The value of sound: Passive acoustic monitoring for terrestrial vertebrate biodiversity assessments

Thesis submitted by

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Ethics and copyright

This research has been conducted in accordance with the James Cook University Animal Research Ethics Committee approval number A2727, the QPWS (Queensland Research Permit P-PTUKI-100066861 and WA0033038), and NSW Government (New South Wales Scientific Licence SL102511).

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Abstract

Biodiversity is essential for ecosystem health and resilience, providing vital resources for humans and animals. An ecosystem rich in biodiversity is more resilient and stable and thus identifying changes to biodiversity is crucial. Traditionally, biodiversity assessments rely on time-consuming and expensive observer-based monitoring (OBM) methods, which are often impractical or impossible in certain areas. Passive acoustic monitoring (PAM) has emerged as a promising remote sensing technique to gain valuable information about vocalising species, including presence and absence, activity patterns, habitat use, community ecology. However, the value of PAM for comprehensive terrestrial vertebrate biodiversity assessments remains unclear. The overarching aim of my thesis was to investigate the value of PAM for assessing terrestrial vertebrate biodiversity by comparing it to traditional OBM efforts and camera trapping for mammals (**Chapter 2**), frogs (**Chapter 3**), and reptiles (**Chapter 4**). Specifically, I conducted extensive fieldwork for two years at six sites spanning a large latitudinal range along eastern Australia, comparing PAM, OBM, and camera trapping for assessing species richness, community composition, and species accumulation while considering survey effort, time investment, and financial costs (**Chapters 2-4**). I also evaluated the effectiveness of the BirdNET deep-learning model to analyse a cumulative total of 36 years of audio recordings and deliver detections of vocalising species.

In **Chapter 1**, I conducted a comprehensive review of 41 studies comparing PAM and OBM across all major terrestrial vertebrate classes. This review revealed that PAM performed equally well or better than OBM in 61% of cases, with no statistical difference in total species detected across vertebrate classes (excluding reptiles). I 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%). 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. These findings emphasise the need for further studies comparing evaluating PAM performance in non-avian vertebrates in different geographical regions to understand the value of PAM and identify the factors that may influence PAM performance.

Chapter 2 focused on mammal biodiversity assessments, comparing PAM, OBM, and camera trapping. Using embeddings from the BirdNET deep-learning model, I efficiently analysed a cumulative total of 317,410 hours of continuous audio data (equivalent to 36 years) from six sites, successfully detecting all 17 target vocal mammal species. While OBM

performed best for detecting the entire mammal community (recording the highest species richness and accumulating species the quickest), PAM significantly outperformed other methods for vocal mammals when leveraging long-term audio data. Furthermore, PAM only required 7% of the overall time investment compared to OBM. Despite the benefits, the inability of passive acoustic monitoring to detect non-vocal mammals underscores the necessity of combining it with other survey methods such as camera trapping or observer-based monitoring to provide the most comprehensive assessment of terrestrial mammal biodiversity.

In **Chapter 3**, I investigated frog biodiversity assessment, comparing PAM and OBM methods. For the short-term (28-day) survey period, OBM proved more effective due to its ability to include visual detections. However, when considering the entire study period, PAM detected the highest number of frog species across all sites. This discrepancy highlights the importance of survey duration in frog monitoring. Frog vocal activity is closely linked to rainfall, and short survey or recording periods risk missing significant rain events and thus failing to detect vocalising species. Extending the monitoring period to at least a year significantly improved species detection, capturing the highest number of species overall. Notably, summer and spring sampling periods provided the quickest accumulation of species, coinciding with more frequent and intense rain events. These findings emphasise the value of long-term PAM for comprehensive frog biodiversity assessment and underscore seasonal sampling bias.

Chapter 4 examined reptile biodiversity assessment, comparing seven survey methods across different latitudes. Pitfall and funnel traps proved most effective, especially in combination, accounting for nearly 90% of all reptile species detected. However, with a decrease in latitude reptile diversity increased and other survey methods became necessary to document the full extent of the reptile communities. Reptile assemblages captured by different survey methods varied significantly, except for the communities captured by pitfall and funnel traps. No single method captured all species, and no species was detected by every method. Passive acoustic monitoring failed to detect any reptiles and may not be viable for assessing reptile biodiversity in Australia. When possible, to maximize species richness, survey designs should incorporate an array of concurrently deployed methods, particularly in regions with higher overall species richness.

The research presented in this thesis demonstrates that PAM, combined with automated analysis techniques using deep-learning models like BirdNET, can be very effective for assessing biodiversity of vocal fauna, particularly over long monitoring periods. However, its inability to detect non-vocal species necessitates a combined approach of PAM for vocal fauna

and targeted OBM efforts or other remote sensing methods (e.g., camera trapping) for non-vocal species to provide the most comprehensive assessment of terrestrial vertebrate biodiversity. This approach offers a more detailed understanding of ecosystems, potentially enhancing future large-scale, long-term biodiversity monitoring and supporting effective conservation practices.

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Chapter 1. General introduction[1]

1.1 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 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

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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). Large-scale, long-term 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.

1.2 Methods

I 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. I 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, I examined the bibliographies of the resulting references for further relevant literature. I selected only references on terrestrial vertebrates that directly compared PAM with OBM from data collected in the same year. From each paper, I 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, I 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. I used two approaches to compare PAM and

OBM. First, I provided a descriptive overview of the literature, and to aid in that description, I 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, I extracted studies that specifically looked at species richness and used them to statistically compare PAM and OBM.

1.2.1 Statistical analysis (richness)

To investigate whether there was a difference in the total number of species detected (richness) *via* PAM and OBM, I 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, I 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, I 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). I controlled for the study by adding it as a random effect in the model. I 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, I 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, I 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 2024).

1.3 Results

I 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 1.1). 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.

Table 1.1. *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 sec/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

Source	Taxa	Location	OBM	Acoustic analysis	Recording period	Better performance	Longer sampling duration	Notes
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 x 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	
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	

Source	Taxa	Location	OBM	Acoustic analysis	Recording period	Better performance	Longer sampling duration	Notes
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
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 x 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 >100m (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

Source	Taxa	Location	OBM	Acoustic analysis	Recording period	Better performance	Longer sampling duration	Notes
								but PAM performed better over an extended recording period
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
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

Source	Taxa	Location	OBM	Acoustic analysis	Recording period	Better performance	Longer sampling duration	Notes
								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*)
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*);

Source	Taxa	Location	OBM	Acoustic analysis	Recording period	Better performance	Longer sampling duration	Notes
								PAM detected males where OBM failed (low-density areas)
Kalan et al. 2015	Non-flying mammals	Ivory Coast	Point counts	Automated	Targeted (30 min/hour 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 x 3 min)	OBM (richness)	OBM	All reptiles captured were non-vocal species

1.3.1 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 1.1). 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 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.

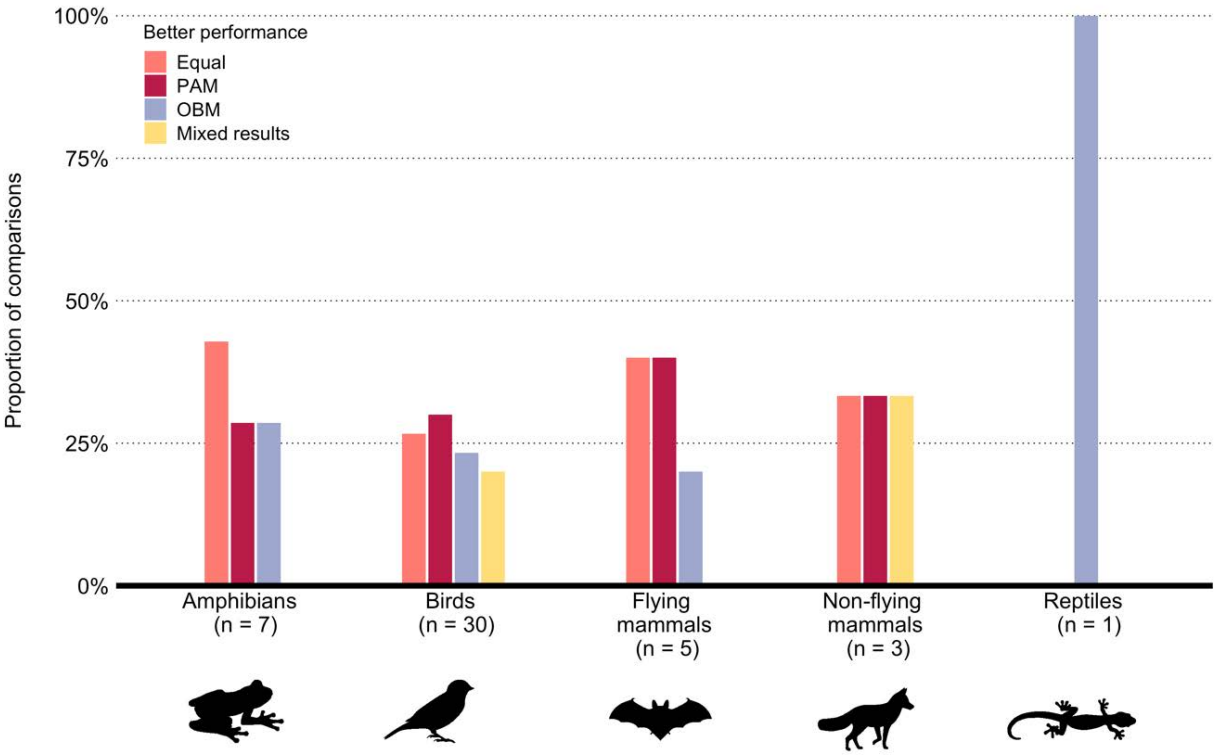

Figure 1.1. *Proportion of comparisons (n = 46) reporting on the detection performance (either richness, species-specific detection, density or occupancy) of each terrestrial vertebrate class using passive acoustic monitoring (PAM) and observer-based monitoring (OBM). In seven studies, performances varied 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.*

1.3.1.1 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 1.1). 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 (>100m) by humans.

1.3.1.2 Amphibians

For amphibian species richness, the performance of PAM was equal to or better than OBM in five out of seven (71%) comparisons (Figure 1.1). 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.

1.3.1.3 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 1.1). 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 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*).

1.3.1.4 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 1.1). 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.

1.3.2 Geographic location

Comparisons of PAM and OBM have mostly been conducted in the northern hemisphere (70%), largely in North America (Figure 1.2). 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 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.

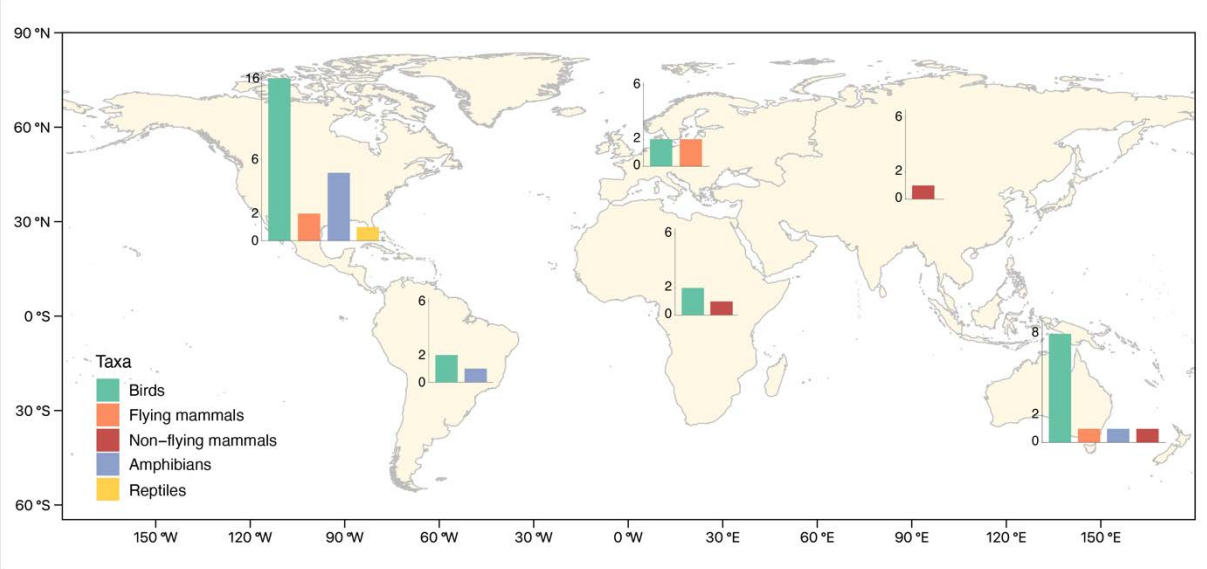

Figure 1.2. *Number of comparisons in the performance of passive acoustic monitoring (PAM) with observer-based monitoring (OBM) for each major terrestrial vertebrate class across geographical regions.*

1.3.3 PAM recording period

Recording periods for PAM differed among studies (Table 1.1) 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.

1.3.4 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.

1.3.5 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 1.1). 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 1.3). 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 (Supplementary Table A1.1). 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 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 (Supplementary Table A1.2). 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.

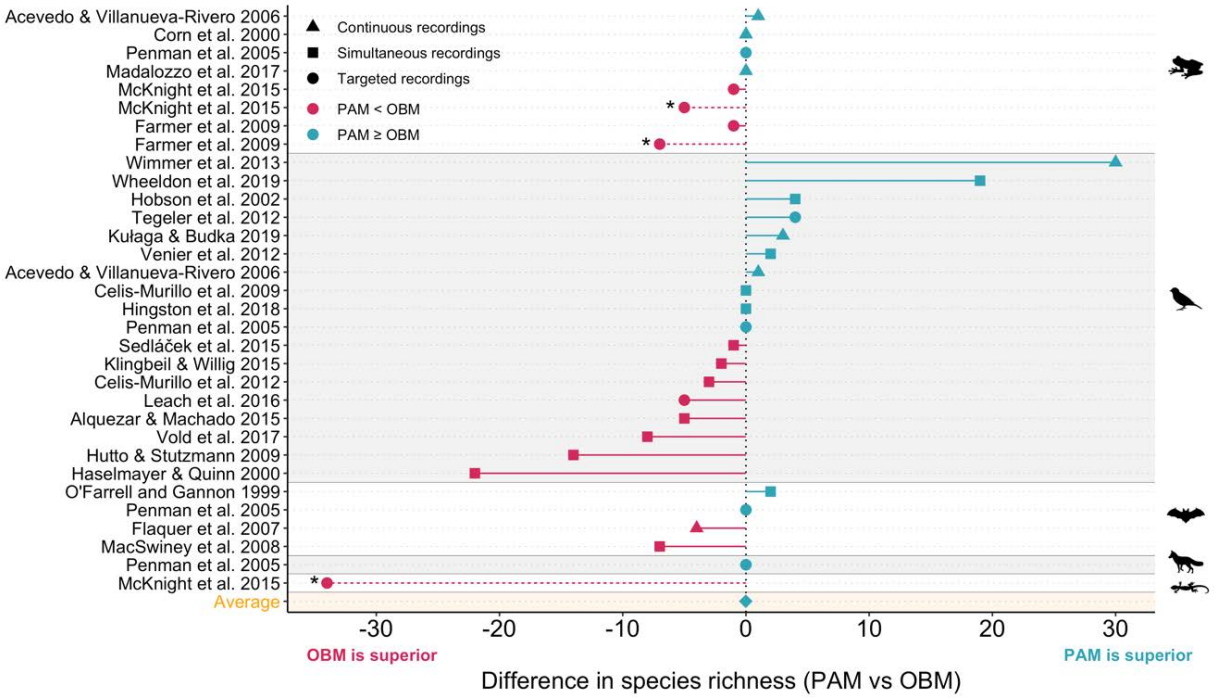

Figure 1.3. *Results of studies specifically examining species richness, displayed as difference in the total species richness assessed via passive acoustic monitoring (PAM) versus observer-based monitoring (OBM) in 30 comparisons in 25 studies separated by vertebrate class and the average difference 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.*

1.4 Discussion

Here, I 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 my 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, I 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) (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 100m) (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 I found that most studies used fixed recording periods, rather than collecting continuous recordings. In my review, there was great variation among studies in recording durations and times. Even though different recording periods produced different outcomes for PAM, I found that, for most terrestrial vertebrates, PAM achieved results comparable to OBM. My 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. I 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 is 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, I was 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, I was 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.

