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Passive acoustic monitoring in terrestrial vertebrates: a review

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ABSTRACT
Passive acoustic monitoring (PAM) has become increasingly popular in ecological studies, but its efficacy for assessing overall terrestrial vertebrate biodiversity is unclear. To quantify this, its performance for species detection must be directly compared to that obtained using traditional observer-based monitoring (OBM). Here, we review such comparisons across all major terrestrial vertebrate classes and identify factors impacting PAM performance. From 41 studies, we found that while PAM-OBM comparisons have been made for all major terrestrial vertebrate classes, most comparisons have focused on birds (65%) in North America (52%). PAM performed equally well or better (61%) compared to OBM in general. We found no statistical difference between the methods for total number of species detected across all vertebrate classes (excluding reptiles); however, recording period and region of study influenced the relative performance of PAM, while acoustic analysis method and which method sampled for longer overall showed no impact. Further studies comparing PAM performance in non-avian vertebrates using standardised methods are needed to investigate in more detail the factors that may influence PAM performance. While PAM is a valuable tool for vertebrate surveys, a combined approach with targeted OBM for non-vocal species should achieve the most comprehensive assessment of terrestrial vertebrate communities.

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Introduction

Biodiversity is essential to provide both humans and animals with resources vital for survival. Clean air, clean water, soil formation, crop pollination, climate control, and nutrient cycling are just some of the essential services provided by diverse, functioning ecosystems (Fisher et al. 2009). Species-rich ecosystems are also more stable and resistant to change than those that are species-poor (Tilman et al. 2006). Globally, biodiversity is in decline (Pimm et al. 2014) because of human activities, which could lead to the degradation or collapse of ecosystems (MacDougall et al. 2013), with catastrophic consequences

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for nature and humanity (Myers et al. 2013; Malhi et al. 2020). Therefore, identifying changes to biodiversity, in particular, biodiversity loss, is crucial to detecting adverse anthropogenic impacts, and comprehensive monitoring efforts are required to identify where and how to allocate conservation actions. Crucially, long-term monitoring is needed to disentangle the natural variability of biodiversity from changes in species' assemblages caused by human activities at both local and global levels (Magurran et al. 2010).

Monitoring can be defined as the long-term assessment of a community *via* repeated surveys. Although animals are the most commonly sampled organisms in biodiversity monitoring programmes (Henry et al. 2008; Troudet et al. 2017; Moussy et al. 2022), they can be difficult to monitor as they are often mobile and cryptic (Elzinga et al. 2001). To comprehensively monitor animal biodiversity, repeated faunal assessments, ideally conducted long-term, and at large spatial scales, are needed to detect changes to the composition of a community (Lindenmayer et al. 2012). Terrestrial vertebrate biodiversity is usually surveyed by observers in the field, and methods to detect specific vertebrate taxa are well developed (e.g. Sutherland 2006). However, observer-based field surveys require significant effort, and therefore conducting consistent, long-term faunal monitoring is extremely challenging.

Assessing overall vertebrate biodiversity with observers in the field is constrained by several factors. First, observer-based assessments are expensive. Acquiring specialised gear and materials needed for live animal trapping, transporting people and equipment to remote locations, and remunerating expert staff is costly (Darras et al. 2019), and costs increase with survey duration and spatial extension. Second, observer-based assessments require a substantial time investment. Ideally, vertebrate communities are sampled over several years, by conducting repeated field trips, requiring multiple days or weeks per year (e.g. Sutherland 2006; Eyre et al. 2018). Third, observer-based field surveys may be extremely challenging to conduct, or impossible in some areas. Dense vegetation may reduce the visibility of species during active searches (Wintle et al. 2005) and natural barriers, such as rugged terrain and waterbodies, can render some areas inaccessible. Additionally, extreme weather events, such as floods or wildfires, can make some areas entirely inaccessible for lengthy periods (pers. obs.). Finally, to obtain a comprehensive understanding of the terrestrial vertebrate community, various sampling methods must be applied that accommodate differences in the behaviour, ecology and morphology of the target groups. Terrestrial vertebrate fauna is typically surveyed by human observers using a combination of observer-based monitoring (OBM) methods such as active searches during the day or night, point and transect counts, and live animal trapping, often specific to particular taxa (Sutherland 2006; Eyre et al. 2018). Therefore, experts with knowledge of detection and identification, typically of different vertebrate classes, are required but may not be available for a target region (Wheeldon et al. 2019), potentially prohibiting observer-based survey efforts that rely on identification in the field. Furthermore, field observers vary in their expertise, which may limit direct comparisons of surveys conducted by observers with different levels of skill (Farmer et al. 2012) and their presence may negatively impact detectability of certain species (Darras et al. 2018).

Due to these challenges, direct observer-based fauna assessments are often limited, conducted only in small accessible areas, and typically over a few days, at specific times of the year (Eyre et al. 2018), which may decrease the accuracy of biodiversity estimation although there are some notable exceptions to this (e.g. Nichols and Grant 2007; Morecroft et al. 2009). Long-term monitoring of biodiversity is required to assess the direction and significance of changes to ecological communities (Magurran et al. 2010), and without it, we may risk failing to detect detrimental changes to species composition of native species or the presence of introduced species and concurrent reductions in the stability of ecosystems.

Remote sensing technologies provide passive alternatives to observer-based field surveys that can overcome some of the limitations of observer-based fauna assessments and enable monitoring across larger spatiotemporal scales. Camera trapping, for example, has been used for over 50 years to detect various fauna and assess the biodiversity of terrestrial animals while also requiring relatively short periods in the field and saving expenses on trained field personnel (e.g. Winkler and Adams 1968; Seydack 1984; Griffiths and van Schaick 1993; see O'Connell et al. 2011 for a comprehensive overview of the use of camera trapping in animal ecology). Similarly, unmanned aerial systems and satellite imagery have been used to remotely survey some large mammalian vertebrate species, and they have delivered promising results at low field personnel costs (Linchant et al. 2015; Xue et al. 2017).

More recently, passive acoustic monitoring (PAM) has been used to remotely survey vocal fauna using automated acoustic recorders (Cato et al. 2006; Blumstein et al. 2011). In PAM, environmental sounds are collected using passive acoustic sensors, the recorded audio subsequently analysed, and features of interest extracted to gain information on species or entire communities (Obrist et al. 2010; Blumstein et al. 2011; Gibb et al. 2018; Pavan et al. 2022). There is some evidence that PAM is an effective tool for species monitoring. Darras et al. (2019) reviewed the performance of PAM for detecting the most bird species, and while traditional point counts had some advantages over PAM, namely vocally cryptic species could be detected visually and vocalisations could be detected and identified from greater distances by human observers, the authors found that, overall, PAM outperformed human observers in the field. The authors argued that using sound recorders for bird biodiversity assessments was cheaper and more scalable than observer-based survey efforts, making acoustic survey methods more practical and enabling assessments at higher temporal and spatial resolution. PAM has the potential to provide many benefits over OBM and may be useful to monitor various vertebrate taxa (Gibb et al. 2018). However, the effectiveness of PAM for monitoring entire vertebrate communities is not well understood.

