




Review article

Impacts of offshore wind farms on migratory bats in British waters

Jack Hooker^{a,b,*} , Paul Lintott^b, Katherine Boughey^a, Lisa Worledge^a,
Kirsty Park^c, Jan Collins^a

^a The Bat Conservation Trust, Studio 15 Cloisters House, 8 Battersea Park Road, London SW8 4BG, UK

^b School of Applied Sciences, University of the West of England, Bristol, England BS16 1QY, UK

^c Biological and Environmental Sciences, School of Natural Sciences, University of Stirling, Stirling FK9 4LA, UK

ARTICLE INFO

Keywords:

Bats
Europe
Wind energy
Wind turbines
Collision mortality
Bat migration
Bat mitigation
Offshore
Renewable energy
Barriers
Avoidance

ABSTRACT

Offshore wind energy projects are developing at pace with ambitious Net Zero targets in place across Europe and understanding the evidence base for the environmental effects of offshore wind development and operation is essential. The evidence for bats moving across seas surrounding the UK is growing, making it critical to better understand the impact of offshore wind energy on bats. We review the literature examining bat migration within and between the British Isles and Europe as well as the interaction of bats with wind energy infrastructure. Based on data available, *Nathusius' pipistrelle* (*Pipistrellus nathusii*) are the most commonly recorded species offshore and are considered a regular migrant to the British Isles therefore putting them at the highest risk for interactions with offshore wind turbines. We also review evidence to suggest that long distance migratory *Nyctalus* spp. may migrate between the British Isles and Europe or Scandinavia as well as highlighting potential impacts of non-migratory activity offshore. We find that whilst it is widely assumed that bat behaviour around offshore wind turbines is likely to be similar to onshore, there is currently a lack of studies specifically reporting how bats interact with offshore wind turbines. A number of hypotheses have been proposed to explain why bats are killed by wind turbines and a likely negative consequence of wind turbine-related mortality is the cumulative impact on bat populations across Europe, particularly for migratory species. To close key gaps in the evidence, future studies should focus on migration routes, phenology and behaviour of bat species crossing open sea including future wind energy development scenarios. It is also important that future work aims to establish the specific impact on bat species in the offshore environment including; if bats are killed at offshore wind turbines, the number of casualties and what conditions influence collisions.

1. Introduction

Global biodiversity is facing a crisis unprecedented in modern history with impacts being witnessed in every habitat on earth (Pimm et al., 2014; Ceballos et al., 2015; Cowie et al., 2022). Yet despite climate change and biodiversity being interdependent, they are primarily tackled in siloes (Pettorelli et al., 2021). This can cause problems when objectives underlying each crisis may be conflicting and the resulting 'green-green' dilemmas can be particularly challenging as they involve two or more necessary goals, yet with

* Corresponding author at: The Bat Conservation Trust, Studio 15 Cloisters House, 8 Battersea Park Road, London SW8 4BG, UK.

E-mail addresses: JHooker@bats.org.uk (J. Hooker), Paul.Lintott@uwe.ac.uk (P. Lintott), KBoughey@bats.org.uk (K. Boughey), LWorledge@bats.org.uk (L. Worledge), k.j.park@stir.ac.uk (K. Park), JCollins@bats.org.uk (J. Collins).

<https://doi.org/10.1016/j.gecco.2025.e03911>

Received 9 June 2025; Received in revised form 13 October 2025; Accepted 14 October 2025

Available online 15 October 2025

2351-9894/Crown Copyright © 2025 Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

detrimental counter-effects (Straka et al., 2020).

One such green-green dilemma is the worldwide promotion and development of wind energy infrastructure (Straka et al., 2020). While transitioning from fossil to renewable energy sources is identified as one of the most important actions to combat the global climate crisis (Shukla et al., 2022), the ongoing negative impact of renewable energy installations on biodiversity is an urgent conservation issue (Voigt et al., 2015; Thaker et al., 2018). Not only is wind power an efficient way of producing energy that generates negligible greenhouse gas emissions when compared to fossil fuels (Lueken et al., 2012; Zhou et al., 2012), the approximate greenhouse-gas payback time (i.e. the time in which the system must operate to offset the emissions embedded in its production) for wind turbines in Europe is now only a few months (Dammeier et al., 2019). However, despite their many benefits, wind farms can have negative impacts on biodiversity (Gibson et al., 2017; Pörtner et al., 2021). During the construction phase of development, all energy production infrastructure will impact the habitats where they are installed through the functional loss or fragmentation of habitats. Moreover, wind energy also has the potential to impact the surrounding aerosphere and cause direct mortality in flying vertebrates during the operational phase (Leroux et al., 2023).

1.1. Potential for Impacts between wildlife and wind energy infrastructure

During their operation, wind turbines create significant airflow disturbances in a so-called “wake effect” that is generated by increased turbulences and decreased wind speed up to a few kilometres on the downwind side of the wind turbine depending on meteorological conditions or turbine array layout (Porté-Agel et al., 2020). This wake effect, coupled with increased noise, vibration, light, and increased human presence may decrease habitat suitability and resource availability near wind turbines (e.g., Campedelli et al., 2014) as well as creating antagonistic behavioural responses within and between species (Dai et al., 2015; Gibson et al., 2017). Turbines can alter habitat use by flying vertebrates by generating attraction (Richardson et al., 2021; Guest et al., 2022) or avoidance responses (Minderman et al., 2012, 2017; Barfé et al., 2018; Gómez-Catasús et al., 2018) at different spatial scales. Attraction may increase fatality risk in the immediate vicinity of wind turbines (micro-scale, Cryan and Barclay, 2009; Marques et al., 2021; Tolvanen et al., 2023) while avoidance can occur at the level of the entire wind farm (macroscale) or within the wind farm (meso-scale). Avoidance impacts include displacement of migrating and commuting routes as well as functional barriers to foraging habitats and roosting opportunities (Roscioni et al., 2014; Tolvanen et al., 2023).

The first observations that onshore wind turbines were causing bat mortalities were made in the 1970s (Hall and Richards, 1972), however serious questioning of their impacts only emerged at the end of the twentieth century, with increasing observations of dead bats at onshore wind farms (reported in Ahlén, 2003; Johnson et al., 2003). Bat casualties have been identified at onshore wind farms for two decades (e.g. Table 1; Rydell et al., 2010; EUROBATS, 2023) and during this time 29 species have been identified among recorded casualties in Europe, with the majority consisting of common pipistrelle (*Pipistrellus pipistrellus*, 22 %), Nathusius' pipistrelle (*P. nathusii*, 16 %), noctule (*Nyctalus noctula*, 15 %) and Leisler's bat (*Nyctalus leisleri*, 7 %) (Table 1; EUROBATS, 2023). Relative to the reported bat casualties, the real extent of bat mortality at onshore wind turbines is likely to be much higher since only the fatalities reported to EUROBATS Intersessional Working Group (IWG) members are officially documented. These casualties are recorded as gross totals between 2003 and 2019 and no account is taken of biases resulting from the non-standardised and often opportunistic nature of the surveys (EUROBATS, 2023). Nonetheless, the reported casualties suggest *Pipistrellus* spp. (57 % of casualties) and *Nyctalus* spp. (23 % of casualties) are likely to be most at risk from wind turbines whereas relatively few casualties have been recovered of other common and widespread species such as brown long-eared bats (*Plecotus auritus* 0.08 %) or *Myotis* spp. (0.5 %) (EUROBATS, 2023). Whilst this could suggest that these species are at lower risk than species in the *Nyctalus* and *Pipistrellus* genera, it may also be a consequence of the open environments from which most of the data is derived, as there is a general paucity of research on wind turbines 'key-holed' into woodlands. The studies that do exist of forest-dwelling bats such as *Myotis* and *Plecotus* spp. have found lower bat activity or general avoidance in forest areas with wind turbines, suggesting that wind energy development in these habitats could functionally exclude bats from important foraging or commuting areas (Roemer et al., 2017; Ellerbrok et al., 2022; Gaultier et al., 2023; Reusch et al., 2023). Current knowledge on fatality risk in bats suggest that the species most prone to collisions with onshore wind turbines are aerial hawkers such as *Pipistrellus* spp. and *Nyctalus* spp. that have echolocation characteristics, wing shape and flight speeds adapted for movement in open space and for hunting flying prey farther from the ground or landscape features. In contrast, the lower-risk species such as *Myotis* spp. or *Rhinolophus* spp. hunt close to surfaces or directly in the vegetation, which decreases the time that they spend in the turbine rotor swept zone, reducing the probability of collision (Table 1; Rydell et al., 2010; Roemer et al., 2017).

1.2. Wind turbine induced mortality in bats

Bats are killed at wind turbines either by direct collision (blunt-force trauma) with the moving blades or by barotrauma i.e. tissue damage, particularly in the lungs and ears, caused by rapid changes in air pressure near the turbine blades (Baerwald et al., 2008; Grodsky et al., 2011). The relative importance of these two mechanisms is unclear and research suggests that most bats with barotrauma also have evidence of direct collision (Rollins et al., 2012). Bat mortality due to barotrauma is the subject of much debate as empirical evidence documenting the impacts of pressure changes on bats is not feasible due to ethical considerations (i.e. subjecting live bats to lethal pressure changes). Furthermore, modelling simulations of wind turbines attempting to characterise the sudden pressure changes bats may experience when flying near a utility-scale wind turbine, concluded that the pressure changes required to cause barotrauma are so close to the turbine blade (i.e. bats would have to skim the surface of the blade) that it is highly unlikely that a bat could experience barotrauma without also being struck by the moving blade (Lawson et al., 2020).

It is important to note that the study by Lawson et al. (2020) was based on a 5 MW reference turbine with a rotor diameter of 126 m

Table 1

Reported bat fatalities in Europe by species and country from 2003 to 2019. Data comprises records submitted to EUROBATS Intersessional Working Group members of bat fatalities found either accidentally or during post-construction monitoring. Table reproduced from data from [EUROBATS \(2023\)](#). Key: AT = Austria, BE = Belgium, CH = Switzerland, CR = Croatia, CZ = Czech Rep., DE = Germany, DK = Denmark, ES = Spain, EE = Estonia, FI = Finland, FR = France, GR = Greece, IL = Israel, IT = Italy, LV = Latvia, NL = Netherlands, NO = Norway, PT = Portugal, PL = Poland, RO = Romania, SE = Sweden, UK = United Kingdom.

Species Name	AT	BE	CH	CR	CZ	DE	DK	ES	EE	FI	FR	GR	IL	IT	LV	NL	NO	PT	PL	RO	SE	UK	Total
<i>Nyctalus noctula</i>	46	1		2	31	1200		1			131	10						2	16	85	14	11	1550
<i>N. lasiopterus</i>								21			7	1						9					38
<i>N. leisleri</i>		2	1	21	3	180		15			174	58		2				273	5	19			753
<i>Nyctalus spp. & Nlei/Vmur</i>				1				2			5							17		8			33
<i>Eptesicus serotinus</i>	1	2			11	63		2			29	1				2			3	1			115
<i>E. isabellinus</i>								117										2					119
<i>E. serotinus/isabellinus</i>								98										17					115
<i>E. nilssonii</i>	1				1	6			2	6					13		1		1	1	13		45
<i>Vespertilio murinus</i>	2	1		15	6	145					12	1			1				8	15	2		208
<i>Myotis myotis</i>						2		2			4												8
<i>M. blythii</i>				1				6			1												8
<i>M. dasycneme</i>						3																	3
<i>M. daubentonii</i>						7												2					9
<i>M. bechsteinii</i>											1												1
<i>M. emarginatus</i>								1			2							1					4
<i>M. brandtii</i>						2																	2
<i>M. mystacinus</i>						3					3	1											7
<i>M. nattereri</i>						1																1	2
<i>Myotis spp.</i>						2		3			1									4			10
<i>Pipistrellus pipistrellus</i>	2	36	7	7	16	702		211			930			1		15		323	3	11	1	46	2311
<i>P. nathusii</i>	13	6	6	50	7	1066	2				285	35		1	23	8			16	111	5	1	1635
<i>P. pygmaeus</i>	4			6	2	134					172				1			42	1	5	18	52	437
<i>P. pipistrellus/pygmaeus</i>	1		3					271			39	55						38	1	3			411
<i>P. kuhlii</i>				126				44			199		22					51		15			457
<i>P. pipistrellus/ kuhlii</i>				12							1							19					32
<i>Pipistrellus spp.</i>	8	4		60	9	91		25			211	1			2			109	2	48		12	582
<i>Hypsugo savii</i>	1			206		1		50			54	28		12				56		2			410
<i>Barbastella barbastellus</i>						1		1			4												6
<i>Plecotus austriacus</i>	1					8																	9
<i>P. auritus</i>						7																1	8
<i>Tadarida teniotis</i>				10				23			2							39					74
<i>Miniopterus schreibersii</i>								2			5							4					11
<i>Rhinolophus ferrumequinum</i>								1					1										2
<i>R. mehelyi</i>								1															1
<i>Rhinolophus spp.</i>								1															1
<i>Rhinopoma microphyllum</i>													5										5
<i>Taphozus nudiventris</i>													3										3
Unidentified bat spp.	1	1		48	1	77		320	1		317	8	2	1				120	3	7	30	9	946
Total	81	53	17	565	87	3701	2	1218	3	6	2588	200	33	17	40	25	1	1124	29	335	83	133	10371

whereas the next generation of offshore wind turbines will have a rotor diameter of 200 m or more. To maintain the optimal ratio of blade-tip speed to wind speed (i.e., tip-speed ratio; [Manwell et al., 2010](#)), rotor revolutions per minute (RPM) must increase linearly with turbine radius. If bats fly mostly near the nacelle, where the blades of large turbines move relatively slowly, the number of fatalities per MW of installed capacity may be reduced for large offshore turbines. However, if bats interact with the turbine blades away from the hub where blade speed is high the opposite may be true. Evidence from studies onshore have identified that mortality not only depends on the dimensions and the location of the wind turbine within the wind farm ([Baerwald and Barclay, 2009](#)) but also tower height and rotor diameter, which could potentially make offshore turbines more dangerous due to their increased size ([Rydell et al.,](#)

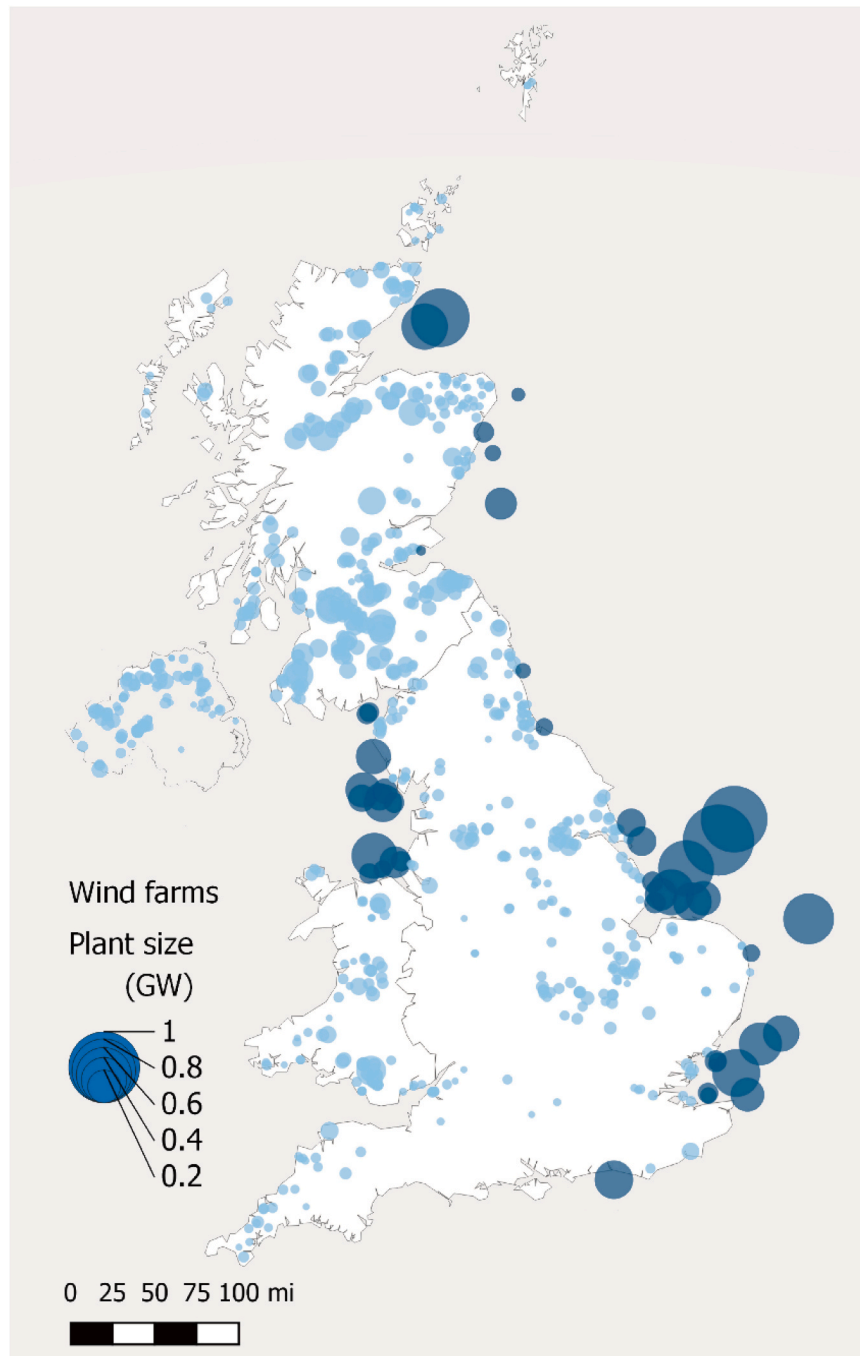


Fig. 1. Operational onshore and offshore wind farms in the UK as of 2022 with a capacity of 0.5 GW or more. There are approx. 9000 sites below this threshold as well as other sites that are excluded due to the lack of location data. The locations in this graphic are representative and not exact. Reproduced from DUKES map data by permission of the Department of Energy Security and Net Zero © Crown copyright 2023.

