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Comparing acoustic survey data for European bats: do walked transects or automated fixed-point surveys provide more robust data?

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Bat surveying and monitoring often rely on detection and identification of echolocation calls. Common methods involve using mobile handheld devices on transect-based activity surveys (good spatial coverage; poor temporal coverage) or passive fixed-point monitoring (good temporal coverage; poor spatial coverage). There have been few published accounts that directly compare data from the different acoustic survey methods. We use 2,349 hrs of acoustic data, on which 12 European bat species were recorded, to identify strengths/weaknesses of each method and highlight how they could be combined to improve accuracy, precision and reliability.

Abstract

Context: Monitoring schemes provide vital data on the distribution and population dynamics of species. This information can be used to inform conservation management and, especially for legally-protected species, ensure legislative compliance in development contexts. For bats, acoustic activity surveys are widely used and often involve: (1) deployment of automated fixed-point detectors; or (2) using bat detectors on walked or driven transects. Transect surveys are typically performed for two hours commencing around sunset; automated fixed-point surveys record continually between sunset and sunrise, often over multiple consecutive nights.

Aims: Despite both walked transects and fixed-point surveys being common methods used to survey bat activity in many parts of the world, often just one technique is used per site. We test the similarity of these two survey methods by comparing acoustic data encompassing 12 species of European bat to determine whether data from different surveys are directly comparable.

Methods: In this study, we use acoustic data covering 2,349 survey hours over a three-year period to investigate the relative effectiveness of walked activity transects and automated fixed-point methods for 12 species of European bats.

Key results: A greater number of bat species were recorded via the fixed-point method. Three species – greater horseshoe (*Rhinolophus ferrumequinum*), lesser horseshoe (*Rhinolophus hipposideros*) and Daubenton's (*Myotis daubentonii*) – were only recorded using automated detectors, possibly because the survey window encompassed the entire night rather than the period immediately after sunset. However, activity transects recorded a significantly higher mean species richness per hour compared to fixed-point surveys. When both methods were carried out at the same sites on the same nights, providing paired data for direct comparison, detection of brown long-eared (*Plecotus auratus*) and soprano pipistrelle (*Pipistrellus pygmaeus*) bat activity was significantly higher for transect surveys.

Conclusions and implications: This study demonstrates important differences in the data resulting from different bat survey methods and highlights the potential for combining acoustic survey types to obtain rigorous and reliable monitoring data for bat populations.

Keywords

Activity surveys; anabat; bat surveying; bat detector, echolocation; ultrasonic detection

Introduction

There are approximately 1400 species of bats globally (Bat Conservation International, 2021), many of which are declining due to natural and/or anthropogenic processes (Hutson et al., 2001; O'Shea et al. 2016). Direct causes of mortality include disease and extreme weather events, which often differ spatially: for example, White Nose Syndrome is a major cause of mortality in North America while extreme heat is a major cause of mortality in Australia (O'Shea et al. 2016). Indirect threats are often more varied and affect bats through loss of, or disturbance to, roosts or feeding grounds (Walsh and Harris 1996b; Hutson et al. 2001). For example, bats are extremely sensitive to habitat change and fragmentation, agricultural intensification, and deforestation or sub-optimal forest management (Walsh and Harris 1996a, b; Willig et al. 2007; Lintott et al. 2016; O'Shea et al. 2016; Alder et al. 2020). Climate change is likely to become an increasing threat worldwide (Jones et al. 2009), while pesticides and pollutants can also pose substantial threats to regional or national populations (O'Shea and Johnston 2009).

Bat data are important in establishing species' distribution, quantifying population metrics, and understanding ecological relationships, as well as assessing temporal trends in relation to environmental change and conservation initiatives (Hutson et al. 2001; Walsh et al. 2004; Barlow et al. 2015). Because of the ecological importance of bats and the ecosystem services they provide, as well as their vulnerability to anthropogenic processes, bats can be a useful bioindicator of habitat quality and climate change (Jones et al. 2009; Russo and Jones, 2015). Population change is thus often used as an indicator of ecosystem health (e.g. in the USA: Treanor et al. 2019; throughout Europe under EUROBATS scheme) and to monitor progress towards sustainable development (e.g. UK: JNCC 2019).

In addition to monitoring bats spatially and temporally through national-level initiatives, such as the North American Bat Monitoring Programme and EUROBATS, site-level bat surveying is often undertaken in research contexts and, in parts of the world where bats are legally protected, site-level survey data are often required to allow planning authorities to make informed decisions on infrastructure development (Drayson et al. 2015; Goodenough and Hart, 2017). For example, in Europe, a considerable amount of bat survey effort is driven by the need for compliance with the EC Habitats Directive (92/43/EEC) and European Protected Species licensing framework, as well as national legislation through which these are implemented (Goodenough et al. 2015). Site-based bat surveys are thus often undertaken within mandatory Ecological Impact Assessments (EcIAs) to quantify bat presence and abundance, assess potential development impacts, and devise suitable mitigation and compensation measures (Treweek 2009; CIEEM 2018), as well as to support license applications to permit work around bat roosts that would otherwise be illegal (Mitchell-Jones 2004).