Animal vocalisations have long been used to study the ecology and behaviour of animals (Bradbury and Vehrencamp 1998; Obrist et al. 2010; Pavan et al. 2022). The introduction of autonomous recording units (ARUs), in conjunction with recent improvements in battery and data storage technology, has led to increased attention to animal vocalisations for ecological research, particularly monitoring (Sugai et al. 2019). While there are some limitations to the use of ARUs, e.g. poor knowledge of species-specific and habitat-specific detection distances and an inability to detect silent fauna on audio recordings, these devices can record vast amounts of environmental sound while being left completely unsupervised. Audio recordings can subsequently be either manually or automatically analysed to identify vocalisations of animals, and the resulting data can be used to detect or confirm the presence of a particular species, describe an entire vocal community in an environment, or investigate various aspects of the ecology and behaviour of target species (Blumstein et al. 2011).

For species inventory, manual (i.e. listening to recordings and visually scanning spectrograms) and automated audio data analyses have different costs and benefits. For example, the time required to listen to a large number of audio recordings can be prohibitive and may require expert knowledge to identify species (Wimmer et al. 2013; Zhang et al. 2015). Thus, typically, only subsets of acoustic recordings are analysed manually (Madalozzo et al. 2017; Hingston et al. 2018). These subsets are created and selected based on biological information on the target species (e.g. analysing only nocturnal recordings for nocturnal species (Zwart et al. 2014)), by breaking recording or analysis periods down to specific number of minutes every hour for some period (Gunzburger 2007; Wimmer et al. 2013), or by removing recording periods with particularly disruptive background noise (e.g. heavy rain or strong wind (Depraetere et al. 2012)). Automated analyses, such as using algorithms to cluster audio clips with similar properties (Ross et al. 2018), using species-specific algorithms or templates to detect calls (so-called 'recognisers'; Eichinski et al. 2022) or using acoustic indices (Allen-Ankins et al. 2023), enable researchers to utilise entire acoustic data sets to make species lists, search for target fauna, or broadly characterise entire soundscapes (Tegeler et al. 2012; Sueur et al. 2014). Further, examining all available acoustic data may be necessary to detect rare species or species that call infrequently or at unexpected times (La and Nudds 2016). On the other hand, high false-negative and false-positive error rates for species detection can be serious problems for practical use of automated methods (Waddle et al. 2009; Digby et al. 2013). These errors are often caused by the complexity of the soundscape, sound qualities of target species or low numbers of available sound examples to train detection algorithms (Gibb et al. 2018). Nevertheless, automated analysis may be as, or even more, accurate and time-efficient than manual analysis (Digby et al. 2013; Wimmer et al. 2013; Holmes et al. 2014).

Even given the difficulties of data analysis, PAM may represent a cost-effective option for conducting single repeated or long-term fauna surveys, which can overcome some of the shortcomings of traditional OBM methods in terrestrial environments, and could allow comprehensive vertebrate biodiversity monitoring at far greater temporal and possibly spatial scales (Collins et al. 2006; Furnas and Callas 2015). Long-term, large-scale monitoring *via* continuous, unattended audio recordings could offer a greater insight into community composition and changes due to various biotic and anthropogenic factors. The ability to deploy recorders at times and in areas impractical for human observers may enable detection of species for which there are no other records, or even new species discoveries (Brewer 2018). However, it remains unclear whether PAM can be effectively used for comprehensive vertebrate faunal assessments and whether it can replace, or should supplement, OBM. Summaries of acoustic data that do not provide species information, such as acoustic indices, may represent valuable proxies for ecosystem quality, biodiversity and species richness (Alcocer et al. 2022; Schoeman et al. 2022; Allen-Ankins et al. 2023), but to assess complex vertebrate community structure, and obtain more detailed information on species richness and its fluctuations, identification of individual species is required. Thus far, detailed species richness data obtained from PAM exist primarily for bats and birds (Sugai et al. 2019), and relatively little effort has been expended to determine how well PAM reflects species presence for other terrestrial vertebrates. Over the last 10 years, there has been a great increase in research interest in PAM (Obrist et al. 2010; Sugai et al. 2019; Pavan et al. 2022); however, to quantify the effectiveness of PAM for terrestrial vertebrate biodiversity assessments, we must identify the fauna that can reliably be detected using PAM, and these data must be compared to those obtained using traditional OBM. Additionally, factors driving differences between PAM and OBM performances need to be investigated across a broad range of taxa to understand the limitations and applications of passive acoustic monitoring. This review aims to assess the value of PAM for terrestrial vertebrate biodiversity monitoring, by comparing the effectiveness of species detection *via* acoustic and OBM for all classes of terrestrial vertebrates for which such studies have been conducted, and, as far as possible, identify factors driving differences in PAM and OBM performances.

Material and methods

We conducted a literature review using literature searches in Google Scholar and the Web of Science online platform, spanning all available years (1968–present) on 3 April 2021 and 10 December 2021. We used the following search terms: 'passive acoustic monitoring*' OR 'acoustic biodiversity monitoring*' OR 'acoustic monitoring*' OR 'automated recognition*' OR 'acoustic and manual biodiversity survey*' OR 'efficacy acoustic biodiversity survey*' OR 'automated recording unit methods comparison*' OR 'passive acoustic methods comparison*' OR 'survey methods comparisons*' OR 'acoustic survey*' OR 'automated recording unit*' OR 'autonomous recording unit*' followed by the terms 'bird*' OR 'frog*' OR 'amphibian*' OR 'anuran*' OR 'reptile*' OR 'bat*' OR 'mammal*'. Additionally, we examined the bibliographies of the resulting references for further relevant literature. We selected only references on terrestrial vertebrates that directly compared PAM with OBM from data collected in the same year. From each paper, we collected information on the geographic location of the study, the OBM used by human observers, the recording period and time of PAM, the overall sampling period for PAM and OBM, the acoustic analysis method, and the target fauna. Furthermore, we extracted information on the performance of both methods for detecting target fauna to assess the value of PAM compared to the current standard for terrestrial vertebrate assessments of the respective taxonomic group. We used two approaches to compare PAM and OBM. First, we provided a descriptive overview of the literature, and to aid in that description, we classified the performance of either method as 'better' when it led to at least 5% more species or individual detections, and otherwise considered them equal. While this threshold is fairly arbitrary, it was chosen in an attempt to avoid describing one method as 'better' when the difference was very small.

