

Activity and behaviour of *Nathusius' pipistrelle* *Pipistrellus nathusii* at low and high altitude in a North Sea offshore wind farm

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Several bat species are known to migrate long distances between summer and winter roosts. During migration, many bats even cross the North Sea. The developments of offshore wind farms in the North Sea could therefore pose a collision risk for migrating bats. While bats have been observed inside offshore wind farms, their activity at turbine rotor height yet remains unknown. We therefore installed acoustic bat detectors at wind turbines in the Belgian part of the North Sea. Seven detectors were installed on the service platform of the transition piece (16 m above mean sea level) and four were installed on the nacelle of the turbines, in the centre of the rotor swept area (93 m above mean sea level). A total of 151 recordings of call sequences of *Pipistrellus nathusii* (*Nathusius' pipistrelle*) were made during 20 nights over an entire autumn migration season (8 August – 30 November 2017). 45 recordings contained more than 10 calls. These were further investigated for behavioural clues. We identified 32 recordings of animals in transit and 10 sequences of animals passing by while simultaneously exploring. Only three detections contained feeding buzzes and/or intense exploratory behaviour. The number of recordings at 93 m were around 10% of the number of recordings made at 16 m. This indicates that the activity of *P. nathusii* at our study site, measured at that particular altitude is low. Our observations therefore suggest that the collision risk might be lower than what could be expected from low altitude observations. However, a low number of recordings at nacelle height does not necessarily mean that only a low number of bats will collide with the turbines. The activity in the outer parts of the rotor swept zone, outside the detection range of our acoustic detectors, remains unknown and should be further investigated.

Key words: bats, bat activity, *Nathusius' pipistrelle*, *Pipistrellus nathusii*, offshore wind turbines, nacelle height, collision risk

INTRODUCTION

To tackle global climate change, developments of wind farms on land and at sea are ever increasing. Negative impacts of wind farms on land on bats, a taxon in global decline, have been described in multiple studies (e.g., Rydell *et al.*, 2010; Voigt *et al.*, 2012; Baerwald and Barclay, 2014; Lehnert *et al.*, 2014; Rodrigues *et al.*, 2015). Increased mortality of bats is caused by collisions with turbines and barotrauma (Baerwald *et al.*, 2008; Grodsky *et al.*, 2011; Rollins *et al.*, 2012). Given the known impact of wind turbines on land, offshore wind farms could also cause problems for bats (Skiba, 2007; Rydell *et al.*, 2014). Local and migrating bats can be affected when wind turbines are built in coastal and nearshore areas. However, most offshore wind farms are located further offshore and are consequently out of the foraging range of local bats, but

migratory bats still remain at risk. Bats undertake seasonal migration from summer roosts to wintering areas. Several species e.g., *Pipistrellus nathusii* (*Nathusius' pipistrelle*), *Nyctalus noctula* (common noctule), *Vesperilio murinus* (parti-coloured bat) and *Nyctalus leisleri* (Leisler's bat) migrate long distances of up to 2000 km (Hutterer *et al.*, 2005; Krapp and Niethammer, 2011; Arthur and Lemaire, 2015). *Pipistrellus nathusii* is known to migrate from Scandinavia and central Europe to western Europe, and vice versa (Kurvits *et al.*, 2011).

During migration, bats can cross large areas of open sea (Ahlén *et al.*, 2009; Rodrigues *et al.*, 2015). In the Southern North Sea, sightings of bats have been reported regularly on ships and oil rigs (e.g., Skiba, 2003, 2007; Walter *et al.*, 2007; Boshamer and Bekker, 2008; Lagerveld *et al.*, 2014; Brabant *et al.*, 2016). In 2013, a *P. nathusii* individual that had been banded in the UK, was found in

the Netherlands (Leopold *et al.*, 2014), proving bats can cross the North Sea during their long-distance migration. Lagerveld *et al.* (2014) report regular occurrences of bats in the Dutch offshore wind farms, generally limited to periods with calm weather suitable for long-distance migration.

Most research on the spatio-temporal patterns of bats at sea was based on recordings made by acoustic detectors, registering the echolocation calls of bats, installed well below rotor height (e.g., Lagerveld *et al.*, 2014, 2017a; Rydell and Wickman, 2015; Hüppop and Hill, 2016). In these studies, detector height was between 5 m and 26 m above mean sea level (MSL). Hüppop and Hill (2016) suggest that migrating bats might be missed in the aforementioned studies as they, possibly, fly at altitudes above 100 m under tailwind conditions. The height distribution of migratory bats at sea therefore remains a point of discussion. Besides echolocation, bats use vision during flight and might react to the visual stimulus of turbines as they do to tall trees (Cryan, 2008). It remains unclear if bats are attracted to offshore wind turbines or if they maintain their flight path when passing an offshore wind farm during migration. Voigt *et al.* (2018) showed that *P. nathusii* is attracted to red light, which is not the case for warm-white light. As turbine lighting is in most cases red, there can be an attraction effect of turbines on *P. nathusii* individuals, leading to an increased collision risk.