1.5 Aims and thesis outline

The overall objective of this thesis is to investigate the value of passive acoustic monitoring for terrestrial vertebrate biodiversity assessments. To determine how PAM can be effectively used to assess biodiversity, it is essential to identify what fauna can reliably be detected using PAM and compare these data to those obtained using traditional monitoring methods such as observer-based monitoring and camera trapping.

Chapter 2 examines the value of PAM for mammal biodiversity assessments by comparing the effectiveness of PAM, camera trapping, and OBM in terms of species richness, community composition, and survey effort through species accumulation. Given the inherent inability of passive acoustic monitoring to detect non-vocalising species, I considered the mammal community in two ways: i) entire mammal community, and ii) vocal mammals only.

Chapter 3 investigates the efficacy of PAM and OBM for frog biodiversity assessments. This chapter compares both monitoring approaches for species richness, community composition, and survey effort *via* species accumulation. Since frog vocal activity is closely linked to rainfall, which varies seasonally, I also examined the seasonal effects on species accumulation.

Chapter 4 investigates whether PAM can be useful for reptile biodiversity assessments by comparing the effectiveness of PAM, camera trapping, and OBM in terms of species richness, community composition, survey effort through species accumulation, and detectability. To better understand the value of each survey methods in capturing a comprehensive picture of the reptile community, I divided the reptile community in ground-dwelling and arboreal reptiles.

Finally, **Chapter 5** concludes with a general discussion, where I propose the most effective monitoring approach for biodiversity assessments of mammals, frogs, and reptiles. This chapter provides a financial cost comparison, highlights limitations, and offers conclusions

from my work, along with an outlook on future directions for passive acoustic monitoring for terrestrial vertebrate biodiversity assessments.

Chapter 2. Sensors vs Surveyors: Comparing passive acoustic monitoring, camera trapping and observer-based monitoring for terrestrial mammals

2.1 Introduction

Globally, mammal biodiversity is in decline, with more than 25% of species threatened with extinction due to habitat alteration, introduced species, and many other anthropogenic pressures (Hoffmann et al. 2010, Ceballos et al. 2015). This decline is particularly concerning in Australia, which has experienced over one-third of the global modern mammal extinctions (Woinarski et al. 2015). Many Australian mammals are endemic, with highly restricted ranges, and play vital roles in ecological communities as predators, prey, grazers, ecosystem engineers, and even pollinators (Holt et al. 2013, Lacher et al. 2019). Therefore, monitoring mammal biodiversity and detecting further declines in populations is crucial, necessitating comprehensive, large-scale monitoring efforts (Woinarski et al. 2011, Schmeller et al. 2015).

A variety of methods have been developed for surveying and monitoring mammals, many of which rely on direct observation in the field (Hoffmann et al. 2016, Eyre et al. 2018). For example, drift fences, coupled with pitfall traps, funnel traps, and Elliott or Sherman traps have been effectively used across many studies to capture small mammals (e.g., Brenner et al. 1992, Tasker and Dickman 2001, Nicolas et al. 2010, Amori and Luiselli 2011). Cage traps are commonly employed for medium-sized mammals (e.g., Garden et al. 2007, Thompson and Thompson 2007), while spotlighting and thermal cameras have proven to be effective for detecting nocturnal and arboreal mammals (Catling et al. 1997, Doggart et al. 2006, Vinson et al. 2020, Burt et al. 2021). While all these methods are effective for detecting a range of mammals across various habitats, they are limited in their spatiotemporal coverage due to high manual labour requirements (Kitzes and Schricker 2019).

More recently, remote sensing has enabled the large-scale and long-term monitoring of many mammals (Leyequien et al. 2007, Rodofili et al. 2022, Gonsalves et al. 2024). Techniques such as satellite imagery, unoccupied aerial vehicles (UAVs), and camera traps have all been employed to effectively survey and monitor mammals (McCallum 2013, Linchant et al. 2015, Wang et al. 2019). Camera trapping has been widely adopted for over a century, allowing continuous, non-invasive observations of wildlife, which is critical for answering questions related to population ecology, animal behaviour, conservation, and wildlife management (O'Connell et al. 2011, Meek et al. 2015). Camera traps have been used across a broad

spectrum of mammals including many medium to large-sized species (Bridges et al. 2004, Wegge et al. 2004, Claridge et al. 2010, Moolman et al. 2019), and they have proven highly useful for studying cryptic and nocturnal species (Kelly 2008, Vine et al. 2009). Furthermore, camera trapping has been more effective for detecting some medium-sized and small mammals compared to observer-based methods (De Bondi et al. 2010, Dundas et al. 2019), while reducing ongoing costs and the need for experts in the field.

Passive acoustic monitoring (PAM) is another remote sensing technique that has recently gained increased interest for detecting terrestrial vertebrates (Sugai et al. 2019). This method utilises automated recording units (ARUs) programmed to operate on a predefined sampling schedule to gain information on vocal fauna (Blumstein et al. 2011, Rhinehart et al. 2020). While most PAM research on mammals has focused on bats (Sugai et al. 2019), a wide range of other species have been successfully detected using PAM, including primates (Heinicke et al. 2015, Kalan et al. 2015), elephants (Wrege et al. 2017), deer (Enari et al. 2017), wolves (Suter et al. 2017, Barber-Meyer et al. 2020), koalas (Law et al. 2020, Whisson et al. 2023), possums (Penman et al. 2005), and gliders (Whisson et al. 2021). A significant challenge associated with PAM is the amount of audio data it collects, which is often too extensive for manual processing (Rempel et al. 2005, Swiston and Mennill 2009). To effectively manage and analyse large acoustic datasets, it is essential to integrate automated acoustic analysis pathways, which enable PAM to be applied across extensive temporal and spatial scales.

Automated acoustic analysis methods have been rapidly advancing in recent years, particularly through the application of machine learning, which has dramatically improved processing times and detection accuracy (Priyadarshani et al. 2018, Brodie et al. 2020, Kahl et al. 2021, Ghani et al. 2023). BirdNET is one such machine learning model, using deep artificial neural networks (DNNs), capable of identifying thousands of species within extensive audio recordings, and has been successfully applied to detect a wide range of bird species (Toenies and Rich 2021, Manzano-Rubio et al. 2022, Wood et al. 2022, Bota et al. 2024). This large acoustic model is regularly being extended to include even more species from different vertebrate classes (BirdNET v2.4 includes 41 anurans and seven mammals), and with recent updates, BirdNET has been able to successfully identify several species of frogs (Pérez-Granados et al. 2023, Wood et al. 2023b, Bota et al. 2024), a primate (Wood et al. 2023a), and wolves and coyotes (Sossover et al. 2023). In addition to detecting the classes present in a pre-trained model, the embeddings from deep-learning models can be used to search target vocalisations. These embeddings are numerical representations of acoustic signals learned by a model which capture essential features of a call and map them into a high-dimensional

space. By comparing the embeddings of a user-provided example call to those in an unknown audio dataset, target vocalisations can be discovered even from just a single example call (Ghani et al. 2023, Allen-Ankins et al. 2025). While the use of BirdNET embeddings seems promising for detecting novel sound classes within unknown audio recordings and has been able to distinguish between different call types of the same species (McGinn et al. 2023), their utility for mammal biodiversity assessments has not been explored.

Here I compared the performance of passive acoustic monitoring (PAM) in combination with BirdNET embeddings to traditional observer-based monitoring methods and camera trapping for assessing terrestrial mammal biodiversity. I evaluated the effectiveness of this remote sensing approach by examining: (i) species richness, (ii) community composition, (iii) survey effort and (iv) time investment.

2.2 Methods

2.2.1 Study sites

This study was undertaken as part of a large-scale terrestrial vertebrate assessment project, with the objective of evaluating the efficacy of passive acoustic monitoring for terrestrial vertebrate biodiversity surveys across Australia. I chose six sites (Figure 2.1A) within open eucalypt woodland where acoustic recording units (ARUs) had previously been deployed as part of the Australian Acoustic Observatory project (Roe et al. 2021). All six sites were situated within natural reserves (Rinyirru National Park: 15.044°S, 144.243°E; Undara National Park: 18.187°S, 144.540°E; Duval Nature Reserve: 30.402°S, 151.625°E) or private properties without public access (Wambiana Station: 20.531°S, 146.113°E, Mourachan Conservation Property: 27.779°S, 149.032°E – Australia Zoo, Tarcutta Hills Reserve: 35.369°S, 147.697°E – Bush Heritage Australia). I established a 1-ha survey plot, with each plot edge within 50 m of an ARU, resulting in four survey plots (2 x "wet" [within 50 m of a body of water], 2 x "dry" [at least 500 m from a waterbody]) per site (Figure 2.1B). Hereafter, I use the term "site" to refer to the six reserves or private properties, and "plot" to denote the four 1-ha areas surveyed within each site. I conducted observer-based monitoring (OBM), camera trapping, and passive acoustic monitoring (PAM) simultaneously at each plot over a seven-day period per survey trip. Each survey trip lasted eight calendar days, although survey days have been considered as one of the seven 24 h periods (12 pm – 12 pm) used in the analysis.

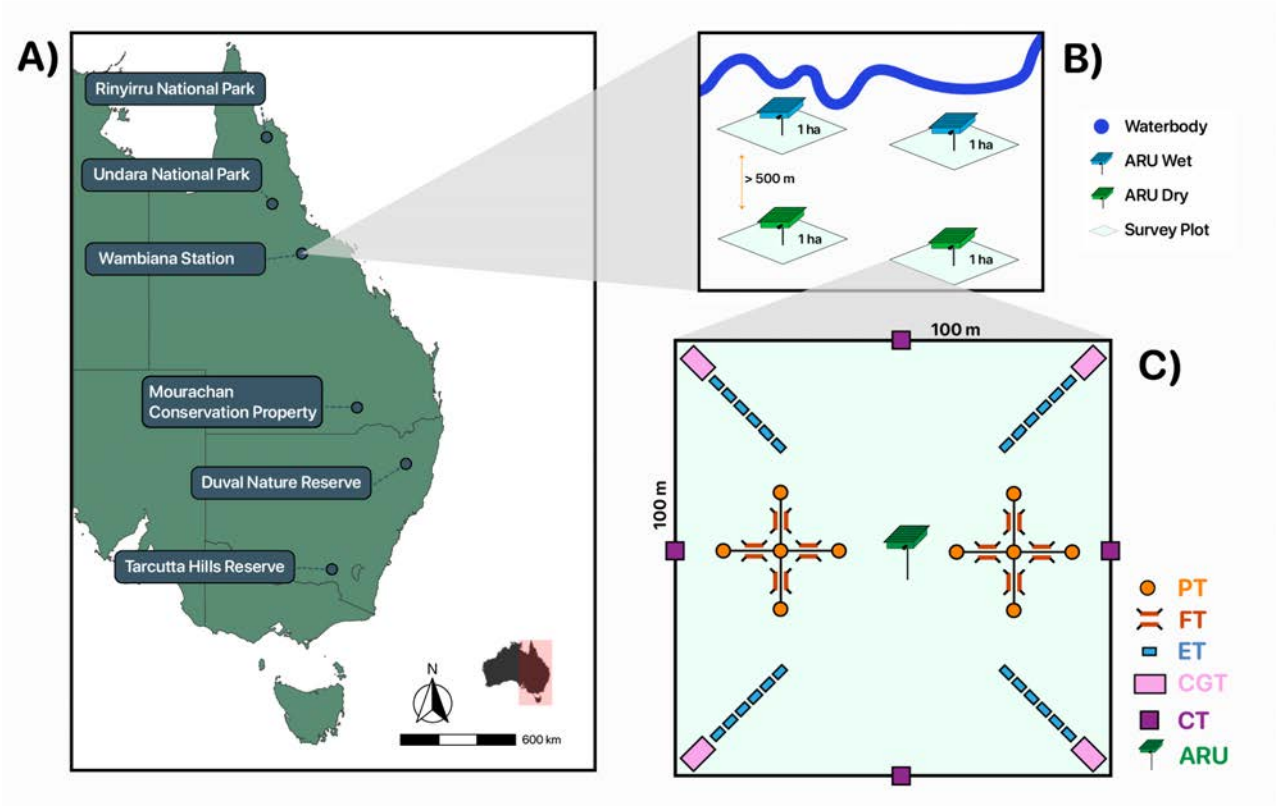

Figure 2.1. *Schematic of (A) the six study sites throughout eastern Australia with (B) a diagram of the acoustic design for each site and (C) a summary of the survey methods employed at each survey plot (four per site) to target mammals within a 1 ha plot near each acoustic recording unit (ARU; adapted from Hoefer et al. 2024). At each site, four ARUs were installed in a comparable habitat type, with two positioned within 50 m of a body of water (ARU Wet – blue) and two more than 500 m away from a water source (ARU Dry – green). Abbreviations used: PT = Pitfall Trap, FT = Funnel Trap, ET = Elliott Trap, CGT = Cage Trap, CT = Camera Trap, ARU = Automated Recording Unit.*

2.2.2 Observer-based monitoring (OBM)

I conducted observer-based surveys to detect terrestrial mammals in Australian spring/summer (Sep – Nov) and autumn/winter (Apr – Aug) in 2021 and 2022 at each site, except for Mourachan and Duval, which were inaccessible during spring 2021 due to high rainfall (Table 2.1; Supplementary Table A2.2). To sample the mammal community, I used six different OBM methods within each plot (spatial arrangement shown in Figure 2.1C): i) pitfall traps, ii) funnel traps, iii) Elliott traps, iv) cage traps, v) nocturnal active area searches (spotlighting), and vi) incidental encounters (i.e., animals observed while not conducting active searches or checking traps).

Within each plot, I installed two drift fences with five pitfall and eight funnel traps each, 24 Elliott traps, and four cage traps. Drift fences (30-cm high) were set up in a cross design with four 10-m arms and five 20-L pitfall traps (one central and four at the ends). Two funnel traps (Thompson and Thompson 2007) were placed at the centre of each arm between the two pitfall traps. For each funnel trap, I attached smaller additional fences or "wings" at the openings to broaden the funnel and enhance capture efficiency (McKnight et al. 2013). Shade cloth was used to cover all funnel traps, while wet sponges were placed within every pitfall and funnel trap to mitigate desiccation and overheating of the trapped animals (McDiarmid et al. 2012). Elliott and cage traps were arranged in a line, 5-m apart, originating from every corner and extending towards the centre of the plot, each placed alongside a tree or log near vegetation cover (Friend 1978, Tasker and Dickman 2001). Each Elliot and cage trap was baited with peanut-butter-oat balls to attract mammals (Garden et al. 2007). When temperatures were low at the southern sites, Elliot traps were placed inside opened plastic bags and cotton wool was inserted into each trap to provide protection against the cold (Tasker and Dickman 2001).

All plots were surveyed by two teams of two trained observers familiar with the local fauna. To minimise observer bias, the observers in each search team were rotated, as was the order in which plots were surveyed during each survey trip. Funnel and pitfall traps were checked twice daily. Elliot and cage traps were checked early in the morning prior to sunrise to alleviate stress on nocturnal mammals, and they were closed during daylight hours. Each captured mammal was marked with a veterinary-grade pink antiseptic spray (ChloromideTM) before release, to ensure any recaptured mammals within the survey trip were not mistaken for new captures. Mammals recaptured within a survey period were removed from the data for community analyses. Nocturnal active area searches, or spotlighting, were conducted by two observers every day after sunset. For 15 minutes, the entire plot was searched, and all individual mammals detected visually or aurally were recorded.

