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 (Stebbings & 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

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**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).
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, deleterious effects, 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 (Stebbings & 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...
Drivers of European bat population change

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

<table>
<thead>
<tr>
<th>Burns et al. (2016) drivers</th>
<th>Proposed drivers</th>
<th>Evidence quality</th>
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<tbody>
<tr>
<td>• Decreasing human disturbance</td>
<td>Human disturbance</td>
<td>Reasonable</td>
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<td>• Intensive management of agricultural land</td>
<td>Agricultural practices</td>
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<td>• Low-intensity management of agricultural land</td>
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<tr>
<td>• Decreasing forest age</td>
<td>Woodland loss and management</td>
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<td>• Increasing native forest area</td>
<td>Onshore wind turbines</td>
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<td>• Increasing forest management</td>
<td>Roads</td>
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<td>• Mining and energy production</td>
<td>Artificial light</td>
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<td>• Transport infrastructure</td>
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<td>• Increasing light pollution</td>
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<td>• Urbanisation</td>
<td>Urbanisation</td>
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<td>• Mining and energy production</td>
<td>Offshore wind turbines</td>
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<td>• Increasing climate change</td>
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<td>• Decreasing water pollution</td>
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<td>• Hydrological change</td>
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<tr>
<td>• Decreasing human disturbance</td>
<td>Legislation and mitigation measures</td>
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<td>• Invasive or problematic species</td>
<td>Driver interactions</td>
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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 (Hambler 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 leisleri (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.
Drivers of European bat population change

**Drivers of European bat population change**

**Reasonable evidence for impact**
- Human disturbance
- Agricultural practices
- Woodland loss & management

**Poor or conflicting evidence for impact**
- Offshore wind turbines
- Water pollution
- Urbanisation
- Climate change
- Legislation & mitigation measures
- Driver interactions

**Direction of impact**
- Positive
- Negative
- Mixed

**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 kuhlii* 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 schemes (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).
to be investigated. Long-term fitness and population declines of bats have yet impacted road avoidance and vehicle collisions have on the echolocation to detect insect prey (Dietz et al. 2009). The and suggests that some species, such as Pipistrellus pipistrellus and Pipistrellus pygmaeus, exploit the insects attracted to the light (Rydell 2006, Lacoeuilhe 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, Lacoeuilhe 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 Pippistrellus 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 synuric 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

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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
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 daubentoni (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 garner use by bats is negligible (Berthinusen & 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 (Berthinusen 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 (Berthinusen 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 (Kloeper & 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 (Rebello 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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**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.