Gaining insight in the altitudinal distribution of bats at sea and the associated collision risk, as well as in possible exploratory behaviour near turbines, were identified as research priorities by EUROBATS (Rodrigues, 2015). This study simultaneously investigated the activity and behaviour of bats at low altitude and at nacelle height in an offshore wind farm in the Belgian part of the North Sea during an autumn migration period.

MATERIALS AND METHODS

The C-Power wind farm is located on the Thorntonbank in the Belgian part of the North Sea at approximately 27 km from the nearest point off the Belgian coastline (Fig. 1). The wind farm consists of 54 wind turbines and one offshore transformer platform. Six turbines have a capacity of five megawatt (MW), the other 48 are 6.15 MW turbines. The nacelle height of the turbines is ca. 93 m above MSL, depending on turbine location. Rotor diameter is 126 m, resulting in a rotor swept zone ranging from 30 to 156 m above MSL.

Each turbine has aviation safety lighting at the nacelle and on the turbine tower. The nacelle is equipped with two red blinking lights of medium intensity (intensity: 100 cd). The tower has continuous red obstacle lights of low intensity (intensity: 10 cd)

at approximately 41 m above MSL. Navigation lights are installed on the service platform (ca. 16 m above MSL) of the turbines on the corners of the wind farm, ensuring visibility from all directions. These are yellow lights (intensity: 100 cd) flashing the Morse code 'U'.

We installed 11 ultrasonic recorders (Batcorder 3.0/3.1 EcoObs Ltd., Germany) on seven different wind turbines in the C-Power wind farm (Fig. 1). Seven batcorders were installed on the turbine service platforms at approximately 16 m above MSL, and four were installed on the helicopter winching platform at the back of the nacelle, at 93 m above MSL (Fig. 2). Each recorder was powered by a solar panel. The recorded data were locally stored on SD memory cards. All Batcorders were installed on turbines in the northeastern part of the wind farm, assuming these are the first turbines bats will encounter when following the Dutch coastline and crossing the North Sea during autumn migration. The Batcorders were installed on 8 August 2017 and were operational until 30 November 2017. We made full spectrum recordings in .RAW format (sampling rate: 500 kHz, record quality: 20, amplitude resolution: 16 bit, threshold amplitude (sensitivity): -36 dB, post trigger: 400 ms, threshold frequency (sensitivity): 30 kHz). A threshold frequency of 30 kHz was deliberately chosen to avoid that the SD cards were primarily filled with wind turbine generated noise. This had to be avoided as the opportunities to visit the wind farm were limited and reaching the detectors to replace SD cards was logistically challenging. This setting implies that species using lower frequencies for echolocation (e.g., *Eptesicus* sp., *N. noctula*, *N. leisleri*) were not reliably recorded. In this study we therefore only focus on the genus *Pipistrellus*. Several previous studies already indicated that the most common species at the North Sea is *P. nathusii* (Lagerveld *et al.*, 2014, 2017a; Brabant *et al.*, 2016; Hüppop and Hill, 2016; L. Bach, P. Bach, H. Pommeranz, R. Hill, C. C. Voigt, M. Götsche, M. Götsche, H. Matthes, and A. Seebens-Hoyer, in litt.). Recordings were processed and visualised with the software program Sonochiro 3.3.3 (Biotope, France). Automated species identifications were verified by a bat expert.

Call sequences with more than 10 calls per recording were explored for behavioural characteristics. We classified the recordings in three types of behaviour as described by Skiba (2003): (1) exploratory behaviour and feeding buzzes, (2) transiting individual and (3) search calls in an obstacle-rich environment. The echolocation used for exploratory behaviour and feeding buzzes by *P. nathusii* is characterized by a change from the 'normal' FM-QCF (frequency modulated — quasi constant frequency) calls to calls with an increasingly shorter QCF-part, increasing FM and decreasing length of time intervals between consecutive calls (Barataud, 2015). Calls of transiting *P. nathusii* have virtually no FM, a peak frequency between 35 and 39 kHz and longer time intervals. The third type of recordings also has longer intervals between calls but strong frequency modulation. Sequences with fewer than 10 calls were not used for this purpose as we considered them too short to get a clear view of the bat's behaviour.

RESULTS

General Observations

All Batcorders were operational without failure during 114 nights from 8 August until 30 November