Table 2.1. *A summary of survey durations across six study sites, including total number of days for field surveys, camera trapping days, and number of days of acoustic recordings during the survey period and for all available audio data. Total survey days are expressed as the number of survey days per site (max 28 days) multiplied by the four survey plots. Total camera trapping days represent the total number of days all 16 camera traps were active at each site.*

Site	First survey	Second survey	Third survey	Fourth survey	Total survey days	Total camera trapping days	Total acoustic recordings (survey period) in days	Total acoustic recordings (all audio) in days
Rinyirru	14/6/2021 – 21/6/2021	8/10/2021 – 15/10/2021	7/8/2022 – 14/8/2022	23/10/2022 – 30/10/2022	112	441	98	1297
Undara	3/6/2021 – 10/6/2021	29/9/2021 – 6/10/2021	8/5/2022 – 15/5/2022	13/10/2022 – 20/10/2022	110	448	84	1660
Wambiana	5/7/2021 – 12/7/2021	10/11/2021 – 17/11/2021	12/6/2022 – 19/6/2022	28/9/2022 – 5/10/2022	112	448	97	3280
Mourachan	9/5/2021 – 16/5/2021	NA	19/6/2022 – 26/6/2022	2/11/2022 – 9/11/2022	84	336	60	1956
Duval	18/4/2021 – 25/4/2021	NA	28/4/2022 – 5/5/2022	12/11/2022 – 19/11/2022	70	273	65	2122
Tarcutta	29/4/2021 – 6/5/2021	18/10/2021 – 25/10/2021	8/5/2022 – 15/5/2022	22/11/2022 – 29/11/2022	112	434	109	2910

2.2.3 Camera trapping

Inside each plot, I installed four camera traps (Campark T85) on individual trees at about 50 cm above ground between two corners, facing into the plot (Figure 2.1C). Due to limited availability of camera traps, I deployed cameras only for the same period OBM was conducted. Each camera trap was baited with a can of sardines and peanut-butter-oat balls fixed to the ground and was set to "high" sensitivity, to take three consecutive photos and one 10-second video when triggered.

2.2.3.1 Camera trap data analysis

I analysed all available camera trapping data using the MegaDetector image recognition algorithm (Beery et al. 2019) and Timelapse2 (Greenberg 2022a). There were three stages of analysis to generate species-level identification. In the first stage, I classified images as either "wildlife" or "non-wildlife" using the MegaDetector for each site and each survey. In stage two, I validated "non-wildlife" classifications following the workflow described in the Timelapse Image Recognition Guide (Greenberg 2022b). To decrease the likelihood of failing to detect mammals in my camera trap data, I used a more conservative confidence threshold of 0.5 to validate "wildlife" classifications. In the final stage, all images classified as "wildlife" were identified and labelled to species level by an expert observer.

2.2.4 Passive acoustic monitoring (PAM)

I conducted passive acoustic monitoring to assess its effectiveness for evaluating mammal biodiversity in Australia. Each ARU (Frontier Labs Solar BAR) consisted of a charge controller, battery, solar panel, and recorder in a weather-sealed unit equipped with an external omnidirectional microphone (Primo EM172) and installed on a star picket with enough clearance to prevent damage from wildlife. The ARUs recorded in mono at 16-bit 22,050 Hz with FLAC lossless compression in two-hour file blocks stored on two 512 GB SD cards (for more details on the ARU setup and specifications, see (Roe et al. 2021). This design enabled a continuous collection of acoustic data for up to twelve months without maintenance, at which point the SD cards were replaced and recording resumed.

2.2.4.1 Acoustic data analysis

I used the BirdNET-Analyzer (Kahl et al. 2021) to gain information about the presence of vocal mammals in my audio recordings. Specifically, I created feature embeddings *via* BirdNET, which are numerical representations of sound data in a multidimensional space (Ghani et al. 2023), to search for novel sounds in my audio recordings. For this, I selected up to three example calls for each of the 17 Australian mammals that produce vocalisations within the

human audible frequency range (Rosenfeld and Hoffmann 2021), and for which I was able to attain audio samples of their characteristic calls (hereafter referred to as "vocal mammals"), which resulted in 46 example calls (Supplementary Table A2.1). Eastern grey kangaroos and common wallaroos were grouped as "macropod" and grey-headed flying-fox, little red flying-fox, and black flying-fox were grouped as "fruit bat". While I was able to obtain example calls of these individual species, I was unable to differentiate the individual species during validation. The 46 example calls were subsequently used to examine the acoustic data collected during the same seven-day periods when other survey methods were in use (PAM during survey period: 12,303 hours) and to examine all acoustic data available (PAM all audio: 317,410 hours). I created feature embeddings for my six survey sites using all acoustic data available in the A2O data repository (Roe et al. 2023) and for the 46 example mammal calls following the instructions in the BirdNET-Analyzer github repository (https://github.com/kahst/BirdNET-Analyzer). I then calculated the Euclidean distances between feature embeddings of the mammal example calls and the unknown audio in the acoustic dataset. Finally, I extracted the top detections (lowest Euclidean distances) for each example call for every day of recording at each survey site and used Kaleidoscope (https://www.wildlifeacoustics.com/products/kaleidoscope) to both aurally (sound clip) and visually (spectrogram) verify and confirm species detections (199,604 detections). I examined the prediction probabilities of true positive detections for each example call and found that, overall, true positives were predicted by lower Euclidean distances, suggesting that extracting the lowest daily distance should lead to species detections when present (Supplementary Figure A2.1).

2.2.5 Statistical analysis

All statistical analyses, conducted for all mammals and vocal mammals only, were performed in R statistical environment (R Core Team 2023, v4.3.2). My reproducible code and the data can be accessed at: https://github.com/cheloniax/Hoefer2024.git. I explored the relationship between species richness and assessment method using hierarchical models in a Bayesian framework. I modelled the total number of species for each survey plot against the different assessment methods assuming a Poisson distribution and weakly informative priors using the package *brms* (Bürkner 2017). The Bayesian models included three chains, each of 5000 iterations, thinned to a rate of 5, and excluded the first 1000 iterations (warmup). I compared several candidate models and selected the final model based on LOO information criterion values (Vehtari et al. 2017). The best model was well mixed and converged (all Rhat <1.05) on a stable posterior and was validated via DHARMa residuals (Hartig 2022). I used post hoc pairwise comparisons to make specific inferences (i.e., comparing differences in species

richness for each combination of assessment methods). I encountered ARU and camera trap failure over the course of the study. To enable a fair comparison of the methods I excluded data from plots for surveys where either the acoustic recorder collected less than 70% of the possible full audio data or more than one camera trap failed (Supplementary Table A2.2). Initially, I analysed the individual OBM methods separately for species richness comparisons against camera trapping and PAM. However, aside from spotlighting, which performed better than the other OBM techniques (Supplementary Figure A2.3), the differences among the individual OBM methods were minimal. Moreover, comprehensive mammal surveys typically involve deploying multiple techniques rather than relying on a single method. Consequently, the individual OBM methods were combined into one category for the subsequent analyses.

2.2.5.1 Community composition and species accumulation curves

I performed nonmetric multidimensional scaling (nMDS) based on Jaccard (presence-absence) dissimilarities to evaluate community differences for each assessment method at each survey site. To assess dissimilarity differences between assessment methods, I conducted pairwise permutational analysis of variance using the packages *vegan* (Oksanen et al. 2022) and *EcolUtils* (Salazar 2022). To examine the sampling effort necessary to reach an asymptote, I used the *vegan* package (Oksanen et al. 2022) to construct species accumulation curves for total species richness throughout the 28-day surveys (combining all four plots per site) and all available audio recording days. Additionally, I examined the time required for PAM to reach the total species richness recorded by OBM at each survey site for vocal mammals only. I permuted the survey day sequence randomly to provide more robust estimates of species richness by accounting for potential biases introduced by day order.

2.2.6 Time investment

I estimated the time investment required for each method to generate species inventories, providing an important proxy for financial costs in mammal biodiversity assessments. While each day of sampling with OBM required less than 24 hours of active searches and live animal trapping, observers spent the full 24 hours on site in the field. Therefore, I calculated the time investment for OBM by multiplying the 24-hour periods spent in the field by the total number of survey days (28) across each of the six survey sites and added the time needed for setup and takedown of all traps. For PAM and camera trapping, I calculated the time needed to analyse and validate the 317,410 hours of audio recordings and approximately 100,000 images, respectively. For both methods, I used timestamps embedded in the validation files created during data analyses and therefore time of analysis could be easily

calculated. For validation, I used stopwatches to accurately record the time required to validate acoustic and camera trapping data. I also added the time needed for the initial setup and regular maintenance of PAM and set up and takedown of camera traps.

2.3 Results

Across the six sites, I identified a total of 45 species of mammals, of which 17 were classified as "vocal mammals" (Supplementary Table A2.3). For all mammals combined, OBM recorded the highest species richness (45/45 species), followed by camera traps (25/45 species), PAM using all available audio (17/45 species), and PAM using audio matching the survey period only (13/45 species). Overall, OBM detected 11 unique species not detected by any other method (Supplementary Table A2.3). The highest number of vocal mammals were detected by PAM using all audio (17/17 species) and OBM (17/17 species), followed by PAM using audio recorded only during the survey period (13/17 species), and camera traps (11/17 species). The maximum total species richness achieved varied among survey sites and did not follow a strict latitudinal trend (Table 2.2). However, species richness was highest at the most southern sites, with Tarcutta (24 total mammals/14 vocal mammals) and Duval (19 total/11 vocal) recording the highest number of species, followed by Wambiana (19 total/11 vocal), Undara (18 total/9 vocal), Mourachan (16 total/9 vocal), and Rinyirru (16 total/9 vocal).

Table 2.2. *Maximum total species richness, number of days to reach the maximum total species richness, the percentage of total richness achieved after 28 days, 90 days, 180 days, and 365 days of passive acoustic monitoring (PAM) of vocal mammals at each survey site, as well as the mean value across all sites.*

Site	PAM (maximum total richness)	Days to max total richness	PAM proportion of max richness			
			28 days	90 days	180 days	365 days
Tarcutta	13	968	0.66	0.78	0.86	0.94
Duval	10	676	0.72	0.86	0.91	0.95
Mourachan	7	782	0.68	0.86	0.89	0.92
Wambiana	10	760	0.79	0.91	0.96	0.99
Undara	7	771	0.50	0.75	0.86	0.92

Rinyirru	9	487	0.61	0.79	0.87	0.96
Average (all sites)	9	741	0.66	0.82	0.89	0.95

2.3.1 Species richness

2.3.1.1. All mammals

Over the same 28-day survey period, OBM detected significantly more species on average than PAM (2.46x more species, 95% highest density interval [HDI]: 1.85-3.12) and camera traps (1.44x species, 95% HDI: 1.15-1.77; Figure 2.2). PAM recorded significantly fewer species than camera traps during this period (0.58x species, 95% HDI: 0.43-0.74). When all available audio data was used, PAM detected significantly more species than when PAM was limited to the survey period only (2.13x species, 95% HDI: 1.62-2.72), but did not differ significantly from OBM (0.86x, 95% HDI: 0.69-1.04) or camera traps (1.25x species, 95% HDI: 0.99-1.52).

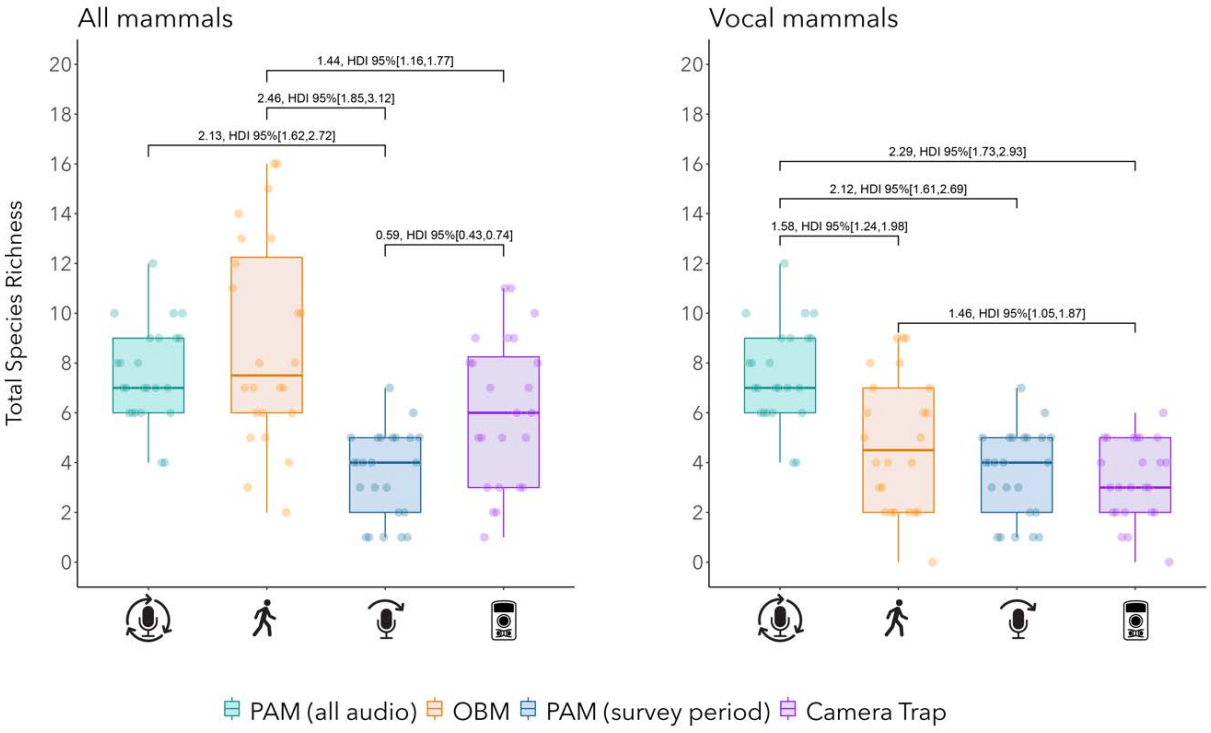

Figure 2.2. *Total species richness for all mammals (left) and vocal mammals only (right) as captured by each assessment method: passive acoustic monitoring using all available audio*

(PAM (all audio), green with microphone icon with three arrows), observer-based monitoring (OBM, orange with human icon), passive acoustic monitoring with audio from only the survey period (PAM (survey period), blue with microphone icon with one arrow), and camera trapping (purple with camera trap icon). Jittered points indicate species richness per survey plot. Average fractional differences and 95% Highest Density Intervals, signifying statistical significance, are displayed above the boxplots. Vocal mammals constituted 42% of all mammals in this study.

2.3.1.2. Vocal mammals only

Considering vocal mammals only, over the same 28-day survey period, OBM detected significantly more species than camera traps on average (1.46x more species, 95% HDI: 1.05-1.87; Figure 2.2). However, there was no significant difference in the average number of species detected by OBM compared to PAM (1.34x species, 95% HDI: 0.99-1.74). Similarly, no significant difference was found between PAM and camera traps (1.08x species, 95% HDI: 0.79-1.43). Using all available audio data, PAM identified significantly more vocal mammal species than OBM (1.58x species, 95% HDI: 1.24-1.98), camera traps (2.29x species, 95% HDI: 1.73-2.93), as well as PAM using audio data only recorded during the survey period (2.12x species, 95% HDI: 1.61-2.69). Using Pearson's correlation, I found a significant moderately positive correlation between the species richness of vocal mammals detected via PAM and the species richness of the entire mammal community detected via OBM ($r_{22} = 0.46$, $R^2 = 0.21$, $P = 0.02$, Supplementary Figure A2.3).

2.3.2 Community composition

2.3.2.1. All mammals

Mammal communities surveyed via OBM were significantly different from those sampled through PAM during the same 28-day survey period (Jaccard index, $R^2 = 0.216$, $P = 0.015$; Figure 2.3). However, communities surveyed by OBM did not differ significantly from camera traps (Jaccard, $R^2 = 0.145$, $P = 0.212$), nor from PAM for all audio (Jaccard, $R^2 = 0.199$, $P = 0.057$). Camera traps recorded significantly different assemblages compared to both PAM over the survey period (Jaccard, $R^2 = 0.327$, $P = 0.016$) and PAM for all audio (Jaccard, $R^2 = 0.331$, $P = 0.006$). Notably, PAM using all audio and PAM over the survey period captured similar mammal communities (Jaccard, $R^2 = 0.109$, $P = 0.291$).