2010; Mathews et al., 2016; Thaxter et al., 2017).

The timing of bat collisions with operating onshore turbines in Europe have been extensively studied, with fatalities occurring primarily during autumn migration, roughly from August to mid-September, with a smaller peak also noted during spring for certain migration pathways across Europe (Rydell et al., 2010; Schuster et al., 2015; O'Shea et al., 2016; Roemer et al., 2019; Gaultier et al., 2020). Migratory activity, an established risk factor for wind turbine collisions in Europe and North America, was until recently thought to be absent among bats in the British Isles. However, evidence gathered through a suite of methods (e.g. acoustic surveys, ring recaptures, stable isotope analysis and radio telemetry) of bat movement between the UK and mainland Europe, as well as between distinct areas of the British Isles, is highlighting the extent of migration habits of Britain's bats, particularly in the *P. nathusii* population (National Nathusius' Pipistrelle Project, 2024). Whilst not considered a form of migratory movement, infrequent immigration of bats into the UK from mainland Europe has also been demonstrated through disease transmission studies whereby passive surveillance of *Eptesicus serotinus* recorded a previously absent strain of European bat lyssavirus 1 (EBLV-1) into the UK (Folly et al., 2021).

The exact timings of fatalities can vary geographically across Europe with southern latitudes generally experiencing a longer collision risk window (Georgiakakis et al., 2012; Sánchez-Navarro et al., 2020). Collision risk was found to be correlated with favourable weather conditions for foraging and commuting, with nights of low wind speed, warmer temperatures and no precipitation associated with the highest collision risk (Arnett and Baerwald, 2013; Cryan et al., 2014; Rydell, 2010). However, in North America it has been observed that macro-scale weather phenomena (i.e. high-pressure, low humidity, etc.) can be a more accurate indicator for predicting bat-turbine collisions than local weather conditions (Arnett et al., 2008).

At present most work on wind turbines and bats is focused on onshore impacts. However, as offshore wind projects are developing at pace with ambitious Net Zero targets in place across Europe (HM Government, 2021; European Commission, 2019), the potential for offshore wind farms to impact migrating bat species is moving up the international agenda (CMS, COP 14, 2024; UNEP-WCMC, 2024).

Due to its geographic location, the UK has some of the most favourable conditions for wind power generation in the world and as a result, wind energy is seeing consistent growth year on year (Asif and Muneer, 2007; RenewableUK, 2023). In addition to being popular with the public (YouGov, 2018, 2021), wind energy offers the most cost-effective choice for new electricity in the UK and as of 2022 domestic wind energy generation totalled 28,493 MW, making the UK the third largest wind energy producer in Europe (WindEurope, 2023). By the end of 2023, 8985 onshore wind turbines had been installed across 2629 projects, creating an operational capacity of 14,972 MW (RenewableUK, 2023; DUKES, 2023). Offshore, a similar operational capacity of 14,735 MW has also been achieved, albeit from only 2766 turbines spread across 44 projects (RenewableUK, 2023; DUKES, 2023; Fig. 1).

The rapid increase in offshore turbines has resulted in the UK becoming a world leader in offshore wind energy, representing 46 % of the total operational capacity of European offshore wind energy. Indeed, the UK commissioned the world's current largest wind farm, Hornsea Two, which has an operational capacity of 1386 MW and in 2022 the last of its 110 turbines (924 MW) were connected

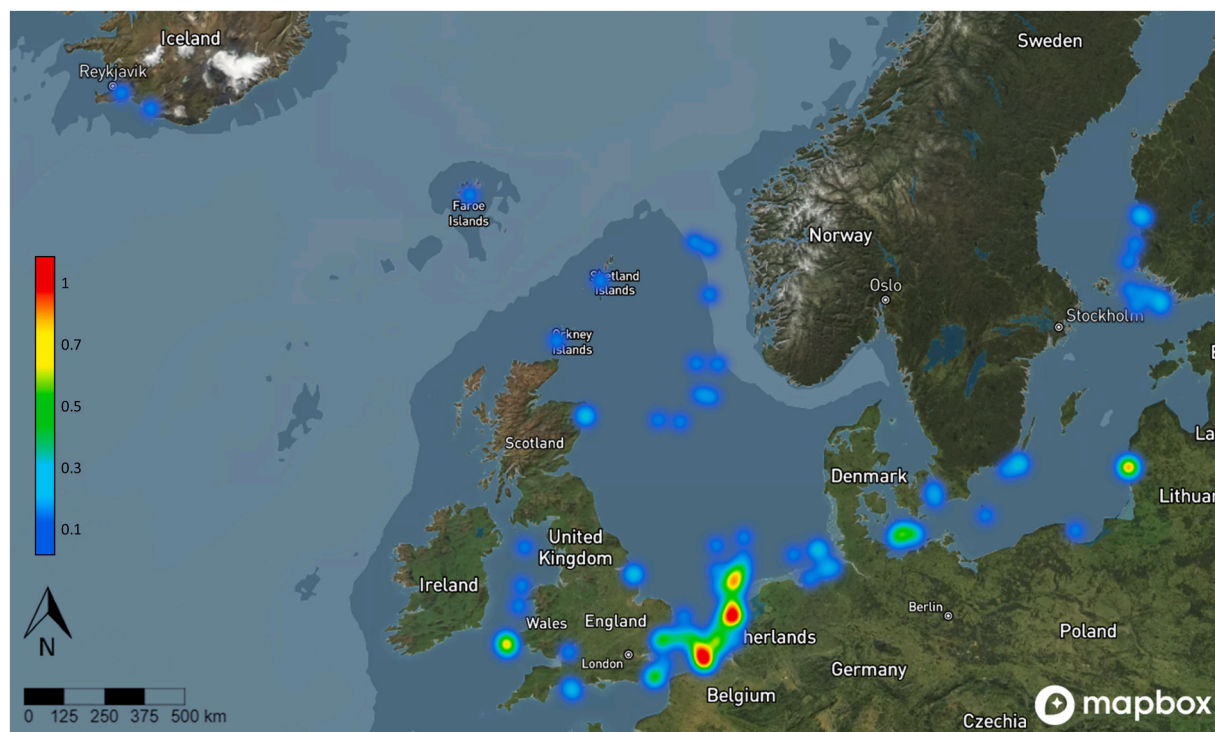


Fig. 2. Heat map displaying regional distribution of studies on bat migration over marine areas in NW Europe included within this review. © Mapbox © OpenStreetMap.



Fig. 3. Potential bi-directional migration corridors across the North Sea between the British Isles, Europe and Scandinavia. Orange arrows indicate possible migration corridors as identified during the literature and evidence review (arrow size is not significant). The evidence for migration across these broad fronts varies geographically and should only be taken as an indication. Detailed discussion of the evidence base surrounding each of these corridors is discussed further within this review. © Mapbox © OpenStreetMap.

to the energy grid ([WindEurope, 2023](#)). Furthermore, as of December 2023, Ørsted are progressing with what will become the world's single largest offshore wind farm, Hornsea Three, which will have a capacity of 2.9 GW and is expected to be completed around the end of 2027 ([Ørsted, 2023](#)).

Understanding the evidence base for the effect of offshore wind development and operation upon different species/habitats is an integral component that underpins government policy for offshore wind development. In the UK, the assessment of offshore wind

project assessments with respect to Environmental Impact (EIA), Habitats Regulations (HRA) and Marine Conservation Zones (MCZ) have identified a likely significant effect/impact pathway for seabirds, marine mammals, benthic (i.e. seafloor habitats and species) and designated fish species, but not bats. Bats remain a poorly understood receptor for marine offshore developments in seas surrounding the British Isles, with a limited evidence base for interactions.

Whilst the migratory movements of bats have been described for over a century (Miller, 1897), evidence of seasonal migration in and out of the UK has historically been largely anecdotal. So far, most information pertaining to the migratory ecology of bats has been gathered through studies in terrestrial habitats, with scientific knowledge on bats migrating over open sea being scarce. In this review, we aim to evaluate the current understanding of bat migration throughout the British Isles and between the British Isles and continental Europe, as well as bat interactions with offshore wind turbines, highlighting any evidence gaps or areas of uncertainty. We review the current knowledge on species-specific bat migration routes, spatial patterns of migrations and environmental drivers of movement, including potential collision risk from offshore turbines, population and barrier effects.

2. Methodology

2.1. Literature search

We conducted a systematic literature review following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) protocols (Page et al., 2021). We searched for studies that examined bat migration within the British Isles and between the British Isles and Europe, including the use of monitoring technologies or approaches to investigate migration pathways. We also searched for studies on the interaction of bats with offshore wind energy infrastructure including established or novel technologies to monitor and mitigate interactions of bats with wind turbines.

We searched the ISI Web of Science Core Collection (<http://www.isiwebofknowledge.com>), Scopus (<https://www.scopus.com>), and Google Scholar (<https://scholar.google.co.uk>) for English language peer-reviewed publications published on all continents. The search fields varied by options available in respective databases, for Google scholar we conducted a full article search (default parameters for keyword searches), whilst for Web of Science-indexed databases and Scopus, we searched using the title-abstract-keyword search. For all databases we included an index search of citation records to include publications that may not be available on the respective databases. We used the following search terms to find studies on the migration of bats within and between the British Isles and Europe: ('bat*' OR 'Chiroptera') AND (migration* OR movement* OR dispersal* OR migratory OR dispersion). An additional search was also completed using the same protocol using the following search terms to find studies on the interactions between bats and offshore wind farm developments: ('bat*' OR 'Chiroptera') AND 'wind' AND (farm* OR energy* OR windfarm* OR industry* OR wind-farm* OR park* OR development*). To comprehensively address our research questions, we also searched manually for accessible grey literature in online repositories, archives and databases which comprised conference proceedings, personal communications, technical reports, non-indexed publications and unpublished data. The final search was carried out in December 2024.

2.2. Article screening and classification

For the review process, all articles that appeared in each search string were exported into the Rayyan intelligent systematic review tool (Ouzzani et al., 2016) which was used to deduplicate repeated references across databases. Reviewers then used an inclusion/exclusion protocol to make final decisions for each article in Rayyan after screening the title, abstract and full-text levels. The articles retrieved from indexed databases were first screened by title and abstract and documents were excluded that did not study either the migration of bats, the impacts of wind energy infrastructure on bats, or techniques and technologies used to monitor and mitigate impacts to bats. More specifically, we interpreted interactions as any measured effect whether positive, negative or neutral, in response to the construction or operation of wind energy infrastructure. We included impacts that were either explicitly measured through observational or experimental studies or predicted based on modelling, molecular or genetic approaches.

As the aim of this review was to establish a baseline on the overall current state of knowledge of bat migration within and between the British Isles and Europe, including current knowledge on the potential impacts of offshore wind, we excluded studies focused only on onshore wind development from the systematic literature search section of this review. Furthermore, whilst we included studies on the interactions between bats and offshore wind turbines internationally, we only included studies on bat migration in North-west Europe and on species relevant to a British context.

2.3. Evidence review

To complement the systematic literature review and to further inform our understanding of potential impacts of offshore wind on bats we also conducted an evidence review of knowledge gained from theoretical and empirical studies in other landscapes (e.g. onshore) or with other non-bat taxa (e.g. birds) that did not form part of the systematic review process. Specific literature on the interaction of bats and onshore wind has been used to inform our understanding of the impacts of offshore wind on bats. This was deemed necessary due to the significant evidence gaps identified during the systematic literature review, consequently knowledge gained onshore represents the only viable source of information in which to draw inferences. Due to the high volume of literature on this topic we undertook a targeted literature review to inform our current knowledge using the same databases as the systematic literature review as well as through expert-led consultation. This consultation consisted of two structured, online workshop sessions in February 2024 that were designed to enable in-depth discussions and knowledge exchange among a panel of cross-sector experts in the

fields of bat migration and/or wind energy. This non-systematic review of the evidence focused on the most up to date studies and reviews, taking an in-depth but not systematic approach to the subject.

3. Results

We retrieved 55 studies were directly related to bat migration over marine areas in northwest Europe. In addition, 37 studies were indirectly related to offshore bat migration in this region (e.g. covering topics such as migration behaviour over land, population dynamics, genetic/molecular studies and general modelling approaches). We assessed the studies by geographical area and topic, with three relating to the Northern North sea, 34 to the southern North sea, five to the English Channel, four to the Celtic and Irish Sea, and nine to the Baltic Sea. Several studies included results related to more than one geographical area. Twenty-four studies looked at the behaviour of migrating bats, 10 studies considered migration through either molecular or genetic techniques and three were based on modelling techniques. A total of 11 European bat species were identified within the literature as being present over marine areas in north-west Europe. The number of retrieved studies identifying the occurrence of these species is summarised in Table 2. A list of research that pertains to bat migration within the British Isles and between the British Isles and Europe is in Appendix 1.

A total of 53 studies were directly related to bat interactions with offshore wind turbines. We assessed the studies by topic, with 21 relating to bat activity around offshore wind turbines, seven relating to the impacts of offshore turbines on bats, two relating to mitigation of impacts and 10 to monitoring of bat activity at offshore turbine locations. In addition, 10 reviews were included that had direct relevance to the interactions of bats with offshore infrastructure. An overview of research that pertains to bat interactions with offshore wind turbines is in Appendix 2.

4. Discussion

4.1. Bat Migration within the UK and between the UK and Europe

Bat migration between summer and winter areas is a widespread phenomenon in temperate climates (Fleming and Eby, 2003; Popa-Lisseanu and Voigt, 2009; Krauel, McCracken, 2013; Ciechanowski et al., 2016; Lehnert et al., 2018), with bats exhibiting three broad spatial patterns of behaviour: regional (typically 100–500 km) or long-distance (> 1000 km) seasonal movements, or partial migration. This is known to occur in a number of European bat species including *Nyctalus* spp. and *Pipistrellus* spp. (Krauel, McCracken, 2013; Rydell et al., 2014).

4.1.1. Bat migration across the English Channel

Whilst the English Channel offers potential for bi-directional migration corridors between the British Isles and continental Europe (Fig. 4), due to the distinct lack of survey effort conducted, there are few documented offshore occurrences of bats in this area. Our literature review did not retrieve any studies specifically documenting bats over open sea in this area.

It is known that migratory species such as *P. nathusii*, *N. noctula* and *N. leisleri* are present across the south coast including the Isle of Wight and Channel Islands (Russ et al., 2001; NBN Atlas, 2024; National Nathusius' Pipistrelle Project, 2024; Bicker, in prep.). However, these are largely restricted to terrestrial records, with direct evidence for bats crossing the English Channel limited to an individual male *P. nathusii* landing on a fishing vessel halfway between Cherbourg and Start Point in Devon in September 1998 (Russ et al., 2001). Furthermore, a ringing recovery reported as part of the National Nathusius' Pipistrelle Project (2024) confirmed a long-distance migration of an individual *P. nathusii* ringed in East Sussex flying to Belgium in September 2018. Whilst the exact route of the bat cannot be determined, it is likely that the bat crossed the eastern English Channel.

Acoustic surveys undertaken along the south coast in the UK have recorded *P. nathusii* activity along the coastline with peaks of activity coinciding with the established autumn migration period. Furthermore, registrations were primarily recorded between 1 and 3 h after sunset suggesting that bats may have flown a substantial distance from their roosts before arriving at the survey location along the coast (Long, 2011; Bicker, 2023). A similar pattern of behaviour has been found along the Northern Baltic Sea where *P. nathusii*

Table 2

Number of retrieved studies/reports identifying the occurrence of European bat species over marine areas in north-west Europe.

Species	Geographic Area				
	Northern North Sea	Southern North Sea	English Channel	Celtic and Irish Sea	Baltic Sea
<i>Nyctalus noctula</i>	1	11			3
<i>N. leisleri</i>	1	4			1
<i>Eptesicus serotinus</i>		2			2
<i>E. nilssonii</i>	1	3			1
<i>Vespertilio murinus</i>	1	7			1
<i>M. dasycneme</i>					1
<i>M. daubentonii</i>		1			1
<i>Pipistrellus pipistrellus</i>		6	1		2
<i>P. nathusii</i>	1	22	1		4
<i>P. pygmaeus</i>		1			3
<i>P. auritus</i>					1



Fig. 4. Potential bi-directional migration corridors across the English Channel between England, the Channel Islands and France and potential corridors between the UK and Ireland including the Isle of Man. Orange arrows indicate possible migration corridors as identified during the literature and evidence review. The evidence for migration across these broad fronts varies geographically and should only be taken as an indication. Detailed discussion of the evidence base surrounding each of these corridors is discussed further within this review. © Mapbox © OpenStreetMap.

aggregate along coastlines during migration windows (Ahlén, 2009; Ijäs et al., 2017). In addition, further acoustic surveys undertaken in spring 2019 provides possible evidence of migration from France and the Channel Islands during April with a strong surge of activity through the Solent at the end of May, coinciding with a similar pattern of migratory activity along the Brittany coast (Bicker, pers. comm.).