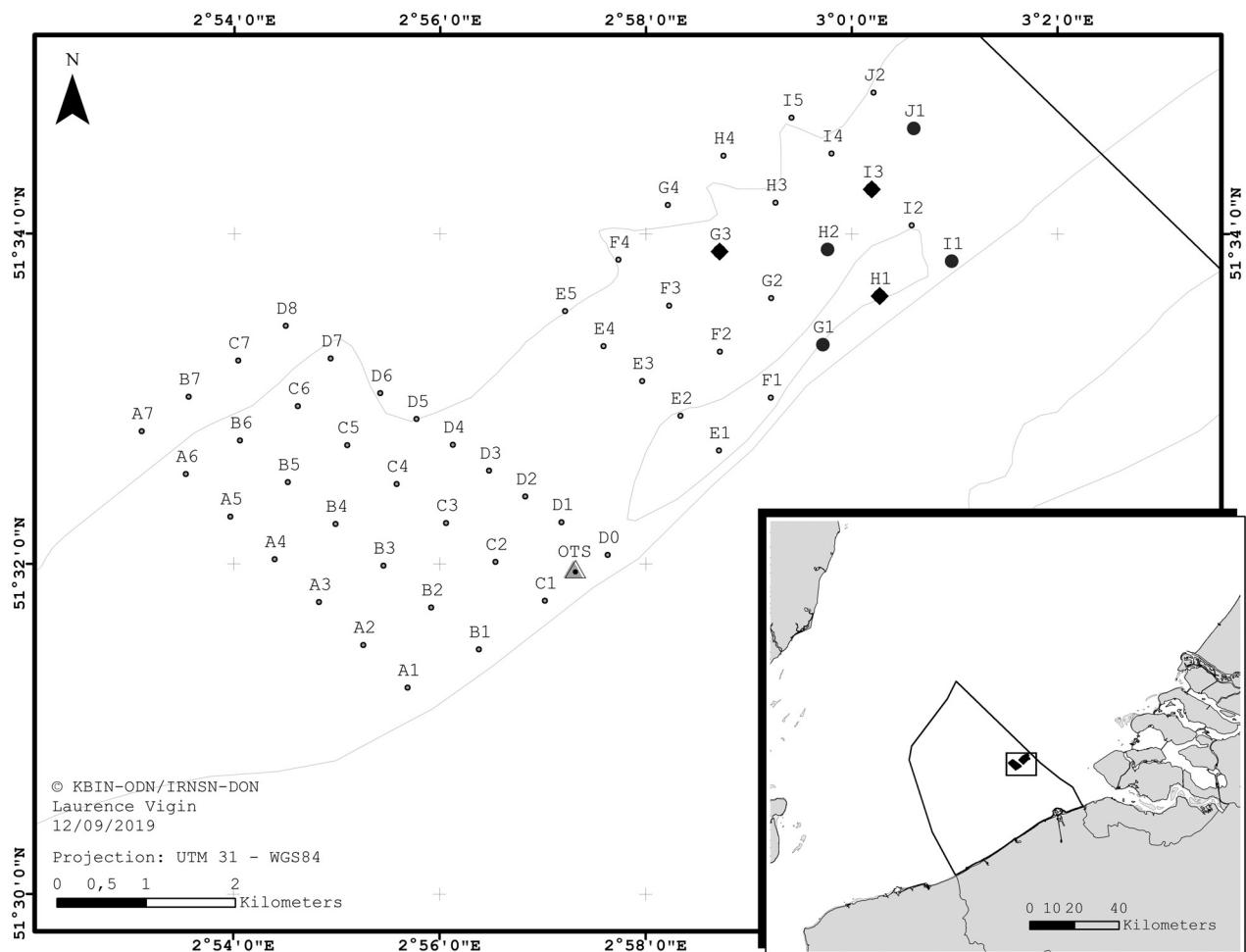


FIG. 1. Lay-out of the C-Power wind farm on the Thorntonbank in the Belgian part of the North Sea. Each dot represents a wind turbine. Turbines G1, H2, I1 and J1 (●) were equipped with two Batcorders each (at 16 m and 93 m above mean sea level, MSL). Turbines G3, H1 and I3 (◆) were equipped with a Batcorder only at 16 m MSL

2017. During that period, a total of 151 recordings of bats were made by the eleven Batcorders. All recordings, including the ones made by the detectors on the nacelle platforms, have a good signal to noise ratio. In some cases, a noise trace originating from the rotor movement, is present with a frequency around 20 kHz. This is not interfering with the bat calls and therefore did not prevent identifying the calls.

Bats were registered throughout the entire study period (Fig. 3). The first record dates from 29 August and the last one from 25 November, with a peak in activity during the second half of September where 63% of the call sequences were recorded. All echolocation calls were identified as calls from the species *P. nathusii*. Bat activity was recorded during 20 different nights. All Batcorders recorded at least one bat, except for the recorder installed on the nacelle of turbine J1 (Table 1). All but one recordings were made between two hours after sunset and

throughout the entire night. Three recordings were made after sunrise.

The seven detectors at 16 m MSL made on average 20.3 recordings. The average number of recordings made by the four detectors at 93 m MSL was 2.3 (Table 1). The number of recordings made at 93 m above MSL was always lower (ranging from 77 to 100% lower) than the number of recordings made at 16 m above MSL on the same turbines.