Bat surveys can involve counting bats visually (roost counts: Barlow et al. 2015; Warren and Witter 2002) or trapping bats in flight (harp traps or mist netting: Law et al. 1998; O'Farrell and Gannon 1999). However, non-invasive acoustic surveys are commonly undertaken whereby ultrasonic devices are used to detect echolocation calls. Acoustic surveys typically involve either: (1) automated fixed-point ultrasonic detectors to record bats continually between sunset and sunrise or (2) transect surveys using ultrasonic detectors in real-time (Collins 2016). Automated fixed-point surveys are used worldwide, including throughout Europe, North America and Oceania, but also increasingly in Asia and Africa (Sedlock et al. 2014; Weier et al. 2020). In contrast, transect acoustic survey methodologies vary between countries. Where activity is typically monitored across large geographic scales, such as in the USA and Canada, ultrasonic detectors may be fitted to vehicles to enable transects to be driven (Braun de Torrez et al. 2017; D'Acunto et al. 2018). However, throughout Europe, walked transects with handheld detectors are more commonly used (Russo and Jones, 2003; Ciechanowski et al. 2007; Stahlschmidt and Bruhl 2012; Henkens et al. 2014; Goodenough et al. 2015; Collins 2016). Outside of Europe, walked transects are used in Oceania (O'Donnell 2000; O'Donnell and Sedgeley, 2001; Scanlon and Petit 2009; Lavery et al. 2020), Africa (Bambini et al. 2006; Taylor et al. 2013; Musila et al. 2019), and Asia (Pottie et al. 2005; Lee et al. 2017; Mullin et al. 2020). In addition to use in formal surveys for research, legislative complacence, and long-term monitoring, walked transects are increasingly being used in citizen science or volunteer-led bat surveys, for example in the Bat Walks Programme by Bat Conservation International and the National Bat Monitoring Programme in the UK. Better insight into how such survey data compare to data derived from more formal automated fixed-point surveys would thus be beneficial.

For any form of monitoring to be effective, underpinning data must be collected in a consistent and rigorous manner appropriate to the aim of the survey (Collins 2016). Survey methods need to be logistically-feasible, robust, and comparable (Balmford et al. 2003; Collins 2016) and account for the influence of spatiotemporal and abiotic factors (Perks and Goodenough, 2020). This is particularly important in applied settings when legally-protected species are affected by resulting actions, either through conservation interventions (Barlow et al. 2015) or development decisions (Mitchell-Jones 2004). In fixed-point detection, spatial coverage is limited to a (very) few points per site, but temporal coverage is extensive with detectors usually recording sunset to sunrise for 5-21 consecutive nights. This allows the entire nocturnal period to be sampled over multiple nights as per the recommendations of Law et al. (1998) and Hayes (1997). In the case of transects (walked or driven), coverage is restricted temporally – often to a two-hour period commencing at or near sunset (O'Donnell 2000; Goodenough et al. 2015; Braun de Torrez et al. 2017) – but a much wider spatial area is covered.

Although the need to monitor bat populations is recognised (Barlow et al. 2015), and there are commonly-used acoustic techniques to achieve this, there have been few attempts to either compare the efficacy of different acoustic surveys or determine whether data from different survey types are directly comparable. This is important because although both transect and fixed-point methods are commonly used and industry-standard techniques, it is common for just one method to be used to survey bats at a specific site. Published evidence that has focused on comparing automated fixed detection with transects surveys is limited to Tonos et al. (2014) in Indiana, USA, and Braun de Torrez et al. (2017) in Florida, USA. Work to date, therefore, has compared automated detection and *driven* transects on American Chiropteran guilds. In this study, we empirically compare automated fixed-point acoustic surveys with *walked* transect acoustic surveys for a European Chiropteran guild. We examine overall bat activity as well as species-specific activity for 12 European bat species and two wider genera (*Myotis* sp. and *Nyctalus* sp.) at the same sites to determine: (1) differences between the survey methods over exactly the same time period (i.e. walked transect acoustic surveys starting two hours post sunset with automated fixed-point acoustic surveys over the same two hour window) and (2) differences between the survey methods over a longer timeframe (i.e. one two-hour walked transect acoustic survey that commenced at sunset compared with whole-night automated fixed-point acoustic surveys for multiple nights within a 21 night window). Undertaking both comparisons enables full exploration of the ability to passively monitor bats whole and consecutive nights, as opposed to the traditional survey window of two hours post sunset. We also use the automated data to quantify hourly bat activity patterns, to explore how peak levels of activity varies throughout the night and how this related to the two-hour walked survey transect period. Our conclusions and recommendations are necessarily related primarily to European bat species, but we also make tentative broader comments relating to walked bat transects in other geographical regions, and for other species, with appropriate caveats.

Materials and methods

Data collection

We used a paired survey design whereby data were collected from 14 sites across the south of England, encompassing a range of habitat types. Most of the sites (n = 9) comprised agricultural land with dividing hedgerows, but other sites included high quality rural habitat or lakeside (n = 3) and green spaces within more urbanised areas (n = 2). At each site, the bat community was surveyed in two ways: (1) walked transect acoustic surveys, and (2) automated fixed-point acoustic surveys.

