern direction ( $157^\circ$ ) about 1 h after sunset (Figure 1a) at light tailwind (see Data S1). The estimated travel time to the mainland was 2 h and 49 min. Once having arrived on the mainland, the bat moved within a range of maximal 50 km for the subsequent 11 nights. During the following westward 3-day journey, the signal was picked up at several stations along the Dutch coastline until the last recording on the 20th of September southwest of Rotterdam. The bat migrated in five out of the 17 monitored nights, covering a total distance of minimal 517 km (Figure 1a). Nightly travel distances of the male bat averaged 103 km per night when the bat migrated, and 30 km per night for all monitored nights, including stopover nights.

The female bat remained on Helgoland for 8 nights before leaving one hour after sunset on the 14th of September, also at light tailwind (see Data S1). The animal arrived at an East Friesian island (Spiekeroog) next to the coastline, about 45 km distance in south-southwestern direction ( $202^\circ$ , Figure 1b). The total travel time was 1 h and 35 min for crossing the sea between Helgoland and the island just off the mainland. Once at the mainland, the bat continued its migration along the German coastline westwards until it reached the estuary of the river Ems at the German–Dutch border (see Figure 1b, night 9). Its signal was picked up by several stations along the Dutch coastline until it was last registered at the Belgian coast near the French border three nights after its departure from Helgoland (Figure 1b). The female bat migrated in four out of the 12 monitored nights and flew a total distance of 525 km, which is equivalent to an average travel distance of 131 km per night during the migration, and 44 km per night when considering of all monitored nights.

### 4 | DISCUSSION

We documented continuous offshore flights of two *Nathusius'* pipistrelles over distances of 45–58 km from the island of Helgoland to the mainland/an island just off the mainland by detecting them on the island and at the coast using radio-telemetry. Both bats traveled across the open sea for 1.5 and 3 h, respectively. Furthermore, migration of tagged bats was interrupted for stopover and bats followed the coastline westwards until the transmitter signal was lost. In the following, we will discuss aspects of the offshore movements, stopovers, coastline migration, and discuss implications for the development of wind farms in the offshore area.

That bats travel between islands and the mainland is known in the context of foraging (Hurme et al., 2019) and migration (Ciechanowski et al., 2015; Cryan & Brown, 2007; Skiba, 2007).

Knowing the travel speed of bats when crossing large waterbodies is relevant for assessing the reachability of offshore wind farms for bats. Estimating ground speeds based on our dataset bears the intrinsic difficulty of not knowing the exact routes that bats took when moving between receiver stations. For the reason of simplicity, we assume that bats flew in straight lines. To derive reasonable estimates of migratory speeds, it is important to account for the effective detection range of stations. A previous study demonstrated for 5- and 6-element yagi antennas a maximum detection distance of around 6 km for radio-transmitters under the specific conditions of this study (Lagerveld et al., 2017). Following a rather conservative approach, we therefore assume an average detection range of 6 km. Consequently, we define the minimum linear flight distance between Helgoland and the first receiving mainland station to be the airline between the two stations minus 12 km ( $2 \times 6$  km maximum detection range), resulting in a maximum (airline) and minimum (airline minus max. detection range) migration speed. Based on these assumptions, the male covered a linear distance of 46–58 km in 2 h and 49 min, which yields a ground speed of 4.5–5.7 m/s. The female traveled over a distance of 33–45 km in 1 h and 35 min, resulting in a ground speed of 5.8–7.9 m/s. The differences between these two estimates may be caused by different wind parameters (see Data S1), individually differed airspeeds or by some violations of the underlying assumptions, for example, a curved rather than a straight flight. Yet, the estimates fall within the range of flight speeds measured before for *Nathusius'* pipistrelles at the Baltic Sea coastline (Troxell et al., 2019), and within the range of values expected from aerodynamic theory (Hedenström, 2019).

We observed stopover behavior of tagged bats before departing from Helgoland (the female) and when arriving at the mainland: After reaching the mainland, the male bat spent several days without moving longer distances before continuing its westward journey. Yet, in case of these stopovers, the underlying motivation remains unclear and might be manifold (Schmaljohann et al., 2022). Refueling fat stores, resting or recovering before continuing the journey might be possibilities. Overcoming adverse ambient conditions, such as strong headwinds or rainfall, may also explain stopover behavior, especially at large barriers, such as marine waterbodies or lakes (Ahlén et al., 2009; Lagerveld et al., 2021; McGuire et al., 2012). Possibly, the extended stopover on the island of Helgoland was caused by waiting for favorable weather conditions (low wind speed, tail wind) for crossing the large barrier of the North Sea (see Data S1).

