


REVIEW

Drivers of European bat population change: a review reveals evidence gaps

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ABSTRACT

1. Bat populations are thought to have suffered significant declines in the past century throughout Europe. Fortunately, there are some signs of recovery; for instance, of the 11 species monitored in the UK, population trends of five are increasing. The drivers of past losses and recent trends are unclear; identifying them will enable targeted conservation strategies to support further recovery.
2. We review the evidence linking proposed drivers to impacts on bat populations in Europe, using the results of a previous cross-taxa semi-quantitative assessment as a framework. Broadly, the drivers reviewed relate to land-use practices, climate change, pollution, development and infrastructure, and human disturbance. We highlight where evidence gaps or conflicts present barriers to successful conservation and review emerging opportunities to address these gaps.
3. We find that the relative importance or impacts of the potential drivers of bat population change are not well understood or quantified, with conflicting evidence in many cases. To close key gaps in the evidence for responses of bat populations to environmental change, future studies should focus on the impacts of climate change, urbanisation, offshore wind turbines, and water pollution, as well as on mitigation measures and the synergistic effects of putative drivers.
4. To increase available evidence of drivers of bat population change, we propose utilising advances in monitoring tools and statistical methods, together with robust quantitative assessment of conservation interventions to mitigate threats and enable the effective conservation of these protected species.

INTRODUCTION

Despite global commitments in the Convention on Biological Diversity to reduce or halt biodiversity declines, targets are perpetually missed by governments (Mace et al. 2018, Convention on Biological Diversity 2019). Monitoring population trends has been a key part of frameworks set by governments, yet more ambitious actions are required,

moving from reducing losses to active gains in biodiversity (Convention on Biological Diversity 2019). Understanding not only how wildlife populations are faring, but also the factors driving population change, is essential to reversing negative trends.

Monitoring bioindicator species, such as bats (Russo & Jones 2015), is considered an efficient means of assessing the health of the habitats and species they rely on. Bats

provide valuable ecosystem services globally, including insect pest control, pollination, and seed dispersal (Kunz et al. 2011), and they are threatened by anthropogenic activities globally (O'Shea et al. 2016). Bat populations in Europe are thought to have experienced significant declines in the last century, and some species have undergone significant range contractions (Stebbins & Griffith 1986, Harris et al. 1995, Haysom et al. 2010). Proposed drivers of these historic declines include agricultural intensification and loss of habitat and roosts through development and exclusion from buildings (Hutson et al. 2001, Jones et al. 2009). Analysis of data collected by the UK's National Bat Monitoring Programme shows that, since 1997, populations of the bat species that are monitored are stable or increasing (Barlow et al. 2015, Bat Conservation Trust 2019). This is reflected in a prototype bat population trend indicator developed using data from nine European countries (van der Meij et al. 2015). The factors driving these recoveries are not fully understood, and it is unclear whether these trends are representative for all European species, as rarer species are missing from these data.

A recent semi-quantitative assessment of the 'broad drivers' of biodiversity loss in the UK identified agricultural management and climate change as the most important causes of population change for the species assessed, which included mammals, birds, amphibians, reptiles, insects, and vascular plants (Burns et al. 2016). Drivers most strongly affecting bats (Fig. 1) differed from those affecting all other assessed taxa (Burns et al. 2016). However, evidence

linking changes in the sizes of bat populations (bat population change) to external drivers is either lacking or low in quality (Figs 1 and 2, Appendix S1), and six of the UK's 17 breeding bat species were not assessed due to lack of evidence. Similarly, a recent review of British mammal populations lacked data for five bat species (Mathews et al. 2018).

We review current understanding of proposed drivers of European bat population change, using the 'broad drivers' proposed by Burns et al. (2016) as a framework. We highlight key evidence gaps and how they may be resolved using innovative data collection and statistical methods to provide a robust evidence base for mitigating the impacts of environmental change on European bat populations.

METHODS

To compile a list of potential drivers of bat population change in Europe, we used the 'broad drivers' proposed by Burns et al. (2016), supplementing them with others proposed elsewhere in the literature. To identify relevant studies, Web of Science and Google Scholar were searched using the following keywords: agriculture, agri-environment, artificial lighting, bat, climate, development, disease, disturbance, habitat fragmentation, habitat loss, human conflict, land-use, predation, pollution, road, roost loss, temperature, urbanisation, water, weather, wind turbine, woodland, and woodland management (Sutherland et al. 2006, Jones et al. 2009). Abstracts were reviewed, and we

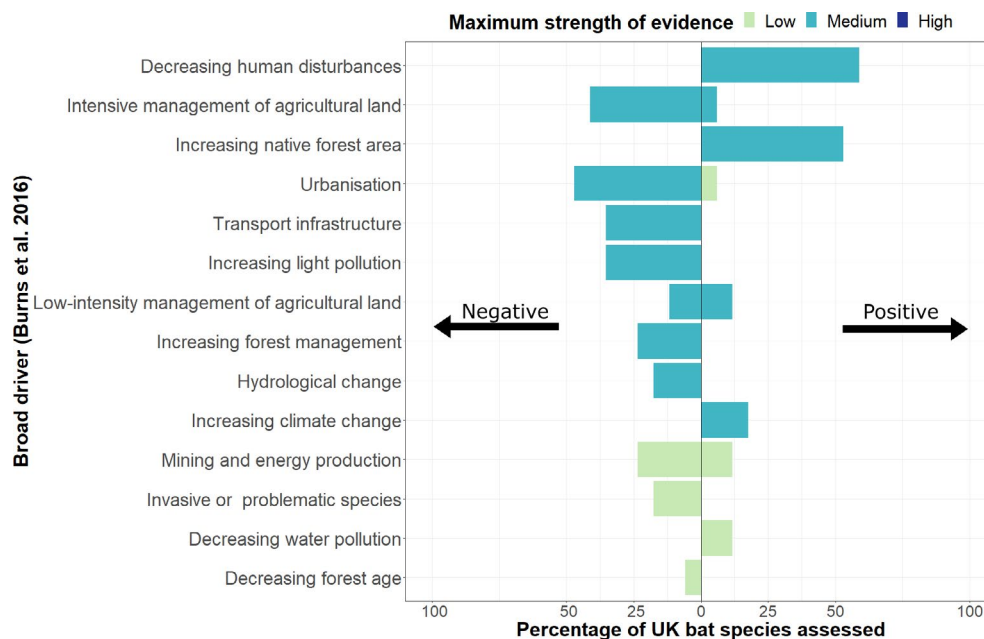


Fig. 1. The percentage of UK bat species assessed for each 'broad driver' included in the impact assessment by Burns et al. (2016), with direction of impact for each species. The maximum strength of evidence for each driver is shown by the shading of the bars and the direction of impact on the x-axis. The strength of evidence was not considered to be 'high' for any driver. Data used to create this Figure are from Burns et al. (2016).

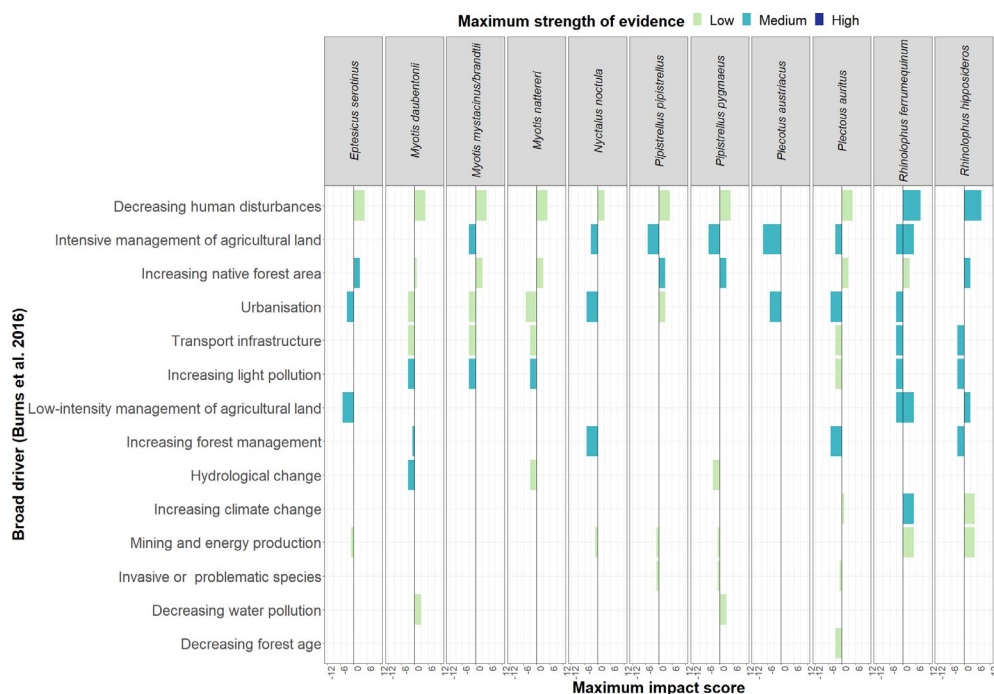


Fig. 2. The maximum impact of 'broad drivers' on each of the 11 UK bat species included in the impact assessment by Burns et al. (2016), with direction of impact (positive or negative) on the x-axis. The maximum strength of evidence is shown by the shading of the bars. The strength of evidence was not considered to be 'high' for any driver. Data used to create this Figure are from Burns et al. (2016).

sourced full manuscripts for papers containing information relevant to one or more of the above topics, and for those that provided some measure of impact on bat populations, abundance, reproductive success, mortality risk, or activity. Using the framework in Burns et al. (2016, Appendices S2–S4), we placed proposed drivers in two categories, separating those with 'reasonable evidence' for impacts on bat abundance, reproductive success, mortality risk, or activity indicating possible population-level change, and those with 'poor or conflicting evidence', where evidence for population-level impacts is lacking or conflicting (Table 1, Fig. 3). Due to limited evidence availability for impacts on European bats, driver topics 'disease' and 'predation' are discussed in conjunction with other proposed drivers (Appendix S5).