Walked transect acoustic surveys were conducted in accordance with the Bat Conservation Trust Guidelines (Collins 2016) using Anabat SD1 detectors (Titley Scientific, Ballina, Australia). These two-hour surveys commenced at sunset and were carried out by two surveyors; either walking in opposite directions around a single perimeter transect (n = 7 sites), or walking separate transects on larger sites (n = 7 sites). Automated fixed-point acoustic surveys were conducted using Anabat Express Units (Titley Scientific, Ballina, Australia). Deployment and positioning of these units was carried out in a consistent manner at all sites with units mounted about 1.75m above the ground adjacent to a suitable hedgerow or treeline to ensure detection of commuting and foraging activity along linear features. The SD1 detectors enabled audio allowing fieldworkers to identify the bats present *in situ*, whereas the Express units were weatherproof and had long battery life and facilitated extended periods of automated recording of sound files to a memory card where sound output was unnecessary. In both cases, the default or recommended settings were used (data division ratio = 8 on both SD1 and Express; sensitivity = 6 on SD1 and 8 on Express): both units had identical frequency ranges.

In total, 24 walked transect acoustic surveys were carried out across the 14 sites. These surveys were matched with data from automated fixed-point acoustic surveys from multiple (minimum of 3) nights within a 21-night window. The 21-night window was set to ensure that seasonality did not confound method comparison analyses. This gave 24 cases where walked transect data (for two hours post sunset on a single night) were matched to automated fixed-point data (encompassing the entire period between sunset and sunrise over several nights) at the same site at the same time of year. This is henceforth referred to as the multi-night dataset. A subset of 14 transects coincided exactly with automated fixed-point surveys so that there were data from the same two-hour window, on the same night, at the same site, from the two different methods. This gave 14 cases of directly-matched data, which are henceforth referred to as the concurrent dataset.

Post fieldwork, all data, which were in zero crossing format, were downloaded from internal SD cards in the bat detectors for sonogram analysis. Sonogram analysis was performed using AnalookW software version 4.1z (Titley Scientific, Ballina, Australia) developed specifically for Anabat detectors. Initially recordings were processed on a night-by-night basis and then data were subdivided into hourly units relative to sunset. Species identification was carried out by assessment of the frequency range and peak frequency, together with shape of each sonogram in terms of pitch and amplitude over time using information in Russ (2012). As is typical for acoustic surveys (Russ 2012), *Myotis* bats were challenging to identify to species level. Where possible, Daubenton's (*Myotis daubentonii*) and Natterer's (*Myotis nattereri*) bats were identified as separate species.

Brandt's bat (*Myotis brandtii*) and whiskered bat (*Myotis mystacinus*) were generally distinguishable from other *Myotis* bats but not from one another and were grouped accordingly. Indistinguishable *Myotis* bats were grouped at genus level. In most cases, noctule (*Nyctalus noctula*) bats could be distinguished to species level but some calls could not be differentiated from Leisler's (*Nyctalus leisleri*) and were thus grouped at genus level.

Statistical analysis

To compare overall species richness recorded in exactly the same two-hour window at the same site via the two different survey methods (i.e. the concurrent data), paired sample t-tests were used for the comparison of mean values between matched samples. This approach was also used to compare total activity of bats (regardless of species) and species-specific or genus-specific activity when there was sufficient data and for species that were recorded in both survey types. To undertake these analyses, walked transect survey data and automated fixed-point survey data were converted to mean bat passes per hour and then log transformed (*ln*+1). Parametric assumptions were met for these transformed data (i.e. the difference between the mean bat passes per hour for the two survey types – the difference scores – were normally distributed in all cases). To compare species richness, total activity, and species-specific activity of bats recorded via the walked transect surveys compared to multi-night data from automated fixed-point surveys, the same paired-sample approach was used. This was adopted on the basis that although the data were not exactly matched in time, they were still exactly matched in space and very similar in time. Again, data were converted to mean bat passes per hour and then log transformed (*ln*+1) to meet parametric assumptions.

To explore nightly activity patterns, trends in bat activity across the night were examined for each species using the automated fixed-point data from the multi-night dataset. Data were grouped on an hourly basis and graphed. Significant deviations from a uniform distribution throughout the night were tested using Kolmogorov-Smirnov two-sample tests. This allowed better understanding of possible differences between walked transect data (which were temporally restricted) and automated fixed-point data (which spanned the entire night). All statistical analysis was carried out in IBM SPSS version 24.

Results

Data were collected on 223 nights of automated fixed-point acoustic recording and 24 walked transect acoustic surveys giving a combined sample size of 2,349 hrs of bat recording data summarising 47,915 individual bat passes.