Second, to provide a more rigorous quantitative assessment, we extracted studies that specifically looked at species richness and used them to statistically compare PAM and OBM.

Statistical analysis (richness)

To investigate whether there was a difference in the total number of species detected (richness) *via* PAM and OBM, we used a generalised linear mixed-effects model (*glmmTMB*, v1.1.4) with total richness as the response and sampling regime (PAM or

OBM) as the predictor. Additionally, we controlled for study and taxonomic group by including them as random effects in the model. Additionally, to understand which factors might drive differences in the total species richness detected by PAM and OBM, we used another generalised linear mixed-effects model, with the proportional difference between PAM and OBM ([PAM richness-OBM richness]/OBM richness) as the response and taxa (vertebrate class sampled), region (geographic location of the study), recording period (time period the acoustic sensor was active and recording or the subset of the acoustic data that was used for analysis in the study; continuous = full 24 h recordings, partially continuous = 24 h recordings but only for a proportion of each hour, target = recordings during hours of expected peak activity, simultaneous = recordings of the same time and duration as observer-based surveys), acoustic analysis method (extraction process used on the acoustic data to provide information on species [i.e. manual or automated]), and overall longer sampling duration (whether PAM or the OBM had sampled for longer to obtain the data; PAM = PAM sampled for more days than OBM, OBM = OBM sampled for more days than PAM, Equal = PAM sampled for as many days as OBM) as the predictors (note that this model was examining which factors would affect the magnitude of difference between PAM and OBM, rather than directly comparing PAM and OBM). We controlled for the study by adding it as a random effect in the model. We tested for the significance of the main effect between the factors using an ANOVA (*car*, v3.1–0) and conducted post-hoc pairwise comparisons (*emmeans*, v1.7.5) to determine the significance of the factors of interest. While it is important to acknowledge that PAM will not be effective for non-vocal taxa and, therefore, may not capture the entire community, for comparisons of richness, we decided to focus only on vocal taxonomic groups. Therefore, the reptiles in McKnight et al. (2015) and the caudates in McKnight et al. (2015) and Farmer et al. (2009) were not included in these analyses. Furthermore, because only two studies used continuous recording periods in their analyses, we combined continuous and partially continuous (continuous for only a proportion of each hour) recording periods as ‘continuous’. All statistical analyses were conducted in R (Version 4.2.1) statistical and graphical environment (R Core Team 2023).

Results

We found a total of 41 studies containing 46 direct comparisons of the performance of PAM and OBM (either richness, species-specific detection, density, or occupancy) for terrestrial vertebrates (Table 1). PAM performed equally well (within ±5% of OBM; n = 14) or better (>5% of OBM; n = 14) compared to OBM in 61% of the 46 direct comparisons. In 11 comparisons (24%), OBM outperformed PAM, and in 7 comparisons (15%), results were mixed.

Target fauna

Direct comparisons between PAM and OBM have focused mostly on birds (65%), whereas amphibians (15%), mammals (11% flying mammals; 7% non-flying mammals) and reptiles (2%) have received relatively little attention (Figure 1). Comparisons between PAM and OBM focused mainly on assessing species richness by focusing on an entire assemblage (76%) compared to targeting specific species (24%). In nearly all

Table 1. Studies comparing performance of Passive Acoustic Monitoring (PAM) to Observer-based Monitoring (OBM) across all major terrestrial vertebrate classes. 'OBM' lists the survey methods applied by an observer in the field to assess biodiversity. 'Acoustic analysis' summarises the extraction process used on acoustic data to provide information on species. 'Recording period' refers to the time period the acoustic sensor was active and recording (the table notes subsetted recording periods used in the analysis of data). 'Better performance' indicates whether PAM or OBM produced better results for the purpose of the particular study (species richness, species-specific detection, population density or occupancy) and 'Longer sampling duration' indicates whether PAM or OBM had sampled for longer to obtain the data.

Source	Taxa	Location	OBM	Acoustic analysis	Recording period	Better performance	Longer sampling duration	Notes
Amphibians								
Acevedo and Villanueva-rivera (2006)	Amphibians	Puerto Rico	Line transect	Manual	Partially continuous (7 min/h)	PAM (richness)	Equal	PAM performed 20% better
Corn et al. (2000)	Amphibians	United States	Aural surveys + area search	Manual	Partially continuous (12 s/30 min)	Equal (richness)	PAM	OBM detected one non-vocal species (*Ambystoma tigrinum*); when this species is excluded PAM performed 10% better
Farmer et al. (2009)	Amphibians	United States	Funnel traps + Crayfish traps + dipnets + PVC refugia	Manual	Targeted (1 min/h for 11 h)	OBM (richness)	Equal	OBM performed 30% better (OBM detected six non-vocal salamanders); when these species were excluded OBM performed 4% better
Gunzburger (2007)	Amphibians	United States	Traps + dipnets + area search	Manual	Targeted (1 min/h for 14 h)	PAM (richness)	Equal	
Madalozzo et al. (2017)	Amphibians	Brazil	Area search + dip nets	Manual	Partially continuous (only 1 min/15 min used for analyses)	Equal (richness)	Equal	Continuous recording occurred but was subsetted for analysis (1 min every 15 min)
McKnight et al. (2015)	Amphibians	United States	Pitfall traps + funnel traps + turtle traps + artificial cover objects	Manual	Targeted - (3 × 3 min)	OBM (richness)	OBM	OBM performed 24% better (OBM detected four non-vocal salamanders); when excluding non-vocal amphibians OBM performed 7% better
Penman et al. (2005)	Amphibians	Australia	Point counts	Manual	Targeted (3 min/h for three h)	Equal (richness)	Equal	

(*Continued*)

Table 1. (Continued).