DRIVERS OF BAT POPULATION CHANGE WITH REASONABLE EVIDENCE

Human disturbance

Bats are often brought into direct conflict with humans due to roost choice, which has led to disturbance, deliberate persecution, and roost exclusion. Roost disturbance causes declines in bat abundance, distribution shifts within the roost, reductions in adult female survival (Grol et al.

2011, López-Roig & Serra-Cobo 2014), and reductions in bat community diversity (Galán et al. 2019). Many bats have adapted to use buildings for roosting, and historically, the use of remedial timber treatment chemicals resulted in large numbers of roosting bat deaths throughout Europe (Stebbins & Griffith 1986, Mitchell-Jones et al. 1989), likely contributing to hypothesised historic population declines. More recently, renovations or conversions of old buildings using new techniques and materials have caused roost disturbance and exclusion (Waring et al. 2013). Although roost exclusion may not immediately impact populations (Stone et al. 2015), reproductive success may be reduced (Brigham & Fenton 1986).

Woodland loss and management

Bats use woodland for foraging and roosting (e.g. Davy et al. 2007, Hill & Greenway 2008). Burns et al. (2016) found evidence of positive responses to increasing native forest cover in nine bat species. Globally, old-growth forests are important bat habitats (Crampton & Barclay 1998, Law & Chidel 2002, Altringham 2011), as they contain a diversity of microhabitats and complex canopies. Loss of old, native woodland most negatively affects species that benefit from a high level of canopy cover, including *Plecotus auritus* and *Barbastella barbastellus*, and those that rely

Table 1. List of 'broad drivers' published by Burns et al. (2016) and shown in Figs 1 and 2, and their relationship to the 'proposed drivers' discussed in this review, with the evidence quality grouping

Burns et al. (2016) drivers	Proposed drivers	Evidence quality
<ul style="list-style-type: none"> • Decreasing human disturbance • Intensive management of agricultural land • Low-intensity management of agricultural land 	<ul style="list-style-type: none"> Human disturbance Agricultural practices 	Reasonable
<ul style="list-style-type: none"> • Decreasing forest age • Increasing native forest area • Increasing forest management • Mining and energy production • Transport infrastructure • Increasing light pollution 	<ul style="list-style-type: none"> Woodland loss and management 	
<ul style="list-style-type: none"> • Urbanisation • Mining and energy production • Increasing climate change • Decreasing water pollution • Hydrological change • Decreasing human disturbance • Invasive or problematic species 	<ul style="list-style-type: none"> Onshore wind turbines Roads Artificial light Urbanisation Offshore wind turbines Climate change Water pollution Legislation and mitigation measures Driver interactions 	Poor or conflicting

on snags and tree holes for maternity roosts, such as *Myotis bechsteinii* (Russo et al. 2007, Dietz & Pir 2009, Murphy et al. 2012). Bats preferentially roost in trees with the large diameters, which are rare in young forests but can support larger colonies (Crampton & Barclay 1998, Law & Anderson 2000, Russo et al. 2004, 2010). Woodland management practices, such as significant canopy thinning, results in reduced tree age and reduced numbers of snags and tree holes. Loss of these features is thought to be a major driver of extinction in bats and other vertebrate groups (Hamblen et al. 2011), and is likely to have played a role in historic bat population declines.

Lack of roosting habitat is considered the primary reason for fewer occurrences of woodland specialists in plantation coniferous forest (Russo et al. 2010). However, small-scale felling in commercial plantations is thought to benefit open and edge space foragers such as *Pipistrellus* spp. and other mixed-space foragers (Tibbels & Kurta 2003, Kirkpatrick et al. 2017a, b, Thomas et al. 2019). Bats' high mobility enables resilience to local forest disturbance, unless perturbations are frequent and suitable alternative patches are scarce (Regnery et al. 2013). Forest fragmentation typically results in an edge-to-interior ratio ill-suited to bat species requiring large areas of continuous forest (Meyer et al. 2007). European forest loss and fragmentation remains a concern for specialist woodland species, such as *Myotis bechsteinii* (Hill & Greenway 2008, Dietz & Pir 2009), as it results in inbreeding in populations with access to less than ~25 ha of woodland, either in a single block or closely connected blocks (Greenway & Hill 2004, Durrant et al. 2008). Bat colonies in old-growth patches within intensive landscapes are sensitive to woodland degradation (Dietz et al. 2020). Burns et al. (2016)

highlighted that the bat species most frequently under-represented in the literature are threatened woodland specialists (Barova et al. 2018). It is currently unclear what the fine-scale habitat associations of many woodland bats are, and continued fragmentation or modification of remaining patches is a threat, given the reliance of all bats on woodland for various parts of their life histories. However, woodland heterogeneity is likely to be important in the landscape to satisfy the requirements of all species (Fuentes-Montemayor et al. 2013).

Agricultural practices

Agricultural expansion and intensification affect bat fitness and activity by reducing insect prey availability (Roeleke et al. 2020), increasing pesticide exposure, degrading foraging areas or reducing access to them (Department for Environment Food and Rural Affairs 2005), and reducing habitat connectivity (Frey-Ehrenbold et al. 2013). Intensive management of agricultural land was identified as negatively impacting six bat species by Burns et al. (2016). Several studies demonstrate that intensively managed arable habitats are avoided by bats such as *Nyctalus leislerii* (Waters et al. 1999), *Eptesicus serotinus* (Robinson & Stebbings 1997), and *Rhinolophus hipposideros* and *Rhinolophus ferrumequinum* (Duvergé & Jones 2003, Bontadina et al. 2008). However, high levels of activity of *Nyctalus*, *Eptesicus*, *Myotis*, and *Plecotus* spp. have been recorded over intensively managed (improved) grasslands (Vaughan et al. 1997, Linton 2009). High pesticide use due to agricultural intensification is also correlated with insect prey population declines (Conrad et al. 2006, Hallmann et al. 2014) and is likely to be affecting bat populations through ingestion

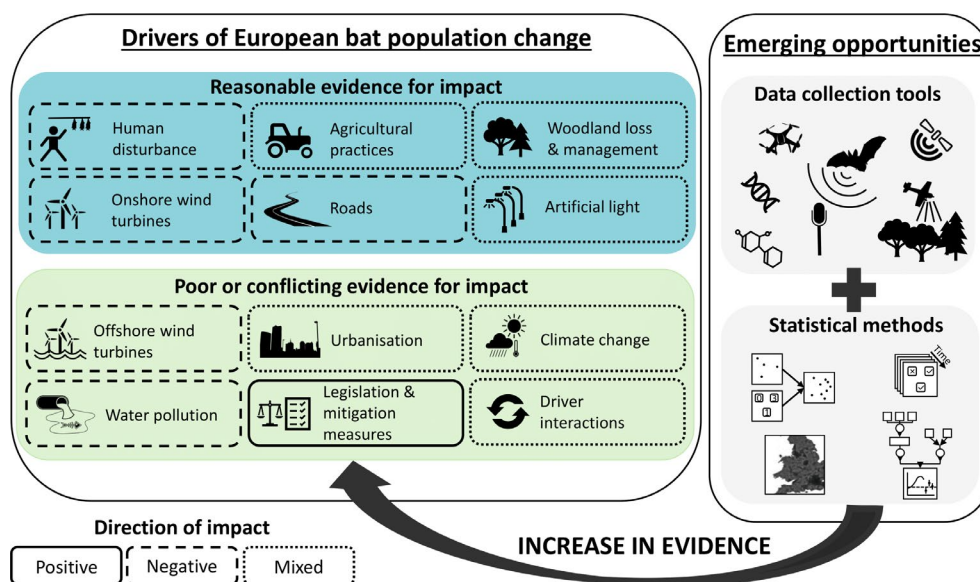


Fig. 3. Schematic of review, showing the proposed driver groupings based on evidence for impact, the direction of impact on bats (positive, negative, and mixed), and the emerging opportunities for increasing available evidence.

of contaminated prey (Stahlschmidt et al. 2017), as it affects insectivorous bird populations in the Netherlands (Hallmann et al. 2014).