2.3.2.2. Vocal mammals only

For the communities of vocal mammals only, OBM sampled a similar suite of species compared to PAM during survey period (Jaccard, $R^2 = 0.115$, $P = 0.698$), PAM with all audio data

(Jaccard, $R^2 = 0.06$, $P = 0.698$), and camera traps (Jaccard, $R^2 = 0.178$, $P = 0.296$; Figure 2.3). The only significant difference in mammal communities sampled was between camera traps and both PAM for all audio (Jaccard, $R^2 = 0.295$, $P = 0.045$), and PAM over the survey period (Jaccard, $R^2 = 0.306$, $P = 0.03$). The assemblages of vocal mammals did not differ significantly between PAM all audio and PAM over the survey period only (Jaccard, $R^2 = 0.109$, $P = 0.698$).

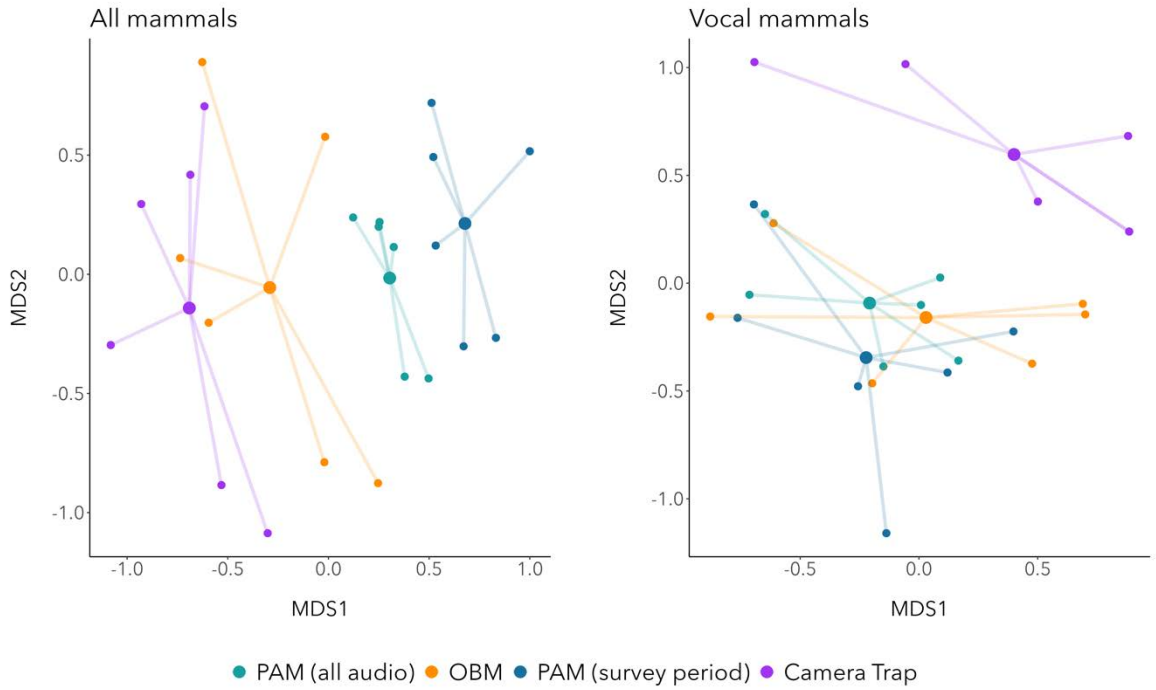

Figure 2.3. *Non-metric multidimensional scaling (NMDS) ordination of mammal communities (all mammals [left] and vocal mammals only [right]) based on Jaccard dissimilarity (presence-absence) captured by the different assessment methods at each survey site. Each point represents a survey site and larger points mark the centroids for every assessment method, with connecting lines to individual sites belonging to each method.*

2.3.3 Survey effort

Passive acoustic monitoring reached its maximum total species richness at an average of nine species across all sites, ranging from seven (Undara and Mourachan) to 13 species (Tarcutta; Table 2.2). It took on average 741 days to reach this maximum total richness, with a range of 487 days (Rinyirru) to 968 days (Tarcutta). After 28 days of sampling, I captured 66% of the maximum total species richness on average, with a high variability of 29% across sites (Table 2.2). After 90 days of recording, the average proportion was 82% and the maximum variability decreased to 16%. After 180 days of sampling, the average proportion was 89% and maximum variability between sites decreased to 10%. After 365 days of recordings the average

proportion of the maximum total species richness at a site was 95% and the maximum variability between sites was 7%.

Species accumulation curves of PAM did not approach an asymptote at any survey site, except for Wambiana where the maximum species richness was accumulated after 760 of 1235 days (Supplementary Figure A2.4). The number of days required to reach equal vocal mammal species richness to OBM at each survey site varied greatly from 12–676 days (Tarcutta: 320 days; Duval: 676 days; Mourachan: 88 days; Wambiana: 17 days; Undara: 175 days; Rinyirru: 12 days; Supplementary Figure A2.4). The number of days required to match camera trap varied less, ranging from 9–35 days (Tarcutta: 9 days; Duval: 12 days; Mourachan: 17 days; Wambiana: 12 days; Undara: 35 days; Rinyirru 12 days).

Species richness accumulation over the 28-day survey period revealed that OBM detected the greatest richness for all mammals, and more quickly, followed by camera traps and PAM (Supplementary Figure A2.5). For vocal mammals only, OBM accumulated greater species richness at four sites and did so more quickly, while PAM accumulated species more quickly and reached greater final numbers at two sites. A combined remote sensing approach with PAM and camera traps offered quicker accumulation and higher species numbers than OBM at four sites for vocal mammals and achieved higher richness at one site for all mammals.

2.3.4 Time investment

The time required to conduct each survey type and process data varied greatly. By considering the time required to actively conduct surveys, analyse, and validate data at each site using each survey method, OBM was more time intensive than PAM or camera trapping. OBM required the greatest time investment for conducting surveys and collecting data in the field (observers spent 24 hours in the field, totalling 4,032 hours over the survey period; Supplementary Table A2.4), whereas processing the data was done following collection and completed within the same 24-hour daily time investment. In contrast, PAM and camera trapping required an initial short time investment for installation and setup (PAM: 12 hours, camera trapping: 64 hours), as well as additional brief visits for maintenance (SD card and battery changes) but required the greatest time investment for processing and validating the collected data (PAM: 299 hours, camera trapping: 181 hours). For each day of sampling and data processing with OBM, observers spent 24 hours in the field to generate a species list. In comparison, each day of sampling and processing data required 0.02 hours (1.2 min) for PAM and 1.1 hours (66 min) for camera trapping. Therefore, the time investment per survey day for PAM and camera traps amounted to less than 0.1% and 4.6% of OBM's time, respectively, with

PAM taking 1.8% of the time required by camera traps. With 4,032 hours of OBM (45 species detected), 299 hours of PAM (17 species), and 181 hours of camera trapping (25 species), detection of each individual species took 90 hours for OBM, 18 hours for PAM, and 7 hours for camera trapping.

2.4 Discussion

In this study, I compared the efficacy of passive acoustic monitoring (PAM) to observer-based monitoring (OBM) and camera trapping for assessing terrestrial mammal biodiversity in eastern Australia. Using embeddings from the BirdNET deep-learning model, I efficiently analysed a cumulative total of 317,410 hours of continuous audio data (equivalent to 36 years) from six sites, successfully detecting all 17 target vocal mammal species. Given the inherent inability of PAM to detect non-vocalising species, I considered the mammal community in two ways: i) entire mammal community, and ii) vocal mammals only. For the entire mammal community, the greatest species richness was detected by OBM (45 species), followed by camera traps (25) and PAM (17). For vocal mammals only, PAM detected at least equal numbers of species and identified a similar suite of the community compared to other survey methods while only requiring a fraction of the time investment. The time needed to capture more than 95% of the total species richness possible with PAM varied across sites, but on average, required 365 days of sampling. The species richness detected via PAM reflected the overall species richness, as sites with higher vocal mammal species richness also exhibited higher overall species richness.

2.4.1 Species richness

This study showed that all survey methods conducted in the 28-d survey period detected similar species richness of terrestrial vocal mammals. However, the species richness detected by long-term recordings of PAM was significantly greater than all other survey methods conducted over the 28-d survey period. It is well established that species richness is an important metric when assessing biodiversity and the overall health of an ecosystem (Gotelli and Colwell 2001, Tilman et al. 2006). Similarly, long-term monitoring generally results in the detection of greater species richness (e.g., long-term camera trapping for medium- to large mammals (Mashintonio et al. 2022), or longer duration live animal trapping for small mammals (Conard et al. 2008)). It is therefore unsurprising that long-term data from PAM significantly outperformed all other methods for species richness (see also Klingbeil and Willig 2015, Kułaga and Budka 2019 for reports in other terrestrial vertebrates). This is likely because although shorter overall recording periods and non-continuous daily sampling schedules can effectively detect some species (Shirose et al. 1997, Thompson III et al. 2002), long-term, continuous audio

recordings provide the advantage of detecting additional cryptic or infrequently vocalising species (Digby et al. 2013, Klingbeil and Willig 2015, Gibb et al. 2018). Indeed, I detected six species in the long-term PAM data which may be considered cryptic or nocturnal, and were not detected by any other survey method at some sites (e.g., squirrel gliders (*Petaurus norfolcensis*), sugar gliders (*Petaurus breviceps*), common brushtail possums (*Trichosurus vulpecula*)). Although I designed sampling for all methods to capture multiple seasons and times of day, the six species detected exclusively by long-term PAM at some sites emphasise that as technological advancements and innovations in autonomous audio recorders progress, the collection of more audio data is achievable and desirable (Aide et al. 2013, Rhinehart et al. 2020). For the monitoring data collected only within the survey period, all methods detected comparable numbers of vocal mammal species, and it is therefore plausible that greater species richness may also be achieved with longer sampling periods for OBM and camera trapping.

2.4.2 Community composition

While species richness is a fundamental aspect of biodiversity, relying solely on this metric is unlikely to provide adequate ecological information (Brown et al. 2001, Fleishman et al. 2006). Considering species richness without broader community data prevents understanding of important impacts on communities, such as native species replacements by invasive species, changes in species interactions, and reductions in species performing specific functional roles within the community, which are critical for understanding ecosystem processes and stability (Tilman et al. 1997). Community composition, which includes the variety of species within a community, provides an additional perspective by highlighting the community structure and identifying potentially important species contributing to ecosystem functionality and health (Díaz and Cabido 2001). This metric may be particularly important in the context of effective conservation action, where failing to identify keystone species may risk the health of an ecosystem (Power et al. 1996). In this study, I found that the similarity between the communities sampled by PAM and OBM differed depending on whether the analysis considered either vocal or non-vocal species. By considering only vocal mammals, the two methods detected a similar assemblage. However, when considering the entire community, including non-vocal mammals, I found that the assemblages detected were not similar. Other studies have also shown that PAM may detect a different part of the community compared to observer-based methods (Acevedo and Villanueva-Rivera 2006, Lintott et al. 2013, Wheeldon et al. 2019). This is most obviously due to the simple limitation of PAM to detect non-vocal species and species with vocalisations indetectable by the recorders (e.g., outside of the sampling rate of

the recorder or vocalising at low decibels), or those that vocalise infrequently. Indeed, the 28 species detected by OBM that were not detected by PAM are not known to produce vocalisations or vocalise very infrequently (Menkhorst and Knight 2011, Rosenfeld and Hoffmann 2021). However, for species that do vocalise, PAM can detect arboreal species difficult to detect without specialised camera trapping (Moore et al. 2021). Furthermore, recording at higher sampling rates could lead to additional detections of mammals vocalising in ultrasonic frequencies, which remained undetected by PAM in this study.

Although camera trapping identified the fewest vocal mammal species of all methods, the assemblage of vocal mammals it captured varied significantly from that detected by PAM. Notably, camera trapping detected cats (*Felis catus*) and pigs (*Sus scrofa*) at certain sites where PAM did not. This is likely because camera traps were baited, which attracted cats and pigs and facilitated detection. Given that these animals do not vocalise as readily and frequently as other terrestrial mammals, detecting them solely through sound is likely to pose a significant challenge. However, increasing the number of call examples used within BirdNET analyses, particularly from a variety of different regions, could enhance detection rates. Vocalisations of the same species can vary regionally due to dialects and different call types (Henry et al. 2008, Luís et al. 2021), and thus constructing a robust, trained recogniser with a variety of call examples may yield more reliable detections of cats and pigs.

2.4.3 Survey effort

The 28-d survey period used in this study followed the recommendations of survey guidelines for OBM and camera trapping for terrestrial mammals in the region (Eyre et al. 2018). However, there is currently no consensus on the optimal deployment duration for PAM, and most studies vary widely in the overall deployment and daily sampling period for acoustic recorders (Sugai et al. 2019, 2020, Hoefer et al. 2023). While shorter deployment periods may reduce maintenance demands (i.e., changing SD cards and batteries), this can lead to less complete species inventories (Wimmer et al. 2013, Klingbeil and Willig 2015, Kułaga and Budka 2019). I found that for the short-term (28-d) monitoring period, OBM was most effective, as it accumulated the greatest species richness and at a faster rate than any other method alone. However, a combined remote sensing approach with PAM and camera trapping achieved similar species richness. The combined strengths of camera trapping and PAM (i.e., the ability of camera traps to detect non-vocalising species and the ability of PAM to detect arboreal species and species from any direction) may allow similarly effective biodiversity assessments compared to traditional OBM, whilst offsetting time and financial investment involved with survey efforts.

Sampling over short periods of time may risk missing species that vocalise seasonally, rarely vocalise, or are cryptic (Digby et al. 2013, Zwart et al. 2014), and some species detections may be masked by anthrophony, geophony or even other biophony (Pijanowski et al. 2011). I found that continuously sampling with PAM for 28 days led to an average detection of only 60% of all vocal mammals, compared to 95% of the total species richness detected by PAM after 365 days. Given its temporal and spatial scalability, deploying ARUs for extended periods is crucial for achieving comprehensive species inventories. If long-term monitoring is not possible, the combination of short-term PAM and camera traps or targeted OBM may be the most effective way to detect the greatest number of terrestrial mammal species using remote methods.

2.4.4 Time investment

A critical consideration for any biodiversity assessment is the resource investment required to effectively detect species present. The amount of time needed is a reasonable proxy of financial expenses and often acts as a constraint for comprehensive survey efforts (Gardner et al. 2008). Therefore, reducing the time required by personnel to detect species in an area is not only desirable but vital for long-term biodiversity monitoring (Darras et al. 2019). For vocal mammals, I found that long-term PAM, in combination with BirdNET embeddings significantly decreased the time needed to conduct species inventories, with at least equal detection performance compared to OBM and camera traps for vocal species. This study allowed me to analyse a cumulative total of 36 years of continuous audio recordings (24 ARUs x 6 sites x hours of available audio data for each ARU; Supplementary Table A2.2) and compile species lists in less than two weeks, with each 24 hours of continuous audio recordings only requiring about one minute to analyse. Compared to OBM, this represented less than 0.1% of the time required (when considering OBM in terms of total necessary in-field days) and only 2% of the time needed for camera trapping. These significant time savings could considerably reduce costs, particularly for large-scale, long-term biodiversity assessments.

2.4.5 Conclusions

Here I show that passive acoustic monitoring in combination with BirdNET embeddings were an effective method for assessing the biodiversity of terrestrial vocal mammals in Australia. By analysing a cumulative total of 317,410 hours (equivalent to over 36 years) of continuous audio recordings from six sites across eastern Australia, I demonstrated that the ability of PAM to detect vocal mammal species was at least equal to traditional methods such as observer-based monitoring and camera trapping. PAM significantly reduced time investment compared to traditional methods, further emphasising its value in biodiversity assessments, especially over large spatial and temporal scales. The use of embeddings from deep-learning

models like BirdNET offers a low-cost and time-efficient method for exploring extensive acoustic datasets. Despite the benefits, the inability of PAM to detect non-vocal mammals necessitates the combination of PAM with other monitoring methods like camera trapping or observer-based methods to provide the most comprehensive assessment of mammal biodiversity. This combined approach will likely improve future biodiversity monitoring, offering a more detailed understanding of ecosystems and support effective conservation practices.