Source	Taxa	Location	OBM	Acoustic analysis	Recording period	Better performance	Longer sampling duration	Notes
Birds								
Acevedo and Villanueva-Rivera (2006)	Birds	Puerto Rico	Point counts	Manual	Partially continuous (7 min/h)	PAM (richness)	Equal	
Alquezar and Machado (2015)	Birds	Brazil	Point counts	Manual	Simultaneous	OBM (richness)	Equal	OBM performed 6% better (detected two species visually not detected via PAM)
Bobay et al. (2018)	Birds	United States	Point counts	Automated	Targeted (~16 h from dawn to dusk)	Mixed results (species-specific detection)	OBM	PAM performed 30% better for Black Rail (*Laterallus jamaicensis*) and OBM performed 26% better for Least Bittern (*Ixobrychus exilis*)
Borker et al. (2015)	Birds	United States	Area search	Automated	Targeted (3 h at dawn)	Equal (species-specific detection)	PAM	Targeted marbled murrelet (*Brachyramphus marmoratus*)
Campbell and Francis (2011)	Birds	Canada	Point counts	Manual	Simultaneous	PAM (richness)		
Castro et al. (2018)	Birds	New Zealand	Point counts (aural only)	Manual	Simultaneous	PAM (species-specific detection)		PAM performed 7% better; Playback experiment; targeted brown kiwi (*Apteryx mantelli*) little spotted kiwi (*Apteryx owenii*) and southern boobook (*Ninox novaeseelandiae*)
Celis-Murillo et al. (2009)	Birds	United States	Point counts	Manual	Simultaneous	Equal (richness)	Equal	
Celis-Murillo et al. (2012)	Birds	Mexico	Point counts	Manual	Simultaneous	Equal (richness)	Equal	
Digby et al. (2013)	Birds	New Zealand	Point counts	Manual/ automated	Simultaneous	OBM (species-specific detection)	Equal	Targeted little spotted kiwi (Apteryx owenii); OBM performed 20% better compared to PAM using manual acoustic analysis and 60% better compared to PAM using automated acoustic analysis; automated acoustic analysis required <3% of the time compared to OBM

(*Continued*)

Table 1. (Continued).

Source	Taxa	Location	OBM	Acoustic analysis	Recording period	Better performance	Longer sampling duration	Notes
Furnas and Callas (2015)	Birds	United States	Point counts	Manual	Simultaneous	Equal (occupancy)	Equal	NA
Haselmayer and Quinn (2000)	Birds	Peru	Point counts	Manual	Simultaneous	OBM (richness)	Equal	OBM performed 13% better; 22 species detected only via OBM (15 were visual only encounters, three inconspicuous calls, four detected at >100m distance)
Hingston et al. (2018)	Birds	Australia	Point counts	Manual	Partially continuous (56–58 min/h) - only subset used for analyses (simultaneous to OBM)	Equal (richness)	PAM	Continuous recording but subsetted for analysis; PAM detected species from beyond 100m
Hobson et al. (2002)	Birds	Canada	Point counts	Manual	Simultaneous	PAM (richness)		PAM performed 13% better
Holmes et al. (2014)	Birds	Canada	Point counts	Automated	Targeted (12 × 10 min/day) – 9 at dawn 3 at dusk	Mixed results (species-specific detection)	PAM	PAM performed 8% better for Acadian Flycatcher (*Empidonax virescens*) and 12% better for Cerulean Warbler (*Setophaga cerulea*) but OBM performed 67% better for Prothonotary Warbler (*Protonotaria citrea*)
Hutto and Stutzman (2009)	Birds	United States	Point counts	Manual	Targeted (5 h at dawn) - only subset used for analyses (simultaneous to OBM)	OBM (richness)	Equal	OBM performed 17% better; species only detected via OBM mainly due to detections at >100 m (52.7%) and visual encounters (14.8%)
Klingbeil and Willig (2015)	Birds	United States	Point counts	Manual	Simultaneous	Mixed results (richness)	PAM	OBM performed better for same duration surveys but PAM performed better over an extended recording period

(*Continued*)

Table 1. (Continued).

Source	Taxa	Location	OBM	Acoustic analysis	Recording period	Better performance	Longer sampling duration	Notes
Kułaga and Budka (2019)	Birds	Poland	Point counts	Manual	Continuous (only subset used for analyses – 15 min before OBM simultaneous to OBM same time but next day)	Mixed results (richness)	Equal	OBM performed 14% better for same duration surveys but PAM performed 4% better over a longer recording period
Lambert and McDonald (2014)	Birds	Australia	Point counts	Manual	Simultaneous	PAM (population density)		Targeted bell miners (*Manorina melanophrys*)
Leach et al. (2016)	Birds	Australia	Point counts	Manual	Targeted (150 min at dawn + 120 min at dusk) - only 5 x 2 min used for analyses	OBM (richness)	Equal	OBM performed 10% better
Penman et al. (2005)	Birds	Australia	Point counts	Manual	Targeted (3 min/h for three h)	Equal (richness)	Equal	
Sedláček et al. (2015)	Birds	Cameroon	Point counts	Manual	Simultaneous	Equal (richness)	Equal	
Sidie-Slettedahl et al. (2015)	Birds	United States	Playbacks	Manual	Targeted (12 x 40 min/h at night)	OBM (species-specific detection)	PAM	OBM performed 60% better for Le Conte's Sparrow (*Ammodramus leconteii*), 76% better for Nelson's Sparrow (*Ammodramus nelsoni*) and 101% better for Yellow Rail (*Coturnicops noveboracensis*); superior OBM performance likely because of detections at great distances

(*Continued*)

Table 1. (Continued).

Source	Taxa	Location	OBM	Acoustic analysis	Recording period	Better performance	Longer sampling duration	Notes
Tegeler et al. (2012)	Birds	United States	Point counts	Manual/ automated	Targeted (5 h at dawn)	Mixed results (richness)	OBM	OBM performed 16% better for same duration surveys and 6% better for longer PAM recording periods when using manual acoustic analysis but PAM performed 5% better when using automated acoustic analysis
Van Wilgenburg et al. (2017)	Birds	Canada	Point counts	Manual	Simultaneous	Equal (population density)	Equal	
Venier et al. (2012)	Birds	Canada	Point counts	Manual	Simultaneous	Mixed results (richness)	Equal	PAM performed 3% better when both PAM methods were combined but OBM performed 3–6% better compared to only one PAM method
Vold et al. (2017)	Birds	United States	Point counts	Manual	Simultaneous	OBM (richness)	Equal	OBM performed 22% better; because of detections at great distances and visual encounters
Wheeldon et al. (2019)	Birds	Kenya	Point counts	Manual	Simultaneous	PAM (richness)	Equal	PAM performed 23% better
Williams et al. (2018)	Birds	New Zealand	Point counts	Manual	Simultaneous	PAM (species-specific detection)	Equal	PAM performed 14% better; targeted Australasian bittern (Botaurus poiciloptilus); PAM about half the cost of OBM
Wimmer et al. (2013)	Birds	Australia	Area search	Manual	Partially continuous (1 min/30 min)	PAM (richness)	Equal	PAM performed 31% better; highest species richness was detected when analysing the full acoustic dataset rather than shorter subsets
Zwart et al. (2014)	Birds	United Kingdom	Line transect	Automated	Targeted (6.5 h at night)	PAM (species-specific detection)	Equal	PAM performed 18% better for same duration surveys and 59% better for longer PAM recording periods; Targeted European Nightjar (*Caprimulgus europaeus*)

(*Continued*)

Table 1. (Continued).