Species richness

Over the entire study, more species were detected using automated fixed-point surveys (n = 11 species plus *Myotis* sp. and *Nyctalus* sp.) than using walked activity surveys (n = 8 species plus *Myotis* sp. and *Nyctalus* sp.). However, mean species richness per hour was significantly higher in the walked transect acoustic surveys compared to the automated fixed-point acoustic surveys when considering both the concurrent data (2.89 ± 0.29 SEM versus 1.96 ± 0.31 species per hour, respectively: paired samples t-test $t = 3.501$, $n = 14$ pairs, $P = 0.004$) and the multi-night data (2.92 ± 0.22 SEM versus 1.32 ± 0.12 SEM species per hour, respectively: paired samples t-test $t = 9.338$, $n = 24$ pairs, $P < 0.001$).

Species prevalence

In the concurrent dataset, lesser horseshoe bats (*Rhinolophus hipposideros*) were only detected in automated fixed-point acoustic surveys. Common pipistrelle (*Pipistrellus pipistrellus*), soprano pipistrelle (*Pipistrellus pygmaeus*), noctule (*Nyctalus noctula*), serotine (*Eptesicus serotinus*), brown long-eared (*Plecotus auritus*) and Natterer's bats, in addition to bats identified at *Myotis* and *Nyctalus* genus level only, occurred on both survey types but were more prevalent in the walked transect acoustic surveys (Figure 1a). Conversely, Brandt's/whiskered (*Myotis* spp.) and barbastelle (*Barbastella barbastellus*) occurred on both survey types but were more prevalent in the fixed-point acoustic surveys (Figure 1a). Greater horseshoe (*Rhinolophus ferrumequinum*) and Daubenton's bats (*Myotis daubentonii*) were absent in both survey types.

In the multi-night dataset, common pipistrelle, soprano pipistrelle, noctule, serotine, brown long-eared, Brandt's/whiskered, barbastelle and Natterer's bats, in addition to bats identified as *Myotis* and *Nyctalus* genus level occurred in both survey types, but were more prevalent in walked transect acoustic surveys (Figure 1b). Two species that were not detected in the concurrent data (greater horseshoe, Daubenton's) were detected in the multi-night dataset in the automated fixed-point surveys only. Lesser horseshoe, which was detected at very low levels in the automated fixed-point surveys in the concurrent dataset, increased in prevalence marginally (<1%) in the multi-night dataset. The three species that only occurred in the automated fixed-point surveys (greater and lesser horseshoe and Daubenton's) were present in <10% of the total recording hours.