Monitoring from April to October in 2012 and 2013 on the Kent coast at the eastern end of the English Channel also revealed peaks

in passes of *P. nathusii* in autumn (September and October) and spring (May). The diurnal timing of detections was indicative of migratory movements from adjacent mainland Europe, and the majority occurred in wind speeds of < 4.2 m/s of a westerly or southerly direction (Jennings et al., 2013a,b).

Further evidence of potential migratory movement of bats comes from a large-scale acoustic survey conducted across the Bailiwick of Guernsey since 2021 which provided the first baseline data for bats on the Channel Islands of Guernsey, Alderney, Herm and Sark. Due to the extensive coverage of ultrasonic detectors deployed between April and the end of October, Newson et al. (2022, 2023, 2024) were able to determine the spatiotemporal occurrence of a number of species and provide evidence that populations of these species were migrating across the English Channel.

Reports from bat care networks in coastal locations have also provided some limited evidence to the offshore movement of bat species. In June 2023 an adult female *P. pipistrellus* was found inside a wind turbine at the Rampion offshore wind farm ~24 km off the Sussex coast, UK (Hurstpierpoint Bat Hospital, 2024, pers. comm.). As *P. pipistrellus* are not considered a migratory species, it is not currently known whether this individual was moving across the English channel or foraging offshore.

4.1.2. Bat Migration across the Celtic and Irish Sea

In concurrence with the English Channel, there is a lack of documented occurrences of bats offshore in the Celtic and Irish Seas and our literature review did not retrieve any studies specifically documenting bats over open sea in this area. However, based on the current distributions of migratory bat species and due to the close proximity between the British Isles and Ireland, it is likely that potential bi-directional migration corridors are present in this area (Fig. 4).

It is known that migratory species such as *P. nathusii*, *N. noctula* and *N. leisleri* occur across the west coast of England and Wales including the Isle of Man and Welsh offshore islands, Skomer, Ramsey and Skokholm (Russ et al., 2001; Taylor et al., 2014; Dyer et al., 2019; Pinder, 2020; NBN Atlas, 2024; National Nathusius' Pipistrelle Project, 2024). Both *P. nathusii* and *N. leisleri* are resident breeding species in Ireland (*N. noctula* are absent from Ireland; Aughney et al., 2022; BC Ireland, 2024) and whilst climatic differences between Great Britain and Ireland are less distinct, movement across the Celtic and Irish seas may still be categorised as regional migration whereby roost temperatures rather than seasonal climatic differences are the main driver for movement (Krauel et al., 2018).

Acoustic surveys undertaken at coastal locations and offshore islands along the Welsh coast have shown limited recordings of *P. nathusii* and *N. leisleri* at survey locations on the western most points of the Welsh coast. Although generally recorded in low numbers, for some survey locations there were small peaks noted in May and September that may give some indication of migratory activities. Detectors placed on ferries sailing between Dublin – Holyhead and Rosslare – Fishguard obtained no records of bats whilst at sea, although a number of registrations of both *P. nathusii* and *N. leisleri* were recorded when ferries were in harbour (Dyer, 2019).

During acoustic surveys on the Pembrokeshire islands by Taylor et al. (2014) a peak of activity was observed during the late summer/autumn for species that are known to be long distance migrants in Europe. While this did not confirm that bats are migrating within GB, or between GB and Ireland, it provided an indication that this may be occurring. Lastly, acoustic results have shown use of Pembrokeshire islands by *Rhinolophus ferrumequinum* and *Barbastella barbastellus*, both of which are not known to regularly cross open sea, although both have been recorded on the Isle of Wight (Altringham, 2003). *R. ferrumequinum* were recorded on all islands studied and recordings from each island suggest that this is regular and predictable behaviour and that bats may be commuting to the islands nightly due to their proximity to the mainland (e.g. Ramsey Island ~1 km; Skomer ~1 km; Skokholm ~4 km).

Studies by both Dyer (2019) and Taylor et al. (2014) concluded that whilst no direct evidence of bat migration across the Celtic and Irish Sea was found, both project methodologies were limited by the reliance on a low number of fixed sampling points along the coastline or offshore islands. Recording locations were based on the logic that bats would make the shortest route possible, however bats may make landfall anywhere on the Welsh coast and may be following other routes such as estuaries to take advantage of riparian corridors inland. Furthermore, without knowing the activity and distribution of resident bats in the local area, attempting any assessment of migratory activity from onshore locations is difficult (Taylor et al., 2014; Dyer et al., 2019).

4.1.2.1. Bat Migration across the Northern North Sea.

Unlike the southern portion of the North Sea, there is a paucity of studies into the activity and behaviour of migratory bats and their pathways in the northern North Sea. Our literature review did not retrieve any studies specifically documenting bats over open sea in this area. Information regarding the status of migratory bats in this area primarily comes from a single study which collates occurrence records at offshore islands and oil platforms in the North Sea with seasonal peaks during the main migratory windows (Russ et al., 2001; Petersen et al., 2014; National Nathusius' Pipistrelle Project, 2024).

Pipistrellus nathusii is the most commonly recorded species from northern North Sea installations and the Shetland Islands (Petersen et al., 2014; Harvey, 2014; National Nathusius' Pipistrelle Project, 2024). Occurrence peaks of individuals recorded at these locations coincide with the main autumn migration period and are consistent with suggestions by Gerell (1987) and Ahlén (1997) that *P. nathusii* migrates in a south-westerly direction from Scandinavia, where it has been found in Norway and Sweden (Syvertsen, 1995; Swenson et al., 2010; Ahlén, 2011) to avoid the harsh winter. The Shetland Islands are one of the windiest locations in the UK (Met Office, 2024). As a result of this extreme climate and lack of tree cover, the Shetland Islands do not support a resident summer population of bats. However, these northerly islands can support overwintering or migratory populations and roosting bats have been found throughout the winter months (Harvey, 2014; National Nathusius' Pipistrelle Project, 2024). As with migratory movements seen further south in the North Sea, the occurrence of migrant bats on the Shetland Islands is associated with strong tailwinds from Scandinavia, which also sees large influxes of migrant bird species arriving on their southward migration (Pennington et al., 2004; Harvey, 2014). The spatiotemporal distribution of these occurrences suggest that *P. nathusii* migrates from Scandinavia to overwinter in the British Isles

where they mix with sedentary resident populations. However, a more concerted surveying effort is required in this area to establish the phenology and activity patterns of bats using this migratory pathway (Russ et al., 2001; Barr, 2020; National Nathusius' Pipistrelle Project, 2024).

Occurrences of other migratory bats have also been reported to a lesser extent from offshore islands and North Sea oil installations and include *Nyctalus leisleri*, *N. noctula* and *Vespertilio murinus* (Petersen et al., 2014; Harvey, 2014). *N. leisleri* is considered to be a long-distance migrant and across Europe displays regular seasonal NE to SW movements between summer and winter habitats (Hutterer et al., 2005; Sheil et al., 2008). Whilst it is unlikely that migration was a factor in most of the records across the northern North Sea due to their occurrence within summer months outside of usual migration windows, a number of records were reported during the spring and autumn migration season (Petersen et al., 2014; Harvey, 2014). Therefore, it cannot be ruled out that the corridor between Scandinavia and the northeast of the British Isles represents a migratory pathway for this species.

Nyctalus noctula has shown both sedentary and migratory behaviour with some individuals covering distances of up to 1600 km during migration, whilst other populations include partial and differential migrants (i.e. those who do not migrate at all or migrate variable distances; Strelkov, 1969, 1997a,b; Hutterer et al., 2005; Dietz et al., 2009; Lehnert et al., 2014). The variability in *N. noctula* migratory behaviour is likely to reflect a strong selection for migratory behaviour in populations at higher latitudes where seasonality in climatic conditions and food availability is most pronounced (Strelkov, 1997a,b; Fleming and Eby, 2003). As such, *N. noctula* is considered to be migratory in northern and eastern Europe but in central and western Europe populations of *N. noctula* do not exhibit the pronounced migration behaviour exhibited by other long-distance migrants such as *N. leisleri* or *P. nathusii* (Strelkov, 1997a,b; Steffens et al., 2004; Hutterer et al., 2005). Despite migratory activity of *N. noctula* being documented in Scandinavia (Ahlén, 1997; Baagøe, 2007; Ahlén et al., 2009) populations are not known to migrate to the British Isles for the winter and records from Orkney, Shetland and North Sea installations are currently regarded as vagrants from Europe and Scandinavia (Mackie et al., 2008).

Lastly, *V. murinus* is also considered to be a long-distance migrant that spends the summer in northern, central and eastern Europe, migrating to southern Europe to overwinter (Hutterer et al., 2005; Fleming 2019). There has been an increase in records of *V. murinus* in the British Isles since 1980, including from Shetland and North Sea installations (Petersen et al., 2014; Harvey, 2014). These records tend to peak in the autumn and spring suggesting that migrants are sometimes deflected from continental Europe (Racey et al., 2008). In southern Sweden a few individuals were recorded in the autumn leaving land and flying out over the sea (Ahlén, 1997). However, the intended destination of these bats is unknown and due to the infrequent records of *V. murinus*, it is currently regarded as a rare vagrant species, with no breeding colonies in the British Isles (Dietz and Kiefer, 2016).

4.1.3. Bat Migration across the southern North Sea

Since the mid-1980s, reports from offshore platforms have indicated the regular movement of bat species across the North Sea (Table 2; Russ et al., 2001; Boshamer and Bekker, 2008). Since this time, the southern North Sea has become a focus of research on bat migration between the UK and Europe and our literature review retrieved the highest number of studies in this area, a total of 34 studies.

Within these studies a total of 9 European bat species were recorded as being present within the marine environment and *P. nathusii* was identified as being the most frequently observed bat species offshore (Table 2). As a result the majority of studies focus on this species and therefore the majority of knowledge surrounding migratory bats in the offshore environment are based on observations of *P. nathusii*.

Pipistrellus nathusii is found from western Europe to Asia Minor (Corbet and Harris, 1991; Strelkov, 1997a,b; Mitchell-Jones et al., 1999) and their main breeding areas are found in central and eastern Europe and into Russia (Vasenkov et al., 2022). *Pipistrellus nathusii* is an example of a partial migrant whereby populations in central Europe are sedentary or migrate over short distances (Sachanowicz et al., 2019), whereas eastern populations are known to perform long-distance seasonal movements with the longest known migration distances in autumn recorded from Latvia to Spain (2224 km; Alcalde et al., 2021) and from Russia to France (2486 km; Vasenkov et al., 2022).

After the breeding season, females and their offspring begin to migrate from their breeding areas in north-eastern Europe to their wintering areas in southern and western Europe (Russ et al., 2001). Along this route, males who may have been holding territories since spring advertise to attract and mate with passing females (Strelkov, 1997a,b; Brosset, 1990; Jahelkova and Horacek, 2011). In late autumn/early winter, after the mating season, individuals from both sexes begin to migrate to lower latitudes further south-west to overwinter in western Europe, while others may hibernate in the same areas (Bastian, 1988; Brosset, 1990; Lina, 1990; Roer, 1995; Petersons, 2004; Sachanowicz et al., 2019). During late spring, migratory populations of *P. nathusii* return to their traditional breeding areas in north-eastern Europe and Russia often across large bodies of water (Hutterer et al., 2005; Alcalde et al., 2021; Petersons et al., 2014).

Pipistrellus nathusii was first recorded in the British Isles in 1940 (Herman, 1992) however, due to the infrequency of historic records, it was initially regarded as a vagrant species (Stebbing, 1988). The species was later afforded 'migrant winter visitor' status due to the presence of hibernating continental populations (Speakman et al., 1991; Hutson, 1997). The status of *P. nathusii* in the British Isles was further updated in the late 1990s after several maternity colonies were documented, indicating that at least part of the UK *P. nathusii* population is resident and breeds successfully (Russ et al., 2001).

In 2014, the National Nathusius' Pipistrelle Project (NNPP) was established by the Bat Conservation Trust with the aims of determining the resident and breeding status of *P. nathusii* in Britain. Surveys conducted as part of the NNPP found that capture rates of *P. nathusii* were highest in early April and late October, corresponding to periods during which migratory individuals are anticipated to be present in Great Britain, having arrived in late summer and early autumn, and departed again in the spring. The seasonal differences in capture rates suggest that the majority of the population of *P. nathusii* in Great Britain is migratory, with a smaller population

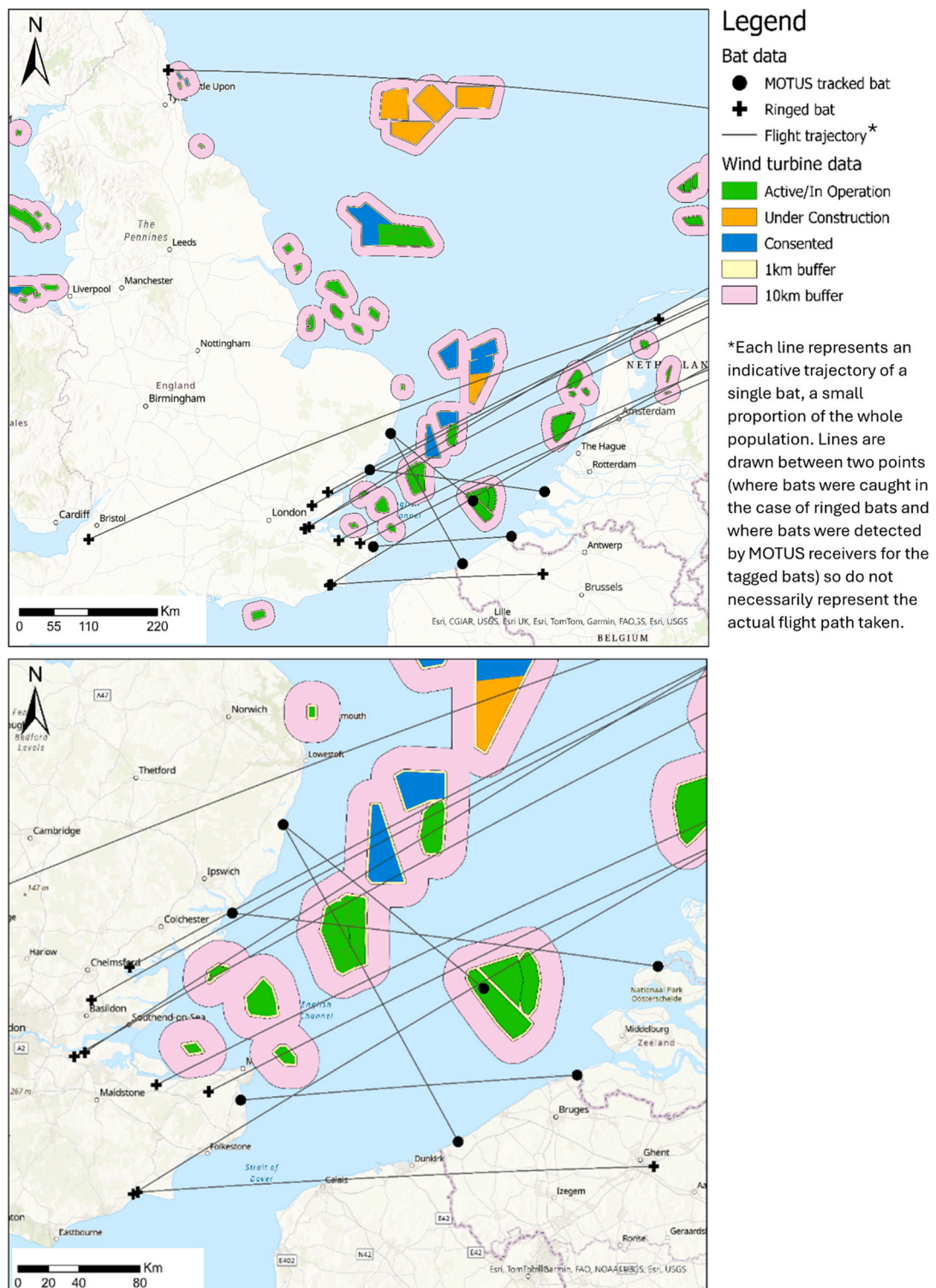


Fig. 5. Straight line ‘flight’ trajectories of single *P. nathusii* bat crossings between England and Europe (based on onshore point data from recapture of ringed bats or MOTUS detections of tagged bats) overlaid on map of operational and projected future wind farms. Buffers around wind farms represent a zone of influence for bat species travelling through these areas based on sensory cues of wind energy facilities and the distances they are likely to be perceived by bats.

remaining during the summer breeding season (Boughey et al., In prep).

These seasonal differences in capture rate contrast with those observed for other *Pipistrellus* spp. surveyed. Both *P. pygmaeus* and *P. pipistrellus* have large breeding populations in Great Britain and had highest capture rates in the summer months, corresponding with the period during which females in particular are most active as they raise their young.

Bat migration across the open sea is now an established phenomenon and the occurrence of bats have been documented either through occurrence records on offshore platforms or from acoustic records from bat detectors placed offshore (e.g. Lagerveld et al., 2017; 2023). However, in recent decades the use of radio telemetry technology combined with a concerted effort to ring migratory bats has allowed for more detailed research into the phenology and behaviour of bat migration over open sea. Ringing recoveries reported as part of the NNPP have confirmed long distance migrations of individuals following an east-northeast (ENE) west-southwest (WSW) route to and from the breeding areas in north-eastern Europe (National Nathusius' Pipistrelle Project, 2024). Similar migratory pathways across the southern North Sea have also been demonstrated using the MOTUS wildlife tracking system which utilises radio telemetry to track animal movement (Taylor et al., 2017).