Behavioural Aspects

Forty-five of the 151 recordings consisted of more than 10 calls, of which only one recorded at 93 m above MSL. Looking into the behavioural characteristics of the recorded sequences, we identified 32 recordings of animals in transit, ten sequences of animals passing by while simultaneously exploring and three recordings of individuals showing



FIG. 2. Batcorder installed on the helicopter winching platform at the back of the nacelle of turbine II at approximately 93 m above MSL

exploratory behaviour and/or feeding buzzes (Fig. 4). These three call sequences were recorded by detectors at low altitude. The QCF calls, with almost no FM and the long time intervals shown in the fig-

ure 4 middle panel, indicate that this individual was transiting. The third sonogram (Fig. 4, lower panel) refers to a bat that is passing by, but the FM suggests that the animal was exploring the area and/or

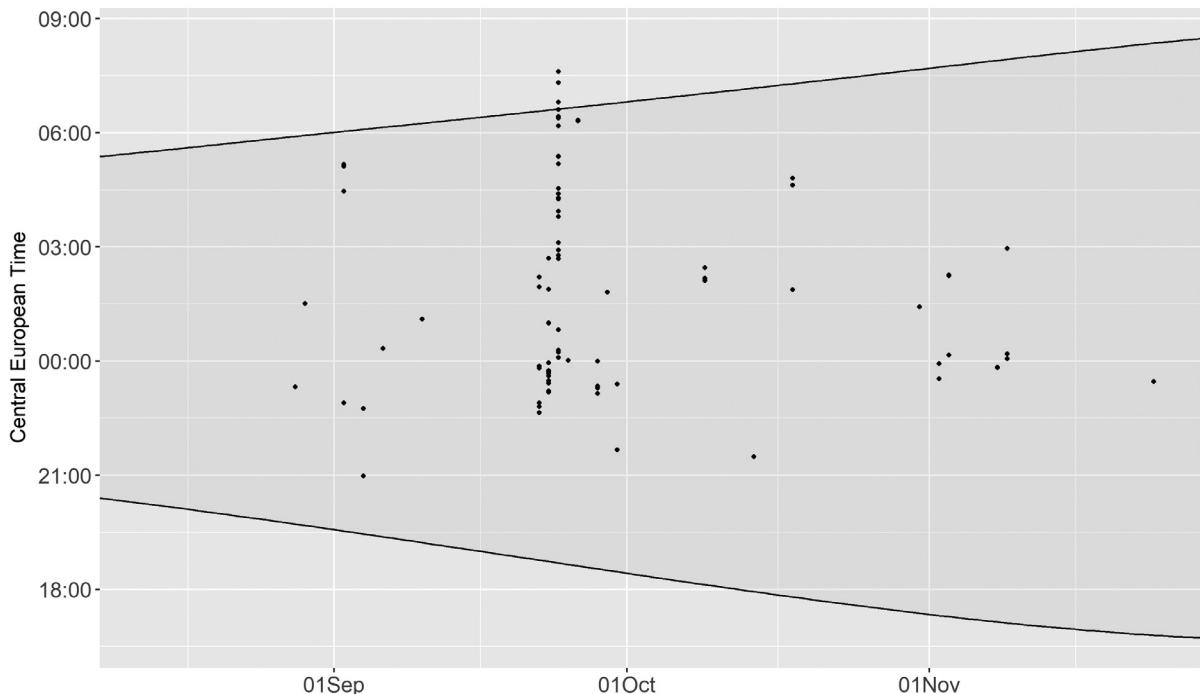


FIG. 3. Actogram of all recordings of bat call sequences during the study period from 8 August until 30 November 2017. Sunrise and sunset are indicated by the black lines

TABLE 1. Number of bat recordings per Batcorder from 8 August until 30 November 2017. Low, number of recordings at 16 m above mean sea level (MSL); High, number of recordings at 93 m above MSL; Records, number of bat recordings

Turbine	Height	Records
G01	Low	23
	High	2
G03	Low	35
H01	Low	11
H02	Low	26
	High	6
I1	Low	17
	High	1
I3	Low	7
J1	Low	23
	High	0
Total		151
Average low		20.3
Average high		2.3

simultaneously on the lookout for prey. Every call in this sonogram is followed by a clear echo, originating from the reflection of the calls on the water surface or a wind turbine.

DISCUSSION

All recordings made during this study concerned *P. nathusii* individuals. This is in line with similar studies (e.g., Lagerveld *et al.*, 2014, 2017a; Hüppop and Hill, 2016; L. Bach, P. Bach, H. Pommeranz, R. Hill, C. C. Voigt, M. Götsche, M. Götsche, H. Matthes, and A. Seebens-Hoyer, in litt.), where *P. nathusii* was the dominant species. The threshold frequency used in this study (30 kHz, to avoid turbine generated noise) however prevented detecting low frequency species like *V. murinus* and *N. noctula*. Most recordings in this study were made between August and mid-October which coincides with the autumn migratory period of *P. nathusii* (Kurvit *et al.*, 2011; Rydell *et al.*, 2014). A few recordings were made as late as the end of November. This might be explained by the warm weather conditions at that time. The distance from the study site to the nearest point off the coast (ca. 27 km) by far exceeds the known foraging distance for *P. nathusii*, which is up to six kilometers (Dietz *et al.*, 2009). Therefore, these recordings at sea, most likely refer to migrating bats and not to extended foraging flights.