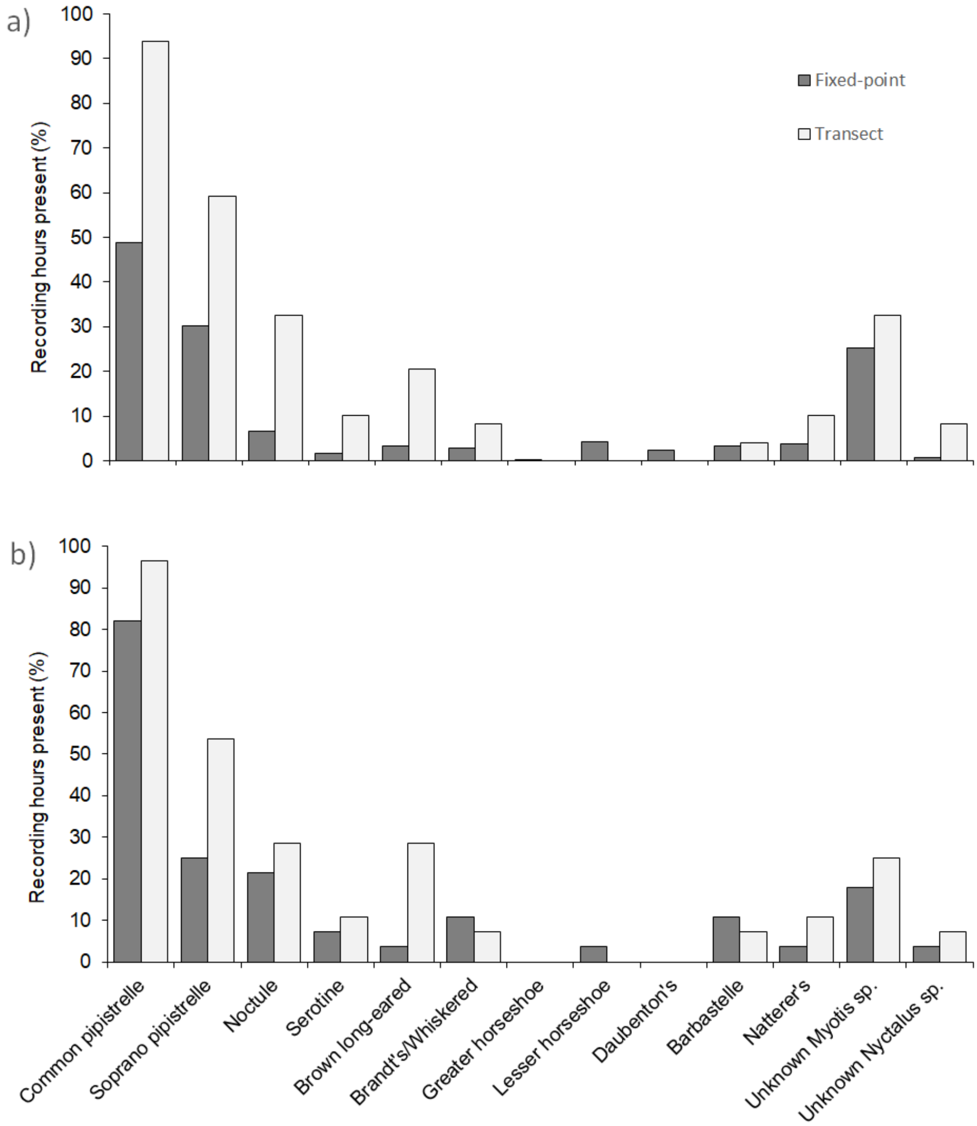

Figure 1 Prevalence of each species/genus in acoustic automated fixed-point and acoustic walked transect surveys (a) within the same two-hour window post-sunset whereby data are directly paired; and (b) using fixed-point data from multiple (minimum of 3) nights within a 21-night window.

Species activity

Within the concurrent data, there was no significant difference in overall bat activity between automated fixed-point surveys and walked transect surveys (19.86 ± 5.65 SEM and 24.18 ± 7.91 SEM, respectively; paired samples t-test: t= 0.870, n= 14 pairs, P= 0.400). However, there was a significant difference between these survey types over multiple nights, with walked transect surveys recording higher overall mean activity (17.53 ± 5.93 SEM, 24.09 ± 5.66 SEM; paired samples t-test: t= 2.610, n = 24 pairs, P= 0.016).

Moreover, there were significant species-specific differences between survey methods. Within the concurrent data, the mean number of brown long-eared bat passes per hour was significantly higher in the walked transect surveys (paired samples t-test: $t = 2.235$, $n = 14$ pairs, $P = 0.044$; Figure 2a). In the multi-night dataset, the mean number of brown long-eared bat passes per hour was also significantly higher during the walked transect surveys than fixed-point surveys (paired samples t-test $t = 2.275$, $n = 24$ pairs, $P = 0.033$: Figure 2b). For common pipistrelle, there was no significant difference between survey methods within the concurrent data, however, within the multi-night data, the mean number of passes per hour was significantly higher during the walked transect surveys, than was recorded in the fixed-point surveys (paired samples t-test: $t = 2.777$, $n = 24$ pairs, $P = 0.011$). For soprano pipistrelle, walked transect surveys recorded a significantly higher number of passes per hour in both the concurrent and multi-night data ($t = 2.228$, $n = 14$ pairs, $P = 0.044$; $t = 2.159$, $n = 24$ pairs, $P = 0.042$, respectively).

Temporal distribution

Analysis of the temporal distributions of each species/genus in relation to hour post sunset is shown in Figure 3. Two sample Kolmogorov-Smirnov tests demonstrated that the activity of all species/genera differed significantly from a uniform distribution ($P \leq 0.046$ in all cases). Most species were detected throughout the night, including within the walked transect survey window (the first two hours post sunset). The exception was the greater horseshoe bats, which were detected in low numbers from 4 hours post sunset onwards. Moreover, although Daubenton's and lesser horseshoe bats were detected in the initial two hours post-sunset they were recorded as frequently (lesser horseshoe) or more frequently (Daubenton's) later in the night. Both pipistrelle species showed a tendency towards being more active in the earlier period of the night, however, the distribution for soprano pipistrelle showed a slight increase in the hours before dawn, making the distribution slightly bimodal.

Discussion

This study found that, for a European bat guild, although more species were recorded via automated fixed-point acoustic surveys than walked transect acoustic surveys in the entire dataset, species richness per hour was substantially and significantly higher in transect surveys. This finding was significant in both the paired dataset (2 hr post sunset) and the multi-night dataset (which fully exploited the recording abilities of the automated method) where per-hour species richness found using walked transects was almost double that found using automated fixed-point acoustic surveys.