Loss of linear landscape elements that are identified as important bat foraging and commuting habitats, such as hedgerows, treelines, and canals (Vaughan et al. 1997, Russ & Montgomery 2002, Frey-Ehrenbold et al. 2013), is a common consequence of agricultural intensification. Increasing energy expenditure and decreasing foraging opportunities affect bat fitness (Russ & Montgomery 2002, Roeleke et al. 2020). *Nyctalus noctula* uses direct flight more in cropland-dominated landscapes where insect prey is more ephemeral than in complex forest-dominated landscapes (Roeleke et al. 2020). A higher amount of semi-natural habitat had a positive impact on *Tadarida teniotis* and *Pipistrellus kuhli* activity in Mediterranean agroecosystems (Kahnonitch et al. 2018). Low-intensity management of agricultural land has positive effects on bat populations (Burns et al. 2016); organic farms are associated with larger hedgerows and higher bat abundance, species richness, and foraging activity (Wickramasinghe et al. 2003, Fuller et al. 2005). Moderate livestock grazing also sustains semi-open habitats and a source of high prey density over dung pats, providing foraging opportunities for many species (Vaughan et al. 1997, Duvergé & Jones 2003, Downs & Sanderson 2010, Ancillotto et al. 2017).

Evidence for the effects of measures to improve agricultural landscapes for biodiversity and bats remains conflicting. Burns et al. (2016) found evidence for positive impacts of sustainable farm practices, including agri-environment schemes, for only *Rhinolophus hipposideros* and

Rhinolophus ferrumequinum. Agri-environment schemes are highly diverse in their nature (Natural England 2012) and effectiveness. For instance, when comparing activity of six bat species on farms under a Welsh agri-environment scheme to conventional management, Angell et al. (2019) found little difference, although they suggest that the measures were not mature enough or present at a large enough spatial scale to be effectual. Untrimmed hedgerows, a management recommendation under many agri-environment scheme (Natural England 2012), are associated with higher bat activity than closely trimmed hedges (Froidevaux et al. 2019). Improving connectivity in intensively managed landscapes with hedgerows and trees is important for species reliant on linear features, such as *Rhinolophus hipposideros* (Froidevaux et al. 2017), and for those with intermediate to high mobility, such as *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus*, and *Nyctalus* spp. Landscape connectivity can reduce energy expenditure and enhance foraging opportunities for bats (Boughey et al. 2011).

Onshore wind turbines

Wind energy production has increased rapidly in recent decades, resulting in conflicts with various wildlife species globally (Sterze & Pogacnik 2008), including bats (Lintott et al. 2016b). Bat mortality at wind farms has been documented, with research showing that migratory species suffer disproportionately, both in North America (Arnett & Baerwald 2013, Frick et al. 2017a) and in Europe (Rydell et al. 2010). Fatalities are concentrated during late summer in the temperate Northern Hemisphere (Rydell et al.

2010, Arnett & Baerwald 2013), with a smaller peak observed in early spring (Rydell et al. 2010), probably due to migratory movements and mating behaviour. Rodrigues et al. (2015) categorised the behaviour of 35 species of European bat in relation to wind farms, and listed 21 species considered to be at risk of collision, which were primarily edge or open habitat foragers. Bat activity at onshore wind turbines depends on factors such as wind speed, which is negatively correlated with bat activity in the rotor zones (Wellig et al. 2018). Indirect impacts of wind energy development include a loss of foraging habitat or roosts through replacement or fragmentation of natural habitat (Rodrigues et al. 2015, Kirkpatrick et al. 2017b).

Roads

Bat-specific impacts of roads include mortality from vehicle collisions, habitat destruction and fragmentation, edge effects, barrier effects, road avoidance, chemical pollution, and disturbance from light and noise (Forman & Alexander 1998, Berthinussen & Altringham 2012b). Burns et al. (2016) found evidence for negative impacts of increased transport infrastructure for six species. High numbers of bats are killed on roads (Fensome & Mathews 2016); casualties are especially high for low-flying species and when roads cut through important bat habitat (Gaisler et al. 2009, Lesiński et al. 2010, Medinas et al. 2012). Bats actively avoid large roads; activity of *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus*, *Nyctalus*, and *Myotis* spp. is positively correlated with distance from the road (Berthinussen & Altringham 2012b). Roads also create acoustic barriers: bat activity is reduced at least 20 m from traffic noise playback, even in the absence of the physical features such as cars (Finch et al. 2020). Foraging time and prey capture success is reduced up to 60 m from a highway, due to traffic noise masking the sounds of insect movements (Schaub et al. 2008, Siemers & Schaub 2011). This suggests that areas close to highways are less suitable for gleaning species, such as *Myotis bechsteinii* and *Plecotus* spp., which use passive listening as well as echolocation to detect insect prey (Dietz et al. 2009). The impacts road avoidance and vehicle collisions have on the long-term fitness and population declines of bats have yet to be investigated.

Artificial light

Burns et al. (2016) found a lack of evidence for the impact of light pollution on bat populations; however, recently the number of studies assessing the impacts of artificial light at night (ALAN) on bats has increased. Evidence suggests that some species, such as *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*, exploit the insects attracted to

the light (Rydell 2006, Lacoëuilhe et al. 2014, Zeale et al. 2018). However, species that prefer low-light conditions for emergence or foraging, such as *Rhinolophus ferrumequinum*, *Rhinolophus hipposideros*, *Myotis emarginatus*, *Myotis oxygnathus*, and other *Myotis* spp., are adversely affected by ALAN and display reduced activity (Downs 2003, Boldogh et al. 2007, Stone et al. 2009). Bats also respond differently to differences in light intensity: *Myotis* spp. are more active in areas of lower light intensity, but *Pipistrellus pipistrellus* activity increases with intensity (Rowse et al. 2018). Individual fitness may be reduced in light-shy species such as *Nyctalus leislerii*, *Myotis* spp., and *Plecotus* spp., due to their avoidance of lit areas to prevent exposure to predators, or because insects are attracted away from dark foraging patches (Fure 2012). This may increase energetic expenditure and reduce foraging time (Stone et al. 2012, Lacoëuilhe et al. 2014), resulting in increased mortality and population losses, yet direct evidence for this is lacking.

EVIDENCE GAPS: DRIVERS OF BAT POPULATION CHANGE WITH POOR OR CONFLICTING EVIDENCE

Urbanisation

Urban environments present both ecological constraints and opportunities for biodiversity and are projected to triple in area by 2030 (Seto et al. 2012), yet, evidence of the impact of urbanisation on bats is conflicting. Urbanisation includes ALAN and roads, as well as providing roosting opportunities for bats in buildings. In central Europe, the 'urban heat island' effect is thought to be facilitating a northward range expansion of *Pipistrellus nathusii* and *Hypsugo savii* (Ancillotto et al. 2018, Sachanowicz et al. 2019). A recent global meta-analysis identified bat traits associated with urban tolerance, including flexible roosting requirements, higher aspect ratios and edge and open space foraging (Jung & Threlfall 2018), exhibited by *Pipistrellus nathusii* and *Pipistrellus pipistrellus* (Hale et al. 2012, Lintott et al. 2015). In contrast, Lintott et al. (2016a) suggest that *Pipistrellus pipistrellus* is negatively impacted by urbanisation, like *Myotis* spp., *Plecotus* spp., and *Eptesicus serotinus*, which are rarely found in urban environments (Vaughan et al. 1997, Lintott et al. 2015). Even where synurbic species' population densities are high in urban areas, reproductive success and body condition may be low, leading to longer term population declines (Coleman & Barclay 2011). Improving urban landscapes by increasing tree canopy height and the percentage tree and vegetation understory cover may promote bat activity and mediate the impact of ALAN (Threlfall et al. 2017, Straka et al. 2019). However, the extent to which green infrastructure

mitigates negative impacts of urbanisation on bats is likely to be species-specific and has not been clearly established (Hale et al. 2012, Pearce & Walters 2012).

Climate change

The impact of climate change on biodiversity is well documented (e.g. Parmesan & Yohe 2003, Spooner et al. 2018). Temperatures have increased over the past four decades; in 2018, global average temperature was increased by >1 °C, and precipitation was below average in northern regions and above average in southerly regions (Copernicus Climate Change Service 2019). Mild winter temperatures as a result of climate warming over the last 20 years are thought to have contributed to the recovery of UK populations of *Rhinolophus hipposideros* and *Rhinolophus ferrumequinum* (Battersby 2005, Schofield 2008), with increased spring temperatures and reduced spring precipitation also benefitting the latter (Froidevaux et al. 2017). Burns et al. (2016) were able to assess just three UK bat species for impacts of increasing climate change, yet identified it as the second most important driver of changes to UK biodiversity. Bowler et al. (2015) found no relationship between species population trends and temperature niche for bats in Germany, and suggest that the effects of climate change may currently be masked by the success of conservation measures following population declines in the latter half of the 20th Century. It is unlikely that climate change is currently a major driver of the population trends of most European bat species, and it is improbable that it was a factor in the hypothesised historic declines.