Chapter 3. Passive acoustic monitoring for frog biodiversity assessments in Australia

3.1 Introduction

Anurans are among the most threatened groups of terrestrial vertebrates and have experienced rapid declines globally (Cox et al. 2022, Luedtke et al. 2023). The decline in frog biodiversity is driven by a combination of factors, including habitat loss, climate change, and the spread of diseases (Alford and Richards 1999, Sodhi et al. 2008, Collins 2010). While conservation efforts are in place for some species, numerous others still require further action (Gillespie et al. 2020, IUCN 2024). Many species still need to be assessed and could be declining so rapidly that they may disappear completely even before the detection of such declines (Skerratt et al. 2007). Therefore, comprehensive monitoring efforts are required to evaluate the conservation status of many frogs, assess the success of conservation action, and detect potential future declines in frog populations and biodiversity.

Traditionally, anurans are surveyed and monitored using a variety of field-based methods, each designed for specific habitats and taxa (Heyer et al. 1994, Eyre et al. 2018). These methods often include visual encounter surveys (e.g., Rödel and Ernst 2004), auditory surveys to detect calling males (e.g., Lotz and Allen 2007), and pitfall and funnel trapping (e.g., McKnight et al. 2015). Surveying frogs directly in the field via observers has its benefits. Incidental encounters are a highly effective method for increasing estimates of species richness (McKnight et al. 2015). Further, observer-based monitoring (OBM) efforts are necessary when surveying females or tadpoles (Gunzburger 2007). Each survey technique has its strengths and limitations, and a combination of these methods typically yields the best results for frog biodiversity monitoring (Sutherland 2006). However, even when combining methods, observer-based surveys may still fail to detect some species (Gardner et al. 2007). Additionally, observer bias in identifying frog calls is a significant issue, with misidentification rates reaching up to 20% (Lotz and Allen 2007, Mcclintock et al. 2010). Furthermore, observer-based monitoring requires substantial financial, time, and labour investments, and is often ineffective for rare or cryptic species (Gibb et al. 2018). As a result, observer-based monitoring in the field is limited in its spatial and temporal coverage.

Remote sensing has been used across various groups of terrestrial vertebrates to overcome some of the limitations inherent in OBM efforts (Pimm et al. 2015). For frogs, passive acoustic monitoring (PAM) is particularly useful, as nearly all frogs actively produce

vocalisations. Indeed, PAM has proven effective for detecting various frog species and has performed as well as many observer-based survey efforts (Acevedo and Villanueva-Rivera 2006, Gunzburger 2007, Madalozzo et al. 2017, Melo et al. 2021, Barnes and Quinn 2023). While PAM substantially reduces financial and time investments, especially for long-term monitoring, it is typically employed for short durations and on non-continuous recording schedules (Hoefer et al. 2023).

Long-term continuous PAM data is lacking and only available from a few large-scale sensor networks (Ross et al. 2018, Roe et al. 2021). Typically, collected audio data represents only snapshots of the day and year, as recording schedules are often limited to periods of expected vocal activity (Corn et al. 2000, Penman et al. 2005, Farmer et al. 2009, Xie et al. 2017, Dutilleux and Curé 2020). These limited recording schedules are typically driven by the constraints of manual data analysis, making it challenging to process large data volumes efficiently (Priyadarshani et al. 2018). However, frogs may vocalise at unexpected times, such as during the day (Callaghan and Rowley 2020), outside of typical wet seasons (Taylor et al. 2017), or with a delayed responses following rain events (Brodie et al. 2021). Consequently, shorter recording schedules risk missing these vocalisations, emphasising the need for long-term continuous PAM.

The use of automated acoustic analysis, such as deep learning models or Convolutional Neural Networks (CNNs), could enable long-term continuous PAM, providing a more comprehensive understanding of frog biodiversity (Priyadarshani et al. 2018, Kahl et al. 2021, Ghani et al. 2023). BirdNET, a deep learning model that has shown success in detecting various species through audio recordings (Wood et al. 2022, 2023a, Bota et al. 2023, Sossover et al. 2023, Sethi et al. 2024), has already identified several frog species (Pérez-Granados et al. 2023, Wood et al. 2023b, Bota et al. 2024) but is not yet trained to detect Australian frogs. However, this model provides "embeddings," numerical representations of acoustic signals that capture key features of a call and map them into a high-dimensional space. By comparing the embeddings of a user-provided example call to those in an unknown audio dataset, target vocalisations can be discovered from just a single example call (Ghani et al. 2023, Allen-Ankins et al. 2025), demonstrating potential for frog biodiversity assessments. This approach has been successful for mammalian biodiversity assessments (**Chapter 2**), but its effectiveness for frog biodiversity assessments remains untested.

In this study, I compared the performance of PAM combined with automated detection using BirdNET embeddings to in-field observer-based monitoring efforts for assessing frog

biodiversity. I compared the performance between methods for: a) species richness, b) community composition, and c) survey effort. Additionally, I investigated a seasonal sampling bias for PAM.

3.2 Methods

3.2.1 Study sites

For this study, I used the same six sites (Figure 3.1A) within open eucalypt woodlands as were used in **Chapter 2**, which were situated within national parks (Rinyirru, Undara, Duval) or private properties with no public access (Wambiana, Mourachan, Tarcutta). I also used the same survey plot design with four acoustic recording units (ARUs) at each site (Figure 3.1B). Observer-based monitoring (OBM) and passive acoustic monitoring (PAM) was conducted simultaneously within each of the 1-ha survey plots across all sites for seven days per survey trip. Acoustic recording units (ARUs) were left recording on a continuous schedule at the end of each survey trip. Camera trapping data was excluded from this study due to the absence of any frog detections, as the setup was specifically designed to target mammals (see Camera Trapping in **2.2.3**). See **2.2.1** for more details on study sites.

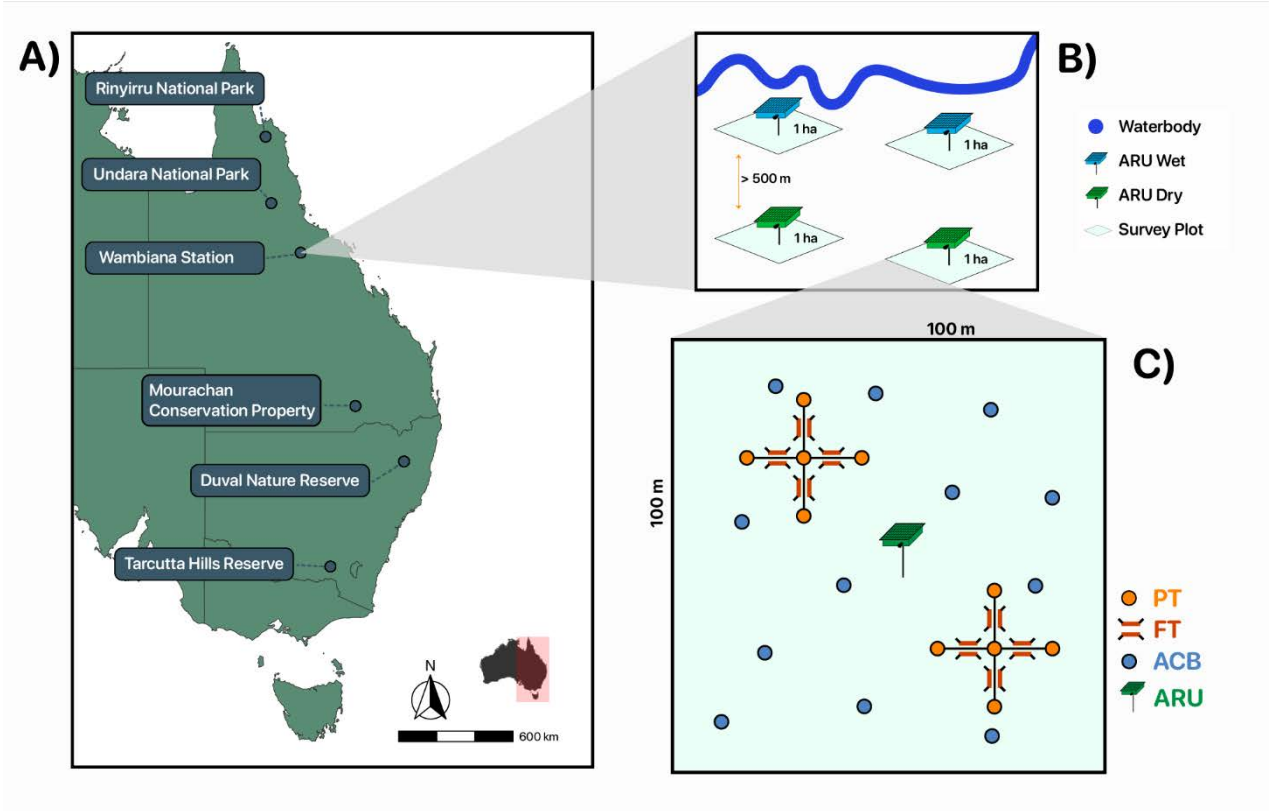

Figure 3.1. *Illustration of (A) the six study sites throughout eastern Australia, (B) the acoustic design layout for each site and, (C) a summary of the survey methods used at each of the four survey plots (1 ha area each) per site to target frogs (adapted from Hoefer et al. 2024). At each site, four ARUs were installed in similar habitat types, with two recorders placed within 50*

m of a body of water (ARU Wet – blue) and two recorders placed more than 500 m away from any water source (ARU Dry – green). Abbreviations used: PT = Pitfall Trap, FT = Funnel Trap, ACB = Arboreal Cover Board, ARU = Automated Recording Unit.

3.2.2 Observer-based monitoring (OBM)

I conducted observer-based surveys to detect frogs as part of the overall observer-based monitoring efforts to detect all terrestrial vertebrates (see mammals in **Chapter 2** and reptiles in **Chapter 4**), therefore, survey periods were identical (Table 2.1; Supplementary Table A2.2). To sample the frog community, I used five different OBM methods within each plot (Figure 3.1C): i) pitfall traps, ii) funnel traps, iii) arboreal cover boards, iv) nocturnal active area searches (spotlighting), and v) incidental encounters (detections of animals while not actively searching or checking traps). In addition to the design and procedure of the overall OBM efforts (See **2.2.2** for more details on observer-based monitoring), I deployed arboreal cover boards (ACB) which consisted of soft foam mats (50 x 50 x 1 cm) strapped to the trunk of twelve haphazardly selected trees at about 1.5 m above the ground to act as artificial refugia for arboreal frogs (Nordberg and Schwarzkopf 2015). It is important to note that the frog detections in this study represent observations rather than individual counts. Since I did not permanently mark each frog, I was unable to distinguish between different individuals across multiple encounters.

3.2.3 Passive acoustic monitoring (PAM)

I conducted passive acoustic monitoring in the same way as in **2.2.4** using Frontier Labs Solar BARs equipped with an external omnidirectional microphone (Primo EM172) sampling in mono at 16-bit 22,050 Hz on a continuous recording schedule.

3.2.3.1 Acoustic analysis

To analyse all audio recordings and detect frog vocalisations, I created feature embeddings for my target species and 3-sec clips of all available audio data from my sites using the BirdNET-Analyzer, following the instructions in the github repository (https://github.com/kahst/BirdNET-Analyzer). I then calculated the Euclidean distances between feature embeddings of the frog example calls and the unknown audio in the acoustic dataset. I selected 115 example calls of 50 Australian frog species with predicted ranges overlapping my study sites (Cutajar et al. 2022, Supplementary Table A3.1). I was, again, interested in comparing OBM to the acoustic data collected during the survey period (12,303 hours) and all acoustic data available (317,410 hours). Hereafter, I will use the term “short-term PAM” to refer to PAM using audio data matching only the survey period, and “long-term PAM” for PAM using all audio data available. Following the creation of feature embeddings, I extracted the

top detections (lowest Euclidean distances) for each frog example call for every day of audio data at each survey site, and aurally and visually confirmed species detections (251,315 detections). After examining the prediction probabilities of true positive detections for each example call, I concluded that, overall, lower Euclidean distances between the example calls and all the other data tended to be true positives, suggesting my approach of extracting the lowest daily distance to confirm species presence at a survey plot was valid (Supplementary Figure A3.1). See Methods in **2.2.4.1** for more details on acoustic analysis.

3.2.4 Statistical analysis

All statistical analyses were conducted in the R statistical environment (R Core Team 2023, v.4.4.0). My reproducible code and the data for my analyses can be accessed here: https://github.com/cheloniax/Hoefer2024.git. I excluded data from survey plots where acoustic recorders collected less than 70% of the total possible amount of audio data due to battery or SD card malfunctioning (Supplementary Table A2.2). For species richness, I explored the relationship between the total number of species per survey plot for each assessment method using hierarchical models in a Bayesian framework, assuming a Poisson distribution and weakly informative priors using the package *brms* (Bürkner 2017). I compared several candidate models and selected the final model based on LOO information criterion values (Vehtari et al. 2017) and validated the best model via DHARMa residuals (Hartig 2022). Finally, I used post hoc pairwise comparisons to make specific inferences on the value of the different assessment methods for detecting high frog species richness. To gain information on the similarity of the frog community sampled by each assessment method, I performed nonmetric multidimensional scaling (nMDS) based on Jaccard (presence-absence) dissimilarities and conducted pairwise permutational analysis of variance using the packages *vegan* (Oksanen et al. 2022) and *EcolUtils* (Salazar 2022). The nMDS ordination was performed with two dimensions and 1000 random starts to ensure convergence. Each unique combination of site and plot was treated as a separate data point in the analysis, with assessment method as the main factor of interest. To evaluate the sampling effort necessary at each site, I constructed species accumulation curves for the 28-day survey period and all available audio recording days, using the *vegan* package (Oksanen et al. 2022) and permutating the sampling day sequence randomly for more robust estimates of species richness accumulation. Additionally, I investigated a seasonal sampling bias in species accumulation by splitting the audio data and species detections into four seasons: summer (Dec-Mar), autumn (Mar-Jun), winter (Jun-Sep), and spring (Sep-Dec). Initially, I examined species richness for each OBM method separately to compare against PAM. However, except from spotlighting, which showed slightly higher average

richness (Supplementary Figure A3.2), the differences among the individual OBM methods were minimal. Furthermore, comprehensive frog surveys rarely employ a single technique and rely on multiple simultaneously deployed methods. Consequently, the individual OBM methods were combined into one category for the analyses.

3.3 Results

Over the course of this study, I detected and identified 35 species of Australian frogs across eight genera and four families (Supplementary Table A3.2). Passive acoustic monitoring using all available audio data (long-term PAM) detected the highest number of species (34 detected/50 possible based on predicted ranges from the Australian Frog Atlas; Cutajar et al. 2022) across all study sites, followed by OBM (23/50), and PAM using audio recordings matching only the survey period (short-term PAM; 21/50).

3.3.1 Species richness

The maximum total species richness varied among sites but followed a latitudinal trend with an increase in the number of detected frog species from South to North (Supplementary Table A3.3). For the matching survey period (28 days), OBM detected significantly more species on average than PAM (1.7x more species, 95% highest density interval [HDI]: 1.27-2.23; Figure 3.2). OBM also recorded higher total numbers of frog species compared to short-term PAM at four sites (Tarcutta, Mourachan, Wambiana, Rinyirru), whereas short-term PAM detected more species than OBM at two sites (Duval, Undara; Supplementary Table A3.3). When all available audio data was considered, PAM detected significantly more species on average than OBM (1.65x more species, 95% HDI: 1.28-1.99) and short-term PAM (2.81x more species, 95% HDI: 2.09-3.55). Long-term PAM recorded the highest species richness at all six survey sites, which was also the highest total species richness (i.e., total richness of all methods combined) at five sites, and only at Rinyirru OBM detected three species not found via PAM (*Limnodynastes terraereginae*: five observations, *Litoria inermis*: one observation, and *Platyplectrum ornatum*: 116 observations; Supplementary Table A3.3).