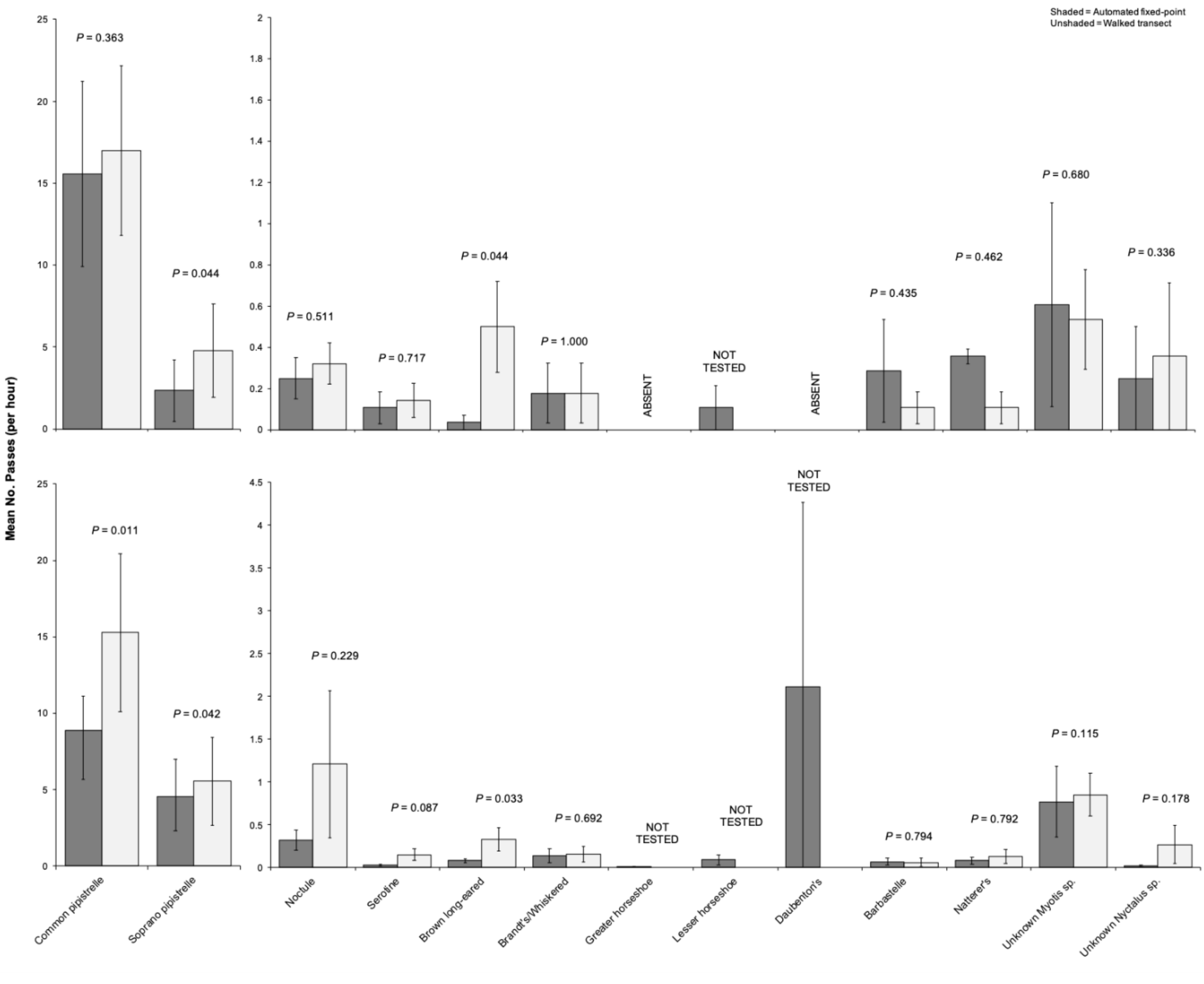

Figure 2 Mean number of bat passes per hour from acoustic automated fixed-point and acoustic walked transect surveys (a) within the same two-hour window post-sunset whereby data are concurrent (significance values from paired samples t-tests undertaken on log-transformed data); and (b) using fixed-point data from multiple (minimum of 3) nights within a 21-night window using the multi-night dataset (significance values from paired samples t-tests undertaken on log-transformed data). Error bars show SEM.

Three species - greater horseshoe, lesser horseshoe and Daubenton's - were not detected on the walked transect surveys, which reduced the species community detected using this method relative to the automated fixed-point surveys. This means that while the walked transects often detect more bat passes, both overall and for some specific species, fixed-point surveys provide a more comprehensive overview of the bat community. Interestingly, the three species not detected on the walked surveys occurred as often (lesser horseshoe), more often (Daubenton's) or exclusively (greater horseshoe) after the two hours post-sunset window when walked transects took place. Greater horseshoes typically emerge late relative to sunset (Collins 2016) and can travel up to 8 km to reach favourable foraging habitat (Billington, 2003a, b; Billington 2004), both of which might mean detection is unlikely during the standard two-hour survey window post sunset as the likelihood of