Source	Taxa	Location	OBM	Acoustic analysis	Recording period	Better performance	Longer sampling duration	Notes
Mammals								
Flaquer et al. (2007)	Flying mammals	Spain	Mist nets + roost surveys	Automated	Continuous	Equal (richness)	Equal	Authors recommend: habitat preference of target species should determine the survey method used; a combination of methods would be best
Lintott et al. (2013)	Flying mammals	United Kingdom	Mist nets + harp traps	Automated	Simultaneous	PAM (species-specific detection)	Equal	
MacSwiney et al. (2008)	Flying mammals	Mexico	Mist nets + harp traps	Manual	Simultaneous	OBM (richness)	Equal	OBM performed 27% better
O'Farrell and Gannon (1999)	Flying mammals	United States	Mist nets + harp traps	Manual	Simultaneous	PAM (richness)	Equal	PAM performed 12% better
Penman et al. (2005)	Flying mammals	Australia	Point counts	Manual	Targeted (3 min/h for three h)	Equal (richness)	Equal	
Enari et al. (2017)	Non-flying mammals	Japan	Spotlighting + camera traps	Manual	Continuous	PAM (species-specific detection)	OBM	PAM performed 40% better; targeted sika deer (*Cervus nippon*); PAM detected males where OBM failed (low-density areas)
Kalan et al. (2015)	Non-flying mammals	Ivory Coast	Point counts	Automated	Targeted (30 min/h for 11 h)	Mixed results (occupancy)	PAM	Targeted chimpanzee (Pan troglodytes verus) Diana monkey (*Cercopithecus diana*) and king colobus (*Colobus polykomos*)
Penman et al. (2005)	Non-flying mammals	Australia	Point counts	Manual	Targeted (3 min/h for three h)	Equal (richness)	Equal	
Reptiles								
McKnight et al. (2015)	Reptiles	United States	Pitfall traps + funnel traps + turtle traps + artificial cover objects	Manual	Targeted - (3 × 3 min)	OBM (richness)	OBM	All reptiles captured were non-vocal species

cases, one vertebrate class was assessed, and only three papers compared the performance of PAM and OBM for two or more vertebrate classes: McKnight et al. (2015) focused on amphibians and reptiles, Acevedo and Villanueva-Rivera (2006) assessed amphibians and birds, and Penman et al. (2005) detected birds, amphibians, flying and non-flying mammals, and the results were treated as separate comparisons for each class.

Birds

For birds, PAM detected species at least equally well as OBM in 17 comparisons (57%, 9 PAM > OBM, 8 PAM = OBM), whereas OBM showed superior detection performance in seven studies (23%; Figure 1). In the remaining six studies, results depended on species identity, recording periods, or acoustic analysis methods. Bobay et al. (2018) and Holmes et al. (2014) compared the detection probabilities of PAM vs. OBM for rare and secretive birds and reported mixed results (i.e. PAM was better at detecting birds with more complex calls but performed worse for species with simple vocalisations). Comparing species richness recorded *via* OBM and two types of ARUs (Wildlife Acoustics Song Meter SM1 and Earthsong series E3A DSS Bio-Acoustic Monitor Kit), Venier et al. (2012) found that OBM detected more species than SM1 recorders but equal numbers to E3A devices and identified differing sensitivities to distant calls as the reason. Tegeler et al. (2012), Klingbeil and Willig (2015) and Kułaga and Budka (2019) all found that species detections were greater using OBM than PAM when the same duration and time periods were compared for the two methods, but PAM detected at least the same number of species when longer recording periods were used to compare to OBM. All seven studies reporting better species detection by OBM compared to PAM relied on targeted recording periods, such that ARUs recorded at a certain time of the day or night, when the target fauna was most likely active. The authors attributed the better performance of OBM mainly to visual encounters during observer-based field surveys and the detection of calls at great distances (>100 m) by humans.

Amphibians

For amphibian species richness, the performance of PAM was equal to or better than OBM in five out of seven (71%) comparisons (Figure 1). Superior OBM performance in the other two studies occurred because OBM detected non-vocal species (salamanders). When excluding non-vocal species and looking only at anurans (frogs and toads), PAM produced similar outcomes (Farmer et al. 2009; McKnight et al. 2015), with only rare species remaining undetected *via* PAM in both studies.

Mammals

Studies comparing PAM and OBM in terrestrial mammals can be separated into those investigating flying mammals (bats) and those targeting non-flying mammals. For detecting the number of species of flying mammals, four studies reported equal ($n = 2$) or better ($n = 2$) PAM performance, compared to OBM, and in one study, OBM outperformed PAM (Figure 1). The authors of that study (MacSwiney et al. 2008) found that even though OBM detected more species than PAM overall, acoustic surveys led to the detection of additional species that had not been captured during observer-based surveys and concluded that a combination of both methods would be best.

In non-flying mammals, one study found that PAM and OBM produced identical species richness for arboreal mammals, and in another comparison, PAM outperformed OBM for

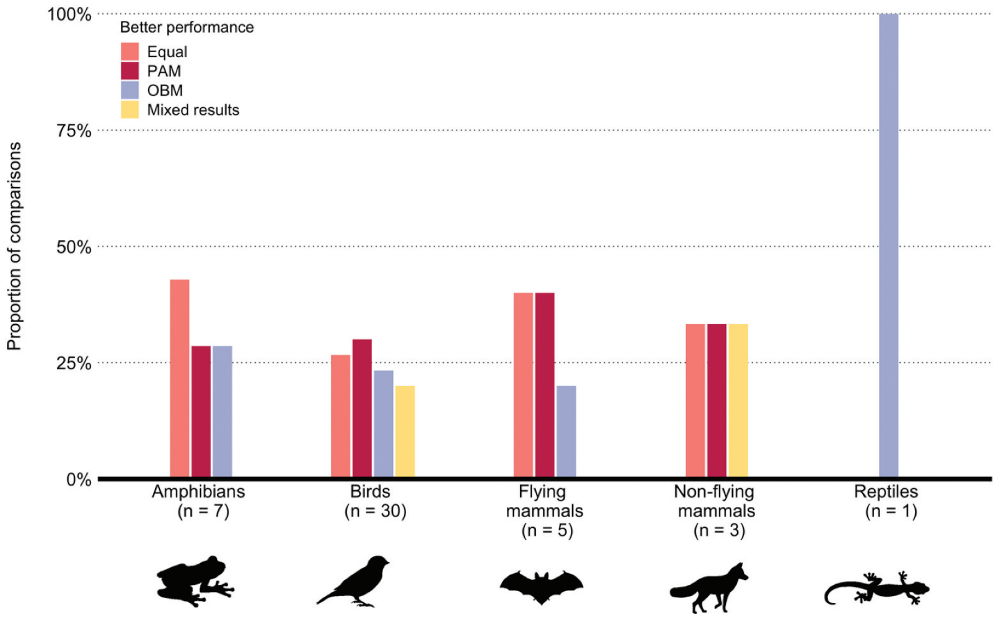

Figure 1. Proportion of comparisons (n = 46) reporting on the detection performance (either richness, species-specific detection, density or occupancy) of each terrestrial vertebrate class using Passive Acoustic Monitoring (PAM) and Observer-based Monitoring (OBM). In seven studies, performances varied for different species, recording periods or acoustic analyses, and were combined in 'Mixed results'. Three studies assessed multiple vertebrate classes and were added as separate data to the relevant taxa.