Given the known flight speed of *P. nathusii* (6.9 ± 0.7 m/s measured by Troxell *et al.*, 2019; 7 m/s by Hedenström, 2009; 11.2–13.2 m/s by Suba, 2014), it takes bats minimum one hour to

reach the wind farm or longer when the wind farm is approached from Northerly directions. This is reflected in our recordings, which were made around two hours after sunset at the earliest. A few recordings are made close to and even after sunrise. These individuals possibly continue their migration during daytime or look for roosting possibilities in the wind farms. The latter was already suggested by Lagerveld *et al.* (2014, 2017a) and is supported by observations of roosting bats in the housing of a utility crane on the turbine service platforms and turbine foundations by maintenance workers of the C-Power wind farm (personal communication).

The bat echolocation calls registered during this study were clear and wind turbine generated noise did not prevent detectors from recording bats at low and high altitude. The difference in number of recordings between the detectors at low and high altitude can therefore not be attributed to the study's set-up. Very few bats were observed at high altitude (nine recordings). We can therefore conclude that there is bat activity at high altitude at sea, but far less than at low altitude. From our data, it is impossible to say if bats migrate at high altitude, as was suggested by Hüppop and Hill (2016), because they can rapidly change altitude when approaching turbines (Ahlén *et al.*, 2009). All migrating bats detected by Ahlén *et al.* (2009) in the Baltic Sea and Kattegat flew at relatively low altitudes except for a few observations of bats investigating turbines and other structures up to 100 m above MSL. *Nyctalus noctula*, a species known to migrate at higher altitude (Kronwitter, 1988), was not within the scope of this study as it uses frequencies lower than the threshold frequency of our detectors (30 kHz).

For echolocation calls of the genus *Pipistrellus*, the detection range by a Batcorder is typically between ca. 17 and 35 m, when a threshold of -36dB is set (Simon *et al.*, 2015). The detection range is influenced by the direction of flight during the echolocation call relative to the device, the environmental conditions (e.g., humidity) and the type of call (i.e., low frequency calls range over longer distances). In general, a detection range of 25 m is assumed for small bat species, like *P. nathusii* (Barataud, 2015; Hüppop and Hill, 2016; Lagerveld *et al.*, 2017a). This means that the Batcorders we installed at 93 m above MSL approximately covered an altitudinal range of 68 to 118 m above MSL. The rotor of the C-Power turbines reaches from 30 m to 156 m above MSL. Therefore, all bats recorded at 93 m above MSL were at risk of colliding with the turbine rotor and our observations provide