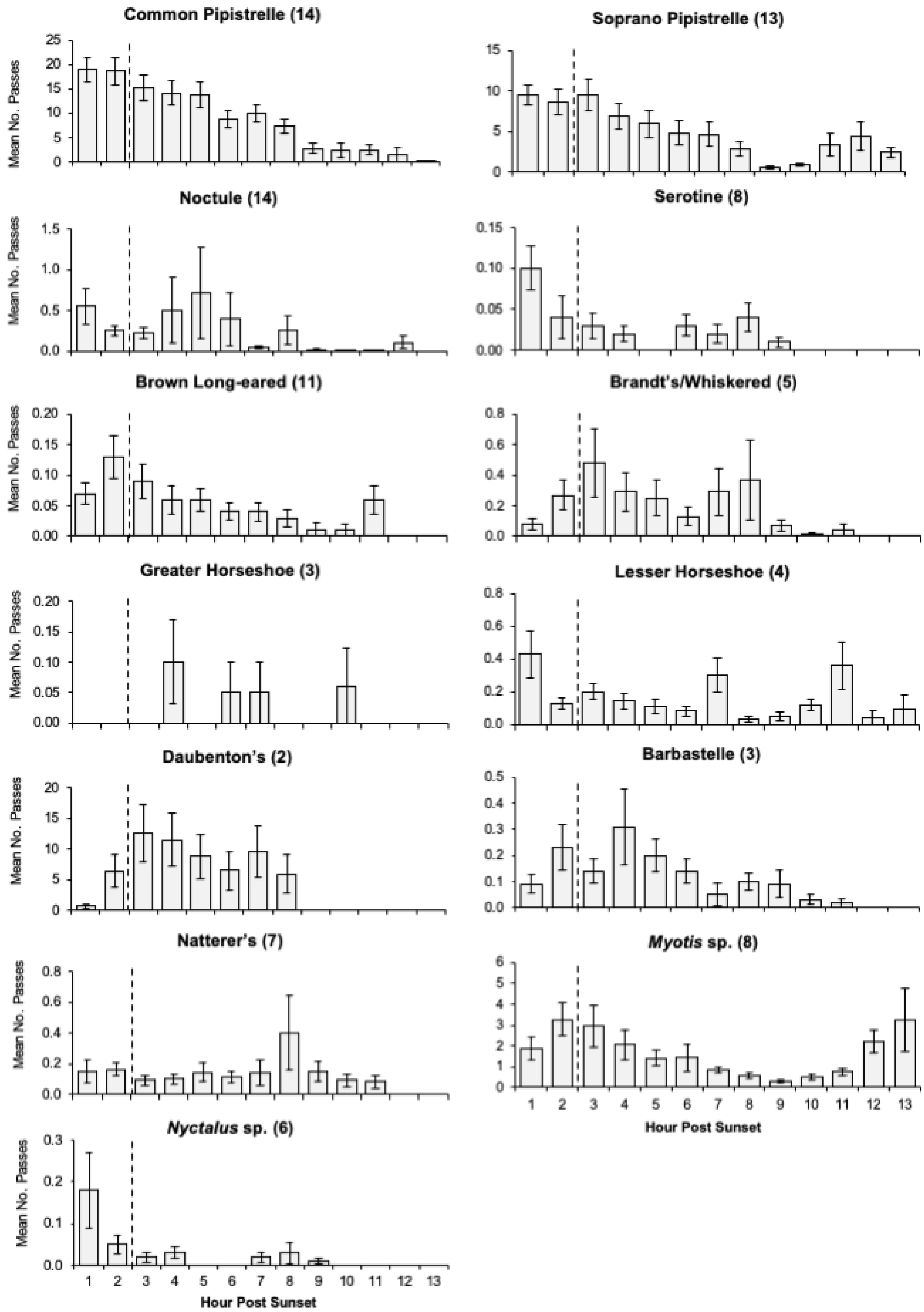

Figure 3 Temporal distribution of each bat species/genus based on mean passes per hour post sunset using automated fixed-point survey data. Number of sites at which species were encountered shown in brackets, the normal transect survey window (two hours post sunset) is shown by the dashed lines. Error bars show SEM.

detecting the species on transects will depend largely on roost proximity. This highlights the importance of secondary data in identification of known roost locations, particularly to target on-ground surveys for legislative compliance in development contexts. Bat mitigation guidelines recommend extending the duration of walked transect acoustic surveys to 3 hours, on sites within commutable distance (4 km) to greater horseshoe roosts (Mitchell-Jones 2004). This aims to account for bat commuting time and minimizes the potential risk of the species being wrongly assumed as absent. However, in this study, greater horseshoes were only detected >4 hrs post sunset, which suggests that this species could still be missed especially if the site constitutes a rich feeding ground that could attract bats from up to 8 km away. Lesser horseshoe bats were detected throughout the night, including within the two-hour transect survey window, but only in the automated fixed-point acoustic surveys. They were always recorded in low densities, probably because they tend to forage within closer proximity to their roosts (Bontadina et al. 2002) and can move easily between roost and foraging grounds throughout the hours of darkness. Given this nocturnal pattern and the comparative rarity of lesser horseshoes, automated fixed-point surveys covering the entire night would be more likely to detect this species. Daubenton's bats were also recorded throughout the night, although they were much more abundant after the end of the transect survey window. Daubenton's roost predominantly in close proximity to the waterways on which they forage (Dietz et al. 2006) and are a later emerging species (Collins 2016), which likely explains their absence from the walked transect acoustic surveys. The decline of activity in both common and soprano pipistrelle throughout the night is also likely responsible for the higher activity of these species in walked transect data compared to fixed-point acoustic data.

The absence of key species from walked transect data emphasises the key advantage of recording for the entire nocturnal period, and over several nights, when surveying bat communities at specific sites: it increases the likelihood of encountering locally rare species or species that emerge (or arrive at foraging grounds) after the widely-used transect survey window two hours post sunset. This is much easier to achieve using fixed-point (passive) surveying, where a fieldworker need not be present, rather than transects. It is not surprising to find different temporal patterns in different bats as multi-species assemblages of insectivorous bats frequently use niche partitioning by selecting different prey, different habitats, or different activity times (Rydell et al. 1996; Milne et al. 2005; Ciechanowski et al. 2007). A similar result was found for US bats whereby three rare species were detected on whole-night automated surveys in Florida, but not on two-hour driven transects that commenced 30 minutes after sunset (Braun de Torrez et al. 2017). Tonos et al. (2014) also found a higher overall species richness on fixed-point surveys relative to driven transects in Indiana. This suggests that although our study has focused on European species and walked transects, this finding is potentially relevant in other bat guilds and for other types of transect including driven and even boat transects (Weier et al. 2020).