Using this system, Harris and Parsons (2020), Briggs et al. (2023) and Lagerveld et al. (2024) have been able to construct probable flight corridors of *P. nathusii* as they cross the southern North Sea and eastern extent of the English Channel, as well as the pre-migratory activity of bats up and down the coastline (see Fig. 5). Data of direct crossings can be combined with both biometric data from tagged bats and weather variables to gain a better understanding of the timings and demography of migration in this area. It should be noted that the data gathered from this method must be assessed in relation to the extent of the receiver network along the coastline. After registration at a MOTUS receiver, bats may continue to move further up or down the coast before crossing, but these movements would not be detected. Furthermore, as there are no current MOTUS receivers stationed offshore, we do not know the behaviour or the exact flight paths of bats once they are over sea.

4.1.4. Seasonal patterns of migration

Acoustic monitoring across offshore wind farms in the southern North Sea indicates that the spatiotemporal occurrence of *P. nathusii* aligns with the main autumn migration window from mid-August to late October. During this period, bat activity peaks from early to late September followed by a subsequent decrease in activity to the middle and end of October (Rydell et al., 2014; Brabant et al., 2019, 2021; Lagerveld et al., 2021, 2023). This peak coincides with departure from breeding areas and is likely to consist of predominantly females and juveniles (Strelkov, 1997a,b; Hüppop and Hill, 2016). A second smaller peak may also occur at the end of October and is likely to reflect sex and/or age-specific differences in migratory movements as males are likely to remain longer on the migration pathway to attract and mate with passing females before moving to hibernation areas (Jahelkova and Horacek, 2011; Lagerveld et al., 2021). Records from bat detectors deployed on ferries transiting the southern North Sea (Felixstowe – Netherlands and Hull - Belgium) equipped have also recorded *P. nathusii* in May, September and October and *Nyctalus* spp. in September up to 66 miles offshore (Hobbs et al., 2014).

In addition to the autumn migration window, studies have also identified a distinct spring migration window. Whilst observed bat activity in spring is not as high as during autumn, it does represent a substantial increase in activity compared to the summer months and correlates with increased capture rates of *P. nathusii* in April across Great Britain (Hüppop and Hill, 2016; Lagerveld et al., 2017a; Seebens-Hoyer et al., 2021; National Nathusius' Pipistrelle Project, 2024). During this period, bat activity peaks from mid-April to mid-May, although this is variable across geographic locations, e.g. in Finland the timing of the migration is 20 days later than in Northern Germany (Rydell et al., 2014). Recent research tracking individual bats across the southern-north sea has found that sex-biased timing of migration also occurs during spring migration with males migrating 25 days later than females (Lagerveld et al., 2024). It is likely that females gain a fitness advantage by arriving early to breeding areas, as early-born pups are more likely to survive their first winter as well being more likely to reproduce in their first year (Frick et al., 2010; Barclay 2012).

The lower intensity of spring migration is also a widespread but poorly documented onshore phenomenon that has been reported in Ireland (Russ et al., 2003), the Dutch coastal provinces (Lagerveld et al., 2017a) as well as further into continental Europe (Perks and Goodenough, 2020). Several hypotheses have been proposed for lower recorded bat activity in spring and include reduced availability of insect prey and faster migratory movements at higher altitudes (Lagerveld et al., 2024). If migratory bat behaviour resembles that of migrant birds, spring migration may be more rapid, occurring at higher altitudes particularly with wind assistance of the prevailing south-westerly tail winds (Lack, 1963, Eastwood, 1967). Therefore, they may use fewer stopovers and fly above the detection range of acoustic detectors leading to an under-recording of their activity. Additionally, a study on insect and bird migration utilising radar technology by Shi et al. (2021) found that insect movements were significantly lower in spring, being non-existent in some areas but had a strong peak in summer and early autumn. This absence of insects offshore in spring might be an additional driver for migrating bats to minimize their time spent foraging above the North Sea, thereby reducing the chance of them being detected.

Limpens et al. (2017) describe a modelling and expert-led approach to estimating migratory populations in the southern North Sea, with their model producing a estimate for bats crossing the Southern North Sea of roughly 40,000 individuals (range 100–1000,000 individuals). The approach in this study aimed to model the migration flux based on either quantitative or estimated parameters defining the population dynamics for the different regions in the relevant geographical population/migration area for the species. Regional bat specialists provided iterative feedback on the structure of the flow model and as a source of information, to help estimate and/or give their expert judgement regarding chosen values.

4.1.5. Environmental patterns of migration

In addition to seasonal considerations, several environmental factors have been found to influence the offshore occurrence of *P. nathusii*. Peaks in migratory activity over sea occur when there are tailwinds, wind speeds < 5 m/s and air temperatures > 15°C in

addition to relatively high atmospheric pressure (Brabant et al., 2019, 2021; Lagerveld et al., 2021, 2023, 2024). Low to moderate wind speeds and wind direction are one of the strongest predictors of bat activity and favourable tailwinds are of particular importance for both spring and autumn migration (Ahlén et al., 2009; Pettit and O'Keefe, 2017; Brabant et al., 2021; Lagerveld et al., 2023, 2024). However, bats will also migrate across open sea with low to moderate headwind or crosswind. Offshore crosswinds are a significant factor driving bat activity in some areas of the southern North Sea, (Hüppop and Hill, 2016). However, it should be noted that whilst certain environmental factors are often shown to be strong predictors of bat activity, the influence of these factors can be variable, with bats showing plasticity in their migratory behaviour in response to environmental conditions. For example, whilst higher temperatures are usually a strong predictor of bat activity, during autumn in the UK, warmer weather is often caused by low pressure fronts with higher wind speeds and stormier conditions offsetting any potential advantage of higher temperatures. Therefore, higher bat activity can often be recorded on colder nights that arise from high pressure systems with lower wind speeds (Met Office, 2024; Bicker, pers. comm.).

4.1.6. Altitudes of migration

During migration over sea, bats have been observed to primarily fly at low altitudes with most activity found in the proximity of offshore wind turbines concentrated around the service platform at the base of the structure (Ahlén et al., 2009; Brabant et al., 2019). However, this can quickly change when they encounter offshore structures, ships, or in response to the distribution of insect prey at different altitudes. Foraging behaviour is often observed during migratory movements, with bats making use of available prey to fuel their onward movements (Ahlén et al., 2009). The majority of bats detected by Ahlén et al. (2009) flew at relatively low altitudes (<10 m) however there were a few observations of bats flying > 40 m and some bats investigating offshore structures up to 100 m above sea level. It has been suggested that low flight altitudes may be restricted to coastal waters, whilst migration further offshore may include a significant high-altitude component, where bats can take advantage of increased wind speeds at height, as is shown for migratory birds and insects (Alerstam, 1993; Chapman et al., 2004; Hüppop and Hill, 2016). Recent research by Lagerveld et al. (2024) has determined that the altitudinal range in which migratory flights can be performed in a particular direction is likely dependant on a combination of wind conditions and airspeed. During this study they calculated that at least two migratory flights over the Southern North sea were undertaken at minimum altitudes of about 400 and 800 m with bats expected to choose altitudes that make use of optimal wind support. Furthermore, findings from this study indicate that undesirable crosswind or headwind at higher altitudes will result in unfeasible combinations of windspeed and airspeed, potentially causing bats to migrate over sea at lower altitudes (Lagerveld et al., 2024).

Research by Seebens-Hoyer et al. (2021) found that activity recorded at varying heights on an offshore platform pole decreased with height with about 20 % of the bat activity recorded at 33 m, 10 % at 66 m and 2 % at 100 m. This behaviour has been documented during aerial surveys off the eastern coast of the United States, where eastern red bats were photographed offshore during tailwind conditions (9–10 m/s) at altitudes of more than 100 m above sea level (Hatch et al., 2013).

Nyctalus noctula, a species known to migrate at higher altitude over land (Kronwitter, 1988; O'Mara et al., 2019), has also been recorded to fly at low altitudes (<10 m) over sea, although radar observations also detected them at > 40 m, changing their altitude quickly near turbines (Ahlén et al., 2009). This behaviour by *N. noctula* is consistent with GPS tracking studies, for example O'Mara et al., (2019) found that individuals used a wide range of airspace including altitudes that put them at increased risk from human-made structures.

4.2. Bat interactions with offshore wind turbines

There are currently no reported records of bat casualties at offshore wind farms, as well as a paucity of studies specifically reporting how bats interact with wind turbines in the offshore environment. The studies retrieved as part of the systematic literature review primarily focused on identifying or monitoring the activity of bats around offshore wind turbines, a total of 31 studies, with other retrieved studies trying to assess the potential offshore wind impact based on these bat activity levels (7 studies). These studies were largely based on acoustic monitoring at offshore wind turbines with some incidental records of bat occurrences on these structures also noted. Our literature search also retrieved two studies focused on trying to establish mitigation strategies with potential in the offshore environment as well as 10 review papers that mention offshore wind in their assessment of impacts to wildlife. This gap in the literature is in part due to more problematic logistical considerations when surveying offshore, coupled with a lack of suitable or affordable technology that can be widely deployed as in the onshore wind energy environment. However, it is widely assumed that bat behaviour around offshore wind turbines is likely to be similar to around onshore wind turbines and therefore offshore wind induced mortality is likely to occur at sea (Ahlén et al., 2009). That being said, it is acknowledged that there are many factors that may influence bat behaviour and activity which would be distinct to an offshore setting and these are discussed where applicable.

4.2.1. Are bats attracted to wind farms?

Our review found no studies specifically reporting how or why bats may be killed at offshore wind turbines and therefore our knowledge of this likely scenario has been translated from the onshore environments. Several hypotheses have been proposed to explain why individual bats are killed by onshore wind turbines, including accidental encounters (particularly by juveniles or along migration pathways), the use of the tall structures as a display site during the breeding season (Kunz et al., 2007; Cryan and Barclay, 2009) or roosting opportunities mid-migration (Brabant et al., 2020) and the accumulation of insects creating increased foraging opportunities near wind turbines. The latter of these is often assumed to be one of the most important factors determining fatality risk for individual bats (Rydell et al., 2010, 2016; Long, 2011; Foo et al., 2017; Voigt, 2021).

Thermal video observations of flight behaviour around onshore wind turbines indicate that some bats may not be randomly colliding with wind turbines but instead are actively and repeatedly approaching wind turbine components (e.g., tower, nacelle, and blades) around the rotor-swept area, even after being buffeted away by the increased turbulence (Cryan et al., 2014; Horn et al., 2008). Furthermore, recent studies have indicated that bats could be attracted to wind energy infrastructure with echolocation activity increasing for some species after wind turbines are constructed (Solick et al., 2020; Richardson et al., 2021). This is further compounded by a lack of predictive relationships between pre-construction bat activity and bat mortality during the operational phase, providing additional evidence that bats are actively attracted to these areas post-construction (Lintott et al., 2016; Solick et al., 2020).

However, after more than a decade of research and considerable advances in our understanding of bat mortality at wind turbines, we still do not have a definitive mechanism of attraction explaining why rates of bat fatalities at wind turbines can be so high. Recent reviews by Jonasson et al. (2024) and Guest et al. (2022) have attempted to summarise our current knowledge on the mechanisms of attraction from studies conducted onshore, taking into account bats' sensory perception, with both concluding that cause(s) and scale(s) remain largely unknown but are likely to be species-specific and not mutually exclusive. Furthermore, these conclusions are likely to be compounded when attempting to evaluate the response of bats in an offshore setting due to the significant differences in scale and attributes of the environment.

4.2.1.1. Sensory stimuli. As bats commute, forage and migrate, they integrate different sensory stimuli that shift in seamless coordination with the current task (Danilovich and Yovel, 2019). As a result, different sensory pollutants (e.g. light, noise, etc.) can contribute to misguidance, obscuring, and diverting of bats as they traverse wind farms, with the mechanisms underlying sensory pollution varying based on proximity and the bats' perceptual faculties. Notably, the sensory inputs that bats prioritise may differ when detecting distant wind farms compared to their immediate interaction with turbine blades (Jonasson et al., 2024).

As bats move across a landscape or seascape their first perception of a wind farm is most likely facilitated by senses such as vision or somatosensation of the turbine wake, i.e. senses associated with navigation during migration or other long-distance movements including mechanoreception (vibration, touch and pressure discrimination) and thermoception i.e. sensations and perceptions of temperature (Romo et al., 2002). Despite common misconceptions, bat vision is often utilised for detecting objects beyond the range of echolocation (Suthers and Wallis, 1970; Boonman et al., 2013) and is well suited for detecting distant objects in dim light (Shen et al., 2010), with homing experiments suggesting that some bats may use visual, topographical cues to orient themselves (e.g. Williams et al., 1966). This orienteering potential may be particularly important when travelling across marine areas as offshore structures such as turbines may represent the only topographical cue in an environment largely devoid of natural features in which bats can navigate by.

One prominent hypothesis of bat attraction to wind turbines is that the tall stand-alone silhouettes of wind turbines could be mistaken for trees and viewed as potential roost structures that may also serve as potential mating sites (Cryan, 2008; Cryan and Barclay, 2009; Jameson and Willis, 2014). The visual detection range of turbine structures at night is species-specific but will generally be within a few kilometres, however the maximum detection distance will be greater for bats with greater visual acuity, under highly contrasted conditions and as object size increases (Boonman et al., 2013; Eklöf et al., 2014).

A bat's ability to visually detect wind turbines at night will depend on both tower size and placement but also ambient illuminance provided by the moon phase and any further artificial illumination of the turbine such as obstruction lighting i.e. mounted blinking lights to provide aviators with clear visual cues during poor visibility (Jonasson et al., 2024). Bat species killed most frequently by onshore wind turbines in temperate areas generally roost in trees, with tree height being an important characteristic for roost selection (Crampton and Barclay, 1998; Kalcounis-Rüppell et al., 2005). Night vision surveys at onshore wind energy facilities have shown bats to use turbines as roosts where they have been observed entering or exiting wind turbine structures at night. Searches at turbine towers, transformers and around turbine doorways have documented the presence of guano from several bat species (Bennett et al., 2017; McAlexander, 2013).

A similar pattern of behaviour has also been found during multiple studies during autumn migration at offshore locations where diurnal stopovers have been recorded along flight routes on structures such as wind turbines, ships, and other offshore structures where bats have been recorded to roost for several days, regularly foraging over the surrounding waters and even flying around turbines emitting territorial or mating calls (Ahlén et al., 2009; Lagerveld et al., 2021). The occurrence of bats at offshore wind turbines have been reported through direct observation of roosting bats by maintenance workers on the outside of turbine foundations and nacelles as well within the utility cranes on the turbine service platforms (Boshamer and Bekker, 2008; Ahlén et al., 2009; Brabant et al., 2020; Lagerveld et al., 2021). Using thermal imaging at onshore wind energy sites, bats have been observed investigating both stationary and moving turbine blades and towers which suggests that they are attracted to these stand-alone structures for potential roosting or foraging opportunities (Arnett et al., 2005; Horn et al., 2008) but this is likely to be highly species-specific (Guest et al., 2022).

As the maximum flight speed of migrating *P. nathusii* is currently recorded to be 40–47 km/h (Suba 2014) and the proximity of offshore monitoring locations where bats have been found are < 30 km from shore, it is assumed that bats departed from land the same night and are using offshore infrastructure as a stopover option. It is suggested that a deterioration in weather conditions offshore or the arrival of daybreak may force bats to interrupt their flight and find a suitable structure at sea to roost, until weather conditions are suited to continue their journey, the next night or later (Lagerveld et al., 2021).

Studies analysing the temporal distribution of *P. nathusii* calls have recorded bats around offshore wind turbines close to dusk when they are known to leave their roost, as well as close to and even after sunrise, suggesting that these animals are spending the day at the monitoring location at sea, or in its vicinity (Dietz et al., 2007; Lagerveld et al., 2014a,b, 2017a,b). However, it is possible that some individuals may continue their migration during the daytime (Lagerveld et al., 2014a,b, 2017a,b).

4.2.1.2. Feeding stations. Bats have also been suggested to perceive turbine sites as potential food sources. Possible explanations for the accumulation of insects at wind turbines includes hill topping behaviour (i.e. congregation of insects at the highest point in the immediate landscape to optimise mating success; Grof-Tisza et al., 2017), insect attraction to the light or heat emitted from wind turbines, and attraction to wind turbine colour (Ahlén et al., 2003; Long, 2011; Jansson et al., 2020; Guest et al., 2022).

Studies suggest that bats adapt their behaviour in the vicinity of offshore structures, often interrupting their migratory flight and changing their altitude for foraging bouts in response to insect prey that may congregate around offshore wind turbines. Evidence of this fly-and-forage strategy is especially common in areas with a high abundance of insects in the air or crustaceans gaffed from the surface of the water (Ahlén et al., 2007, 2009; Suba et al., 2012).