Predicted responses of bat species to future climate warming include northward range shifts (UNEP 2006, Rebelo et al. 2010) as observed for *Pipistrellus kuhlii* and *Hypsugo savii* (Sachanowicz et al. 2006, Ancillotto et al. 2018), resulting in changes to local species diversity. Increased summer temperatures may cause maternity roosts to overheat, reducing reproductive success if suitable alternatives are unavailable (Lourenço & Palmeirim 2004). Shifts to phenology are expected, with earlier spring emergences or more frequent rousing from hibernation during milder winters, leading to increased mortality risk if there is a mismatch with insect prey availability (Jones et al. 2009, Rebelo et al. 2010); this is most likely to affect bat species that are specialist foragers. Aerial-hawking bats are predicted to be highly sensitive to changes in climate (Sherwin et al. 2013), as their activity is dependent on air temperature and insect abundance (Ciechanowski et al. 2007). Generalist bat species are, therefore, most likely to benefit from climate change, as has been shown for butterflies in the UK (Warren et al. 2001). How specialist bat species will respond to climate change remains uncertain.

Offshore wind turbines

Notable evidence gaps remain for impacts of offshore wind turbines, which are increasing in number globally (Arnett et al. 2015). Monitoring collisions of bats with offshore wind turbines is challenging, as injured bats or carcasses are unlikely to be recovered. Twelve European bat species are considered to be long-distance or regional migrants. Many of them cross the North and Baltic Seas (Hutterer et al. 2005), which brings them into contact with offshore wind turbines (Ahlén et al. 2009, Limpens et al. 2017, National Nathusius' Pipistrelle Project, bats.org.uk). It is thought that primarily female *Pipistrellus nathusii* migrate from the UK to northern Europe, where parturition and the rearing of pups occurs. Offshore turbines pose a threat to this species, potentially causing mass mortalities or isolating subsections of the population. The frequency that other species travel over sea is poorly known, but may increase with climate change as European species' range margins move northwards (Rebelo et al. 2010), increasing contact with offshore turbines.

Water pollution

All bats rely on waterbodies for hydration and are at risk of exposure to or ingestion of water pollutants through bioaccumulation (Vaughan et al. 1996), although no direct links have been established to impacts on populations. Indirectly, eutrophication and acidification of water affects insect prey abundance, such as downstream of sewage outputs (Vaughan et al. 1996). Rivers, canals, and lakes are important foraging sites for species such as *Myotis dasycneme* (Sijpe et al. 2004, Heim et al. 2018) *Myotis daubentonii* (Lesiński et al. 2009), *Pipistrellus pygmaeus* (Wickramasinghe et al. 2003) *Pipistrellus pipistrellus*, *Nyctalus leisleri*, and *Nyctalus noctula*, as prey abundance is high near water (Vaughan et al. 1997). Burns et al. (2016) found evidence for the positive impact of decreasing water pollution on five of these species. However, two-thirds of Europe's surface water is estimated to be in poor ecological status (Posthuma et al. 2020), and some pollutants, such as toxic heavy metals, may persist in the environment for many years (Walker et al. 2007). Another pollutant not yet studied in bats is microplastic. Experimental evidence demonstrates that microplastics are transferred ontologically from an insect's aquatic life stage to the terrestrial adult stage (Al-Jaibachi et al. 2018). This has important implications for insectivorous organisms such as bats, as it is likely that ingesting polluted insects results in microplastics building up in bats' bodies. Given the longevity and slow reproductive cycles of bats (Altringham 2011), the full impacts of water pollution on populations may not yet have been realised.

Legislation and mitigation measures

Due to legislation, mitigation measures are required to protect and to reduce the impact of anthropogenic activities and development on bat populations, yet for many there is little evidence of their effectiveness in reducing bat population declines. The European Union legislation introduced in 1991 (EUROBATS 2006) and 1992 (Council of the European Union 1992) protects species across the European Union and is thought to have reduced the amount of deliberate disturbance and persecution suffered by bats. Despite legislation, roost destruction frequently occurs (Stone et al. 2013), suggesting that it is not sufficient. Furthermore, quantifying the impact of these legislative measures on European bat population remains difficult, with no scientific publications providing evidence of impacts of legal protection on population trends in Europe. To comply with legislation and mitigate impacts of building development on bats, bat roost boxes or bat lofts are used, with the latter considered more effective (Lintott & Mathews 2018). Underpasses and overhead gantries (bridges) are installed to mitigate the impacts of road building and the resulting habitat fragmentation. Some species use underpasses (Kerth & Melber 2009); however, evidence for gantry use by bats is negligible (Berthinussen & Altringham 2012a).

Mitigating the mortality risks posed by wind turbines to bats is urgent, yet methods for estimating mortalities and the risks posed to bat populations by wind turbines at local, national, and continental scales are inadequate. Lintott et al. (2016b) show that, even when Environmental Impact Assessments were carried out pre-construction at onshore sites, the risk to bats was not identified accurately at half of the study sites investigated. Recent guidelines suggest requirements for surveying species assemblage, quantifying spatial and temporal activity distribution, and identifying local habitat use by bats prior to turbine placement (Scottish Natural Heritage et al. 2019). Variation in post-construction field surveillance methods used at wind turbines and in calculations of death rates reduces the accuracy of mortality estimations (Berthinussen et al. 2014). Adaptive response measures have been proposed, such as switching off turbines during low nocturnal wind speeds (Wellig et al. 2018) or using deterrents; these could be applied during seasonal periods of high activity such as during migration and mating periods (Rydell et al. 2010, Arnett & Baerwald 2013), to reduce mortalities. Determining the effectiveness of these assessments and measures is particularly pressing at offshore wind energy sites.

To combat the negative impacts of ALAN on bats, mitigation measures suggested include using certain spectra

or part-night lighting (Zeale et al. 2018). The latter is unlikely to benefit bats, as their evening emergence coincides with when ALAN is most needed by humans. Studies in which various spectra were used in light emitting diode (LED) street lights indicate that red lights may benefit slower-flying *Myotis* and *Plecotus* spp. (Spoelstra et al. 2017), whereas *Pipistrellus* spp. were more active under white, green, or orange LED lights (Spoelstra et al. 2017, Zeale et al. 2018). Low-intensity lighting is likely to reduce light spill, mediating the impact on light-averse species (Rowse et al. 2018). The varied responses of bats to the presence of different artificial light types, spectra and intensities suggest that a single mitigation method for ALAN is unlikely to benefit all bat species. There is well-established literature on conservation interventions and mitigation measures for bats that also highlights a lack of quantitative evidence for their effectiveness (Berthinussen et al. 2019).

Driver interactions

We have primarily discussed impacts of drivers individually in this review, yet it is likely that the impact of each on population change in bats is modulated by others. A prime example of this is increasing climate warming, which may allow species to expand their ranges northward, but only if suitable habitat and prey are available. Furthermore, the risk posed by existing and emergent diseases to European bat populations may be exacerbated by climate change. Emergent diseases can devastate populations, as shown by the impact of White Nose Syndrome on bat populations in North America (Frick et al. 2017b). However, there is little evidence available to assess the threat of emergent diseases on European bat populations. The road network presents a further example where many stressors may be acting in tandem on bat populations. It is currently poorly understood how effects of ALAN interplay with risks of collision with vehicles, and whether road noise pollution may exacerbate this by causing disorientation and avoidance. Air pollution is high around roads and in urban areas, yet the combined impacts of pollution, roads, and urbanisation on bat species have not been studied. Increased predation is a possible consequence of urbanisation. Domestic cats are considered to be the most significant predators of bats, killing an estimated 250000 bats per year in the UK; house-roosting species such as *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus*, and *Plecotus auritus* are primarily at risk (Altringham 2011), yet other species may also be vulnerable. Bat captures by tawny owls *Strix aluco* are highest in urban habitats and suburban forests and lowest in forest interiors (Woods et al. 2003). The impacts of predation on bat species are

currently not well understood, particularly how anthropogenic environmental change may conflate existing risks. Identifying synergistic impacts of anthropogenic pressures on bat populations is vital if conservation strategies are to be successful.

EMERGING OPPORTUNITIES

Emerging technologies present exciting opportunities for providing evidence to address evidence gaps identified in this review. Recent advances in passive acoustic monitoring hardware, such as the low-cost AudioMoth (Hill et al. 2018), coupled with improvements to automated call detection (Mac Aodha et al. 2018), allow the geographic and temporal upscaling of bat monitoring and assessment of population-level responses to environmental change. However, automated call classification tools require representative training data, and some species are challenging to monitor with passive acoustic monitoring, particularly *Plecotus* spp., woodland specialists with quiet calls, and *Myotis* spp. due to the difficulties in distinguishing interspecific calls. Thus, there is an urgent need for geographically and taxonomically comprehensive open-source bat call libraries to train classification tools (Gibb et al. 2018). Combining passive acoustic monitoring with technologies such as unmanned aerial vehicles, Light Detection and Ranging (LiDAR), and global positioning system (GPS) data loggers would yield detailed evidence of bat activity patterns. For instance, LiDAR mapping of woodland at a fine scale, paired with passive acoustic monitoring, may provide evidence for the impacts of woodland management and fragmentation on bat activity (Froidevaux et al. 2016) have recently been combined with sensors to assess call modulation by *Tadarida brasiliensis* during roost re-entry in response to flight height or the presence of conspecifics (Klopper & Kinniry 2018). However, use of this technology for monitoring biodiversity is in its infancy and the responses of bats to such airborne devices should be cautiously assessed to prevent harm. GPS data loggers have been too heavy to be used ethically on most European bat species, yet are rapidly decreasing in weight, and, if combined with passive acoustic monitoring, they could enhance our understanding of intra- and interspecific bat communication.