detecting sika deer (*Cervus nippon*). The authors reported that PAM detected deer even at low densities when OBM failed to detect individuals. Kalan et al. (2015) investigated occupancy probabilities in three species of primate and reported mixed results. PAM and OBM performed equally well for Diana monkeys (*Cercopithecus diana*) and king colobus (*Colobus polykomos*), but PAM outperformed OBM for chimpanzees (*Pan troglodytes verus*).

Reptiles

Only one study included a comparison of the performance of PAM and OBM for the detection of reptiles (McKnight et al. 2015; included as part of a broad reptile and amphibian survey utilising and comparing a suite of methods; Figure 1). None of the 34 species of reptiles observed *via* OBM were detected using PAM. All reptile species detected in the study were non-vocal, except for turtles, which can make low-frequency vocalisations (Ferrara et al. 2013); however, detection would require hydrophones placed in bodies of water, which were not used in the study.

Geographic location

Comparisons of PAM and OBM have mostly been conducted in the Northern Hemisphere (70%), largely in North America (Figure 2). Comparisons were most widely distributed for birds and were conducted on five continents in 12 countries, mostly in the United States (30%), Canada (17%) and Australia (17%). Conversely, comparisons for

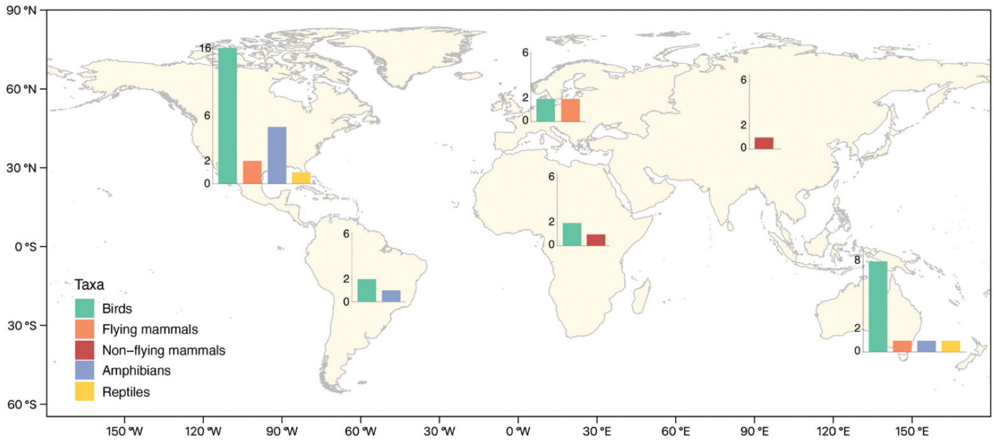

Figure 2. Number of comparisons in the performance of Passive Acoustic Monitoring (PAM) with Observer-based Monitoring (OBM) for each major terrestrial vertebrate class across geographical regions.

amphibians (71%) and reptiles (100%) were almost exclusively conducted in North America. Outside of the United States, studies targeting flying mammals were conducted only in Europe and Australia, and for amphibians only in Australia and South America. Studies targeting non-flying mammals have been conducted only in Asia and Africa.

PAM recording period

Recording periods for PAM differed among studies (Table 1) but can generally be classified as follows: simultaneous with OBM (48%); targeted at specific times of day when target fauna was likely active (35%); partially continuous for a proportion of each hour (11%); and continuous (7%). In most studies, ARUs were active and recorded only for a period of the day or night. Only four comparisons of PAM and OBM performance used continuous PAM recordings. However, only two of these analysed the entire acoustic data set, whereas the other two studies analysed only subsets of the data.

Acoustic analysis method

The primary methods (80% of studies) used to detect species in audio recordings were manual, typically by either listening to audio clips, visually inspecting spectrograms, or a combination of both. In 17% of cases, automated analysis was applied to search PAM recordings for species calls, and 2% of studies applied manual and automated acoustic analysis. Automated analysis methods were mostly used in studies after 2013, except for Flaquer et al. (2007) who used built-in identification algorithms for automated recognition of bat calls offered in the 'BatSound' software (Brigham et al. 2002), whereas manual methods were used in all studies spanning 1999 to 2020. Automated acoustic analyses were applied primarily to detect specific fauna within targeted PAM recordings, rather than entire vertebrate communities.

Total species richness

Of the 41 studies comparing PAM and OBM performance, 25 compared species richness and reported the total species richness for each method (Table 1). Within those 25 studies, 30 comparisons were made between PAM and OBM for the total number of species detected. In 17 comparisons (57%) PAM detected at least as many species in total as OBM, and in 13 comparisons (43%) OBM produced higher total species richness (Figure 3). There was no significant difference in total species richness detected between PAM and OBM (estimate = −0.24, 95% CI [−3.52, 3.04], $p = 0.89$). However, the subsequent analysis examining the factors affecting the performance of PAM relative to OBM revealed a significant effect of recording period ($df = 2$, $p < 0.001$) and region ($df = 4$, $p = 0.003$). Neither the vertebrate class ($df = 3$, $p = 0.89$), method of acoustic analysis (manual or automated; $df = 1$, $p = 0.8$), nor which method sampled for longer overall ($df = 3$, $p = 0.07$), were significant (Table S1). Post hoc analyses of continuous, simultaneous, and targeted recording periods showed evidence only for a positive effect of continuous recordings compared to targeted recordings (estimate = 0.33, 95% CI [0.09, 0.56], $p = 0.008$) and no significant difference between continuous and simultaneous