Due to their scale and extent, wind farms interact with the atmospheric boundary layer, affecting local meteorology and can subsequently increase nightly temperatures for up to 10 km in their wake (Miller and Keith, 2018; Porté-Agel et al., 2020). Whilst the relative importance of these microclimatic patterns in attracting bats is unknown, bats may use temperature as a cue when searching for foraging patches because nocturnal insect activity increases with temperature (Ahlén et al., 2003). Studies have shown that bat activity increases with ambient temperature and prey density (Müller et al., 2012) and ambient nightly temperature is positively correlated with bat mortality at wind farms (Baerwald & Barclay, 2011; Amorim et al., 2012; Grodsky et al., 2012). Studies conducted offshore by Lagerveld et al. (2021), (2023) and Brabant et al. (2021) showed that the majority of bat observations around offshore turbines in the southern North Sea were recorded on nights when average night temperatures were greater than 13–15 °C which in part could be explained by the same increase in insect availability and activity triggered by higher temperatures seen onshore. When higher temperatures coincide with easterly winds, insects may drift offshore, but in addition insects are known to migrate in large numbers over sea, often at heights of several hundred meters above sea level (Chapman et al., 2004; Drake and Reynolds, 2012). This increased insect availability at higher temperatures enables bats to fly-and-forage during offshore migratory flights (Suba et al., 2012). However, increased collision risk may also correlate with an overall increase in bat migration activity during weather fronts that increase ambient temperature (Pettit and O’Keefe, 2017; Jonasson and Guglielmo, 2019).

It is worth noting that, whilst most research is focused on foraging around offshore wind turbines by migratory bats, there is evidence to suggest that resident bat species regularly forage offshore especially for wind energy developments situated closer to the coast. Studies by Ahlén et al. (2007), (2009) in the Baltic Sea have shown that at least 10 species, both migratory and resident, regularly forage offshore and even *Myotis daubentonii* and *Myotis dasycneme* forage up to 10 km from the coast. *Pipistrellus pipistrellus*, a resident non-migratory species, has been recorded offshore throughout the summer season, including at offshore wind turbines on the Sussex coast (Hurstpierpoint Bat Hospital, 2024, pers. comm; Dietz et al., 2007; Ahlén et al., 2007; Lagerveld et al., 2017a,b; Brabant et al., 2016; Seebens-Hoyer et al., 2021).

Whilst it is unclear the extent to which sedentary species utilise offshore areas for foraging or the seasonal or climatic conditions required, it is clear that resident bat species take advantage of invertebrate prey found offshore. In some areas at sea, prey availability is extremely high and is easily accessible because of complete lack of clutter (Ahlén et al., 2009) and therefore non-migratory species should also be considered when mitigating impacts of wind turbines at sea, particularly for wind farms situated within inshore water closer to the coast.

4.2.1.3. Lighting as an attractant. Other theories relating to increased bat activity at wind turbines include bat attraction to lights on turbines or associated infrastructure. Obstruction lights are a requirement at most wind energy facilities and involve either flashing red or white lights mounted at the top of a turbine monopole in order provide aviators with clear visual cues during poor visibility. These lights are likely the most distant stimuli that bats encounter when flying in the vicinity of wind farms and bats may orient towards certain wavelengths during migration or be attracted by insect concentrations near illuminated areas (Voigt et al., 2017, 2018). The influence of artificial light on bats is species-specific and often based on the species’ morphology, with various wavelengths known to exhibit species-specific effects on bats that is dependent on locality and season (Rowse et al., 2016; Voigt et al., 2021).

Bat attraction to obstruction lighting on turbines has predominately been studied in North America in an onshore setting with no clear effects on bat mortality (Johnson et al., 2003, 2004; Arnett et al., 2008; Bennett and Hale, 2014). Studies by Voigt et al. (2017), (2018) have shown that some migrating bat species seem to exhibit movement towards specific wavelengths of light, such as red and green, but not warm, white light. However, like with most studies on the effects of lighting on bats, this attraction to obstruction lighting appears to be both phylogenetically and geographically complex, and conclusions are hindered by studies with little spatiotemporal control for mortality or consideration of how bats view the landscape. In a review of bat attraction hypotheses by Guest et al. (2022) the authors analysed the research conducted at wind farms and concluded that artificial lights do not appear to be the primary cause of bat attraction to wind turbines. However, it is recognised that currently no studies have tested the effect of lighting at the scale of attraction to entire wind farms rather than single turbines. While bat fatalities do not increase at individual turbines with obstruction lights onshore, these lights could attract bats towards areas with wind farms, which aligns with evidence of bat visual acuity and navigation at the scale of kilometres (Jonasson et al., 2024). Furthermore, it is possible that the effect of lighting is exacerbated in environments absent of other navigational cues such as the offshore marine environment.

4.2.2. Are bats displaced from wind farms?

Whilst the potential causes of wind-turbine induced fatalities on bats have been widely investigated on land and to a lesser extent offshore, the impacts on bats through avoidance or displacement, rarely appear in the scientific literature. Consequently, this review did not find any studies covering the avoidance or displacement of bats in the offshore environment and therefore any knowledge of this potential scenario has been translated from the onshore environments

Most of the research in this area has been conducted in Western Europe at onshore wind energy facilities and have generally found lower bat activity the closer you get to wind turbines at the landscape scale, indicating that turbines are directly avoided, or habitats surrounding turbines appear less attractive. This avoidance effect has also been recorded in Pacific Island habitats (see Millon et al., 2018) and indicates that suitable habitat around the turbine is effectively lost to bats (Reusch et al., 2022).

These findings are in contrast to the attraction towards turbines recorded at a finer scale and the reasons for avoidance are currently unknown, although a number of possible causes have been proposed, including turbine lighting and noise emission (Barré et al., 2018; Leroux et al., 2022). Furthermore, studies indicate that all species, regardless of their sensitivity to wind power related mortality, may be displaced from areas of wind farm development (Barré et al., 2018).

Studies researching GPS tagged bats across agricultural and coastal regions of Germany support the hypothesis that bat responses to wind turbines may be scale-dependent where bats are found to be active around turbines at a small spatial scale but avoid them at a broad spatial scale (Reusch et al., 2022, 2023). This larger scale behavioural response has also been recorded in acoustic studies at onshore wind farms across France where a significant negative effect of wind farm proximity was found for most bat species groups (Millon et al., 2015; Barré et al., 2018). Barré et al. (2018) reported a significant drop in activity in a 1000 m radius around wind turbines for both fast flying species (19.6 % reduction; *Barbastella*, *Eptesicus*, *Nyctalus* and *Pipistrellus* genera) and gleaning species (53.8 % reduction; *Myotis nattereri*, *Plecotus* and *Rhinolophus* genera). Similar landscape scale avoidance has been reported in studies at small onshore wind turbines (SWTs) by Minderman et al. (2012, 2017) who found bat activity increased with greater distances from the SWTs.

Depending on the location and layout of the wind farm, avoidance or displacement could have ecological consequences for bats (Rybicki and Hanski, 2013) that may lead to the fragmentation of the habitat through functional barriers that cannot be passed, or areas that are very complex or energetically costly to navigate. For onshore wind farms, the avoidance effect may be considered to form a “no-fly zone” of several square kilometres around each turbine, which bats may avoid depending on context and species (Gaultier et al., 2023).

However, it is currently not known to what degree any avoidance/displacement impacts translate to offshore wind farms as much of the research on land has focused on particular habitat features that are not present in the offshore environment. Studies into the barrier effect offshore in seabirds have shown strong avoidance behaviour/displacement for a range of species that appears to be strongest when the turbine blades are rotating (Dierschke et al., 2016). A recent study by Garthe et al. (2023) found that the distribution and abundance of seabirds from the family Gaviidae (loons) in the North Sea changed substantially when comparing activity before and after offshore wind farm construction. Densities of loons were significantly reduced at distances of up to 9–12 km from the wind farms corresponding to a decline of 94 % within 1 km and 52 % within 10 km of the offshore wind farm. Although, like bats, different seabird species respond differently and sometimes inconsistently to the development of offshore wind farms. A recent review of 20 offshore wind farms in European waters found that behavioural responses by different bird species ranged from strong avoidance to strong attraction (Dierschke et al., 2016).

4.2.3. The influence of offshore wind farms on bat movements

It is not currently known to what extent bats are attracted or displaced from wind farm locations in the offshore environment. Our review found no studies specifically explaining the potential mechanisms of avoidance/displacement offshore and therefore our knowledge of this likely scenario has been translated from the onshore environment. Evidence from studies conducted onshore indicate that the behaviour of bats at wind farms may be different based on scale, with avoidance/displacement at the landscape scale and attraction at finer scales. However, it is not known whether this translates to an offshore setting due to substantial differences in the scale of wind farm arrays and turbine size as well as the nature of the environment and behaviour of bats offshore. As such, accurate collision risk maps are not currently achievable for bats in the offshore environment and instead inferences can only be drawn based on ‘zone of influence’ buffers surrounding offshore wind farms (Fig. 5). These ‘zones of influence’ are based on sensory cues and potential pollutants at wind energy facilities and the distances they are likely perceived by bats (as reviewed in Jonasson et al., 2024).

4.2.4. Impacts on Bat Populations

It is acknowledged that current population risk assessments for UK bats are restricted by a lack of evidence in our understanding of demography, abundance and behaviour (Natural England, 2014). Whilst population trends for UK bat species have been studied through a variety of national monitoring projects (e.g. National Bat Monitoring programme; Bat Conservation Trust, 2023) overall population estimates are uncertain for many species (Mathews et al., 2018), therefore evaluation of the impacts of turbine collision rates on population viability also remains uncertain. It has been suggested that even calculating population impacts for *P. pipistrellus*, one of the most common and widely studied bats in Europe and one of the primary species killed by onshore wind turbines in northern Europe, is restricted by the lack of appropriate demographic data (Lentini et al., 2015).

A likely negative consequence of wind turbine-related collision/mortality is the cumulative impact on bat populations across Europe, particularly for migratory species, which are thought to normally experience low mortality rates during their seasonal migrations (Giavi et al., 2014). Bats are heavily dependent on adult survival owing to their long spans and long maturation period coupled with a low fertility (1–2 offspring per year) (Medinas et al., 2013). These populations are particularly susceptible to increased adult mortality rates due to slow recruitment of juveniles in populations (Jones et al., 2003) and therefore, even minor increases in mortality risks might have large-scale effects on bat populations. This negative impact of increased adult mortality rates has been demonstrated by Erickson et al. (2015) who used models to study the effects of different rates of mortality on two theoretical but representative bat species a long-lived, low fecundity cave bat and a short-lived, moderate fecundity tree bat. They showed that long lived species may seem to have stable populations until a threshold mortality rate is passed, after which even small increases raise the

risk of (local) extinction. In addition to potential large-scale impacts of turbine-induced mortality on bat populations, there is likely to be intraspecific variation in mortality that reflect gender and/or age-related differences in migratory movements. Studies at wind farms across Germany reported a higher percentage of females and juveniles from distant places were killed at wind turbines, suggesting a potential large negative effect of the so-called German “Energiewende”, (i.e. Germany’s policy of increasing the share of renewables and phasing out nuclear power), which could aggravate the negative effects on bat populations in Northeastern Europe (Voigt et al., 2015; Lehnert et al., 2014; Kruszynski et al., 2022).

Reported cases of bat fatalities at onshore wind turbines across Europe show significant variation in both species’ composition and quantity of individuals (Table 1; Rydell et al., 2010). This variation will likely reflect regional variation in species richness and habitat composition across latitudinal/longitudinal gradients as well as differences in applied search protocols (e.g. survey duration). Furthermore, studies have not always considered carcass removal by scavengers and searcher efficiency in the estimation of annual bat fatalities (Arnett et al., 2008; Voigt et al., 2015). Using standardized protocols to control for these biases (Rodrigues et al., 2014), Voigt et al. (2015) estimated that over 250,000 bats are likely killed annually across Germany by onshore wind turbines, whilst 600,000 have been reported in the USA in a single year (Brinkmann et al., 2011; Hayes, 2013). As carcass detection rates in the UK (0–0.18 observed bats per turbine per day; Mathews et al., 2016) are consistent with the range reported across Europe (0–0.11 bats per turbine per day; Rydell et al., 2010), and assuming that bats in the UK experience the same mortality risk as those in Germany, it is estimated that more than 80,000 bats may be killed at onshore wind turbines annually in the UK if mitigation measures (e.g. curtailment or the slowing/stopping of rotor blades below a designated speed) are not applied.

Unlike wind farms on land, the number of bat fatalities at offshore wind farms is very difficult to directly assess through carcass searches. Such searches on offshore wind turbines are only possible at the service platform and whilst theoretically these can be used when detection biases are accounted for, the searched area will be tiny in relation to the area where carcasses potentially may land. In addition, the increased attrition rates of carcasses compared to onshore turbines (e.g. falling into the sea through grates or through wind or wave action) means that carcass monitoring will be logistically and financially impractical as search intervals are typically 2–3 days where practiced onshore, and several wind turbines of multiple offshore wind farms would have to be monitored simultaneously in order to obtain a robust data set.

It has been suggested that the number of bat collisions with offshore turbines is likely to be lower than onshore as the majority of activity is limited to the migration period and in periods of suitable weather conditions. In addition, non-migratory bats, such as *P. pipistrellus*, which makes up the majority of fatalities onshore (Table 1.), are very rare in the offshore environment (Leopold et al., 2014; Lagerveld et al., 2017a; Seebens-Hoyer et al., 2021). Based on the knowledge that fatalities at wind farms in large, open, intensively used agricultural areas are typically around one fatality per turbine per year, Leopold et al. (2014) estimated the number of collisions offshore, based on expert opinion, to be somewhere between zero and one fatality per turbine per year (Rydell et al., 2010; Limpens et al., 2013). However, this was a ‘best guess’ based on the available knowledge at the time, which was very limited in terms of behaviour and knowledge of activity around offshore wind turbines. The real number may be a lot higher as these estimates do not account for other potential attractant factors such as lighting, or bats using offshore wind turbines to roost in inclement weather. Understanding how bats behave as they cross open sea is crucial in being able to extrapolate any fatality estimates from onshore landscapes to offshore settings.

Despite the potential impact on bat populations across Europe, there are a lack of studies quantifying a direct link between wind turbine-related collision/mortality and population level impacts either onshore or offshore. A primary driver of this paucity in research arises from limited baseline data, e.g. of population sizes, recruitment and dispersal rates in the absence and presence of wind turbines (EUROBATS, 2023). This is particularly difficult when trying to relate individual bats killed at wind turbines (particularly those that migrate), to the likely location of their ‘local’ populations. Studies based on stable hydrogen isotopes in fur by Voigt et al. (2012) and Lehnert et al. (2014) have shown that wind turbines kill bats not only from sedentary local populations but also distant migratory populations. This is of particular importance for migratory species such as *P. nathusii*, whose home range may extend from the UK to the Baltic States or from Russia to Greece, and they are likely to be subject to the cumulative impact of all wind farms in those home ranges. In addition to these geographical considerations, when longitudinal demographic studies have been able to establish population estimates and parameters, it is difficult to disentangle the impacts of wind energy infrastructure from confounding factors, such as changes in the management of local habitats, losses of daytime roosts, annual climatic fluctuations and global climate change impacts. The urgent need for evidence synthesis linking empirical datasets to population scale impacts has been highlighted in several reviews (e.g. Tabassum-Abbasi et al., 2014; Köppel et al., 2014; Schuster et al., 2015; Smales, 2015; Voigt et al., 2015; Dai et al., 2015; Arnett et al., 2016).

Current knowledge on potential population level impacts of both onshore and offshore wind energy infrastructure is lacking. This review found no recent studies specifically demonstrating an effect of offshore wind turbines on bat populations in Europe. One long-term study in Germany raised concerns that dramatic declines in *P. nathusii* and *N. noctula* observed in a region where the species only occur during migration could be attributable to onshore wind energy expansion in the area (Bernd, 2021).

Determining the threat of wind energy development on migratory bats highlights the common problem of how to assess threats when critical data is lacking. A number of modelling approaches have been adopted to investigate population-level impacts at onshore wind farms. Studies by Roscioni et al. (2013), (2014) in Italy and Santos et al. (2013) in Portugal combined species distribution models for bats with the spatial distribution of wind turbines at sites that were undergoing wind farm development. These studies modelled the likely occurrence of wind farm developments in bat flight corridors by overlaying existing and planned turbine to determine areas of probable mortality. A similar modelling approach has also been used by Hedenström and Rydell (2013) who showed that deployment of onshore wind turbines in Sweden will have a negative effect on Swedish populations of *N. noctula* if no mitigation measures are adopted.

Research by Diffendorfer et al. (2015), (2019) has attempted to assess population-level effects of wind energy facilities in the USA, including a probabilistic, quantitative assessment method based on fatalities, species demography/range and turbine data, as well as a broader methodology using ecological knowledge, demographic models and the potential biological removal concept i.e. an estimated mortality rate before a population becomes unsustainable. The authors conclude that assessment methodologies are based on simplifying assumptions and suffer from unreliable or absent empirical data, a theme that is common throughout studies on wildlife population-level impacts of wind energy facilities.

When there is a lack of empirical data for a particular species, data from similar species, or structured elicitation of expert opinion, can be used for conservation decision-making or to inform modelling approaches. Frick et al. (2017) used expert elicitation and population forecasting to assess whether wind turbine-induced fatalities could threaten the population viability of *Lasiurus cinereus*, a wide-spread migratory species that comprises the highest proportion of bat fatalities at wind energy facilities in North America (Arnett and Baerwald, 2013). They show that mortality from wind turbines may drastically reduce population size and increase the risk of extinction. For example, if the initial *L. cinereus* population size is near 2500,000 bats and annual population growth rate is similar to rates estimated for other bat species, it is estimated that their population could decline by as much as 90 % in the next 50 years. However, the study also concluded that site or population-specific differences in demographic parameters may affect the validity of extrapolating patterns observed in local studies to broader spatial scales. It is acknowledged that different methodological approaches for scaling up individual impacts to the population level can affect the estimates and that even comprehensive monitoring and advanced modelling may not capture the full complexity of bat interactions with wind turbines (May et al., 2019).