Evidence for large-scale bat movements, including data on home-range size and migration routes, is lacking, and molecular and genetic tools are possible methods for assessing susceptibility to environmental change. Bat population sizes and the impacts of environmental perturbations, such as climate change, can be estimated using molecular tools measuring genetic variation (Rebelo et al. 2012, Razgour et al. 2013). Population genetics

has been used to study the impacts of habitat fragmentation on woodland specialists *Rhinolophus ferrumequinum* in the UK and Ireland (Rossiter et al. 2000, Dool et al. 2016) and *Myotis bechsteinii* in England (Durrant et al. 2008); this research has identified genetically isolated populations as being vulnerable to stochastic events or further habitat perturbations. Stable isotope analysis provides a broader picture than banding and re-capture data for understanding bat migration and movement patterns where conventional tracking methods are unsuitable (e.g. Cryan et al. 2004, Voigt et al. 2016, Lehnert et al. 2018). These methods may be valuable for understanding movements due to range shifts and identifying threats encountered during movements. Furthermore, past range shifts in response to climatic changes can be identified using molecular tools, and estimations of bat population size can be made.

Advances in data collection tools are complemented by improvements to statistical methods, such as species distribution models, occupancy modelling, hierarchical Bayesian models, and data integration. Using the latter to combine the growing, but often disparate, number of existing datasets, from unstructured to structured survey data, can increase the geographic or temporal scale of a study (Isaac et al. 2019, Zipkin et al. 2019). Augmenting count data from roost surveys or captures with acoustic data is particularly useful when assessing population changes in rare species (Banner et al. 2018). False-positive site occupancy models are applied to data with different error sources, such as false-positive identifications (Clement et al. 2014, Banner et al. 2018), a common problem with bat acoustic data even with improving automated call detection and classification tools, due to the plasticity or crypticity in echolocation calls (Russo & Jones 2002, Berger-Tal et al. 2007). Complex hierarchical Bayesian models are becoming increasingly less computationally expensive and further increase the accessibility of spatiotemporal models, as multiple sources of uncertainty may be incorporated (e.g. Isaac et al. 2014, Ruiz-Gutierrez et al. 2016). Using these improved statistical methods, a wider selection of passive acoustic monitoring data, including poorer quality recordings, may be used to track changes to bat populations over time. These statistical tools present opportunities for understanding historic trends in bat populations and for harnessing the rapidly increasing number of data, not only to track population trends in time and space, but also to understand their drivers.

CONCLUSION

In this review, we have synthesised evidence for proposed influences on bat population change in Europe and identified a lack of evidence for impacts on European bat

population trends, finding predominantly evidence for impacts on abundance activity. Key evidence gaps remain in determining the effectiveness of legal protection, the impacts of future climate warming and urbanisation, as well as evaluating synergistic effects of anthropogenic environmental change. Whilst we have focussed on drivers of bat population change in Europe, many are relevant to bats in tropical and sub-tropical regions, such as urbanisation (Liu et al. 2020), agricultural intensification, and deforestation (Meyer et al. 2007). Robust, quantitative assessments of conservation interventions and impacts of environmental change on bat populations are becoming more feasible with the advances in data collection and analysis tools, enabling the relative importance of threats to bat populations in Europe and globally to be disentangled.

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REFERENCES

- Ahlén I, Baagøe HJ, Bach L (2009) Behavior of Scandinavian bats during migration and foraging at sea. *Journal of Mammalogy* 90: 1318–1323.
- Al-Jaibachi R, Cuthbert RN, Callaghan A (2018) Up and away: ontogenic transference as a pathway for aerial dispersal of microplastics. *Biology Letters* 14: 20180479.
- Altringham JD (2011) *Bats – From Evolution to Conservation*. Oxford University Press, Oxford, UK.
- Ancillotto L, Ariano A, Nardone V, Budinski I, Rydell J, Russo D (2017) Effects of free-ranging cattle and landscape complexity on bat foraging: implications for bat conservation and livestock management. *Agriculture, Ecosystems & Environment* 241: 54–61.
- Ancillotto L, Budinski I, Nardone V, Di Salvo I, Della Corte M, Bosso L, Conti P, Russo D (2018) What is driving range expansion in a common bat? Hints from thermoregulation and habitat selection. *Behavioural Processes* 157: 540–546.
- Angell RL, Langton SD, MacDonald MA, Skates J, Haysom KA (2019) The effect of a Welsh agri-environment scheme on bat activity: a large-scale study. *Agriculture, Ecosystems & Environment* 275: 32–41.
- Arnett EB, Baerwald EF (2013) Impacts of wind energy development on bats: implications for conservation. In: Adams RA, Pedersen SC (eds) *Bat Evolution, Ecology, and Conservation*, 435–456. Springer, New York, New York, USA.
- Arnett EB, Baerwald EF, Mathews F, Rodrigues L, Rodríguez-Durán A, Rydell J, Villegas-Patraca R, Voigt CC (2015) Impacts of wind energy development on bats: a global perspective. In: Voigt CC, Kingston T (eds) *Bats in the Anthropocene: Conservation of Bats in a Changing World*, 295–323. Springer International Publishing, Cham, Switzerland.
- Banner KM, Irvine KM, Rodhouse TJ, Wright WJ, Rodriguez RM, Litt AR (2018) Improving geographically extensive acoustic survey designs for modeling species occurrence with imperfect detection and misidentification. *Ecology and Evolution* 8: 6144–6156.
- Barlow KE, Briggs P, Haysom K, Hutson M, Lechiara NL, Racey PA, Walsh L, Langton SD (2015) Citizen science reveals trends in bat populations: the National Bat Monitoring Programme in Great Britain. *Biological Conservation* 182: 14–26.
- Barova S, Striet A, Marchaia G, Thauront M (2018) *Action Plan for the Conservation of All Bat Species in the European Union 2018–2024*. European Commission, Brussels, Belgium.
- Bat Conservation Trust (2019) *National Bat Monitoring Programme Annual Report 2018 2*. London, UK.
- Battersby J (2005) *UK Mammals: Species Status and Population Trends. First Report by the Tracking Mammals Partnership*. JNCC, Peterborough, UK.
- Berger-Tal O, Berger-Tal R, Korine C, Holderied MW, Fenton MB (2007) Echolocation calls produced by Kuhl's pipistrelles in different flight situations. *Journal of Zoology* 274: 59–64. <https://doi.org/10.1111/j.1469-7998.2007.00357.x>.
- Berthinussen A, Altringham J (2012a) Do bat gantries and underpasses help bats cross roads safely? *PLoS One* 7: e38775.
- Berthinussen A, Altringham J (2012b) The effect of a major road on bat activity and diversity. *Journal of Applied Ecology* 49: 82–89.
- Berthinussen A, Richardson O, Altringham J (2014) *Bat Conservation: Global Evidence for the Effects of Interventions*. Synopses of Conservation Evidence, Vol. 5. Pelagic Publishing, Exeter, UK.
- Berthinussen A, Richardson OC, Altringham JD (2019) *Bat Conservation: Global Evidence for the Effects of Interventions 2019 Edition*. Pelagic Publishing, Exeter, UK.