Coastline migration is documented for migratory bats along the shoreline of the Baltic Sea (Petersons, 2004; Šuba et al., 2012; Troxell et al., 2019) and the coastline of the North Sea (Frey et al., 2012; Rydell et al., 2014; see also Kurvits et al., 2011). The tracking data from our study are consistent with the existence of such migratory corridors along the German, Dutch and Belgian coastline. Following the continuous coastline detections and the assumed Motus station detection range of a few km both bats seemed to travel almost exclusively along the western Dutch coastline (Figure 1). Still, as the Motus stations in our study region concentrate along the coastline, the widths of these corridors towards the inland as well as the open sea cannot be depicted. We cannot state on the bats movements where detections are missing like in the northeast of the Netherlands, where there are only few stations (Figure 1). While acknowledging the low sample size of this study, we nonetheless highlight the convergent results with respect to heading directions and migratory routes observed in both individuals. Overall, tagged bats traveled at a migration speed of about 30–40 km per night when considering the whole monitoring period. This falls within the range of migration speeds suggested before (Hedenström, 2019; Petersons, 2004). Yet, it is important to note that *Nathusius'* pipistrelles may cover more than 100 km during a single migration night when traveling along the coastline. Conclusions from our study are limited by the small sample size. By studying more bats in future, we hopefully can identify factors explaining individual differences in migration behavior in detail and with regard to departure decisions and other behavioral aspects.

Still, our study confirms that the Motus radio-tracking method is suitable for elucidating the migration behavior of individual bats moving across marine waterbodies and along coastlines. Migratory *Nathusius'*

pipistrelles alternated between stopover and extended migration efforts, each of these periods covered several days. Our results show that bats fly over the North Sea at relatively high speed compared to measured ground speeds at the Latvian coastline (Troxell et al., 2019), depending on favorable wind conditions (Lagerveld et al., 2021). Assuming migration flights over sea at low altitudes (Ahlén et al., 2009; Skiba, 2007) we expect that bats might cross offshore wind farms while traveling over the open sea, which would make them vulnerable of colliding with offshore wind turbines. Past behavior observations confirmed exploratory behavior of bats at offshore turbines (Ahlén et al., 2009; Brabant et al., 2019), indicating that, once encountered, they may be attracted to and approach such offshore structures. Based on the precautionary principle and the preliminary evidence of this study, we call for cautious actions when establishing offshore wind turbines in future. We recommend monitoring bats at offshore wind turbines and implementing mitigation schemes like it is already done for onshore wind turbines. Specifically, we recommend monitoring bats at least at the nacelle and at the bottom of the blade swept zone for defining curtailment schemes, which could help preventing bats from colliding with rotor blades. Such mitigation schemes are already practiced in a few offshore regions, such as the Netherlands and some coastal waters of Germany. However, we argue for expanding these mitigation schemes for wind turbines across the whole North and Baltic Sea. Past acoustic offshore monitoring point out that bats are only active during a few nights per year (Brabant et al., 2021; Hüppop & Hill, 2016; Lagerveld et al., 2021; Seebens-Hoyer et al., 2021). Therefore, we expect curtailment schemes to be implemented at offshore wind turbines only a few nights. Since migration appears to happen only in nights with low wind speeds, we assume that the loss of energy yield would be minor.

#### AUTHOR CONTRIBUTIONS

Field work: Petra Bach, Matthias Götsche; Installation and maintenance of stations: Vera Brust, O. Hüppop, S. Lagerveld, H. Schmaljohann; analysis of tracking data: P. Bach, V. Brust; study design and original draft: Lothar Bach, Petra Bach, Antje Seebens-Hoyer, Christian C. Voigt; writing, editing and review: all authors; funding: Ommo Hüppop, Sander Lagerveld, Heiko Schmaljohann, Antje Seebens-Hoyer.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The tracking data of the male bat is accessible is accessible via the Motus-Website at <https://motus.org/data/track?tagDeploymentId=29773>, and those of the female bat at <https://motus.org/data/track?tagDeploymentId=29779>. Research on animals was covered by permits of the corresponding animal care and welfare authority (V 244—31231/2020(20/49-6)) and conservation authority (LLUR 515).