Long-term PAM detected 34 species and 13,577 observations of frogs, whereas short-term PAM recorded 21 species and 540 observations. Using OBM, spotlighting recorded the highest number of species (19) and observations (2155), followed by pitfall traps (18 species, 419 observations), incidental encounters (17 species, 263 observations), and funnel traps (16 species, 210 observations). Arboreal cover boards only detected two species, two observations of *Litoria rubella*, and one observation of *Platyplectrum ornatum*.

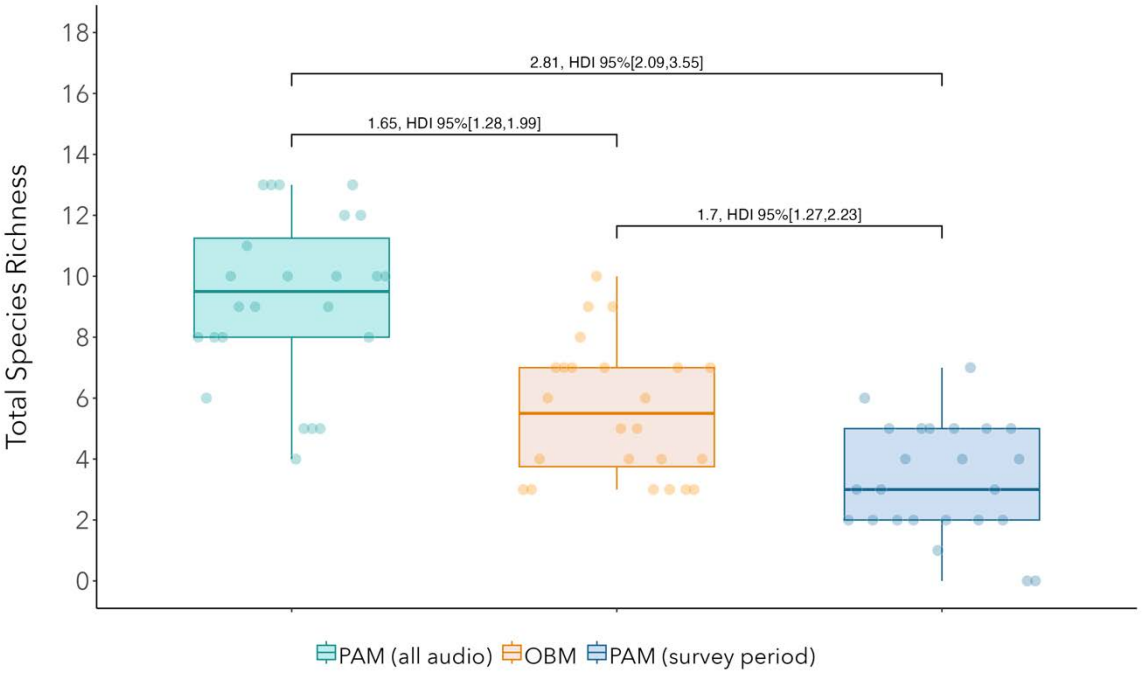

Figure 3.2. *Total species richness of frogs for each survey plot at each site detected by each survey method: passive acoustic monitoring using all available audio data (green), observer-based monitoring (orange), passive acoustic monitoring using only audio data matching the survey period (blue). The average fractional difference and 95% Highest Density Intervals (HDI) are shown above the boxplots, indicating statistical significance.*

3.3.2 Community composition

There were no significant differences in the frog communities predicted by any of the survey methods employed. Short-term PAM did not record significantly different species assemblages to OBM (Jaccard index, R2 = 0.035, *P* = 0.108; Figure 3.3) and long-term PAM (Jaccard, R2 = 0.056, *P* = 0.053). The frog communities sampled by long-term PAM and OBM were also similar, with no significant differences observed (Jaccard, R2 = 0.056, *P* = 0.062). Long-term PAM detected 12 unique frog species not detected by OBM, three of which were also detected in short-term PAM, while OBM detected one species (*Limnodynastes terraereginae*) not recorded by PAM (Supplementary Table A3.2). This species was exclusively detected in pitfall traps (two observations) and funnel traps (three observations) at Rinyirru.

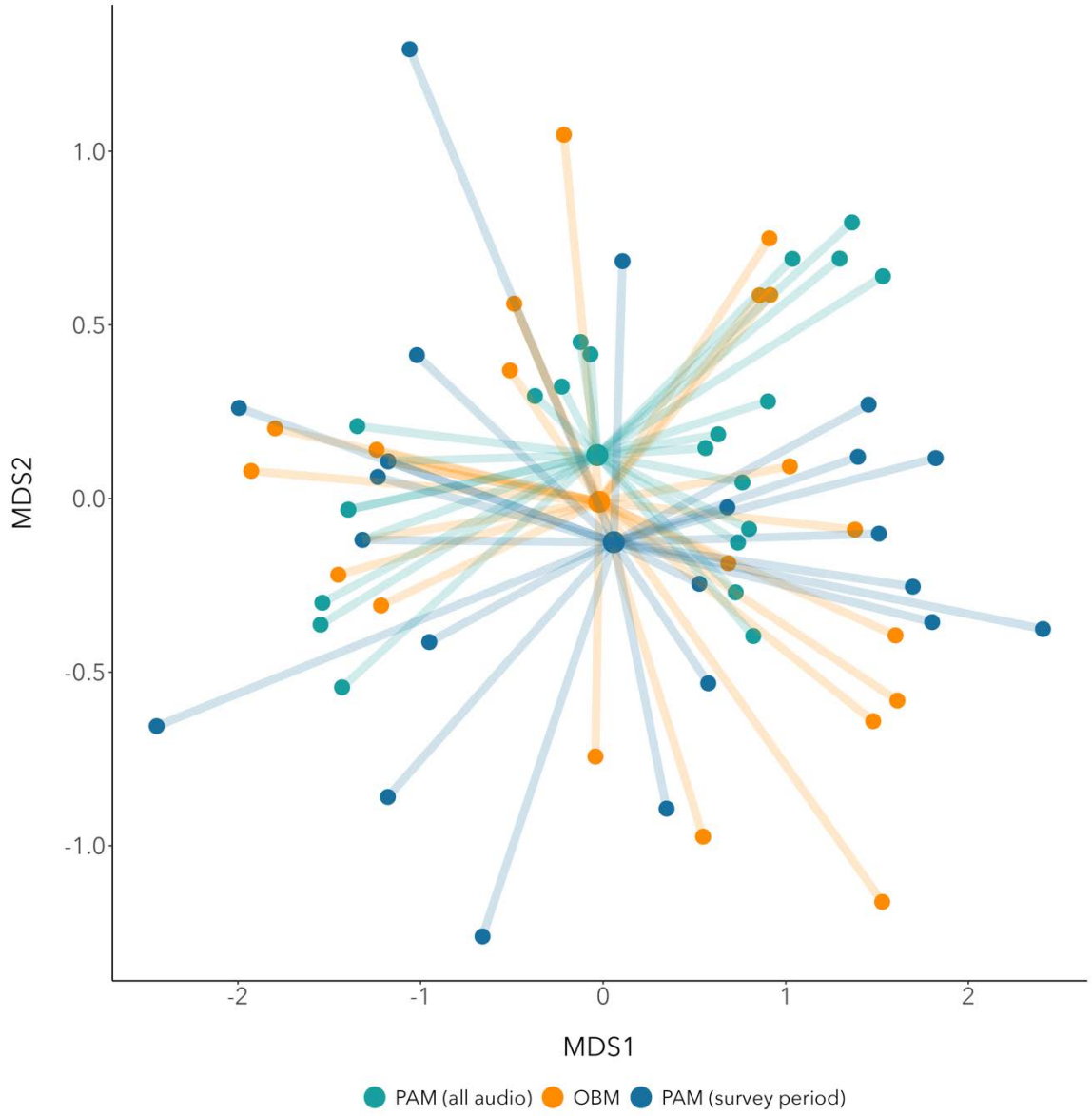

Figure 3.3. *Non-metric multidimensional scaling (NMDS) ordination of frog communities based on Jaccard dissimilarity (presence-absence) captured by the different assessment methods at each survey plot at each site. Each point represents a survey plot and larger points mark the centroids for every assessment method, with connecting lines to individual sites belonging to each method.*

3.3.3 Survey effort

Over the 28-day survey period, species accumulation curves for the total number of species did not reach an asymptote at any site (Figure 3.4). For this short-term period, OBM accumulated species the quickest at all sites and recorded the highest species richness at four sites, whereas PAM recorded higher species richness after 12 days in Duval and 22 days in Undara. Over the 28 days, neither OBM nor PAM alone detected all species present at four of the

sites. Only at the two southernmost sites did a single method detect all species: PAM at Duval and OBM at Tarcutta.

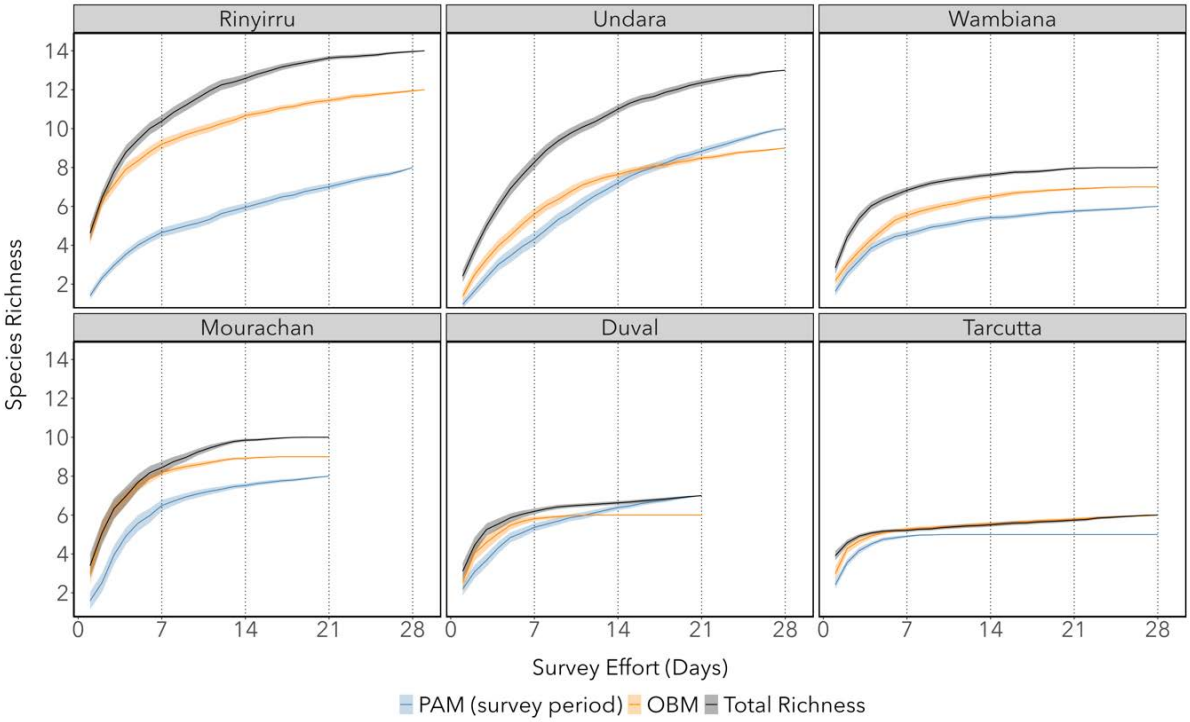

Figure 3.4. *Species accumulation curves for frog communities at six survey sites for each assessment method over up to 28 survey days. The coloured lines represent the different assessment methods: passive acoustic monitoring (blue), observer-based monitoring (orange), and all methods combined (total richness [black]). Shaded areas around each line corresponds to the 95% confidence intervals and dotted vertical lines mark the cumulative effort after each survey.*

With all audio data used, PAM reached its maximum frog species richness at an average of 12 species across all sites, with a range from six at Tarcutta, to 16 at Rinyirru (Table 3.1). To reach this maximum richness required on average 539 days of PAM, ranging from 487 days at Rinyirru to 596 days at Mourachan. After 28-days of PAM, I only recorded 66% of its maximum species richness on average, with a variability of 24% across sites. After sampling for 90 days, the average proportion of the maximum species richness detected was 84%, with a maximum variability of 10% across sites. Extending the sampling period to 180 days increased the average proportion to 93% and reduced the maximum variability between sites to 9%. After a full year (365 days) of recordings, the average proportion of the maximum total species richness at a site was 98%, with a maximum variability of 4% across sites.

Species accumulation curves of long-term PAM approached an asymptote at five sites (Tarcutta after 495 of 986 days, Duval 594 of 679 days, Mourachan 596 of 783 days, Wambiana 560 of 1235 days, and Undara 504 of 780 days; Figure 3.5). The number of days needed for PAM to match the frog species richness of OBM at each survey sites varied but took on average 111 days (Tarcutta: 495 days; Duval: 7 days; Mourachan: 42 days; Wambiana: 19 days; Undara: 35 days; Rinyirru: 68 days; Supplementary Table A3.4). After splitting the audio data and species detections into four seasons, summer and spring sampling accumulated species the quickest and recorded the highest species richness, while winter and autumn sampling led to the poorest results (Figure 3.5). Across all sites, summer sampling detected the most species (67), followed by spring (59), autumn (46) and winter (37). However, some species were only detected in one particular season at certain sites, with six species detected only during summer (Mourachan: Cyclorana verrucosa; Undara: *Cyclorana brevipes, Limnodynastes grayi*; Rinyirru: *Cyclorana brevipes, Litoria latopalmata, Litoria pallida*), and two species only in spring (Duval: *Limnodynastes dumerilii dumerilii*; Mourachan: *Limnodynastes grayi*), but no species was exclusively detected during winter or autumn sampling.