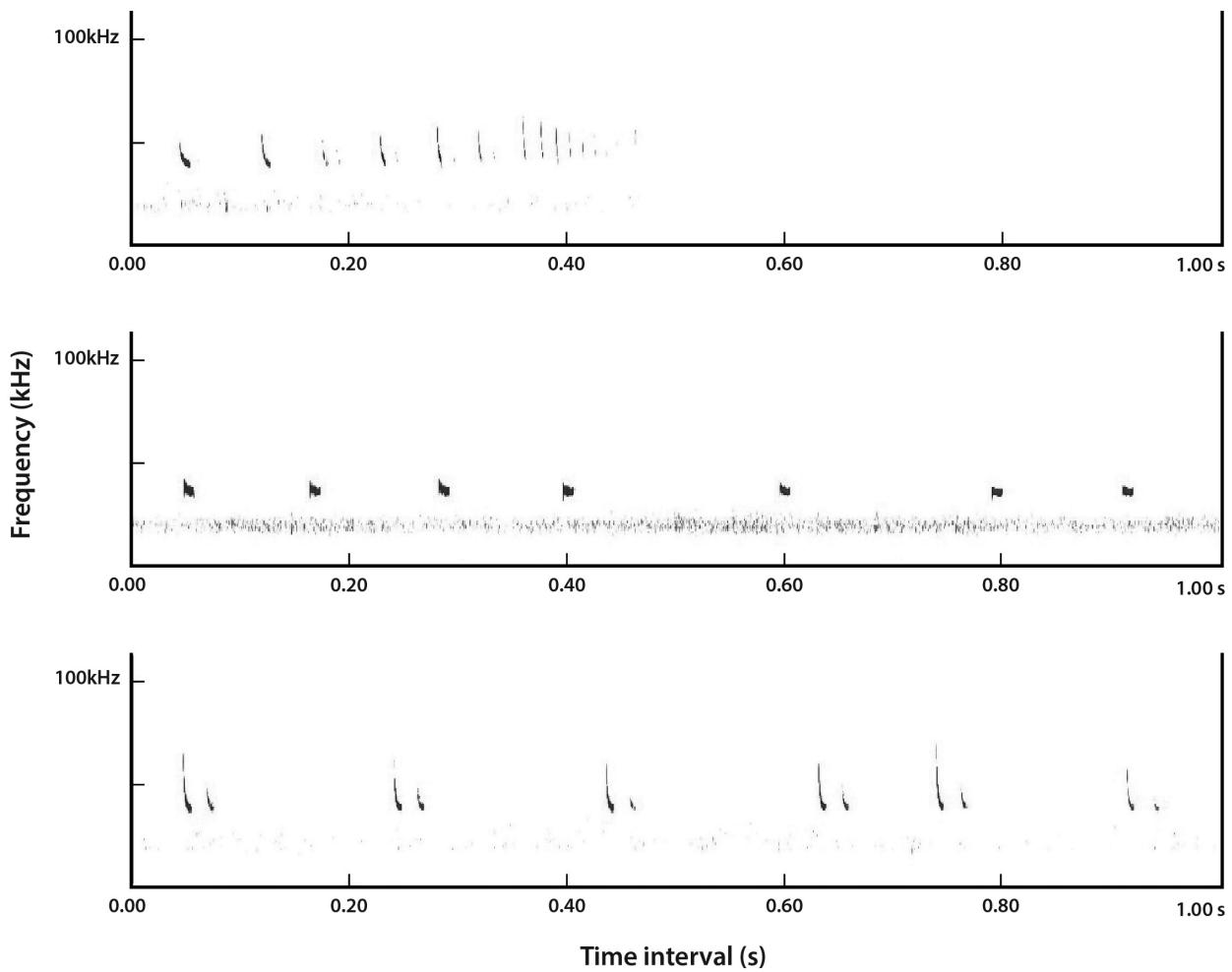


FIG. 4. Three example sonograms (i.e., visual representation of the echolocation calls, indicating frequency, intensity and time) of the different behaviour detected during this study. Upper panel, exploratory behaviour and/or feeding buzzes; middle panel, transit; lower panel, transit and simultaneous exploring

an indication of the activity of bats in the risk-of-collision zone. Ahlén *et al.* (2009) expect that accidents with wind turbines are probably not frequent during migration itself, because bats generally migrate at low altitudes. Our low number of recordings at nacelle height support this hypothesis. However, there are records of bats migrating at high altitude (>100 m) at sea (Hatch *et al.*, 2013). We should thus be cautious to make strong conclusions about the possible number of collisions. A low number of recordings at nacelle height does not necessarily mean that only a low number of bats will collide with the turbines. P. Bach and L. Bach (in litt.) found a high number of collision victims of *P. nathusii* (i.e. 1.6/year/turbine) in an onshore wind farm, for a relatively low number of acoustic detections at nacelle height. This might be explained by the small detection range of the acoustic detectors, ca. 25 m, which is the same for the detector we used.

Furthermore, the limited detection range of the detectors does not allow to record bats in the outer parts of the rotor swept zone. At an onshore wind farm, P. Bach and L. Bach (in litt.) showed that *P. nathusii* activity at the lowest point of the rotor blades was substantially higher than at nacelle height, although not as high as at ground level. Also, offshore wind turbines attract insects (Rydell *et al.*, 2010) and provide habitat for certain flying insect species (e.g., *Telmatobius japonicus* — De Mesel *et al.*, 2015). Collisions become more likely, when bats stop over and forage around turbines. In one case (24 September 2017 at turbine H2), the data suggest that an individual was foraging during a longer time at one turbine and was changing altitude alongside the turbine, as it was first recorded by the upper Batcorder and then by the lower Batcorder. This type of behaviour increases the risk of collision (Ahlén *et al.*, 2009). On the other hand, only three

of the 45 longer recordings that we investigated for behavioural clues referred to bats showing intensive exploratory behaviour and/or feeding buzzes. Thirty-two sequences referred to bats transiting. The remaining ten recordings were call sequences described by Skiba (2003) as “search calls in an obstacle-rich environment”. Possibly these bats were simultaneously transiting and exploring the area and/or on the look-out for prey. This rather fits in the fly-and-forage strategy of migrating birds and bats to keep feeding along the way to take in energy (Suba *et al.*, 2012).

We can conclude that the number of recordings of *P. nathusii* at rotor height is only about 10% of the number of recordings at low altitude in the wind farm in this study. In order to assess the risk of collision, there is a need for studies assessing bat activity at the entire turbine altitude span, including the outermost areas of the rotor where the blade speed is highest, as recommended by Reers *et al.* (2017). Ideally, these studies should also include species with call frequencies lower than 30 kHz, which was not the case in our study. Furthermore, there is a need for studies that can unravel migration routes of bats at sea. A promising technique for the latter is the use of radio-telemetry tags and fixed receiver stations along the coast and at sea (more information in Sjöberg *et al.*, 2015; Lagerveld *et al.*, 2017b; C. M. Francis, P. D. Taylor, and Z. J. Crysler, in litt.).