- Boldogh S, Dobrosi D, Samu P (2007) The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterologica* 9: 527–534.
- Bontadina F, Schmieid SF, Beck A, Arlettaz R (2008) Changes in prey abundance unlikely to explain the demography of a critically endangered Central European bat. *Journal of Applied Ecology* 45: 641–648.
- Boughey KL, Lake IR, Haysom KA, Dolman PM (2011) Improving the biodiversity benefits of hedgerows: how physical characteristics and the proximity of foraging habitat affect the use of linear features by bats. *Biological Conservation* 144: 1790–1798.
- Bowler DE, Haase P, Kröncke I, Tackenberg O, Bauer HG, Brendel C et al. (2015) A cross-taxon analysis of the impact of climate change on abundance trends in central Europe. *Biological Conservation* 187: 41–50.
- Brigham RM, Fenton MB (1986) The influence of roost closure on the roosting and foraging behaviour of *Eptesicus fuscus* (Chiroptera: Vespertilionidae). *Canadian Journal of Zoology* 64: 1128–1133.
- Burns F, Eaton MA, Barlow KE, Beckmann BC, Brereton T, Brooks DR et al. (2016) Agricultural management and climatic change are the major drivers of biodiversity change in the UK. *PLoS One* 11: e0151595.
- Ciechanowski M, Zajac T, Biłas A, Dunajski R (2007) Spatiotemporal variation in activity of bat species differing in hunting tactics: effects of weather, moonlight, food abundance, and structural clutter. *Canadian Journal of Zoology* 85: 1249–1263.
- Clement MJ, Rodhouse TJ, Ormsbee PC, Szewczak JM, Nichols JD (2014) Accounting for false-positive acoustic detections of bats using occupancy models. *Journal of Applied Ecology* 51: 1460–1467.
- Coleman JL, Barclay RMR (2011) Influence of urbanization on demography of little brown bats (*Myotis lucifugus*) in the prairies of North America. *PLoS One* 6: e20483.
- Conrad KF, Warren MS, Fox R, Parsons MS, Woiwod IP (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation* 132: 279–291.
- Convention on Biological Diversity (2019) *Report of the Conference of the Parties to the Convention on Biological Diversity on its Fourteenth Meeting*. Sharm El-Sheikh, Egypt.
- Copernicus Climate Change Service (2019) *European State of the Climate 2018*. <https://climate.copernicus.eu/european-state-of-the-climate>.
- Council of the European Union (1992) *Council Directive 92/43/EEC of 21 May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora*.
- Crampton LH, Barclay RMR (1998) Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. *Conservation Biology* 12: 1347–1358.
- Cryan PM, Bogan MA, Rye RO, Landis GP, Kester CL (2004) Stable hydrogen isotope analysis of bat hair as evidence for seasonal molt and long-distance migration. *Journal of Mammalogy* 85: 995–1001.
- Davy CM, Russo D, Fenton MB (2007) Use of native woodlands and traditional olive groves by foraging bats on a Mediterranean island: consequences for conservation. *Journal of Zoology* 273: 397–405.
- Department for Environment Food and Rural Affairs (2005) *Agricultural Practice and Bats: a Review of Current Research Literature and Management Recommendations*. Project BD2005. Defra, London, UK.
- Dietz C, von Helversen O, Nill D (2009) *Bats of Britain, Europe & Northwest Africa*. A&C Black Publishers Ltd, London, UK.
- Dietz M, Bögelsack K, Krannich A, Simon O (2020) Woodland fragments in urban landscapes are important bat areas: an example of the endangered Bechstein's bat *Myotis bechsteinii*. *Urban Ecosystems* 23: 1359–1370.
- Dietz M, Pir JB (2009) Distribution and habitat selection of *Myotis bechsteinii* in Luxembourg: implications for forest management and conservation. In: Krystufek B, Amori G, Mitchell-Jones A, Zima J (eds) *Mammal Conservation in Europe: Status and Priorities. Collection of Papers from the 5th European Congress of Mammalogy, Siena, Italy, 21–26 September 2007*, 327–340. Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Brno, Czech Republic.
- Dool SE, Puechmaille SJ, Kelleher C, McAney K, Teeling EC (2016) The effects of human-mediated habitat fragmentation on a sedentary woodland-associated species (*Rhinolophus hipposideros*) at its range margin. *Acta Chiropterologica* 18: 377–393.
- Downs N (2003) The effects of illuminating the roost entrance on the emergence behaviour of *Pipistrellus pygmaeus*. *Biological Conservation* 111: 247–252.
- Downs NC, Sanderson LJ (2010) Do bats forage over cattle dung or over cattle? *Acta Chiropterologica* 12: 349–358.
- Durrant CJ, Beebee TJC, Greenaway F, Hill DA (2008) Evidence of recent population bottlenecks and inbreeding in British populations of Bechstein's bat, *Myotis bechsteinii*. *Conservation Genetics* 10: 489–496.
- Duvergé P, Jones G (2003) Use of farmland habitats by greater horseshoe bats. In: Tattersall F, Manley W (eds) *Conservation and Conflict. Mammals and Farming in Britain*, 64–81. The Linnean Society, London, UK.
- EUROBATS (2006) *1991–2006 EUROBATS Celebrates Its 15th Anniversary*. UNEP/EUROBATS, Bonn, Germany.
- Fensome AG, Mathews F (2016) Roads and bats: a meta-analysis and review of the evidence on vehicle collisions and barrier effects. *Mammal Review* 46: 311–323.
- Finch D, Schofield H, Mathews F (2020) Traffic noise playback reduces the activity and feeding behaviour of free-living bats. *Environmental Pollution* 263: 114405.

- Forman RTT, Alexander LE (1998) Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29: 207–231.
- Frey-Ehrenbold A, Bontadina F, Arlettaz R, Obrist MK (2013) Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *Journal of Applied Ecology* 50: 252–261.
- Frick WF, Baerwald EF, Pollock JF, Barclay RMR, Szymanski JA, Weller TJ et al. (2017a) Fatalities at wind turbines may threaten population viability of a migratory bat. *Biological Conservation* 209: 172–177.
- Frick WF, Cheng TL, Langwig KE, Hoyt JR, Janicki AF, Parise KL, Foster JT, Kilpatrick AM (2017b) Pathogen dynamics during invasion and establishment of white-nose syndrome explain mechanisms of host persistence. *Ecology* 98: 624–631.
- Froidevaux JSP, Boughey KL, Barlow KE, Jones G (2017) Factors driving population recovery of the greater horseshoe bat (*Rhinolophus ferrumequinum*) in the UK: implications for conservation. *Biodiversity and Conservation* 26: 1601–1621.
- Froidevaux JSP, Boughey KL, Hawkins CL, Broyles M, Jones G (2019) Managing hedgerows for nocturnal wildlife: do bats and their insect prey benefit from targeted agri-environment schemes? *Journal of Applied Ecology* 56: 1610–1623.
- Froidevaux JSP, Zellweger F, Bollmann K, Jones G, Obrist MK (2016) From field surveys to LiDAR: shining a light on how bats respond to forest structure. *Remote Sensing of Environment* 175: 242–250.
- Fuentes-Montemayor E, Goulson D, Cavin L, Wallace JM, Park KJ (2013) Fragmented woodlands in agricultural landscapes: the influence of woodland character and landscape context on bats and their insect prey. *Agriculture, Ecosystems & Environment* 172: 6–15.
- Fuller RJ, Norton LR, Feber RE, Johnson PJ, Chamberlain DE, Joys AC (2005) Benefits of organic farming to biodiversity vary among taxa. *Biology Letters* 1: 431–434.
- Fure A (2012) Bats and lighting – six years on. *London Naturalist* 91: 69–88.
- Gaisler J, Řehák Z, Bartonička T (2009) Bat casualties by road traffic (Brno-Vienna). *Acta Theriologica* 54: 147–155.
- Galán J, Núñez-Lahuerta C, López-García JM, Cuenca-Bescós G (2019) Did humans disturb bats? Exploring the hominin-chiropter interactions in the Sierra de Atapuerca sites (early to Middle Pleistocene, Spain). *Quaternary Science Reviews* 226: 106018.
- Gibb R, Browning E, Glover-Kapfer P, Jones KE (2018) Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. *Methods in Ecology and Evolution* 10: 169–185.
- Greenway F, Hill DA (2004) *Woodland Management Advice for Bechstein's and Barbastelle Bat*. Natural England, Peterborough, UK.
- Grol BPFE, Voute AM, Verboom B (2011) The influence of a Christmas market on hibernating bats in a man-made limestone cave. *Lutra* 54: 69–88.
- Hale JD, Fairbrass AJ, Matthews TJ, Sadler JP (2012) Habitat composition and connectivity predicts bat presence and activity at foraging sites in a large UK conurbation. *PLoS One* 7: e33300.
- Hallmann CA, Foppen RPB, van Turnhout CAM, de Kroon H, Jongejans E (2014) Declines in insectivorous birds are associated with high neonicotinoid concentrations. *Nature* 511: 341–343.
- Hambler C, Henderson PA, Speight MR (2011) Extinction rates, extinction-prone habitats, and indicator groups in Britain and at larger scales. *Biological Conservation* 144: 713–721.
- Harris S, Morris P, Wray S, Yalden D (1995) *A Review of British Mammals: Population Estimates and Conservation Status of British Mammals Other Than Cetaceans*. JNCC, Peterborough, UK.
- Haysom KA, Jones G, Merrett D, Racey PA (2010) Bats. In: Macelean N (ed) *Silent Summer: the State of Wildlife in Britain and Ireland*, 259–280. Cambridge University Press, Cambridge, UK.
- Heim O, Lenski J, Schulze J, Jung K, Kramer-Schadt S, Eccard JA, Voigt CC (2018) The relevance of vegetation structures and small water bodies for bats foraging above farmland. *Basic and Applied Ecology* 27: 9–19.
- Hill AP, Prince P, Piña Covarrubias E, Doncaster CP, Snaddon JL, Rogers A (2018) AudioMoth: evaluation of a smart open acoustic device for monitoring biodiversity and the environment. *Methods in Ecology and Evolution* 9: 1199–1211.
- Hill DA, Greenway F (2008) Conservation of bats in British woodlands. *British Wildlife* 19: 161–169.
- Hutson AM, Mickleburgh SP, Racey PA (2001) *Microchiropteran Bats – Global Status Survey and Conservation Action Plan*. IUCN, Gland, Switzerland and Cambridge, UK.
- Hutterer R, Ivanova T, Meyer-Cords C, Rodrigues LL (2005) *Bat Migrations in Europe: a Review of Banding Data and Literature*, 28–31. Federal Agency for Nature Conservation (Bundesamt für Naturschutz), Bonn, Germany.
- Isaac NJB, Jarzyna MA, Keil P, Dambly LI, Boersch-Supan PH, Browning E et al. (2019) Data integration for large-scale models of species distributions. *Trends in Ecology & Evolution* 35: 56–67.
- Isaac NJB, van Strien AJ, August TA, de Zeeuw MP, Roy DB (2014) Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution* 5: 1052–1060.
- Jones G, Jacobs DS, Kunz TH, Willig MR, Racey PA (2009) *Carpe noctem: the importance of bats as bioindicators*. *Endangered Species Research* 8: 93–115.