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## REFERENCES

- Ahlén, I., Baagøe, H. J., & Bach, L. (2009). Behavior of scandinavian bats during migration and foraging at sea. *Journal of Mammalogy*, 90(6), 1318–1323.
- Aldridge, H. D. J. N., & Brigham, R. M. (1988). Load carrying and maneuverability in an insectivorous bat: A test of the 5% “rule” of radio-telemetry. *Journal of Mammalogy*, 69(2), 379–382.
- Bégin-Marchand, C., Desrochers, A., Taylor, P. D., Tremblay, J. A., Berrigan, L., Frei, B., Morales, A., & Mitchell, G. W. (2021). Spatial structure in migration routes maintained despite regional convergence among eastern populations of Swainson's thrushes. *Movement Ecology*, 9(1), 23. <https://doi.org/10.1186/s40462-021-00263-9>
- Brabant, R., Laurent, Y., Jonge Poerink, B., & Degraer, S. (2019). Activity and behaviour of Nathusius' pipistrelle *Pipistrellus nathusii* at low and high altitude in a North Sea offshore wind farm. *Acta Chiropterologica*, 21(2), 341–348.
- 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*, 11, 3457. <https://doi.org/10.3390/ani11123457>
- Brust, V., Michalik, B., & Hüppop, O. (2019). To cross or not to cross—Thrushes at the German North Sea coast adapt flight and routing to wind conditions in autumn. *Movement Ecology*, 7, 32. <https://doi.org/10.1186/s40462-019-0173-5>
- Brzustowski, J., & LePage, D. (2021). Motus: Fetch and use data from the Motus wildlife tracking system. R package version 4.0.5. Retrieved from <https://motus.org>
- Ciechanowski, M., Jakusz-Gostomska, A., & Żmihorski, M. (2015). Empty in summer, crowded during migration? Structure of assemblage, distribution pattern and habitat use by bats (Chiroptera: Vespertilionidae) in a narrow, marine peninsula. *Mammal Research*, 61, 45–55. <https://doi.org/10.1007/s13364-015-0249-6>
- Crewe, T. L., Deakin, J. E., Beauchamp, A. T., & Morbey, Y. E. (2019). Detection range of songbirds using a stopover site by automated radio-telemetry. *Journal of Field Ornithology*, 90(2), 176–189.
- Cryan, P. M., & Brown, A. C. (2007). Migration of bats past a remote Island offers clues toward the problem of bat fatalities at wind turbines. *Biological Conservation*, 139(1–2), 1–11.
- Fleming, T. H., & Eby, P. (2003). Ecology of bat migration. In T. H. Kunz & M. B. Fenton (Eds.), *Bat ecology* (pp. 156–208). University of Chicago Press.
- Frey, K., Bach, L., Bach, P., & Brunken, H. (2012). Fledermauszug entlang der südlichen Nordseeküste. *Naturschutz und Biologische Vielfalt*, 128, 185–204.
- 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.
- Global Wind Energy Council (2021). Global Wind Report 2021. Retrieved from <https://gwec.net/global-offshore-wind-report-2021/>
- Hedenström, A. (2019). Optimal migration strategies in bats. *Journal of Mammalogy*, 90(6), 1298–1309.
- Hüppop, O., & Hill, R. (2016). Migration phenology and behaviour of bats at a research platform in the South-Eastern North Sea. *Lutra*, 59(1–2), 5–22.
- Hüppop, O., Michalik, B., Bach, L., Hill, R., & Pelletier, S. K. (2019). Migratory birds and bats. In M. R. Perrow (Ed.), *Wildlife and wind farms, conflicts and solutions, volume 3. Offshore: Potential effects* (pp. 142–173). Pelagic Publishing.
- Hurme, E., Gurarie, E., Greif, S., Herrera, L., Flores-Martinez, J., Wilkinsons, G., & Yovel, Y. (2019). Acoustic evaluation of behavioral states predicted from GPS tracking: A case study of a marine fishing bat. *Movement Ecology*, 7, 21. <https://doi.org/10.1186/s40462-019-0163-7>
- 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.
- Kaldellis, J. K., & Kapsali, M. (2013). Shifting towards offshore wind energy—recent activity and future development. *Energy Policy*, 53, 136–148.
- Kays, R., Tilak, S., Crofoot, M., Fountain, T., Obando, D., Ortega, A., Kuemmeth, F., Mandel, J., Swenson, G., Lambert, T., Hirsch, B., & Wikelski, M. (2011). Tracking animal location and activity with an