5. Conclusions

(1) Bats have several biological and ecological traits that may make them sensitive to the widespread deployment of wind turbines in the offshore environment, yet there is surprisingly little evidence on the movement of bats across waterbodies surrounding the British Isles or how different species of these mammals respond to wind energy development in this environment. Our systematic review assessing the movements of bat species offshore and their interactions with offshore windfarms in British waters highlights important gaps in the literature and the way we study the impacts of wind energy development.

(2) Historically the evidence of seasonal migration in and out of the UK has been largely anecdotal, with most of information pertaining to the migratory ecology of bat species being gathered through studies in terrestrial habitats. However, with the increased availability and deployment of remote sensing technologies, studies are starting to uncover potential migratory pathways across waterbodies surrounding the British Isles. Despite present knowledge on offshore migration of bats around the British Isles being currently limited to specific regions and species, studies have established successful methodologies for analysing seasonal and environmental patterns of migrations, as well as emerging evidence in relation to altitude and air pressure. Furthermore, studies are starting to reveal in more detail the migratory ecology of bat species, with reasonable evidence now available for *P. nathusii*, emerging evidence for *Nyctalus* spp. and limited or absent evidence for all other species.

(3) A wider deployment of established technologies, in addition to exploring novel technological approaches, is required to fill evidence gaps for other offshore regions across the British Isles and for a greater number of species. These should focus on the migration routes, phenology and behaviour of bat species crossing open sea as well as considering how these are likely to change in the future.

(4) Whilst it is widely assumed that bat behaviour around offshore wind turbines is likely to be similar to around onshore wind turbines, there is a paucity of studies specifically reporting how bat species interact with offshore wind turbines. It is not currently known whether the attractant or displacement effects of wind turbines seen in the onshore environment translates to an offshore setting due to substantial differences in the scale of wind farm arrays and turbine size as well as the nature of the environment and behaviour of bats offshore. In this review, we found some emerging evidence for the role of feeding and roosting opportunities in shaping bats interaction with offshore wind turbine but limited or absent evidence for other potential drivers.

(5) Evidence gaps should be progressed in the UK through the funding of academic, NGO and industry-led projects. It is important to establish the specific impact on bat species in the offshore environment including; if bats are killed at offshore wind turbines, the number of casualties and what conditions influence collisions.

CRediT authorship contribution statement

Jan Collins: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jack Hooker:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Paul R Lintott:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Conceptualization. **Katherine Boughey:** Writing – review & editing, Validation, Supervision, Resources, Funding acquisition, Conceptualization. **Lisa Worledge:** Writing – review & editing, Validation, Supervision, Funding acquisition, Conceptualization. **Kirsty Park:** Writing – review & editing, Validation, Supervision, Conceptualization.

Declaration of Competing Interest

Myself (Jack Hooker) or any of the co-authors do not have any conflict of interest to disclose.

Data Availability

Data Availability The data that supports the findings of this study are available in the supplementary material of this article

References

- Ahlén, I., 1997. Migratory behaviour of bats at south Swedish coasts. *Jnt J. Mamm. Biol.* 62, 375–380.
- Ahlén, I. (2003) *Wind turbines and bats—a pilot study*. Report to Swedish National Energy Administration. Swedish University of Agricultural Sciences.
- Ahlén, I. et al. (2007) *Bats and offshore wind turbines studied in southern Scandinavia*.
- Ahlén, I., et al., 2009. Behaviour of scandinavian bats during migration and foraging at sea. *J. MAMMALOGY* 90 (6), 1318–1323. <https://doi.org/10.1644/09-MAMM-S-223R.1>.
- Ahlén, I., 2011. Fladdermusfaunan I sverige. Arternas utbredning och status. Kunskapsläget The bat fauna of Sweden. Present knowledge on distribution and status. *Fauna och Flora* 106 (2), 2–19.
- Alcalde, J.T., et al., 2021. Transcontinental 2200 km migration of a *Nathusius'* pipistrelle (*Pipistrellus nathusii*) across Europe. *Mammalia* 85 (2), 161–163. <https://doi.org/10.1515/mammalia-2020-0069>.
- Alerstam, T., 1993. Bird migration. Cambridge University Press.
- Altringham, J.D., 2003. British bats. HarperCollins.
- Amorim, F., Rebelo, H., Rodrigues, L., 2012. Factors influencing bat activity and mortality at a wind farm in the Mediterranean region. *Acta Chiropterologica* 14, 439–457. <https://doi.org/10.3161/150811012X661756>.
- Arnett, E.B., et al., 2005. Relationships between bats and wind turbines in Pennsylvania and west virginia: an assessment of fatality search protocols, patterns of fatality, and behavioral interactions with wind turbines. *Bat Conservation International*, p. 187.
- Arnett, E.B., et al., 2008. Patterns of bat fatalities at wind energy facilities in North America. *J. Wildl. Manag.* 72 (1), 61–78. <https://doi.org/10.2193/2007-221>.
- Arnett, E.B., et al., 2016. Impacts of wind energy development on bats: a global perspective. In: Voigt, C.C., Kingston, T. (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer International Publishing, Cham, pp. 295–323. https://doi.org/10.1007/978-3-319-25220-9_11.
- Arnett, E.B., Baerwald, E.F., 2013. Impacts of wind energy development on bats: implications for conservation. In: Adams, R.A., Pedersen, S.C. (Eds.), *Bat Evolution, Ecology, and Conservation*. Springer New York, New York, NY, pp. 435–456. https://doi.org/10.1007/978-1-4614-7397-8_21.
- Asif, M., Muneer, T., 2007. Energy supply, its demand and security issues for developed and emerging economies. *Renew. Sustain. Energy Rev.* 11 (7), 1388–1413. <https://doi.org/10.1016/j.rser.2005.12.004>.
- Aughney, T., Roche, N., Langton, S., 2022. Irish BAT MONITORING PROGRAMME 2018-202. National Parks and Wildlife Service.
- Baagøe, H.J., 2007. Dansk pattedyratlas. Gyldendal A/S.
- Baerwald, E.F., et al., 2008. Barotrauma is a significant cause of bat fatalities at wind turbines. *Curr. Biol.* 18 (16), R695–R696. <https://doi.org/10.1016/j.cub.2008.06.029>.
- Baerwald, E.F., Barclay, R.M.R., 2009. Geographic variation in activity and fatality of migratory bats at wind energy facilities. *J. Mammal.* 90 (6), 1341–1349. <https://doi.org/10.1644/09-MAMM-S-104R.1>.
- Baerwald, E.F., Barclay, R.M.R., 2011. Patterns of activity and fatality of migratory bats at a wind energy facility in Alberta, Canada. *J. Wildl. Manag.* 75 (5), 1103–1114. <https://doi.org/10.1002/jwmg.147>.
- Barclay, R.M.R. (2012) 'Variable Variation: Annual and Seasonal Changes in Offspring Sex Ratio in a Bat', *PLoS ONE*. Edited by B. Fenton, 7(5), p. e36344. Available at: <https://doi.org/10.1371/journal.pone.0036344>.
- Barr, K., 2020. The status of *Nathusius'* pipistrelle *Pipistrellus nathusii* in north east scotland: breeding or migratory status? *Br. Isl. Bats* 1.
- Barré, K., et al., 2018. Estimating habitat loss due to wind turbine avoidance by bats: implications for european siting guidance. *Biol. Conserv.* 226, 205–214. <https://doi.org/10.1016/j.biocon.2018.07.011>.
- Bastian, H.-V., 1988. Vorkommen und zug der rauhhauffledermaus (*Pipistrellus nathusii* Keyserling und Blasius, 1839) in Baden-Württemberg. *Z. F. üR. Säugetierkunde* 53, 202–209.
- BC Ireland (2024) *Irish Bats - Bat Conservation Ireland*. (<https://www.batconservationireland.org>). Available at: (<https://www.batconservationireland.org/irish-bats>) (Accessed: 27 March 2024).
- Bennett, V.J., Hale, A.M., 2014. Red aviation lights on wind turbines do not increase bat–turbine collisions. *Anim. Conserv.* 17 (4), 354–358. <https://doi.org/10.1111/acv.12102>.
- Bennett, V.J., Hale, A.M., Williams, D.A., 2017. When the excrement hits the fan: fecal surveys reveal species-specific bat activity at wind turbines. *Mamm. Biol.* 87, 125–129. <https://doi.org/10.1016/j.mambio.2017.08.003>.
- Bernd, D., 2021. Declines of two migratory bat species in the border triangle of hesse, Baden-Wuerttemberg and Rhineland-Palatinate | Rückgänge zweier wanderfledermausarten im Dreiländereck hessen, Baden-Württemberg und Rheinland-Pfalz. *Nyctalus* 19 (4–5), 343–355.
- Bicker, A., 2023. 'Acoustic *Nathusius'* pipistrelle migration study on the Dorset coast, autumn 2017. *Br. Isl. Bats* 4.
- Boonman, A., et al., 2013. 'It's not black or White—on the range of vision and echolocation in echolocating bats'. *Front. Physiol.* 4, 248.
- Boshamer, J.P.C., Bekker, J.P., 2008. *Nathusius'* pipistrelles (*Pipistrellus nathusii*) and other species of bats on offshore platforms in the Dutch sector of the north sea. *Lutra* 51 (1), 17–36.
- Brabant, R., et al., 2016. Bats in the Belgian part of the north sea and possible impacts of offshore wind farms. *Environmental impacts of offshore wind farms in the Belgian part of the North Sea: Environmental impact monitoring reloaded*. OD Natural Environment, Marine Ecology and Management Section. Royal Belgian Institute of Natural Sciences, pp. 235–246.
- Brabant, R., et al., 2019. The influence of meteorological conditions on the presence of *Nathusius'* pipistrelle (*Pipistrellus nathusii*) at sea. *Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Marking a Decade of Monitoring, Research and Innovation*. Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management, Brussels, pp. 117–124.
- Brabant, R., et al., 2020. 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. <https://doi.org/10.3161/15081109ACC2019.21.2.009>.
- Brabant, R., et al., 2021. The relation between migratory activity of *Pipistrellus* bats at sea and weather conditions offers possibilities to reduce offshore wind farm effects. *ANIMALS* 11 (12). <https://doi.org/10.3390/ani11123457>.
- Briggs, P., Briggs, B., Parsons, E., 2023. First motus tag results from bedfont lakes study of *Nathusius'* pipistrelle. *Br. Isl. Bats* 4.
- Brinkmann, R. et al. (2011) 'Windbedingte Verdriftungen von Fledermausschlagopfern an Windenergieanlagen – ein Diskussionsbeitrag zur Methodik der Schlagopfersuche', in, pp. 116–129.
- Brosset, A., 1990. The migrations of *Pipistrellus nathusii*, in France. Possible implication on the spreading of rabies. *Mamm. (Fr.)* 54 (2).
- Campebell, T., et al., 2014. Raptor displacement due to the construction of a wind farm: preliminary results after the first 2 years since the construction. *Ethol. Ecol. Evol.* 26 (4), 376–391. <https://doi.org/10.1080/03949370.2013.862305>.
- Ceballos, G., et al., 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. *Sci. Adv.* 1 (5), e1400253. <https://doi.org/10.1126/sciadv.1400253>.
- Chapman, J.W., et al., 2004. An aerial netting study of insects migrating at high altitude over england. *Bull. Entomol. Res.* 94 (2), 123–136. <https://doi.org/10.1079/BER2004287>.
- Ciechanowski, M., et al., 2016. Empty in summer, crowded during migration? Structure of assemblage, distribution pattern and habitat use by bats (Chiroptera: Vespertilionidae) in a narrow, marine peninsula. *MAMMAL Res.* 61 (1), 45–55. <https://doi.org/10.1007/s13364-015-0249-6>.
- Corbet, G.B., Harris, S. (Eds.), 1991. *The handbook of british mammals*, 3. ed. Blackwell Science, Oxford.

- Cowie, R.H., Bouchet, P., Fontaine, B., 2022. The sixth mass extinction: fact, fiction or speculation? *Biol. Rev.* 97 (2), 640–663. <https://doi.org/10.1111/brv.12816>.
- Crampton, L.H., Barclay, R.M.R., 1998. Selection of roosting and foraging habitat by bats in Different-Aged aspen mixedwood stands. *Conserv. Biol.* 12 (6), 1347–1358. <https://doi.org/10.1111/j.1523-1739.1998.97209.x>.
- Cryan, P.M., 2008. Mating behavior as a possible cause of bat fatalities at wind turbines. *J. Wildl. Manag.* 72 (3), 845–849. <https://doi.org/10.2193/2007-371>.
- Cryan, P.M., et al., 2014. Behavior of bats at wind turbines. *Proc. Natl. Acad. Sci.* 111 (42), 15126–15131. <https://doi.org/10.1073/pnas.1406672111>.
- Cryan, P.M., Barclay, R.M.R., 2009. Causes of bat fatalities at wind turbines: hypotheses and predictions. *J. Mammal.* 90 (6), 1330–1340. <https://doi.org/10.1644/09-MAMM-S-076R1.1>.
- Dai, K., et al., 2015a. Environmental issues associated with wind energy – a review. *Renew. Energy* 75, 911–921. <https://doi.org/10.1016/j.renene.2014.10.074>.
- Dammeier, L.C., et al., 2019. Space, time, and size dependencies of greenhouse gas payback times of wind turbines in northwestern Europe. *Environ. Sci. Technol.* 53 (15), 9289–9297. <https://doi.org/10.1021/acs.est.9b01030>.
- Danilovich, S., Yovel, Y., 2019. Integrating vision and echolocation for navigation and perception in bats. *Sci. Adv.* 5 (6), eaaw6503. <https://doi.org/10.1126/sciadv.aaw6503>.
- Dierschke, V., Furness, R., Garthe, S., 2016. Seabirds and offshore wind farms in European waters: avoidance and attraction. *Biol. Conserv.* 202, 59–68. <https://doi.org/10.1016/j.biocon.2016.08.016>.
- Dietz, C., et al., 2007. Handbuch der Fledermäuse Europas und Nordwestafrikas. Biologie, Kennzeichen, Gefährdung. *Mamm. Biol.* 74 (1), 82–83. <https://doi.org/10.1016/j.mambio.2007.10.005>.
- Dietz, C., et al., 2009. Bats of Britain, Europe and northwest Africa. A & C Black London.
- Dietz, C., Kiefer, A., 2016. *Bats of Britain and Europe*.
- Diffendorfer, J.E., et al., 2015. *Preliminary methodology to assess the national and regional impacts of U.S. wind energy development on birds and bats, scientific investigations report*. U.S. Geological Survey. <https://doi.org/10.3133/sir20185157>.
- Diffendorfer, J.E., et al., 2019. *A methodology to assess the national and regional impacts of U.S. wind energy development on birds and bats, scientific investigations report*. 2018–5157. U.S. Geological Survey. <https://doi.org/10.3133/sir20185157>.
- Drake, A., Reynolds, D.R., 2012. First edition. *Radar Entomology: Observing Insect Flight and Migration*. CABI.
- DUKES (2023) *Renewable sources of energy*. Digest of United Kingdom Energy Statistics (DUKES). Department for Energy Security and Net Zero.
- Dyer, S., 2019. *Bat migration project report (2017–2018)*. NRW evidence report no: 335. Natural Resources Wales, Bangor.
- Eastwood, E. (1967) 'Radar ornithology', (No Title) [Preprint].
- Eklöf, J., Petersons, G., Rydell, J., 2014. Visual acuity and eye size in five European bat species in relation to foraging and migration strategies. *Environ. Exp. Biol.* 12, 1–6.
- Ellerbrok, J.S., et al., 2022. Activity of forest specialist bats decreases towards wind turbines at forest sites. *J. Appl. Ecol.* 59 (10), 2497–2506. <https://doi.org/10.1111/1365-2664.14249>.
- Erickson, R.A., et al., 2015. Assessing local population vulnerability with branching process models: an application to wind energy development. *Ecosphere* 6 (12), 1–14. <https://doi.org/10.1890/ES15-00103.1>.
- EUROBATS (2023) *Report of the Intersectoral Working Group on Wind Turbines and Bat Populations*.
- European Commission, 2019. Going climate-neutral by 2050: a strategic long term vision for a prosperous, modern, competitive and climate neutral EU economy. Publications Office of the European Union, LU. Available at: <https://data.europa.eu/doi/10.2834/02074>.
- Fleming, T.H., Eby, P., 2003. Ecology of bat migration. In: Kunz, T.H., Fenton, M.B. (Eds.), *Bat Ecology*. The University of Chicago Press, Chicago, pp. 156–208.
- Folly, A.J., et al., 2021. Incursion of European bat lyssavirus 1 (EBLV-1) in serotine bats in the United Kingdom. *Viruses* 13 (10), 1979. <https://doi.org/10.3390/v13101979>.
- Foo, C.F., et al., 2017. Increasing evidence that bats actively forage at wind turbines. *PeerJ* 5, e3985. <https://doi.org/10.7717/peerj.3985>.
- Frick, W.F., et al., 2017. Fatalities at wind turbines May threaten population viability of a migratory bat. *Biol. Conserv.* 209, 172–177. <https://doi.org/10.1016/j.biocon.2017.02.023>.
- Frick, W.F., Reynolds, D.S., Kunz, T.H., 2010. Influence of climate and reproductive timing on demography of little brown myotis *Myotis lucifugus*. *J. Anim. Ecol.* 79 (1), 128–136. <https://doi.org/10.1111/j.1365-2656.2009.01615.x>.
- Garthe, S., et al., 2023. Large-scale effects of offshore wind farms on seabirds of high conservation concern. *Sci. Rep.* 13 (1), 4779. <https://doi.org/10.1038/s41598-023-31601-z>.
- Gaultier, S.P., et al., 2020. Bats and wind farms: the role and importance of the Baltic Sea countries in the European context of power transition and biodiversity conservation. *Environ. Sci. Technol.* 54 (17), 10385–10398. <https://doi.org/10.1021/acs.est.0c00070>.
- Gaultier, S.P., et al., 2023. The presence of wind turbines repels bats in boreal forests. *Landsc. Urban Plan.* 231, 104636. <https://doi.org/10.1016/j.landurbplan.2022.104636>.
- Georgiakakis, P., et al., 2012. Bat fatalities at wind farms in North-Eastern Greece. *Acta Chiropterologica* 14, 459–468. <https://doi.org/10.3161/150811012X661765>.
- Gerell, R., 1987. 'Flyttar svenska fladdermöss. Fauna och Flora 82 (2), 79–83.
- Giavi, S., et al., 2014. Seasonal survival probabilities suggest low migration mortality in migrating bats. *PLOS ONE* 9 (1). <https://doi.org/10.1371/journal.pone.0085628>.
- Gibson, L., Wilman, E.N., Laurance, W.F., 2017. How Green is "Green" energy? *Trends Ecol. Evol.* 32 (12), 922–935. <https://doi.org/10.1016/j.tree.2017.09.007>.
- Gómez-Catastús, J., Garza, V., Traba, J., 2018. Wind farms affect the occurrence, abundance and population trends of small passerine birds: the case of the Dupont's lark. *J. Appl. Ecol.* 55 (4), 2033–2042. <https://doi.org/10.1111/1365-2664.13107>.
- Grodsky, S.M., et al., 2011. Investigating the causes of death for wind turbine-associated bat fatalities. *J. Mammal.* 92 (5), 917–925. <https://doi.org/10.1644/10-MAMM-A-404.1>.
- Grodsky, S.M., et al., 2012. Bat mortality at a wind-energy facility in southeastern Wisconsin. *Wildl. Soc. Bull.* 36 (4), 773–783. <https://doi.org/10.1002/wsb.191>.
- Grof-Tisza, P., et al., 2017. Testing predictions of movement behaviour in a hilltopping moth. *Anim. Behav.* 133, 161–168. <https://doi.org/10.1016/j.anbehav.2017.08.028>.
- Guest, E.E., et al., 2022. An updated review of hypotheses regarding bat attraction to wind turbines. *Animals* 12 (3), 343. <https://doi.org/10.3390/ani12030343>.
- Hall, L.S., Richards, G.C., 1972. Notes on *Tadarida australis* (Chiroptera: Molossidae). *Aust. Mammal.* 1 (1), 46–47. <https://doi.org/10.1071/AM72009>.
- Harris, J., Parsons, E., 2020. Developing the MOTUS automated radio-tracking system for studying migratory activity of *Nathusius' pipistrelle*. *Br. Isl. Bats* 1.
- Harvey, P., 2014. The occurrence of bats in Shetland. *Scott. Bats* 6.
- Hatch, S., et al., 2013. Offshore observations of eastern red bats (*Lasiurus borealis*) in the Mid-Atlantic United States using multiple survey methods. *PLOS ONE* 8 (12). <https://doi.org/10.1371/journal.pone.0083803>.
- Hayes, M.A., 2013. Bats killed in large numbers at United States wind energy facilities. *BioScience* 63 (12), 975–979. <https://doi.org/10.1525/bio.2013.63.12.10>.
- Hedenström, A., Rydell, J., 2013. Effect of wind turbine mortality on bat populations in Sweden: predictions from a simple population model. In: *Naturvårdsverket rapport*, 6546. CWE, p. 58.
- Herman, J.S., 1992. The earliest record of *Nathusius' pipistrelle* from the British Isles. *Scott. Bats* 1, 48.
- HM Government, 2021. *Net zero strategy: build back greener*. HM Government. Accessed: 21 December 2023.
- Hobbs, M., Gabb, O., Shepherd, P., 2014. North sea ferry bat migration research report. BSG Ecology. Available at: <https://www.bsg-ecology.com/wp-content/uploads/2015/01/North-Sea-Ferry-Bat-Migration-Research-Report-20141.pdf>.
- Horn, J.W., Arnett, E.B., Kunz, T.H., 2008. Behavioral responses of bats to operating wind turbines. *J. Wildl. Manag.* 72 (1), 123–132. <https://doi.org/10.2193/2006-465>.
- Hüppop, O., Hill, R., 2016. Migration phenology and behaviour of bats at a research platform in the south-eastern North Sea. *Lutra* 59, 5–22.
- Hurstpierpoint Bat Hospital (2024) 'Offshore bat rescues'.
- Hutson, A.M., 1997. Two species of bat new to the UK. *Bat N.* 46 (2), 722.