- Jung K, Threlfall CG (2018) Trait-dependent tolerance of bats to urbanization: a global meta-analysis. *Proceedings of the Royal Society B: Biological Sciences* 285: 20181222.
- Kahnonitch I, Lubin Y, Korine C (2018) Insectivorous bats in semi-arid agroecosystems – effects on foraging activity and implications for insect pest control. *Agriculture, Ecosystems & Environment* 261: 80–92.
- Kerth G, Melber M (2009) Species-specific barrier effects of a motorway on the habitat use of two threatened forest-living bat species. *Biological Conservation* 142: 270–279.
- Kirkpatrick L, Maher SJ, Lopez Z, Lintott PR, Bailey SA, Dent D, Park KJ (2017a) Bat use of commercial coniferous plantations at multiple spatial scales: management and conservation implications. *Biological Conservation* 206: 1–10.
- Kirkpatrick L, Oldfield IF, Park K (2017b) Responses of bats to clear fell harvesting in Sitka Spruce plantations, and implications for wind turbine installation. *Forest Ecology and Management* 395: 1–8.
- Klopper LN, Kinniry M (2018) Recording animal vocalizations from a UAV: bat echolocation during roost re-entry. *Scientific Reports* 8: 7779.
- Kunz TH, Braun de Torrez E, Bauer D, Lobova T, Fleming TH (2011) Ecosystem services provided by bats. *Annals of the New York Academy of Sciences* 1223: 1–38.
- Lacoeuilhe A, Machon N, Julien J-F, Le Bocq A, Kerbirou C (2014) The influence of low intensities of light pollution on bat communities in a semi-natural context. *PLoS One* 9: e103042.
- Law BS, Anderson J (2000) Roost preferences and foraging ranges of the eastern forest bat *Vespardelus pumilus* under two disturbance histories in northern New South Wales, Australia. *Austral Ecology* 25: 352–367.
- Law B, Chidel M (2002) Tracks and riparian zones facilitate the use of Australian regrowth forest by insectivorous bats. *Journal of Applied Ecology* 39: 605–617.
- Lehnert LS, Kramer-Schadt S, Teige T, Hoffmeister U, Popa-Lisseanu A, Bontadina F et al. (2018) Variability and repeatability of noctule bat migration in Central Europe: evidence for partial and differential migration. *Proceedings of the Royal Society B: Biological Sciences* 285: 20182174.
- Lesiński G, Gryz J, Kowalski M (2009) Bat predation by tawny owls *Strix aluco* in differently human-transformed habitats. *Italian Journal of Zoology* 76: 415–421.
- Lesiński G, Sikora A, Olszewski A (2010) Bat casualties on a road crossing a mosaic landscape. *European Journal of Wildlife Research* 57: 217–223.
- Limpens HJGA, Lagerveld S, Ahlén I, Anxionnat D, Aughney T, Baagoe HJ et al. (2017) *Migrating Bats at the Southern North Sea: Approach to an Estimation of Migration Populations of Bats at the Southern North Sea*. Zoogdiervereniging (Dutch Mammal Society), Wageningen Marine Research, the Netherlands.
- Lintott DM (2009) *Bat Ecology and Conservation in Lowland Farmland*. Oxford University Lady Margaret Hall, Oxford, UK.
- Lintott PR, Barlow K, Bunnefeld N, Briggs P, Gajas Roig C, Park KJ (2016a) Differential responses of cryptic bat species to the urban landscape. *Ecology and Evolution* 6: 2044–2052.
- Lintott PR, Bunnefeld N, Park KJ (2015) Opportunities for improving the foraging potential of urban waterways for bats. *Biological Conservation* 191: 224–233.
- Lintott PR, Mathews F (2018) *Reviewing the Evidence on Mitigation Strategies for Bats in Buildings: Informing Best-Practice for Policy Makers and Practitioners*. University of Exeter, Exeter, UK.
- Lintott PR, Richardson SM, Hosken DJ, Fensome SA, Mathews F (2016b) Ecological impact assessments fail to reduce risk of bat casualties at wind farms. *Current Biology* 26: R1135–R1136.
- Liu X, Huang Y, Xu X, Li X, Li X, Ciais P et al. (2020) High-spatiotemporal-resolution mapping of global urban change from 1985 to 2015. *Nature Sustainability* 3: 564–570.
- López-Roig M, Serra-Cobo J (2014) Impact of human disturbance, density, and environmental conditions on the survival probabilities of pipistrelle bat (*Pipistrellus pipistrellus*). *Population Ecology* 56: 471–480.
- Lourenço SI, Palmeirim JM (2004) Influence of temperature in roost selection by *Pipistrellus pygmaeus* (Chiroptera): relevance for the design of bat boxes. *Biological Conservation* 119: 237–243.
- Mac Aodha O, Gibb R, Barlow KE, Browning E, Firman M, Freeman R et al. (2018) Bat detective—deep learning tools for bat acoustic signal detection. *PLoS Computational Biology* 14: e1005995. <https://doi.org/10.1371/journal.pcbi.1005995>.
- Mace GM, Barrett M, Burgess ND, Cornell SE, Freeman R, Grooten M, Purvis A (2018) Aiming higher to bend the curve of biodiversity loss. *Nature Sustainability* 1: 448–451.
- Mathews F, Kubasiewicz LM, Gurnell J, Harrower CA, McDonald RA, Shore RF (2018) *A Review of the Population and Conservation Status of British Mammals: Technical Summary*. Natural England, Peterborough, UK.
- Medinas D, Marques JT, Mira A (2012) Assessing road effects on bats: the role of landscape, road features, and bat activity on road-kills. *Ecological Research* 28: 227–237.
- van der Meij T, van Strien AJ, Haysom KA, Dekker J, Russ J, Biala K et al. (2015) Return of the bats? A prototype indicator of trends in European bat populations in underground hibernacula. *Mammalian Biology* 80: 170–177.

- Meyer CFJ, Fründ J, Lizano WP, Kalko EKV (2007) Ecological correlates of vulnerability to fragmentation in Neotropical bats. *Journal of Applied Ecology* 45: 381–391.
- Mitchell-Jones AJ, Cooke AS, Boyd IL, Stebbings RE (1989) Bats and remedial timber treatment chemicals a review. *Mammal Review* 19: 93–110.
- Murphy SE, Greenaway F, Hill DA (2012) Patterns of habitat use by female brown long-eared bats presage negative impacts of woodland conservation management. *Journal of Zoology* 288: 177–183.
- Natural England (2012) *Entry Level Stewardship. Environmental Stewardship Handbook Fourth Edition – January 2013*. Natural England, Peterborough, UK.
- O’Shea TJ, Cryan PM, Hayman DTS, Plowright RK, Streicker DG (2016) Multiple mortality events in bats: a global review. *Mammal Review* 46: 175–190.
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.
- Pearce H, Walters CL (2012) Do green roofs provide habitat for bats in urban areas? *Acta Chiropterologica* 14: 469–478.
- Posthuma L, Zijp MC, De Zwart D, Van de Meent D, Globevnik L, Koprivsek M, Focks A, Van Gils J, Birk S (2020) Chemical pollution imposes limitations to the ecological status of European surface waters. *Scientific Reports* 10: 14825.
- Razgour O, Juste J, Ibáñez C, Kiefer A, Rebelo H, Puechmaile SJ et al. (2013) The shaping of genetic variation in edge-of-range populations under past and future climate change. *Ecology Letters* 16: 1258–1266.
- Rebelo H, Froufe E, Brito JC, Danilo R, Cistone L, Ferrand N, Jones G (2012) Postglacial colonization of Europe by the barbastelle bat: agreement between molecular data and past predictive modelling. *Molecular Ecology* 21: 2761–2774.
- Rebelo H, Tarroso P, Jones G (2010) Predicted impact of climate change on European bats in relation to their biogeographic patterns. *Global Change Biology* 16: 561–576.
- Regnery B, Couvet D, Kubarek L, Julien JF, Kerbiriou C (2013) Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. *Ecological Indicators* 34: 221–230.
- Robinson MF, Stebbings RE (1997) Home range and habitat use by the serotine bat, *Eptesicus serotinus*, in England. *Journal of Zoology* 243: 117–136.
- Rodrigues L, Bach L, Dubourg-Savage MJ, Karapandza B, Kovac D, Kervyn T et al. (2015) *Guidelines for Consideration of Bats in Wind Farm Projects - Revision 2014*. EUROBATS Publication Series No. 6. Bonn, Germany.
- Roeleke M, Blohm T, Hoffmeister U, Marggraf L, Schlägel UE, Teige T, Voigt CC (2020) Landscape structure influences the use of social information in an insectivorous bat. *Oikos* 129: 912–923.
- Rossiter SJ, Jones G, Ransome RD, Barratt EM (2000) Genetic variation and population structure in the endangered greater horseshoe bat *Rhinolophus ferrumequinum*. *Molecular Ecology* 9: 1131–1135.
- Rowse EG, Harris S, Jones G (2018) Effects of dimming light-emitting diode street lights on light-opportunistic and light-averse bats in suburban habitats. *Royal Society Open Science* 5: 180205.
- Ruiz-Gutierrez V, Hooten MB, Campbell Grant EH (2016) Uncertainty in biological monitoring: a framework for data collection and analysis to account for multiple sources of sampling bias. *Methods in Ecology and Evolution* 7: 900–909.
- Russ J, Montgomery W (2002) Habitat associations of bats in Northern Ireland: implications for conservation. *Biological Conservation* 108: 49–58.
- Russo D, Cistrone L, Jones G, Mazzoleni S (2004) Roost selection by barbastelle bats (*Barbastella barbastellus*, Chiroptera: Vespertilionidae) in beech woodlands of central Italy: consequences for conservation. *Biological Conservation* 117: 73–81.
- Russo D, Cistrone L, Jones G (2007) Emergence time in forest bats: the influence of canopy closure. *Acta Oecologica* 31: 119–126.
- Russo D, Cistrone L, Garonna AP, Jones G (2010) Reconsidering the importance of harvested forests for the conservation of tree-dwelling bats. *Biodiversity and Conservation* 19: 2501–2515.
- Russo D, Jones G (2002) Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. *Journal of Zoology* 258: 91–102.
- Russo D, Jones G (2015) Bats as bioindicators: an introduction. *Mammalian Biology* 80: 157–158.
- Rydell J (2006) Bats and their insect prey at streetlights. In: Rich C, Longcore T (eds) *Ecological Consequences of Artificial Night Lighting*, 43–60. Island Press, Washington, District of Columbia, USA.
- Rydell J, Bach L, Dubourg-Savage M-J, Green M, Rodrigues L, Hedenström A (2010) Bat mortality at wind turbines in northwestern Europe. *Acta Chiropterologica* 12: 261–274.
- Sachanowicz K, Ciechanowski M, Tryjanowski P, Kosicki JZ (2019) Wintering range of *Pipistrellus nathusii* (Chiroptera) in Central Europe: has the species extended to the north-east using urban heat islands? *Mammalia* 83: 260–271.
- Sachanowicz K, Wower A, Bashta A-T (2006) Further range extension of *Pipistrellus kuhlii* (Kuhl, 1817) in central and eastern Europe. *Acta Chiropterologica* 8: 543–548.
- Schaub A, Ostwald J, Siemers BM (2008) Foraging bats avoid noise. *Journal of Experimental Biology* 211: 3174–3180.
- Schofield H (2008) *The Lesser Horseshoe Bat Conservation Handbook*. Vincent Wildlife Trust, Herefordshire, UK.