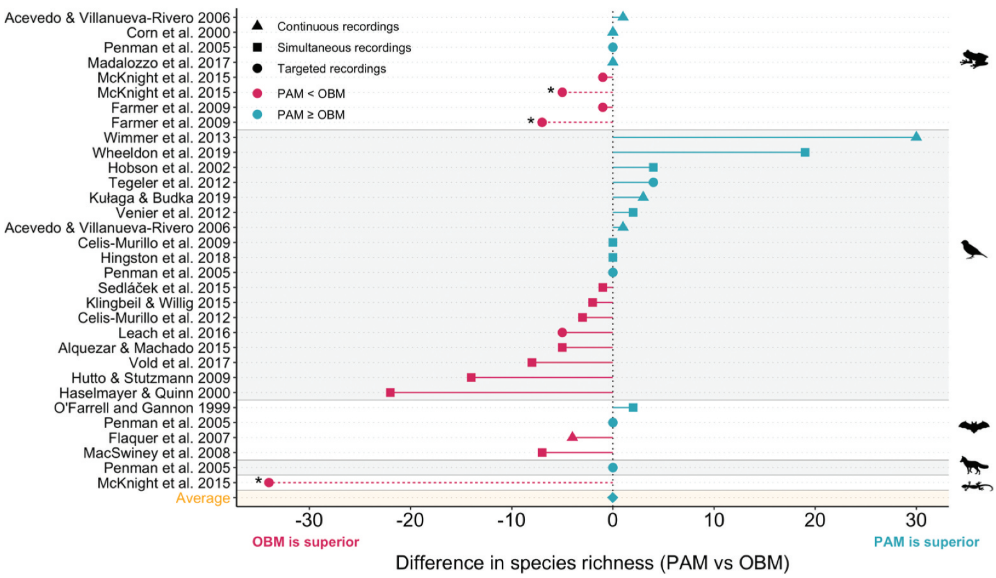

Figure 3. Results of studies specifically examining species richness, displayed as difference in the total species richness assessed via Passive Acoustic Monitoring (PAM) versus Observer-based Monitoring (OBM) in 30 comparisons in 25 studies separated by vertebrate class and the average difference across all comparisons. Icons next to white or grey areas indicate all comparisons for the respective vertebrate class (amphibians, birds, flying mammals, non-flying mammals and reptiles). Shapes represent the recording period used via PAM for the comparison (triangle = continuous, square = simultaneous, circle = targeted; continuous and partially continuous recording periods were combined as 'Continuous recordings'). Red shapes and lines represent higher total species richness via OBM and blue shapes and lines equal or higher total species richness via PAM. Three studies assessed multiple vertebrate classes and were added as separate comparisons to the relevant taxa. Three comparisons indicated by asterisks and dotted lines were not used in the richness model and to calculate the average because they included non-vocal fauna.

recordings (estimate = 0.18, 95% CI [−0.03, 0.39], $p = 0.09$) or between targeted and simultaneous recordings (estimate = 0.15, 95% CI [−0.13, 0.42], $p = 0.73$). While there was a significant main effect of regions in the model, post hoc comparisons did not identify any significant pairwise differences between specific regions (Table S2). Taken together, these results show that while there was no overarching difference in richness between PAM and OBM, there are factors that affect the relative performance of PAM.

Discussion

Here, we reviewed the performance of PAM for species detection, a fundamental aspect of fauna monitoring, across all major classes of terrestrial vertebrates. In many studies, PAM often outperformed or was equal to OBM for estimating species richness and detecting individual species, and our statistical analysis of 25 studies failed to find a significant difference between PAM and OBM for richness. Thus, PAM was useful for monitoring in a variety of situations although, of course, non-vocal species were never detected. Direct comparisons of the performance of PAM and OBM for species detection have been conducted for all terrestrial vertebrates; however, most studies have focused on birds in North America. For total species richness, the period ARUs are active and recording (recording period) and the region of study influenced the relative performance of PAM compared to OBM, whereas the vertebrate class targeted, method of acoustic analysis and which method sampled for longer overall (PAM vs OBM) had little impact. The region where surveys were conducted may have had an influence; however, more research from other parts of the world is needed to assess regional differences of PAM and OBM performances. In general, sample sizes and various classes of methodologies available for comparison were small.

Adequate detection of many species using PAM suggests that acoustic monitoring might be a viable alternative to OBM for many terrestrial vertebrates. However, the effectiveness of PAM for species detection does vary and is better for some species and taxonomic groups. Most obviously, reptiles are largely non-vocal and therefore remain undetected when using PAM (McKnight et al. 2015). However, many species within Gekkota emit territorial and advertisement calls audible at a distance (Marcellini 1974; Brillet and Paillette 1991; Hibbitts et al. 2007) and could potentially be sampled using PAM. Most salamanders (order Caudata) on the other hand, are non-vocal and were the primary reason for superior OBM performance compared to PAM in some studies of amphibians (Farmer et al. 2009; McKnight et al. 2015). When targeting only vocal amphibians, PAM produced results similar to OBM. PAM typically detected bats better than OBM, and only one study found that OBM was better at detecting bats than PAM (MacSwiney et al. 2008), and even this study found that, although estimates of overall richness were higher using OBM, more insectivorous bats of the family Molossidae were detected using PAM. PAM performance was at least equal to OBM for non-flying mammals; however, this conclusion is based on only three studies targeting sika deer (Enari et al. 2017), four species of arboreal mammals (Penman et al. 2005), and three species of primate (Kalan et al. 2015). More comparisons focusing on non-flying mammals are needed to determine if PAM can be used to effectively monitor vocal mammals.

In birds, PAM performed at least equally well as OBM to sample the maximum number of species (also see Darras et al. 2019), but for specific species, we found that the performance of PAM and OBM varied. Bobay et al. (2018) suggested that differences in vocal complexity were the main reasons for the variation in detection performance. Species with less complex vocalisations (one- or two-note calls) were detected less effectively using PAM. This outcome is also typical of studies using automated acoustic analysis methods (Swiston and Mennill 2009; Sidie-Slettedahl et al. 2015; Knight et al. 2017). Careful consideration must be given to the fauna of interest and whether non-vocal species are present or of interest, when planning to use PAM alone for biodiversity assessments. Similarly, some species vocalise regularly and often (e.g. various birds), while others exhibit more irregular seasonal calling patterns (e.g. frogs and many terrestrial mammals). Therefore, the rates at which species call should also be considered, to inform acoustic sampling efforts. An initial survey approach, in which PAM and OBM are combined to provide a first insight into species' identity at a site, could inform the best approach to use for comprehensive vertebrate assessments (Flaquer et al. 2007; Holmes et al. 2014; Wheeldon et al. 2019).