- Hutterer, R. et al. (2005) *Bat migrations in Europe: a review of banding data and literature*. BfN-Schriftenvertrieb im Landwirtschaftsverlag. Available at: (<https://bfn.bsz-bw.de/frontdoor/index/index/docId/928>) (Accessed: 27 March 2024).
- Jahelkova, H., Horacek, I., 2011. Mating system of a migratory bat, *Nathusius' pipistrelle* (*Pipistrellus nathusii*): different Male strategies. *Acta Chiropterologica* 13, 123–137. <https://doi.org/10.3161/150811011X578679>.
- Jameson, J.W., Willis, C.K.R., 2014. Activity of tree bats at anthropogenic tall structures: implications for mortality of bats at wind turbines. *Anim. Behav.* 97, 145–152. <https://doi.org/10.1016/j.anbehav.2014.09.003>.
- Jansson, S., et al., 2020. A scheidpflug lidar used to observe insect swarming at a wind turbine. *Ecol. Indic.* 117, 106578. <https://doi.org/10.1016/j.ecolind.2020.106578>.
- Jennings, L., et al., 2013b. Kent bat migration research baseline report. BSG Ecology.
- Jennings, L., Gabb, O., Betts, S., 2013a. Dungeness. Kent bat migration pilot study. BSG Ecology. Available at: (<https://www.bsg-ecology.com/wp-content/uploads/2015/01/Dungeness-Bat-Study-2012.pdf>).
- Johnson, G.D., et al., 2003. Mortality of bats at a Large-scale wind power development at buffalo ridge, Minnesota'. *Am. Midl. Nat.* 150 (2), 332–342. [https://doi.org/10.1674/0003-0031\(2003\)150\[0332:MOBAAL\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2003)150[0332:MOBAAL]2.0.CO;2).
- Johnson, G.D., et al., 2004. Bat activity, composition, and collision mortality at a large wind plant in Minnesota'. *Wildl. Soc. Bull.* 32 (4), 1278–1288. [https://doi.org/10.2193/0091-7648\(2004\)032\[1278:BACACM\]2.0.CO;2](https://doi.org/10.2193/0091-7648(2004)032[1278:BACACM]2.0.CO;2).
- Jonasson, K.A., Guglielmo, C.G., 2019. Evidence for spring stopover refuelling in migrating silver-haired bats (*Lasionycteris noctivagans*). *Can. J. Zool.* 97 (11), 961–970. <https://doi.org/10.1139/cjz-2019-0036>.
- Jonasson, K.A. et al. (2024) 'A multisensory approach to understanding bat responses to wind energy developments', *Mammal Review*, n/a(n/a). Available at: <https://doi.org/10.1111/mam.12340>.
- Jones, K.E., Purvis, A., Gittleman, J.L., 2003. Biological correlates of extinction risk in bats. *Am. Nat.* 161 (4), 601–614. <https://doi.org/10.1086/368289>.
- Kalcounis-Rüppell, M.C., Psyllakis, J.M., Brigham, R.M., 2005. Tree roost selection by bats: an empirical synthesis using Meta-Analysis. *Wildl. Soc. Bull.* (19732006) 33 (3), 1123–1132.
- Köppel, J., et al., 2014. Cautious but committed: moving toward adaptive planning and operation strategies for renewable Energy's wildlife implications. *Environ. Manag.* 54 (4), 744–755. <https://doi.org/10.1007/s00267-014-0333-8>.
- Krauel, J.J., McCracken, G.F., 2013. Recent advances in bat migration research. In: Adams, R.A., Pedersen, S.C. (Eds.), *Bat Evolution, Ecology, and Conservation*. Springer, New York, NY, pp. 293–313. https://doi.org/10.1007/978-1-4614-7397-8_15.
- Krauel, J.J., McGuire, L.P., Boyles, J.G., 2018. Testing traditional assumptions about regional migration in bats. *Mammal. Res.* 63 (2), 115–123. <https://doi.org/10.1007/s13364-017-0346-9>.
- Kronwitter, F. (1988) *Population structure, habitat use and activity patterns of the noctule bat, Nyctalus noctula Schreb., 1774 (Chiroptera: Vespertilionidae) revealed by radio-tracking*.
- Kruszynski, C., et al., 2022. High vulnerability of juvenile *Nathusius' pipistrelle* bats (*Pipistrellus nathusii*) at wind turbines'. *Ecol. Appl.* 32 (2), e2513. <https://doi.org/10.1002/eap.2513>.
- Kunz, T., et al., 2007. Assessing impacts of Wind-Energy development on nocturnally active birds and bats: a guidance document. *J. Wildl. Manag.* 71, 2449–2486. <https://doi.org/10.2193/2007-270>.
- Lack, D., 1963. Migration across the Southern north sea studied by radar part 4. Autumn. *Ibis* 105 (1), 1–54.
- Lagerveld, S., et al., 2014a. Bats in Dutch offshore wind farms in autumn 2012. *Lutra* 57 (2), 61–69.
- Lagerveld, S., et al., 2017a. *spatial and temporal occurrence of bats in the southern north sea area*. C090/17. Wageningen Marine Research, Den Helder. <https://doi.org/10.18174/426898>.
- Lagerveld, S., et al., 2017b. *bat flight analysis around wind turbines: a feasibility study*. C026/17. Wageningen Marine Research. <https://doi.org/10.18174/417091>.
- Lagerveld, S., et al., 2021. Offshore occurrence of a migratory bat, *pipistrellus nathusii*, depends on seasonality and weather conditions. *ANIMALS* 11 (12). <https://doi.org/10.3390/ani11123442>.
- Lagerveld, S., et al., 2023. Acoustic monitoring reveals spatiotemporal occurrence of *Nathusius' pipistrelle* at the Southern north sea during autumn migration. *Environ. Monit. Assess.* 195 (9). <https://doi.org/10.1007/s10661-023-11590-2>.
- Lagerveld, S., et al., 2024. Migratory movements of bats are shaped by barrier effects, sex-biased timing and the adaptive use of winds. *Mov. Ecol.* 12 (1), 81. <https://doi.org/10.1186/s40462-024-00520-7>.
- Lagerveld, S., Poerink, B.J., Verdaat, H., et al., 2014b. *monitoring bat activity in offshore wind farms owez and pawp in 2013*. C165/14. Wageningen Marine Research.
- Lawson, M., et al., 2020. An investigation into the potential for wind turbines to cause barotrauma in bats. *PLOS ONE* 15 (12), e0242485. <https://doi.org/10.1371/journal.pone.0242485>.
- Lehnert, L.S. et al. (2014) 'Wind Farm Facilities in Germany Kill Noctule Bats from Near and Far', *PLoS ONE*. Edited by {C}J.M. Ratcliffe{C}, 9(8), p. e103106. Available at: <https://doi.org/10.1371/journal.pone.0103106>.
- Lehnert, L., et al., 2018. Variability and repeatability of noctule bat migration in central Europe: evidence for partial and differential migration. *Proc. R. Soc. BBiol. Sci.* 285 (1893). <https://doi.org/10.1098/rspb.2018.2174>.
- Lentini, P.E., et al., 2015. A global synthesis of survival estimates for microbats. *Biol. Lett.* 11 (8), 20150371. <https://doi.org/10.1098/rsbl.2015.0371>.
- Leopold, M. 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*.
- Leroux, C., et al., 2022. Distance to hedgerows drives local repulsion and attraction of wind turbines on bats: implications for spatial siting. *J. Appl. Ecol.* 59 (8), 2142–2153. <https://doi.org/10.1111/1365-2664.14227>.
- Leroux, C., et al., 2023. Disentangling mechanisms responsible for wind energy effects on european bats. *J. Environ. Manag.* 346, 118987. <https://doi.org/10.1016/j.jenvman.2023.118987>.
- Limpens, H. et al. (2013) *Windturbines and bats in the Netherlands - Measuring and predicting*. Available at: <https://doi.org/10.13140/RG.2.1.2356.6889>.
- Limpens, H., et al., 2017. *migrating bats at the southern north sea approach to an estimation of migration populations of bats at the southern north sea*. 2016–0.31. Dutch Mammal Society.
- Lina, P.H.C., 1990. Verre terugmeldingen van *Nathusius' dwergvleermuisen pipistrellus nathusii* gevonden of geringd in nederland. *Lutra* 33 (1), 45–48.
- Lintott, P.R., et al., 2016. Ecological impact assessments fail to reduce risk of bat casualties at wind farms. *Curr. Biol.* 26 (21), R1135–R1136. <https://doi.org/10.1016/j.cub.2016.10.003>.
- Long, C.V. (2011) *The interaction of bats (Microchiroptera) with wind turbines: bioacoustic and other investigations*. © Chloe V. Long.
- Lueken, C., Cohen, G.E., Apt, J., 2012. Costs of solar and wind power variability for reducing CO2 emissions. *Environ. Sci. Technol.* 46 (17), 9761–9767. <https://doi.org/10.1021/es204392a>.
- Mackie, I.J., Racey, P.A., Waters, D.A., 2008. Noctule *nyctalus noctula*. In: Harris, S., Yalden, D.W. (Eds.), *Mammals of the British Isles: handbook*, Fourth edition. The Mammal Society c/o Society for Experimental Biology, Southampton, pp. 338–342.
- Manwell, J.F., McGowan, J.G., Rogers, A.L., 2010. *Wind energy explained: theory, design and application*. John Wiley & Sons.
- Marques, A.T., Batalha, H., Bernardino, J., 2021. Bird displacement by wind turbines: assessing current knowledge and recommendations for future studies. *Birds* 2 (4), 460–475. <https://doi.org/10.3390/birds2040034>.
- Mathews, F., et al., 2016. Understanding the risk to european protected species. University of Exeter.
- Mathews, F., et al., 2018. A review of the population and conservation status of British mammals. Natural England, Peterborough.
- May, R., et al., 2019. Considerations for upscaling individual effects of wind energy development towards population-level impacts on wildlife. *J. Environ. Manag.* 230, 84–93. <https://doi.org/10.1016/j.jenvman.2018.09.062>.
- McAlexander, A.M., 2013. Evidence that bats perceive wind turbine surfaces to be water. Purdue University.
- Medinas, D., Marques, J.T., Mira, A., 2013. Assessing road effects on bats: the role of landscape, road features, and bat activity on road-kills. *Ecol. Res.* 28 (2), 227–237. <https://doi.org/10.1007/s11284-012-1009-6>.