- automated radio telemetry system in a tropical rainforest. *The Computer Journal*, 54(12), 1931–1948.
- Kurvits, T., Nellemann, C., Alftan, B., Kühn, A., Prokosch, P., Virtue, M., & Skallvik, J. F. (2011). *Living planet: Connected planet—preventing the end of the world's wildlife migrations through ecological networks. A rapid response assessment*. UNEP/GRID-Arendal.
- Lagerveld, S., Janssen, R., Manshanden, J., Haarsma, A.-J., De Vries, S., Brabant, R., & Scholl, M. (2017). *Telemetry for migratory bats - a feasibility study. Technical report*. Wageningen University. <https://doi.org/10.18174/417092>
- Lagerveld, S., Jonge-Poerink, B., & Geelhoed, S. C. V. (2021). Offshore occurrence of a migratory bat, *Pipistrellus nathusii*, depends on seasonality and weather conditions. *Animals*, 11(12), 3442. <https://doi.org/10.3390/ani11123442>
- 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*. *Journal of Animal Ecology*, 81(2), 377–385.
- Müller, F., Eikenaar, C., Crysler, Z. J., Taylor, P. D., & Schmaljohann, H. (2018). Nocturnal departure timing in songbirds facing distinct migratory challenges. *Journal of Animal Ecology*, 87(4), 1102–1115.
- Müller, F., Rüppel, G., & Schmaljohann, H. (2018). Does the length of the night affect the timing of nocturnal departures in a migratory songbird? *Animal Behaviour*, 141, 183–194.
- O'Shea, T. J., Cryan, P. M., Hayman, D. T. S., Plowright, R. K., & Streicker, D. G. (2016). Multiple mortality events in bats: A global review. *Mammal Review*, 46, 1–16.
- Packmor, F., Klinner, T., Woodworth, B. K., Eikenaar, C., & Schmaljohann, H. (2020). Stopover departure decisions in songbirds: Do long-distance migrants depart earlier and more independently of weather conditions than medium-distance migrants? *Movement Ecology*, 8, 6. <https://doi.org/10.1186/s40462-020-0193-1>
- Petersons, G. (2004). Seasonal migrations of north-eastern populations of Nathusius' bat *Pipistrellus nathusii* (Chiroptera). *Myotis*, 41(42), 29–56.
- Peterson, T., Pelletier, S., & Giovanni, M. (2016). Long-term bat monitoring on Islands, offshore structures, and coastal sites in the Gulf of Maine, mid-Atlantic, and Great Lakes - Final Report. Stantec, Topsham, ME, USA.
- Rydell, J., Bach, L., Bach, P., Diaz, L. G., Furmankiewicz, J., Hagner-Wahlsten, N., Kyheröinen, E. M., Lilley, T., Masing, M., Meyer, M. M., Petersons, G., Šuba, J., Vasko, V., Vintulis, V., & Hedenström, A. (2014). Phenology of migratory bat activity across the Baltic Sea and the South-Eastern North Sea. *Acta Chiropterologica*, 16(1), 139–147.
- 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.
- Rydell, J., & Wickman, A. (2015). Bat activity at a small wind turbine in the Baltic Sea. *Acta Chiropterologica*, 17(2), 359–364.
- Schmaljohann, H., Eikenaar, C., & Sapir, N. (2022). Understanding the ecological and evolutionary function of stopover in migrating birds. *Biological Reviews*, 97, 1231–1252. <https://doi.org/10.1111/brv.12839>
- Seebens-Hoyer, A., Bach, L., Bach, P., Pommeranz, H., Göttsche, M., Voigt, C., Hill, R., Vardeh, S., Göttsche, M., & Matthes, M. (2021). *Fledermausmigration über der Nord- und Ostsee*. NABU Mecklenburg-Vorpommern.
- Skiba, R. (2007). Die Fledermäuse im Bereich der Deutschen Nordsee unter Berücksichtigung der Gefährdungen durch WEA (WEA). *Nyctalus*, 12(2–3), 199–220.
- 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.
- Taylor, P. D., Crewe, T. L., Mackenzie, S. A., Lepage, D., Aubry, Y., Crysler, Z., Finney, G., Francis, C. M., Guglielmo, C. G., Hamilton, D. J., Holberton, R. L., Loring, P. H., Mitchell, G. W., Norris, D. R., Paquet, J., Ronconi, R. A., Smetzer, J. R., Smith, P. A., Welch, L. J., & Woodworth, B. K. (2017). The Motus wildlife tracking system: A collaborative research network to enhance the understanding of wildlife movement. *Avian Conservation and Ecology*, 12(1), 8. <https://doi.org/10.5751/ACE-00953-120108>
- Troxell, S. A., Holderied, M. W., Petersons, G., & Voigt, C. C. (2019). Nathusius' bats optimize long-distance migration by flying at maximum range speed. *Journal of Experimental Biology*, 222(4), jeb176396. <https://doi.org/10.1242/jeb.176396>
- 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 Review*, 51(4), 559–570.
- Voigt, C. C., Lehnert, L. S., Petersons, G., Adorf, F., & Bach, L. (2015). Wildlife and renewable energy: German politics cross migratory bats. *European Journal of Wildlife Research*, 61(2), 213–219.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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