Walked transect data and automated fixed-point data were also notably different for the brown long-eared bat. This species was not particularly abundant in either of the acoustic survey methods, despite being fairly common in the UK (Russ 2012), but was detected significantly more often in the walked transect data. This finding was consistent regardless of whether paired data or multi-night data were analysed. Brown long-eared bats are principally gleaners rather than aerial hawkers and thus usually take moth and beetle prey directly from plants (Swift and Racey 1983; Russ 2012). Foraging is often undertaken visually or using sound directly (Anderson and Racey 1991; Eklöf and Jones 2003) as echolocation is not always useful in close proximity to vegetation when hunting (Simmons et al*.* 1979). Any echolocation sounds they do produce, therefore, are short and quiet (Russ 2012) and have historically been almost impossible to pick up using an ultrasonic detector (Anderson and Racey 1991). Although technological advances have now made it possible to detect echolocation from a distance of around 5 m (Russ 2012), brown long-eared bats would still have to echolocate very close to the detector to be recorded, which is potentially less likely to occur if the detector is fixed. Moreover, an advantage of walked transect surveys is that light levels at the start of the survey often permit brown long-eared bats to be identified visually (Russ 2012); the surveyor can also manually orient the detector to obtain a clear recording for sonogram analysis, which can significantly improve detection rates as shown by Milne et al. (2004) for Australian bats. Failure to undertake walked surveys might lead to this species being under-represented in data (Russo and Voigt 2016).

Conclusions and recommendations

Compared to walked transect surveys, automated fixed-point surveys are sometimes considered to be a more effective acoustic survey method (Stahlschmidt and Bruhl 2012), primarily because walked transect surveys are difficult to standardise and can miss activity patterns even in homogenous landscapes. However, our study indicates that the survey types have different strengths and different weaknesses, certainly for European bats and potentially for other bat guilds too. This highlights the value of using a combination of the two methods to collect bat activity data, either for specific sites (e.g. for research, legislative complacence, or conservation) and for national monitoring programmes. While this study has focused on comparing data from paired surveys, examining whether multi-year walked transect and automated fixed-point surveys show the same temporal trends in bat activity would be a useful avenue for future research.

Walked surveys that occur in the standard window of two hours post sunset are likely to under-record rare species, especially those that emerge from roosts late and/or travel a considerable distance to foraging grounds. In Europe, if relying on walked activity surveys, especially in legislative compliance contexts, the survey window for at least one site visit should be extended to 4 hours post sunset by conducting two back-to-back transects to maximise the chances of encountering greater and lesser horseshoe bats, especially if the site is within 8 km of a known horseshoe roost.

In terms of specific recommendations for European bat surveys, we suggest:

- Walked transect acoustic surveys should be used if the aim is to obtain initial baseline data on bats at a specific site, since these are effective in recording high levels of activity, and species richness, in a very time-effective way. Gauging differing activity levels across the whole site also aids in determining its ecological value to bat populations spatially, particularly in heterogenous landscapes.
- Automated fixed-point acoustic surveys should be used if the aim is to catalogue the complete bat species assemblage at a site. As this approach provides data over a longer time period, both throughout the night and over several consecutive nights, issues of temporal niche partitioning and different nocturnal activity patterns between species are negated. This method and also allows for differences in activity due to different environmental conditions on different nights.
- Fixed-point surveys are likely to under-record brown long-eared bats, probably because of infrequent and quiet echolocation as a result of their highly-specific foraging strategy. In Europe, walked activity surveys should be conducted where this species is the target (research contexts) or where habitat is favourable and determining presence conclusively is important for legislation compliance or informing conservation decisions. Pending specific research in other geographical areas, it is suggested that where species are known undertake infrequent or quiet echolocation, or for species known to glean as their main foraging strategy rather than being primarily aerial insectivores (e.g. Gould's long-eared (*Nyctophilus gouldi*) and Lesser long-eared (*Nyctophilus geoffroyi*) bats in Australia (Grant 1991); African yellow-winged bat (*Lavia frons*) in sub-Saharan Africa (Vaughan and Vaughan 1986)), transect surveys are undertaken to complement any fixed-point surveying.
- Walked activity and automated fixed-point acoustic surveys are combined where possible for site assessments, and certainly for national monitoring programmes to ensure that data, and any decisions made on those data including in bioindicator metrics or sustainable development indicators, to be comprehensive, valid and robust.

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Data availability statement

The data that support this study cannot be publicly shared due to ethical or privacy reasons because they include locations of legally-protected species. However, partially redacted or summary data may be shared upon reasonable request to the corresponding author.

Conflicts of interest

The authors declare no conflicts of interest

Declaration of funding

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