The main advantages of OBM over PAM for species detection and the reasons OBM outperformed PAM at species detections in some studies were (i) that visual observations could detect silent individuals, and (ii) human observers can often detect species calling from further than can the microphone of ARUs (typically at distances greater than 100 m) (Haselmayer and Quinn 2000; Venier et al. 2012; Furnas and Callas 2015). Visual detections made during observer-based field surveys are often mentioned as major advantages over acoustic methods (Acevedo and Villanueva-Rivera 2006; Hutto and Stutzman 2009; Alquezar and Machado 2015), although some studies found that visual detections did not affect estimates of species composition compared to PAM (Celis-Murillo et al. 2009), and in densely vegetated habitats, acoustic cues may actually be more important for species detections (Kułaga and Budka 2019). When directly comparing both survey methods, specifically using audio recordings made only at the same time as observer-based field surveys, visual encounters can indeed represent a significant advantage (Hutto and Stutzman 2009). During a typical 10–15 min point count survey, some birds might not vocalise and therefore do not appear in recordings. However, many species of birds are detected aurally during point counts (Brewster and Simons 2009), and most birds will vocalise eventually, such that longer recording periods tend to detect higher species richness (Tegeler et al. 2012; Froidevaux et al. 2014; Klingbeil and Willig 2015; Kułaga and Budka 2019; Wood et al. 2021). Therefore, extending the duration of recording and taking advantage of the storage and battery capabilities of modern ARUs should allow detection of species only encountered visually during short recording periods, as well as rare avian or non-avian species or those that do not vocalise frequently. Similarly, extending recording periods could lead to detection of birds observed only at great distances during point counts, because they may eventually approach recorders. Furthermore, human presence affects bird calling activity (Bye et al. 2001), and some birds may avoid spatial proximity to humans (Fernández-Juricic et al. 2001; Darras et al. 2018). Replacing the human observer with an ARU may lead to the detection of species previously deterred by the observer. Further research into the detectability of species of interest over time and distance is critical to enhance the usefulness of PAM.

Collecting acoustic data using ARUs over periods longer than 24 h is often limited by battery life and data storage capacity (Shonfield and Bayne 2017), and we found that most studies used fixed recording periods, rather than collecting continuous recordings. In our review, there was great variation among studies in recording durations and times. Even though different recording periods produced different outcomes for PAM, we found that, for most terrestrial vertebrates, PAM achieved results comparable to OBM. Our analyses suggest that duration of recording period drove differences in PAM and OBM performance for total species richness and that using partially continuous recordings was superior to targeted recording periods at specific times of the day or night. The impact of fully continuous recordings on the performance of PAM for species richness could not be conclusively evaluated, as only two studies utilised continuous recordings. However, extended recording periods, now possible given technological advances, seem likely to improve the species detection performance of PAM (Klingbeil and Willig 2015), and ongoing technological innovations continue to increase battery life and advance data storage options (Aide et al. 2013), enabling the collection of long-term acoustic data sets.

Longer recording periods and more data storage, however, generate larger acoustic data sets to be analysed. We found that most studies comparing PAM to OBM relied on manual acoustic analyses, rather than automated methods. The time required to manually analyse long-duration audio recordings is prohibitive and requires expert knowledge to identify species, and thus, typically only subsets of larger acoustic data sets are manually analysed (e.g. Hutto and Stutzman 2009; Madalozzo et al. 2017; Hingston et al. 2018). Collection and analysis of acoustic data are often conducted only for certain periods of the day when target fauna are likely to be vocalising (Bobay et al. 2018), but some species could be missed when listening to samples. For example, Wimmer et al. (2013) found that avian species richness was about 20% lower for dawn-only samples compared to full-day sampling. The authors focused on birds, but to detect many mammals, frogs, and nocturnal birds, it is important to record at night, and therefore recordings lasting longer than dawn periods are required for comprehensive monitoring. Automated analyses, such as clustering an acoustic data set into categories of similar sound, or using species-specific, automated call 'recognisers' (Priyadarshani et al. 2018), enable researchers to search the entire acoustic data set for target fauna. Automated analyses often suffer from errors, either incorrectly suggesting a sound match (false positive) or missing a target sound (false negative). Reducing the incidence of one type of error usually leads to an increase in the other type, which means that there is a trade-off between incorrectly 'detecting' a species and missing a species' calls altogether (Waddle et al. 2009). Constant improvements in acoustic analysis software and the increasing availability of labelled acoustic data will decrease overall error rates (Priyadarshani et al. 2018) and will mean that eventually, entire long-term recordings can be analysed quickly, reducing the amount of manual effort required (Waddle et al. 2009). Automated processing will likely reduce costs and time compared to conducting observer-based surveys in the field, which collect less data (Holmes et al. 2014; Darras et al. 2019) and may increase achieving the objectives of monitoring, such as detecting patterns of decline.

In this review, we were unable to evaluate the relative impact of some factors on PAM performance for species richness. Even though there was some evidence of regional differences in PAM performance, the low number of available studies comparing PAM and OBM performance directly from regions other than North America limited detailed assessment of regional effects. Similarly, only two studies compared PAM and OBM while utilising fully continuous audio recordings, as opposed to either recording only for some minutes of every hour or subsetting their acoustic data for analysis. As a result, we were forced to combine partially continuous and fully continuous recordings, limiting the insight into the value of fully continuous recording periods. Additionally, other interesting factors that might influence PAM performance, like type of recorder, recording settings or weather conditions were highly inconsistent among studies, prohibiting further statistical investigation. In fact, standardisation among PAM studies is an issue making direct comparisons among studies difficult (Gibb et al. 2018). While a standardised acoustic survey protocol has been proposed for birds in the UK (Abrahams 2018), more studies focusing on comparisons of vertebrates other than birds in North America applying standardised methods are needed, to enable more direct comparisons and a more detailed investigation into the factors that influence PAM performance.

In conclusion, direct comparisons of the performance of PAM and OBM for species detection have been conducted for all terrestrial vertebrate classes, and for detecting vocal species, PAM often performs at least equally well as OBM. However, most studies have focused on birds, and very little research has been directed at investigating the efficacy of PAM for monitoring other terrestrial vertebrates. The duration of recordings analysed likely influences the effectiveness of PAM, and future studies should aim to record continuously and analyse as much of the available audio data as possible, to fully utilise the capabilities of passive acoustic monitoring. More direct PAM-OBM comparisons, for a wider range of terrestrial vertebrates, are needed to understand how PAM can effectively be used for comprehensive biodiversity surveys. However, some form of manual validation and analysis will continue to be necessary. Similarly, observer-based field surveys continue to be necessary to detect non-vocal fauna, and therefore PAM is a tool for enhancing vertebrate surveys, rather than replacing observer-based efforts. Therefore, a combination of targeted observer-based field survey efforts for non-vocal species and PAM to detect most other fauna can provide a comprehensive terrestrial vertebrate community assessment while saving time and financial resources.

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