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LITERATURE CITED

- AHLÉN, I., H. J. BAAGØE, and L. BACH. 2009. Behavior of Scandinavian bats during migration and foraging at sea. *Journal of Mammalogy*, 90: 1318–1323.
- ARTHUR, L., and M. LEMAIRE. 2015. Les chauves-souris de France, Belgique, Luxembourg et Suisse, 2nd edition. Coll. Parthénope, Biotope édition, Mèze, NHBN, Paris, 544 pp.
- BAERWALD, E. F., and R. BARCLAY. 2014. Sciencebased strategies can save bats at wind farms. *Bats*, 32: 2–4.
- BAERWALD, E. F., G. H. D'AMOURS, B. J. KLUG, and R. M. R. BARCLAY. 2008. Barotrauma is a significant cause of bat fatalities at wind turbines. *Current Biology*, 18: 695–696.
- BARATAUD, M. 2015. Acoustic ecology of European bats. Species, identification, study of their habitats and foraging behaviour. Biotope éditions, Mèze, 340 pp.
- BOSHAMER, J. P. C., and J. P. BEKKER. 2008. *Nathusius' pipistrelles (Pipistrellus nathusii)* and other species of bats on offshore platforms in the Dutch sector of the North Sea. *Lutra*, 51: 17–36.
- BRABANT, R., Y. LAURENT, R.-M. LAFONTAINE, B. VANDEN-DRIESSCHE, and S. DEGRAER. 2016. First offshore observation of parti-coloured bat *Vespertilio murinus* in the Belgian part of the North Sea. *Belgian Journal of Zoology*, 146: 62–65.
- CRYAN, P. M. 2008. Mating behavior as a possible cause of bat fatalities at wind turbines. *Journal of Wildlife Management*, 72: 845–849.
- DE MESEL, I., F. KERCKHOF, A. NORRO, B. RUMES, and S. DEGRAER. 2015. Succession and seasonal dynamics of the epifauna community on offshore wind farm foundations and their role as stepping stones for non-indigenous species. *Hydrobiologia*, 756: 37–50.
- DIETZ, C., O. VON HELVERSEN, and D. NILL. 2009. Bats of Britain, Europe and Northwest Africa. A. & C. Black, Publishers Ltd., London, 400 pp.
- GRODSKY, S. M., M. J. BEHR, A. GENDLER, D. DRAKE, B. D. DIETERLE, R. J. RUDD, and N. L. WALRATH. 2011. Investigating the causes of death for wind turbine-associated bat fatalities. *Journal of Mammalogy*, 92: 917–925.
- HATCH, S. K., E. E. CONNELLY, T. J. DIVOLL, I. J. STENHOUSE, and K. A. WILLIAMS. 2013. Offshore observations of eastern red bats (*Lasiorurus borealis*) in the mid-Atlantic United States using multiple survey methods. *PloS ONE*, 8: e83803.
- HEDENSTRÖM, A. 2009. Optimal migration strategies in bats. *Journal of Mammalogy*, 90: 1298–1309.
- HÜPPOP, O., and R. HILL. 2016. Migration phenology and behaviour of bats at a research platform in the south-eastern North Sea. *Lutra*, 59: 5–22.
- HUTTERER, R., T. IVANOVA, C. MEYER-CORDS, and L. RODRIGUES. 2005. Bat migrations in Europe: a review of banding data and literature. *Naturschutz und Biologische Vielfalt*, 28: 1–176.
- KRAPP, F., and J. NIETHAMMER (eds.). 2011. Die Fledermäuse Europas. AULA Verlag, Wiebelsheim, Germany, 1202 pp.
- KRONWITTER, F. 1988. Population structure, habitat use and activity patterns of the noctule bat, *Nyctalus noctula* Schreb., 1774 (Chiroptera: Vespertilionidae) revealed by radio-tracking. *Myotis*, 26: 23–85.
- KURVITS, T., C. NELLEMANN, B. ALFTAN, A. KÜHL, P. PROKOSCH, M. VIRTUE, and J. F. SKAALVIK (eds.). 2011. Living planet: connected planet — preventing the end of the world's wildlife migrations through ecological networks. rapid response assessment. United Nations Environment Programme, GRID-Arendal, 76 pp.
- LAGERVELD, S., B. JONGE POERINK, R. HASELAGER, and H. VERDAAT. 2014. Bats in Dutch offshore wind farms in autumn 2012. *Lutra*, 57: 61–69.
- LAGERVELD, S., D. GERLA, J. T. VAN DER WAL, P. DE VRIES, R. BRABANT, E. STIENEN, K. DENEUDT, J. MANSHANDEN, and M. SCHOLL. 2017a. Spatial and temporal occurrence of bats in the southern North Sea area. Wageningen Marine Research (University & Research centre), Wageningen Marine Research report C090/17, 52 pp.
- LAGERVELD, S., R. JANSSEN, J. MANSHANDEN, A.J. HAARSMA, S. DE VRIES, R. BRABANT, and M. SCHOLL. 2017b. Telemetry for migratory bats: a feasibility study. Wageningen Marine Research (University & Research centre), Wageningen Marine Research Report C011/17, 58 pp.