- Met Office (2024). High and low pressure, Met Office. Available at: (<https://www.metoffice.gov.uk/weather/learn-about/weather/how-weather-works/high-and-low-pressure>) (Accessed: 27 March 2024).
- Miller, G.S., 1897. Migration of bats on cape cod, massachusetts. *Science* 5 (118), 541–543. <https://doi.org/10.1126/science.5.118.541>.
- Miller, L., Keith, D., 2018. Climatic impacts of wind power. *Joule* 2. <https://doi.org/10.1016/j.joule.2018.09.009>.
- Millon, L., et al., 2015. Bat activity in intensively farmed landscapes with wind turbines and offset measures. *Ecol. Eng.* 75, 250–257. <https://doi.org/10.1016/j.ecoleng.2014.11.050>.
- Millon, L., et al., 2018. Wind turbines impact bat activity, leading to high losses of habitat use in a biodiversity hotspot. *Ecol. Eng.* 112, 51–54. <https://doi.org/10.1016/j.ecoleng.2017.12.024>.
- Minderman, J. et al. (2012) 'Experimental Evidence for the Effect of Small Wind Turbine Proximity and Operation on Bird and Bat Activity', *PLoS ONE*. Edited by B. Fenton, 7(7), p. e41177. Available at: <https://doi.org/10.1371/journal.pone.0041177>.
- Minderman, J., et al., 2017. Landscape-scale effects of single- and multiple small wind turbines on bat activity. *Anim. Conserv.* 20 (5), 455–462. <https://doi.org/10.1111/acv.12331>.
- Mitchell-Jones, A.J. et al. (1999) *The atlas of European mammals*. Poyser. Available at: (<https://research.wur.nl/en/publications/the-atlas-of-european-mammals>) (Accessed: 27 March 2024).
- Müller, J., et al., 2012. Aggregative response in bats: prey abundance versus habitat. *Oecologia* 169 (3), 673–684. <https://doi.org/10.1007/s00442-011-2247-y>.
- National Bat Monitoring Program (2023). *National Bat Monitoring Program, Bat Conservation Trust*. Available at: <https://www.bats.org.uk/our-work/national-bat-monitoring-programme> (Accessed: 26 March 2024).
- National Natusius' Pipistrelle Project (2024) *National Natusius' Pipistrelle Project - Explore NBMP Surveys, Bat Conservation Trust*. Available at: (<https://www.bats.org.uk/our-work/national-bat-monitoring-programme/surveys/national-nathusius-pipistrelle-survey>) (Accessed: 26 March 2024).
- Natural England (2014) 'Bats and onshore wind turbines (Interim guidance) - TIN051'. Available at: (<https://publications.naturalengland.org.uk/publication/35010>) (Accessed: 26 March 2024).
- NBN Atlas (2024). *NBN Atlas - UK's largest collection of biodiversity information, NBN Atlas*. Available at: (<https://nbnatlas.org/>) (Accessed: 27 March 2024).
- Newson, S.E., et al., 2022. Bailiwick bat survey: 2021 season report. BTO, Thetford, p. 743.
- Newson, S.E., et al., 2023. Bailiwick bat survey: 2022 season report. BTO, Thetford, p. 750.
- Newson, S.E., et al., 2024. Bailiwick bat survey: 2023 season report. BTO, Thetford, p. 764.
- O'Mara, M., et al., 2019. First three-dimensional tracks of bat migration reveal large amounts of individual behavioral flexibility. *Ecology* 100 (9), e02762. <https://doi.org/10.1002/ecy.2762>.
- O'Shea, T.J., et al., 2016. Multiple mortality events in bats: a global review. *Mammal. Rev.* 46 (3), 175–190. <https://doi.org/10.1111/mam.12064>.
- Ørsted (2023) *Hornsea 3 Final Investment Decision*. Company Announcement 27/2023. Ørsted. Available at: (<https://via.ritzau.dk/ir-files/13560592/8032/12278/Hornsea%203%20FID.pdf>) (Accessed: 21 December 2023).
- Ouzzani, M., et al., 2016. Rayyan—a web and mobile app for systematic reviews. *Syst. Rev.* 5 (1), 210. <https://doi.org/10.1186/s13643-016-0384-4>.
- Page, M.J., et al., 2021. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. *Syst. Rev.* 10 (1), 89. <https://doi.org/10.1186/s13643-021-01626-4>.
- Pennington, M., et al., 2004. *The Birds of Shetland, First Edition*. Helm.
- Perks, S.J., Goodenough, A.E., 2020. Abiotic and spatiotemporal factors affect activity of european bat species and have implications for detectability for acoustic surveys. *Wildl. Biol.* 2020 (2). <https://doi.org/10.2981/wlb.00659>.
- Petersen, A., et al., 2014. A review of the occurrence of bats (Chiroptera) on islands in the north east atlantic and on north sea installations. *Acta Chiropterologica* 16 (1), 169–195. <https://doi.org/10.3161/150811014X683381>.
- Petersons, G., 2004. Seasonal migrations of north-eastern populations of *Nathusius' bat pipistrellus nathusii* (Chiroptera). *Myotis* 41, 29–56.
- Pettit, J.L., O'Keefe, J.M., 2017. Day of year, temperature, wind, and precipitation predict timing of bat migration. *J. Mammal.* 98 (5), 1236–1248. <https://doi.org/10.1093/jmammal/gyx054>.
- Petorelli, N., et al., 2021. Time to integrate global climate change and biodiversity science-policy agendas. *J. Appl. Ecol.* 58 (11), 2384–2393. <https://doi.org/10.1111/1365-2664.13985>.
- Pimm, S.L., et al., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344 (6187), 1246752. <https://doi.org/10.1126/science.1246752>.
- Pinder, N., 2020. When did the Leisler's bat colonise the isle of man? *Br. Isl. Bats* 1.
- Popa-Lisseanu, A.G., Voigt, C.C., 2009. Bats on the move. *J. Mammal.* 90 (6), 1283–1289. <https://doi.org/10.1644/09-MAMM-S-130R2.1>.
- Porté-Agel, F., Bastankhah, M., Shamsoddin, S., 2020. Wind-Turbine and Wind-Farm flows: a review. *Bound. Layer. Meteorol.* 174 (1), 1–59. <https://doi.org/10.1007/s10546-019-00473-0>.
- Pörtner, H.-O., et al., 2021. Scientific outcome of the IPBES-IPCC co-sponsored workshop on biodiversity and climate change (Available at). Zenodo. <https://doi.org/10.5281/ZENODO.5101125>.
- Racey, P.A., Mackie, L.J., Waters, D.A., 2008. *Genus vespertilio*. In: Harris, S., Yalden, D.W. (Eds.), *Mammals of the British Isles: handbook, Fourth edition*. The Mammal Society c/o Society for Experimental Biology, Southampton, pp. 361–362.
- RenewableUK (2023) *Wind Energy Statistics*. Available at: (<https://www.renewableuk.com/page/UKWEDhome>) (Accessed: 26 March 2024).
- Reusch, C., et al., 2022. Coastal onshore wind turbines lead to habitat loss for bats in Northern Germany. *J. Environ. Manag.* 310, 114715. <https://doi.org/10.1016/j.jenvman.2022.114715>.
- Reusch, C., et al., 2023. Wind energy production in forests conflicts with tree-roosting bats. *Curr. Biol.* 33 (4), 737–743.e3. <https://doi.org/10.1016/j.cub.2022.12.050>.
- Richardson, S.M., et al., 2021. Peaks in bat activity at turbines and the implications for mitigating the impact of wind energy developments on bats. *Sci. Rep.* 11 (1), 3636. <https://doi.org/10.1038/s41598-021-82014-9>.
- Rodrigues, L. et al. (2014) *Guidelines for consideration of bats in wind farm projects: Revision 2014*. Bonn: UNEP/EUROBATS (EUROBATS Publication Series).
- Roemer, C., et al., 2017. Bat flight height monitored from wind masts predicts mortality risk at wind farms. *Biol. Conserv.* 215, 116–122. <https://doi.org/10.1016/j.biocon.2017.09.002>.
- Roemer, C., et al., 2019. Influence of landscape and time of year on bat-wind turbines collision risks. *Landsc. Ecol.* 34 (12), 2869–2881. <https://doi.org/10.1007/s10980-019-00927-3>.
- Roer, H., 1995. 60 years of bat-banding in Europe - results and tasks for future research. *Myotis* 32-33, 251–261.
- Rollins, K.E., et al., 2012. A forensic investigation into the etiology of bat mortality at a wind farm: barotrauma or traumatic injury? *Vet. Pathol.* 49 (2), 362–371. <https://doi.org/10.1177/0300985812436745>.
- Romo, R., et al., 2002. From sensation to action. *Behav. brain Res.* 135 (1–2), 105–118.
- Roscioni, F., et al., 2013. Regional-scale modelling of the cumulative impact of wind farms on bats. *Biodivers. Conserv.* 22 (8), 1821–1835. <https://doi.org/10.1007/s10531-013-0515-3>.
- Roscioni, F., et al., 2014. A modelling approach to infer the effects of wind farms on landscape connectivity for bats. *Landsc. Ecol.* 1–13. <https://doi.org/10.1007/s10980-014-0030-2>.
- Rowe, E.G., et al., 2016. Dark matters: the effects of artificial lighting on bats. In: Voigt, C.C., Kingston, T. (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer International Publishing, Cham, pp. 187–213. https://doi.org/10.1007/978-3-319-25220-9_7.
- Russ, J.M., et al., 2001. The status of *Nathusius' pipistrelle* (*pipistrellus nathusii* Keyserling & Blasius, 1839) in the British isles. *J. Zool.* 254 (1), 91–100. <https://doi.org/10.1017/S0952836901000589>.
- Russ, J.M., Briffa, M., Montgomery, W.L., 2003. Seasonal patterns in activity and habitat use by bats (*Pipistrellus* spp. and *Nyctalus leisleri*) in Northern Ireland, determined using a driven transect. *J. Zool.* 259 (3), 289–299. <https://doi.org/10.1017/S0952836902003254>.

- Rybicki, J., Hanski, I., 2013. Species–area relationships and extinctions caused by habitat loss and fragmentation. *Ecol. Lett.* 16 (s1), 27–38. <https://doi.org/10.1111/ele.12065>.
- Rydell, J., et al., 2010. Bat mortality at wind turbines in northwestern Europe. *Acta Chiropterologica* 12 (2), 261–274. <https://doi.org/10.3161/150811010X537846>.
- Rydell, J., et al., 2014. Phenology of migratory bat activity across the Baltic Sea and the south-eastern North Sea. *Acta Chiropterologica* 16 (1), 139–147. <https://doi.org/10.3161/150811014X683354>.
- Rydell, J., et al., 2016. Bats may eat diurnal flies that rest on wind turbines. *Mamm. Biol.* 81 (3), 331–339. <https://doi.org/10.1016/j.mambio.2016.01.005>.
- Sachanowicz, K., et al., 2019. Wintering range of *Pipistrellus nathusii* (Chiroptera) in central Europe: has the species extended to the north-east using urban heat islands? *Mammalia* 83 (3), 260–271. <https://doi.org/10.1515/mammalia-2018-0014>.
- Sánchez-Navarro, S., Rydell, J., Ibáñez, C., 2020. Bat fatalities at Wind-Farms in the lowland Mediterranean of Southern Spain. *Acta Chiropterologica* 21 (2), 349–358. <https://doi.org/10.3161/15081109ACC2019.21.2.010>.
- Santos, H., et al., 2013. Using species distribution modelling to predict bat fatality risk at wind farms. *Biol. Conserv.* 157, 178–186. <https://doi.org/10.1016/j.biocon.2012.06.017>.
- Schuster, E., et al., 2015. Consolidating the state of knowledge: a synoptical review of wind energy's wildlife effects. *Environ. Manag.* 56 (2), 300–331. <https://doi.org/10.1007/s00267-015-0501-5>.
- Seebens-Hoyer, A., et al., 2021. Bat migration over north and Baltic seas. NABU Federal Agency for Nature Conservation.
- Sheil, C.B., Jones, G., Waters, D.A., 2008. Genus *Myotis*. In: Harris, S., Yalden, D.W. (Eds.), *Mammals of the British Isles: handbook, Fourth edition. The Mammal Society c/o Society for Experimental Biology, Southampton*, pp. 334–338.
- Shen, Y.-Y., et al., 2010. Parallel and convergent evolution of the Dim-Light vision gene RH1 in bats (Order: Chiroptera). *PLOS ONE* 5 (1), e8838. <https://doi.org/10.1371/journal.pone.0008838>.
- Shi, X., et al., 2021. Seasonal trends in movement patterns of birds and insects aloft simultaneously recorded by radar. *Remote Sens.* 13 (9), 1839. <https://doi.org/10.3390/rs13091839>.
- Shukla, A.R., et al. (2022) 'Summary for Policymakers', in A.R. Shukla et al. (eds) *Climate Change 2022, Mitigation of Climate Change. Summary for Policymakers*. Cambridge, UK and New York, NY, USA: Cambridge University Press, pp. 3–48. Available at: <https://www.ipcc.ch/report/ar6/wg3/> (Accessed: 26 March 2024).
- Smales, I., 2015. Fauna collisions with wind turbines: effects and impacts, individuals and populations. What are we trying to assess? In: Hull, C., et al. (Eds.), *Wind and Wildlife*. Dordrecht. Springer, Netherlands, pp. 23–40. https://doi.org/10.1007/978-94-017-9490-9_2.
- Solick, D., et al., 2020. Bat activity rates do not predict bat fatality rates at wind energy facilities. *Acta Chiropterologica* 22 (1), 135–146. <https://doi.org/10.3161/15081109ACC2020.22.1.012>.
- Speakman, J.R., et al., 1991. Status of *Nathusius' pipistrelle* (*Pipistrellus nathusii*) in Britain. *J. Zool.* 225 (4), 685–690.
- Stebbins, R.E. (1988) 'The conservation of European bats'.
- Steffens, R., Zöphel, U. and Brockmann, D. (2004) '40th anniversary Bat Marking Centre Dresden: evaluation of methods and overview of results', *Saxon State Office for Environment and Geology, Dresden, Germany* [Printed].
- Straka, T.M., Fritze, M., Voigt, C.C., 2020. The human dimensions of a Green–Green-dilemma: lessons learned from the wind energy — wildlife conflict in Germany. *Energy Rep.* 6, 1768–1777. <https://doi.org/10.1016/j.egyr.2020.06.028>.
- Strelkov, P.P., 1969. Migratory and stationary bats (Chiroptera) of the European part of the Soviet Union. *Acta Zool. Crac.* 16 pp.393–440+.
- Strelkov, P.P., 1997a. 'Breeding area and its position in range of migratory bats species (Chiroptera, Vespertilionidae) in East Europe and adjacent territories—Communication 1'. *Зоологический Журнал* 76 (9), 1079–1082.
- Strelkov, P.P., 1997b. 'Breeding area and its position in range of migratory bats species (Chiroptera, Vespertilionidae) in east Europe and adjacent territories: Communication 2'. *Зоологический Журнал* 76 (12), 1388–1390.
- Šuba, J., Petersons, G., Rydell, J., 2012. Fly-and-Forage strategy in the bat *Pipistrellus nathusii* during autumn migration (Available at). *Acta Chiropterologica* 14 (2), 379–385. <https://doi.org/10.3161/150811012X661693>.
- Suthers, R.A., Wallis, N.E., 1970. Optics of the eyes of echolocating bats. *Vis. Res.* 10 (11), 1165–1173.
- Swenson, et al., 2010. *Pattedyr mammalia*. In: Kålås, J.A., Viken, Å., Henriksen, S., Skjelseth, S. (Eds.), *Norsk Rødliste for arter 2010*. Artsdatabanken, Trondheim, p. 480.
- Syvrtsen, P.O., 1995. A tentative assessment of bat diversity and distribution in Norway'. *Myotis* 32, 183–191.
- Tabassum-Abbasi, et al., 2014. Wind energy: increasing deployment, rising environmental concerns. *Renew. Sustain. Energy Rev.* 31, 270–288. <https://doi.org/10.1016/j.rser.2013.11.019>.
- Taylor, R., et al., 2014. *Pembroke islands bat report*. BSG Ecology. Available at: (https://www.bsg-ecology.com/wp-content/uploads/2014/12/Pembroke_Islands_Bat_Report.pdf).
- Taylor, P.D., et al., 2017. The Motus Wildlife Tracking System: a collaborative research network to enhance the understanding of wildlife movement. *Avian Conserv. Ecol.* 12 (1), art8. <https://doi.org/10.5751/ACE-00953-120108>.
- Thaker, M., Zambre, A., Bhosale, H., 2018. Wind farms have cascading impacts on ecosystems across trophic levels. *Nat. Ecol. Evol.* 2 (12), 1854–1858. <https://doi.org/10.1038/s41559-018-0707-z>.
- Thaxter, C.B., et al., 2017. Bird and bat species' global vulnerability to collision mortality at wind farms revealed through a trait-based assessment. *Proc. R. Soc. B Biol. Sci.* 284 (1862), 20170829. <https://doi.org/10.1098/rspb.2017.0829>.
- Tolvanen, A., et al., 2023. How far are birds, bats, and terrestrial mammals displaced from onshore wind power development? – A systematic review. *Biol. Conserv.* 288, 110382. <https://doi.org/10.1016/j.biocon.2023.110382>.
- UNEP-WCMC, 2024. *State of the World's migratory species report*. UNEP-WCMC, Cambridge, United Kingdom. Accessed: 27 March 2024).
- Vasenkov, D., et al., 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. <https://doi.org/10.1515/mammalia-2021-0139>.
- Voigt, C.C., et al., 2012. The catchment area of wind farms for European bats: a plea for international regulations. *Biol. Conserv.* 153, 80–86. <https://doi.org/10.1016/j.biocon.2012.04.027>.
- Voigt, C.C., et al., 2015. Wildlife and renewable energy: German politics cross migratory bats. *Eur. J. Wildl. Res.* 61 (2), 213–219. <https://doi.org/10.1007/s10344-015-0903-y>.
- Voigt, C., et al., 2017. Migratory bats respond to artificial Green light with positive phototaxis. *PLOS ONE* 12 (5). <https://doi.org/10.1371/journal.pone.0177748>.
- Voigt, C., et al., 2018. Migratory bats are attracted by red light but not by warm-White light: implications for the protection of nocturnal migrants. *Ecol. Evolution* 8 (18), 9353–9361. <https://doi.org/10.1002/eece3.4400>.
- Voigt, C.C., et al., 2021. The impact of light pollution on bats varies according to foraging guild and habitat context. *BioScience* biab087. <https://doi.org/10.1093/biosci/biab087>.
- Williams, T.C., Williams, J.M., Griffin, D.R., 1966. The homing ability of the neotropical bat *Phyllostomus hastatus*, with evidence for visual orientation. *Anim. Behav.* 14 (4), 468–473. [https://doi.org/10.1016/S0003-3472\(66\)80047-7](https://doi.org/10.1016/S0003-3472(66)80047-7).
- WindEurope (2023) *Wind energy in Europe: 2022 Statistics and the outlook for 2023–2027*. WindEurope. Available at: <https://windeurope.org/intelligence-platform/product/wind-energy-in-europe-2022-statistics-and-the-outlook-for-2023-2027> (Accessed: 5 February 2024).
- YouGov, 2018. YouGov / renewable UK survey results 2018. YouGov. Available at: (https://d25d2506sf94s.cloudfront.net/cumulus_uploads/document/3hx70b1nzc/RenewableUK_June18_GB_v.pdf).
- YouGov, 2021. YouGov / renewable UK survey results 2021. YouGov. Available at: (https://d3nkl3psvxxpe9.cloudfront.net/documents/RenewablesUK_Onshore_Wind_210512_W.pdf).
- Zhou, Y., et al., 2012. Evaluation of global onshore wind energy potential and generation costs. *Environ. Sci. Technol.* 46 (14), 7857–7864. <https://doi.org/10.1021/es204706m>.