Table 3.1. *Maximum total species richness, number of days to reach the maximum total species richness, the percentage of total richness achieved after 28 days, 90 days, 180 days, and 365 days of passive acoustic monitoring (PAM) of frogs at each survey site, as well as the mean value across all sites.*

Site	PAM (maximum total richness)	Days to max total richness	PAM proportion of max richness			
			28 days	90 days	180 days	365 days
Tarcutta	6	495	0.78	0.89	0.95	0.99
Duval	10	594	0.75	0.85	0.92	0.97
Mourachan	13	596	0.63	0.84	0.94	0.99
Wambiana	12	560	0.66	0.87	0.96	1
Undara	15	504	0.54	0.83	0.96	1
Rinyirru	16	487	0.63	0.79	0.87	0.96
Average (all sites)	12	539	0.66	0.84	0.93	0.98

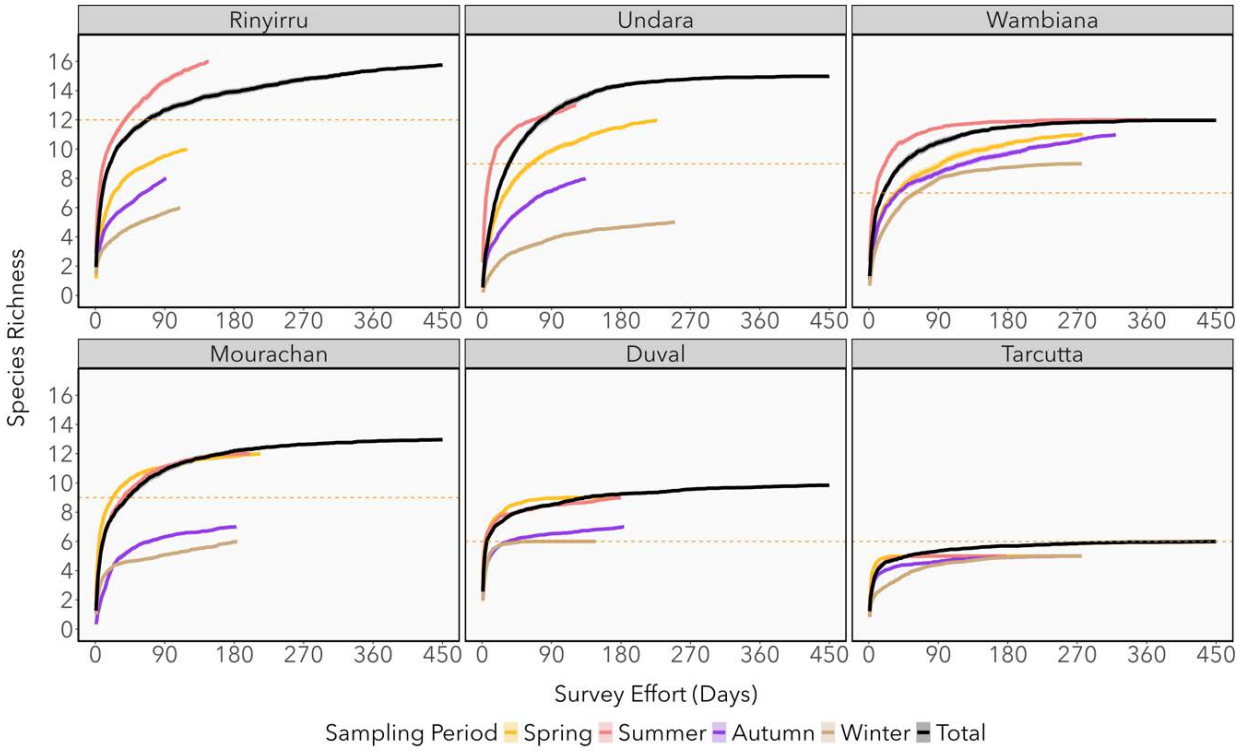

Figure 3.5. *Species accumulation curves for frog communities at six survey sites for each assessment method. The coloured lines represent different sampling periods over the year: sampling only in spring (yellow), summer (red), autumn (purple), winter (brown), and sampling all seasons (all available audio data [black]). Shaded areas around each line corresponds to the 95% confidence intervals and dotted horizontal orange line marks the total species richness detected via observer-based monitoring (OBM) at each site.*

3.4 Discussion

I compared the performance of passive acoustic monitoring (PAM) to observer-based monitoring (OBM) for frog biodiversity assessments across open eucalypt woodlands in eastern Australia. Using feature embeddings from the BirdNET deep-learning model I was able to analyse over 300,000 hours of continuous audio recordings from six sites and detected 34 species of frogs. This method only required as little as a single example call per species without the need to build individual recognisers, which demand a high time investment and in-depth knowledge (Priyadarshani et al. 2018). Across all sites, I detected the most frog species (34) using long-term PAM (i.e., PAM using all available audio data) which was 22% higher than using OBM (23 species) and 26% higher than via short-term PAM (i.e., PAM using the audio time period matching the survey period only: 21 species). The reasons for the absence of 15 species with predicted ranges overlapping my study sites remains unclear. While it is possible that micro-scale environmental factors, such as habitat or climate, are unsuitable for supporting robust

populations of these species at these sites, widespread anuran declines may also play a role in explaining the absence of these species.

During the 28-day survey period, OBM proved more effective than PAM by accumulating species more quickly and recording the highest richness at most sites. The ability of OBM to detect species both visually and aurally, as opposed to aural detection only via PAM, led to generally higher species richness observed with OBM in the short-term. Visual detections have been noted as a significant factor in the superior performance of OBM for detecting some species of birds (Haselmayer and Quinn 2000, Hutto and Stutzman 2009, Alquezar and Machado 2015, Vold et al. 2017). However, OBM alone did not detect all species present, suggesting that a combination of OBM and PAM may be the most comprehensive strategy for short-term monitoring of frogs (see also **Chapter 2**). When extending the recording period to include all available audio data, PAM significantly outperformed OBM and short-term PAM in terms of species richness. Similar findings have been reported in studies on birds, where long-term PAM was more effective than short-term monitoring (Klingbeil and Willig 2015, Kułaga and Budka 2019).

Frogs primarily vocalise for reproductive purposes (Duellman and Trueb 1994, Gerhardt 1994). Since breeding is closely associated with rainfall, increased precipitation typically triggers heightened calling activity in frogs (Hauselberger and Alford 2005, Xie et al. 2017, Brodie et al. In Review). Conducting observer-based surveys in the field or recording audio for only short periods of time may increase the risk of missing rainfall events that trigger breeding calls in some frogs. In my study, restricting the acoustic monitoring period for PAM to only 28 days resulted in missing nine species of breeding frogs that were detected in long-term PAM. Similarly, recording schedules that capture only parts of the day or night may fail to detect unexpected calling activity from some species or individuals (Callaghan and Rowley 2020). Therefore, continuous long-term monitoring should be the goal to capture the highest frog species richness.

Utilising PAM for extended monitoring periods resulted in the highest species richness at all sites, indicating that this is the most effective approach for quantifying overall frog biodiversity. In the short-term (28 days), PAM detected only 66% of the total possible frog species richness, whereas after 365 days, this increased to 98%, demonstrating the substantial benefits of long-term PAM. Importantly, extending the duration of PAM does not generally incur much higher costs compared to site visits, making long-term PAM sampling highly cost-effective (Williams et al. 2018). With recent technological advancements, it is feasible to collect and

store long-term continuous audio data (Aide et al. 2013, Rhinehart et al. 2020), and using deep-learning models like BirdNET allows for efficient analysis of these extensive acoustic datasets, further enhancing the practicality and effectiveness of long-term PAM.

Because increased calling activity in frogs is often linked to rain events (Hauselberger and Alford 2005, Xie et al. 2017, Brodie et al. 2021), I aimed to determine if PAM sampling at different times of the year, when rain is more or less common, would lead to different rates of species accumulation. I found that species were detected fastest, and species richness was highest during spring and summer sampling, which aligns with the periods of more frequent and higher rainfall events. However, I did experience events of high rainfall even during autumn and winter at some sites, which prompted frog calling activity. Sampling continuously for at least 365 days will ensure that researchers capture significant rain events at any time of year that may trigger increased frog calling activity, thereby maximising the detection of frog species. Starting PAM sampling in early spring may be particularly beneficial to ensure a rapid accumulation of species throughout spring and summer as rain events become more frequent.

Observer-based monitoring and both short-term and long-term PAM captured comparable frog communities, indicating no overall differences in species assemblages detected by the different survey methods. Previous studies have shown that OBM and PAM can detect different species, and, in particular, visual detections represent an advantage of OBM (Darras et al. 2019). In fact, non-vocal species or species vocalising outside the sampling rate of the audio recorders can never be detected via PAM and could only be assessed using OBM (see **Chapter 2**). However, since vocalisation is essential for successful reproduction in most frog species, frogs should eventually vocalise, providing the opportunity for detection via PAM. In some cases, frogs with short or quiet calls may remain undetected because their calls could be masked by other species, or environmental noises such as rain, wind, or even anthropogenic sounds (Pijanowski et al. 2011, Luther and Gentry 2013). In fact, I was unable to detect three species (*Limnodynastes terraereginae*, *Litoria inermis*, *Platyplectrum ornatum*) by (even long-term) PAM at Rinyirru and they were only detected in traps or visually during active searches. It is probable that a noisy, insect-dominated soundscape at this site prevented the acoustic detection of these species. Despite not directly overlapping in frequency with the frogs' short calls (< 0.1 seconds), the dominance of insect noise may have masked the acoustic signals, making them difficult for BirdNET embeddings to capture. Notably, these same species were detected via PAM at other sites, suggesting that intense insect noise, combined with potentially subtle call variations at Rinyirru, affected their detection. The transferability of PAM across different habitats or areas remains challenging, as some environments may pose greater

difficulties for species detection (Hill et al. 2013, Kułaga and Budka 2019). However, utilising more example calls from various geographic regions and developing more robust recognisers using Convolutional Neural Networks (CNN) may enhance the detection of difficult-to-detect species, even across large spatial scales.

PAM presented an advantage over OBM for differentiating among species that are most reliably identified by their calls, such as many species within the genera *Crinia* and *Uperoleia*. When these frogs were encountered in traps alone, I was often unable to identify individuals to species level in the field, whereas PAM often allowed accurate detections through vocalisations alone. Furthermore, PAM samples the same communities as OBM, making it a viable option for producing comprehensive species lists, especially in cases where obtaining presence-absence data is the primary goal. Additionally, PAM provided valuable information on the seasonal activity of frogs, helping to identify optimal periods for effective monitoring. However, while PAM excelled at detecting adult male frogs, it cannot capture information on juveniles, females, or sex ratios, limiting its utility for detailed population information. Consequently, certain ecological questions, such as population structure, reproductive output, and morphological data, cannot be answered directly through acoustic recordings alone. In these contexts, observer-based monitoring (e.g., pitfall traps, spotlighting) remains crucial.

3.5 Conclusions

This study demonstrated that passive acoustic monitoring (PAM) combined with BirdNET feature embeddings was highly effective for assessing frog biodiversity in open eucalypt woodlands across eastern Australia. By analysing over 300,000 hours of continuous audio recordings from six sites, while requiring only few example calls per species, I successfully detected 34 frog species. Over 28 days, observer-based monitoring (OBM) was more effective than PAM due to visual detections, however, long-term PAM significantly outperformed both OBM and short-term PAM. PAM sampling in spring and summer was the most effective, but sampling continuously for a full year detected nearly all species across all sites and ensured capturing high rainfall events triggering increased frog calling activity across seasons. Pitfall and funnel trapping were effective for capturing high numbers of species and individuals, including females and juveniles, but these methods missed arboreal species and required substantial financial and time investments. Spotlighting was the single most effective OBM method, requiring comparatively little time and cost while targeting both ground-dwelling and arboreal species through visual and aural detection. Overall, these findings support the use of long-term PAM for extensive and cost-efficient species inventories, but underscore the value of combining PAM with OBM for more detailed population ecology research and conservation outcomes.

Chapter 4. Diverse Methods for Diverse Systems: A Large-Scale Comparison of Reptile Sampling Methods[2]

4.1 Introduction

Reptiles are a critical part of biodiversity. They play a vital role in ecological communities, serving as predators, prey and even seed dispersers, and contribute to the overall stability and health of ecosystems (Valido and Olesen 2007, Valencia-Aguilar et al. 2013, Dodd 2016). However, they are increasingly threatened due to habitat loss, climate change, and other anthropogenic factors, with every fifth species currently facing the risk of extinction (Cox et al. 2022). Given the importance of reptiles in ecological communities, identifying changes in reptile biodiversity, particularly biodiversity loss, is crucial, and comprehensive monitoring efforts are required (Böhm et al. 2013, Webb et al. 2014).

Numerous sampling techniques have been developed to survey terrestrial reptile communities (McDiarmid et al. 2012, Dodd 2016). These often involve observer-based monitoring methods, such as pitfall traps, funnel traps, visual encounter surveys, and artificial refugia (e.g., Thompson and Thompson 2007, Ribeiro-Júnior et al. 2008, Sung et al. 2011, Michael et al. 2012). The effectiveness of these methods varies across taxa, and their use can impact the detection of biodiversity patterns (Whitworth et al. 2017). For instance, pitfall traps are widely used and highly effective for capturing small to medium-sized lizards and small snakes, but less effective for medium and large snakes (Greenberg et al. 1994, Todd et al. 2007, McKnight et al. 2015). In contrast, funnel traps effectively capture medium-sized snakes and lizards but are less effective for small snakes and lizards (Thompson and Thompson 2007, Todd et al. 2007). Common artificial refugia, such as corrugated sheet metal, plywood, or roof tiles, are useful in detecting nocturnal thigmothermic reptiles (Engelstoft and Ovaska 2000, Michael et al. 2012, Kolanek and Bury 2021). While many of these survey methods target terrestrial species, visual encounter surveys, including diurnal active searches and nocturnal spotlighting, successfully detect many arboreal reptiles (Rodda et al. 1999, Lardner et al. 2013, Vanderduys et al. 2013, Nordberg and Schwarzkopf 2015, Kutt and Colman 2023). Additionally, arboreal cover objects and traps have been employed to sample arboreal reptiles (Davis et al. 2008, Bell 2009, Nordberg and Schwarzkopf 2015). Despite their varying effectiveness for specific species, most of these commonly used methods require considerable labour and can incur high personnel and equipment costs (Garden et al. 2007, Molyneux et al. 2018).

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Technological advancements have led to the development of more cost-effective and less time-intensive biodiversity assessment tools, such as remote sensing and eDNA sampling (Adams et al. 2017, Ezat et al. 2018, Welbourne et al. 2020, Kyle et al. 2022). Camera traps, for example, can offer reduced long-term costs and increase scalability for reptile biodiversity assessments (Ariefiandy et al. 2013, Welbourne et al. 2017, Moore et al. 2020), but face challenges in identifying small reptiles and fail to detect nocturnal species (Welbourne et al. 2015, Richardson et al. 2017). Passive acoustic monitoring (PAM), has demonstrated potential as a non-invasive and cost-effective method for detecting a range of vocal terrestrial vertebrates (Sugai et al. 2019), including reptiles (Yu et al. 2011, Hopkins et al. 2021), but research on the application of PAM in reptile biodiversity assessments remains limited (McKnight et al. 2015). This limited exploration of PAM in reptile assessments may be attributed to its inability to detect non-vocal species, which are more prevalent among reptiles than other vertebrate taxa (Capshaw et al. 2021). However, it is important to not dismiss the potential of PAM prematurely.

The substantial behavioural and morphological diversity of reptiles and cryptic nature of many species present challenges for accurate biodiversity assessments, resulting in insufficient data for evaluating the conservation status of numerous species (Böhm et al. 2013, Cox et al. 2022). Given the limitations of individual survey techniques, it has been suggested that multiple complementary techniques should be employed to assess reptile assemblages (Garden et al. 2007). However, implementing various survey methods simultaneously can increase costs and time spent field sampling (De Bondi et al. 2010, Richardson et al. 2017). While a variety of studies have compared survey methods for reptiles, most have been conducted in a single area, targeting a single community (often in a single season), and few studies have employed replicate surveys over a broad geographic area (Thompson and Thompson 2007). The relative effectiveness of different methods may, however, vary substantially in different areas or for different communities, and studies that take a broader approach would be valuable. To address these knowledge gaps and inform effective conservation strategies, it is essential to implement reliable and efficient methods for detecting and monitoring reptile communities.

In this study, I aimed to simultaneously compare the effectiveness of seven methods for assessing reptile biodiversity—pitfall traps, funnel traps, spotlight surveys, arboreal cover boards, camera traps, incidental encounters, and PAM—over two years and across an extensive spatial scale. My objectives were to evaluate the performance of each method in terms of species richness, sampling effort, and detectability, while also considering potential biases and limitations associated with each technique. By providing a comprehensive comparison of sampling methods, I contribute to the development of best practices for reptile biodiversity

monitoring, ultimately supporting more effective conservation efforts for this ecologically important group of animals.

4.2 Methods

4.2.1 Study sites

This study was conducted as part of a large-scale terrestrial vertebrate assessment project, evaluating the efficacy of acoustic monitoring for terrestrial vertebrate biodiversity surveys in Australia. I selected six sites (Figure 4.1A) in open eucalypt woodland, where acoustic recording units (ARUs) had previously been deployed for the Australian Acoustic Observatory project (Roe et al. 2021). All six sites were located within natural reserves (Rinyirru, 15.044007°S, 144.242852°E; Undara, 18.187058°S, 144.539753°E; Duval, 30.402213°S, 151.624706°E; datum = WGS84) or private properties (Wambiana, 20.53071°S, 146.113426°E, Lyons family; Mourachan, 27.778986°S, 149.032006°E, Australia Zoo; Tarcutta, 35.368525°S, 147.696893°E, Bush Heritage; datum = WGS84) with no public access. I established a 1 ha survey plot within 50 m of each ARU, resulting in four survey plots (2 x Wet, 2 x Dry) per site (Figure 4.1B). Note that throughout I will use the term "site" to refer to the six reserves/private properties and "plot" to refer to the four 1 ha areas surveyed within each site. I employed all seven methods simultaneously at each plot over seven days per survey trip.