- Scottish Natural Heritage, Natural England, Natural Resources Wales, RenewableUK, Scottish Power Renewables, Ecotricity Ltd, University of Exeter, Bat Conservation Trust (2019) *Bats and Onshore Wind Turbines: Survey, Assessment and Mitigation*.
- Seto KC, Guneralp B, Hutyra LR (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences of the United States of America* 109: 16083–16088.
- Sherwin HA, Montgomery WI, Lundy MG (2013) The impact and implications of climate change for bats. *Mammal Review* 43: 171–182.
- Siemers BM, Schaub A (2011) Hunting at the highway: traffic noise reduces foraging efficiency in acoustic predators. *Proceedings of the Royal Society B: Biological Sciences* 278: 1646–1652.
- Sijpe M van de, Vandendriessche B, Voet P, Vandenberghe J, Duyck J, Naeyaert E, Manhaeve M, Martens E (2004) Summer distribution of the pond bat *Myotis dasycneme* (Chiroptera, Vespertilionidae) in the west of Flanders (Belgium) with regard to water quality. *Mammalia* 68: 377–386. <https://doi.org/10.1515/mamm.2004.037>.
- Spoelstra K, van Grunsven RHA, Ramakers JJC, Ferguson KB, Raap T, Donners M, Veenendaal EM, Visser ME (2017) Response of bats to light with different spectra: light-shy and agile bat presence is affected by white and green, but not red light. *Proceedings of the Royal Society B: Biological Sciences* 284: 20170075.
- Spooner FEB, Pearson RG, Freeman R (2018) Rapid warming is associated with population decline among terrestrial birds and mammals globally. *Global Change Biology* 24: 4521–4531.
- Stahlschmidt P, Hahn M, Brühl CA (2017) Nocturnal risks - high bat activity in the agricultural landscape indicates potential pesticide exposure. *Frontiers in Environmental Science* 5: 62.
- Stebbins R, Griffith F (1986) *Distribution and Status of Bats in Europe*. Institute of Terrestrial Ecology, Abbots Ripton, Huntingdon, UK.
- Sterze J, Pogacnik M (2008) The impacts of wind farms on animal species. *Acta Veterinaria* 58: 615–632.
- Stone EL, Jones G, Harris S (2009) Street lighting disturbs commuting bats. *Current Biology* 19: 1123–1127.
- Stone EL, Jones G, Harris S (2012) Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. *Global Change Biology* 18: 2458–2465.
- Stone EL, Jones G, Harris S (2013) Mitigating the effect of development on bats in England with derogation licensing. *Conservation Biology* 27: 1324–1334.
- Stone E, Zeale MRK, Newson SE, Browne WJ, Harris S, Jones G (2015) Managing conflict between bats and humans: the response of soprano pipistrelles (*Pipistrellus pygmaeus*) to exclusion from roosts in houses. *PLoS One* 10: e0131825.
- Straka TM, Wolf M, Gras P, Buchholz S, Voigt CC (2019) Tree cover mediates the effect of artificial light on urban bats. *Frontiers in Ecology and Evolution* 7: 91.
- Sutherland WJ, Armstrong-Brown S, Armsworth PR, Brereton T, Brickland J, Campbell CD et al. (2006) The identification of 100 ecological questions of high policy relevance in the UK. *Journal of Applied Ecology* 43: 617–627.
- Thomas JP, Reid ML, Jung TS, Barclay RMR (2019) Site occupancy of little brown bats (*Myotis lucifugus*) in response to salvage logging in the boreal forest. *Forest Ecology and Management* 451: 117501.
- Threlfall CG, Mata L, Mackie JA, Hahs AK, Stork NE, Williams NSG, Livesley SJ (2017) Increasing biodiversity in urban green spaces through simple vegetation interventions. *Journal of Applied Ecology* 54: 1874–1883.
- Tibbels AE, Kurta A (2003) Bat activity is low in thinned and unthinned stands of red pine. *Canadian Journal of Forest Research* 33: 2436–2442.
- UNEP (2006) *Migratory Species and Climate Change: Impacts of a Changing Environment on Wild Animals*. United Nations Environment Programme/CMS Secretariat, Bonn, Germany.
- Vaughan N, Jones G, Harris S (1996) Effects of sewage effluent on the activity of bats (Chiroptera: Vespertilionidae) foraging along rivers. *Biological Conservation* 78: 337–343.
- Vaughan N, Jones G, Harris S (1997) Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. *Journal of Applied Ecology* 34: 716–730.
- Voigt CC, Lindecke O, Schönborn S, Kramer-Schadt S, Lehmann D (2016) Habitat use of migratory bats killed during autumn at wind turbines. *Ecological Applications* 26: 771–783.
- Walker LA, Simpson VR, Rockett L, Wienburg CL, Shore RF (2007) Heavy metal contamination in bats in Britain. *Environmental Pollution* 148: 483–490.
- Waring SD, Essah EA, Gunnell K, Bonser RHC (2013) Double jeopardy: the potential for problems when bats interact with breathable roofing membranes in the United Kingdom. *Architecture & Environment* 1: 1–13.
- Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B et al. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414: 65–69.
- Waters D, Jones G, Furlong M (1999) Foraging ecology of Leisler's bat (*Nyctalus leisleri*) at two sites in southern Britain. *Journal of Zoology* 249: 173–180.
- Wellig SD, Nusslé S, Miltner D, Kohle O, Glairoz O, Braunisch V, Obrist MK, Arlettaz R (2018) Mitigating the negative impacts of tall wind turbines on bats: vertical activity profiles and relationships to wind speed. *PLoS One* 13: e0192493.

- Wickramasinghe LP, Harris S, Jones G, Vaughan N (2003) Bat activity and species richness on organic and conventional farms: impact of agricultural intensification. *Journal of Applied Ecology* 40: 984–993.
- Woods M, McDonald RA, Harris S (2003) Predation of wildlife by domestic cats *Felis catus* in Great Britain. *Mammal Review* 33: 174–188.
- Zeale MRK, Stone EL, Zeale E, Browne WJ, Harris S, Jones G (2018) Experimentally manipulating light spectra reveals the importance of dark corridors for commuting bats. *Global Change Biology* 24: 5909–5918.
- Zipkin EF, Inouye BD, Beissinger SR (2019) Innovations in data integration for modeling populations. *Ecology* 100: e02713.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Assessment of drivers of change for each bat species, ordered by 'broad driver' (Burns et al. 2014).

Appendix S2. Summary of impact assessment method.

Appendix S3. Details of scoring scheme for the strength of impact on species.

Appendix S4. Details of scoring scheme of the strength of evidence used by assessors in the impact assessment.

Appendix S5. Literature search topics and their relation to proposed drivers.