- LEHNERT, L. S., S. KRAMER-SCHADT, S. SCHÖNBORN, O. LINDECKE, I. NIERMANN, and C. C. VOIGT. 2014. Wind farm facilities in Germany kill noctule bats from near and far. PLoS ONE, 9: e103106.
- LEOPOLD, M. F., M. BOONMAN, M. P. COLLIER, N. DAVAASUREN, R. C. FLIN, A. GYIMESI, J. DE JONG, R. H. JONGBLOED, B. JONGE POERINK, J. C. KLEYHEEG-HARTMAN, *et al.* 2014. A first approach to deal with cumulative effects on birds and bats of offshore wind farms and other human activities in the Southern North Sea. IMARES Report C166/14, 188 pp.
- REERS, H., S. HARTMANN, J. HURST, and R. BRINKMANN. 2017. Bat activity at nacelle height over forest. Pp. 79–98, *in* Wind energy and wildlife interactions (J. KÖPPEL, ed.). Springer, Cham, Switzerland, 289 pp.
- RODRIGUES, L., L. BACH, M. J. DUBOURG-SAVAGE, B. KARAPANDŽA, D. KOVAC, T. KERVYN, J. DEKKER, A. KEPEL, P. BACH, J. COLLINS, *et al.* 2015. Guidelines for consideration of bats in wind farm projects: revision 2014. EUROBATS Publication Series No. 6. UNEP/EUROBATS Secretariat, Bonn, 133 pp.
- ROLLINS, K. E., D. K. MEYERHOLZ, G. D. JOHNSON, A. P. CAPARELLA, and S. S. LOEW. 2012. A forensic investigation into the etiology of bat mortality at a wind farm: barotrauma or traumatic injury? Veterinary Pathology, 49: 362–371.
- RYDELL, J., and A. WICKMAN. 2015. Bat activity at a small wind turbine in the Baltic Sea. Acta Chiropterologica, 17: 359–364.
- RYDELL, J., L. BACH, M.-J. DUBOURG-SAVAGE, M. GREEN, L. RODRIGUES, and A. HEDENSTRÖM. 2010. Bat mortality at wind turbines in northwestern Europe. Acta Chiropterologica, 12: 261–274.
- RYDELL, J., L. BACH, P. BACH, L. G. DIAZ, J. FURMANKIEWICZ, N. HAGNER-WAHLSTEN, E.-M. KYHERÖINEN, T. LILLEY, M. MASING, M. M. MEYER, *et al.* 2014. Phenology of migratory bat activity across the Baltic Sea and the south-eastern North Sea. Acta Chiropterologica, 16: 139–147.
- SIMON, R., K. HOCHRADEL, J. MAGES, M. NAGY, A. NAUCKE, I. NIERMANN, N. WEBER, and O. BEHR. 2015. Methoden der akustischen Erfassung der Fledermausaktivität an Windenergieanlagen. Pp. 39–80, *in* Reduktion des Kollisionsrisikos von Fledermausen an Onshore-Windenergieanlagen (RENEBAT II) (O. BEHR, R. BRINKMANN, F. KORNER-NIEVERGELT, M. NAGY, I. NIERMANN, M. REICH, and R. SIMON, eds.). Umwelt und Raum, 7: 1–368.
- SJÖBERG, S., T. ALERSTAM, S. ÅKESSON, A. SCHULZ, A. WEIDAUER, T. COPPACK, and R. MUHEIM. 2015. Weather and fuel reserves determine departure and flight decisions in passerines migrating across the Baltic Sea. Animal Behaviour, 104: 59–68.
- SKIBA, R. 2003. Europäische Fledermäuse, 2nd edition. Neue Brehm-Bücherei 648. Westarp Wissenschaften, Hohenwarsleben, Germany, 218 pp.
- SKIBA, R., 2007. Die Fledermäuse im Bereich der Deutschen Nordsee unter Berücksichtigung der Gefährdungen durch Windenergieanlagen (WEA). Nyctalus (N.F.), 12: 199–220.
- SUBA, J. 2014. Migrating *Nathusius' pipistrellus* (*Pipistrellus nathusii*) (Chiroptera: Vespertilionidae) optimise flight speed and maintain acoustic contact with the ground. Environmental and Experimental Biology, 12: 7–14.
- TROXELL, S. A., M. W. HOLDERIED, G. PETERSONS, and C. C. VOIGT. 2019. *Nathusius'* bats optimize long-distance migration by flying at maximum range speed. Journal of Experimental Biology, 222: jeb176396.
- VOIGT, C. C., A. G. POPA-LISSEANU, I. NIERMANN, and S. KRAMER-SCHADT. 2012. The catchment area of wind farms for European bats: a plea for international regulations. Biological Conservation, 153: 80–86.
- VOIGT, C. C., K. REHNIG, O. LINDECKE, and G. PETERSONS. 2018. Migratory bats are attracted by red light but not by warm-white light: implications for the protection of nocturnal migrants. Ecology and Evolution, 8: 9353–9361.
- WALTER, G., H. MATTHES, and M. JOOST. 2007. Fledermauszug über Nord- und Ostsee — Ergebnisse aus Offshore-Untersuchungen und deren Einordnung in das bisher bekannte Bild zum Zuggeschehen. Nyctalus (N.F.), 12: 221–233.

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