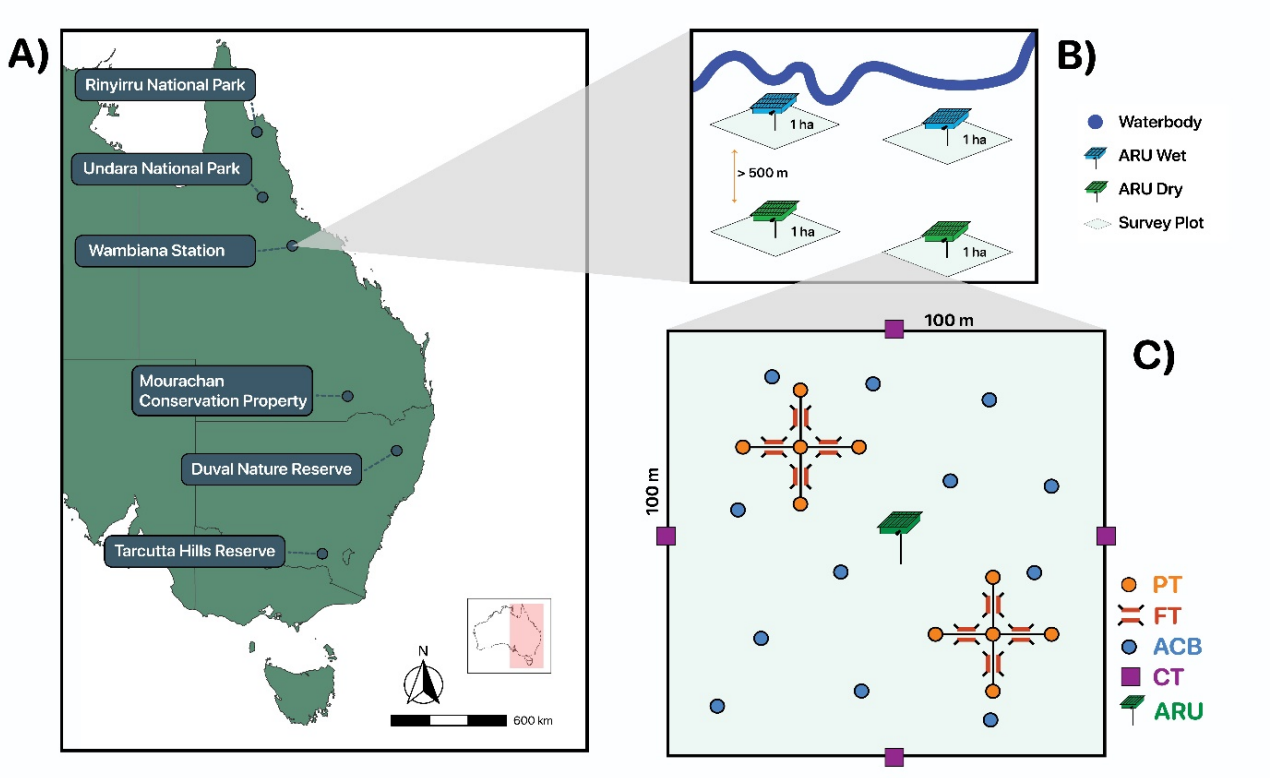

Figure 4.1. *Overview of (A) the six field sites across eastern Australia with (B) a schematic of the acoustic setup for each of the field sites and (C) an overview of the survey methods*

deployed at each survey plot (four per site), targeting reptiles within a 1 ha plot at each acoustic recording unit (ARU). Four ARUs, two within 50 m of a body of water (ARU Wet = blue) and two > 500 m from a water source (ARU Dry = green), were deployed in a similar habitat type. PT = pitfall trap, FT = funnel trap, ACB = arboreal cover board, CT = camera trap, ARU = automated recording unit.

4.2.2 Survey methods

I conducted surveys to detect terrestrial reptiles in spring/summer (September–November) and autumn/winter (April–August) in 2021 and 2022 at each site, except for Mourachan and Duval, which were inaccessible during spring 2021 due to high rainfall (Table 4.1; Supplementary Table A2.2). To comprehensively sample the reptile community, I used seven different survey methods within each plot (spatial arrangement shown in Figure 4.1C): (1) passive acoustic monitoring (PAM), (2) pitfall traps, (3) funnel traps, (4) arboreal cover boards, (5) nocturnal active area searches or spotlighting, (6) camera traps, and (7) incidental encounters (i.e., animals detected outside of a trap while not conducting active searches such as a lizard observed on the ground while a researcher was walking to a trap).

Passive acoustic monitoring (PAM) was conducted to evaluate whether reptile biodiversity in Australia can be assessed via sound. Each site had four automated recording units (ARUs; Frontier Labs Solar BAR), two within 50 m of a body of water (classified as Wet) and two at least 500 m from a waterbody (classified as Dry). Each recorder was placed at least 500 m from any other, to avoid detecting the same individuals across multiple recorders at the same time (Figure 4.1B). Each ARU consisted of a solar panel, battery, charge controller and recorder in a weather-sealed unit equipped with an external Primo EM172 omnidirectional microphone and was installed on a fence post (star picket) with enough clearance to prevent damage from wildlife and livestock. The ARUs recorded in mono at 16-bit 22,050 Hz with FLAC lossless compression in 2-h file blocks stored on two PNY Elite-X SDXC 512 GB SD cards (for more details on the ARU setup and specifications, see Roe et al. 2021). The design and setup of the ARUs enabled a continuous collection of acoustic data for up to 12 months without maintenance, at which point the SD cards were swapped out and recording resumed.

Inside each plot, I set up two drift fences with five pitfall and eight funnel traps each, 12 arboreal cover boards, and four camera traps. Drift fences (30 cm high) were installed in a cross design with four 10-m arms, accompanied by five 20-L pitfall traps (one central and four terminal). A pair of funnel traps (Thompson and Thompson 2007) were placed in the centre of each arm between the two pitfall traps. I equipped the openings of each funnel trap with

additional smaller fences, acting as wings to create a larger funnel and increase capture rates (McKnight et al. 2013). I covered all funnel traps with shade cloth and placed wet sponges in each pitfall and funnel trap to prevent desiccation and overheating of captured animals (McDiarmid et al. 2012). Arboreal cover boards (ACB) consisted of soft foam mats (50 x 50 x 1 cm) and were strapped to the trunk of haphazardly selected trees at about 1.5 m above the ground to act as artificial refugia for arboreal species (Nordberg and Schwarzkopf 2015). Additionally, I installed four camera traps (Campark T85, Campark Electronics Co., LTD.) on individual trees about 50 cm above ground between two corners facing into the plot. Each camera trap was baited with a can of sardines and peanut-butter-oat balls and set to high sensitivity, to take three consecutive photos and one 10-s video when triggered. Camera traps were active for the same 7-d period as the other survey methods. As camera traps were part of the overall vertebrate biodiversity assessment design, their setup followed a more generalized approach (Eyre et al. 2018), rather than a reptile-specific setup (Welbourne et al. 2017); however, baiting camera traps with meat has previously been used for surveying large, active predatory reptiles such as monitor lizards (Ariefiandy et al. 2013, Moore et al. 2020).

Each plot was surveyed by two trained observers familiar with the fauna of the region. Funnel and pitfall traps were checked twice daily (morning and evening), and ACBs were checked each morning. I also conducted active area searches every day after sunset (spotlight survey); for 15 min, two observers searched each entire plot, and recorded all individual reptiles detected visually or aurally. To minimize observer bias, members of each search team and the order at which plots were visited were alternated during each survey trip. I marked each captured reptile with a non-toxic permanent marker pen before release, to avoid mistaking recaptures for new captures within the survey trip. Recaptures within a survey period were excluded from the data for community analyses.

Table 4.1. *Overview of the survey periods and the total number of survey days for each of the six study sites. Dates are expressed as day/month/year. Total survey days are expressed as the number of survey days per site (max 28 days) multiplied by the four survey plots.*

Site	First survey	Second survey	Third survey	Fourth survey	Total number of survey days
Tarcutta	29/4–6/5/21	18/10–25/10/21	8/5–15/5/22	22/11–29/11/22	112
Duval	18/4–25/4/21	NA	28/4–5/5/22	12/11–19/11/22	70
Mourachan	9/5–16/5/21	NA	19/6–26/6/22	2/11–9/11/22	84
Wambiana	5/7–12/7/21	10/11–17/11/21	12/6–19/6/22	28/9–5/10/22	112
Undara	3/6–10/6/21	29/9–6/10/21	8/5–15/5/22	13/10–20/10/22	110
Rinyirru	14/6–21/6/21	8/10–15/10/21	7/8–14/8/22	23/10–30/10/22	112

4.2.3 Acoustic data analysis

To extract information about the presence of vocal reptiles, acoustic data were analysed using species-specific call recognizers created using *monitoR* (Katz et al. 2016). To my knowledge, members of the family Gekkonidae are the only Australian terrestrial reptiles producing audible calls for communication (Capshaw et al. 2021), but only few species have been witnessed vocalising. I created call recognizers for three species (*Hemidactylus frenatus*, *Gehyra dubia*, *Heteronotia binoei*) from example calls provided by J. Hopkins, Phongkangsananan et al. (2014) and S. Zozaya, respectively. These call recognizers were subsequently used to analyse the acoustic data for the same 7-d periods I employed the other surveys methods. Resulting positive matches were aurally (sound clip) and visually (spectrogram) reviewed and validated by one of the authors to identify and confirm species detections.

4.2.4 Camera trap data analysis

I used all camera trapping data available, and images were analysed using Timelapse2 (Greenberg 2022a) and the MegaDetector image recognition pipeline (Beery et al. 2019). There were three stages of analysis to generate species lists from the camera trap data. In the first stage, I used the MegaDetector to classify images as either wildlife or non-wildlife for each site and each survey. In stage two, non-wildlife classifications were validated following the workflow described in the Timelapse Image Recognition Guide (available at https://saul.cpsc.ucalgary.ca/timelapse/uploads/Guides/TimelapseImageRecognitionGuide.pdf). In the final stage, all images classified as wildlife were identified and labelled to species

level by an expert observer. Each wildlife categorization by MegaDetector comes with a confidence value indicating the certainty of the classification. While the guide suggests a confidence threshold of 0.8, I opted for a more conservative threshold of 0.5 for validating wildlife classifications. This was done to reduce the likelihood of false negative errors and failing to detect reptiles in my camera trap data.

4.2.5 Statistical analysis

All statistical analyses were carried out in R (v4.2.2) statistical and graphical environment (R Core Team 2023), and the full reproducible code is available at https://github.com/cheloniax/Hoefer2023. The relationship between species richness and survey method was explored using hierarchical models in a Bayesian framework. Specifically, the total number of species for each survey plot was modelled against the different survey methods assuming a Poisson distribution and weakly informative priors. Additionally, a spatial effect was investigated by including the latitude of each plot as a predictor. The Bayesian models included three chains, each of 5,000 iterations, thinned to a rate of 5, and excluded the first 1,000 iterations (warmup). Several candidate models were compared, and the final model was selected based on LOO information criterion values (Vehtari et al. 2017). The best model was well mixed and converged (all Rhat < 1.05) on a stable posterior and was validated via DHARMa residuals (Hartig 2022). The influence of the priors on the final model outcomes was assessed by visually comparing the prior and posterior distributions via overlaid density plots for each parameter. Specific inferences (comparing differences in species richness for each combination of survey methods at the six survey sites) were explored using exceedance probabilities and post hoc pairwise comparisons. For exceedance probabilities, I calculated the proportion of the posterior distribution above 0, to indicate the probability that one method is more effective than the other (henceforth referred to as $P_{(0)}$). A $P_{(0)}$ value of 1 would indicate that 100% of the posterior distribution are above 0, meaning that there is a 100% likelihood of a difference.

4.2.5.1 Species accumulation curves and community composition

To investigate the sampling effort required to reach an asymptote, I used the *vegan* package (Oksanen et al. 2022) to calculate species accumulation curves for the total species richness over the course of the 28 survey days (all four plots combined per site). I randomly permuted the order of survey days to provide more robust estimates of species richness by accounting for potential biases introduced by the order of days. Additionally, I performed Nonmetric Multidimensional Scaling (NMDS) using Jaccard (presence–absence) and Bray–Curtis (relative abundance) dissimilarities to assess community differences for each survey

method at each plot of each survey site. To test for differences in dissimilarity between the survey methods, I performed pairwise PERMANOVA analyses using the *vegan* (Oksanen et al. 2022) and *EcolUtils* (Salazar 2022) packages.

4.2.5.2 Detectability

I calculated the probability of capturing each species at any given survey day for each survey method within each plot for each study site. My aim was to compare detection probabilities among survey methods and not to conduct occupancy modelling; therefore, for each plot, I only examined species that were confirmed to be present at that plot (i.e., detected at least once by at least one method). To explore the relationship between detection and survey method I used hierarchical models in a Bayesian framework. I modelled the number of days a species was detected at each survey plot against the different survey methods with a negative binomial family and weakly informative priors and investigated a spatial effect by including the latitude of each plot as a predictor. Finally, I was interested in evaluating the efficacy of each survey method for detecting arboreal and ground-dwelling reptiles and distinctions between those species were made following Cogger (2014).

4.3 Results

Overall, I detected 3,323 reptiles of 93 species, including 295 recaptures of 30 species (Supplementary Table A4.3). An additional 129 reptiles escaped before species-level identification (*Scincidae* = 94, *Gekkota* = 32, *Serpentes* = 3) and were not included in the analyses. Pitfall traps recorded the highest number of reptile observations (978), followed by funnel traps (944), spotlighting (706), arboreal cover boards (514), incidental encounters (152) and camera traps (29). I was unable to detect any reptiles in my continuous acoustic recordings and, therefore, removed acoustic monitoring from further analyses.

4.3.1 Species richness

In total, funnel traps recorded the highest species richness (69), followed by pitfall traps (60), incidental encounters (42), spotlighting (28), arboreal cover boards (11) and camera traps (5). Funnel traps also detected the highest number of unique species (i.e., species not observed by any other method at a given site) across all plots (33; Supplementary Table A4.3). Pitfall traps and spotlighting detected the second and third highest number of unique species (13 and 7, respectively), incidental encounters and camera traps both detected three unique species, and arboreal cover boards detected two unique species. I recorded a latitudinal increase in species richness from south to north with the lowest number of species at Duval (11) and Tarcutta (14) and the highest richness at Undara (42) and Rinyirru (34).

On average, pitfall traps detected 2.49 and 3.04 times more species than incidental encounters and spotlighting respectively, 4.8 times more than arboreal cover boards, and 11.89 times more than camera traps. Similarly, funnel traps yielded 2.45 and 2.96 times more species than incidental encounters and spotlighting respectively, 4.69 times more than arboreal cover boards, and 11.56 times more than camera traps. However, pitfall and funnel traps did not differ significantly from each other (1.02, 95% highest density interval (HDI) = 0.8–1.27, $P_{(0)}$ = 0.588; Figure 4.2; Supplementary Table A4.1). Incidental encounters and spotlighting did not differ in the number of species detected (1.21, 95% HDI = 0.79–1.81, $P_{(0)}$ = 0.812) but detected up to four times more species than camera traps. Arboreal cover boards detected about two times fewer species than incidental encounters (1.93, 95% HDI = 1.11–2.97, $P_{(0)}$ = 0.997) and spotlighting (1.58, 95% HDI = 0.94–2.56, $P_{(0)}$ = 0.966). Camera traps detected the lowest number of species, with 2.5 times fewer species than arboreal cover boards (2.48, 95% HDI = 1.14–4.38, $P_{(0)}$ = 0.998) and up to 12 times fewer species compared to pitfall traps (11.89, 95% HDI = 6.39–20.14, $P_{(0)}$ = 1).

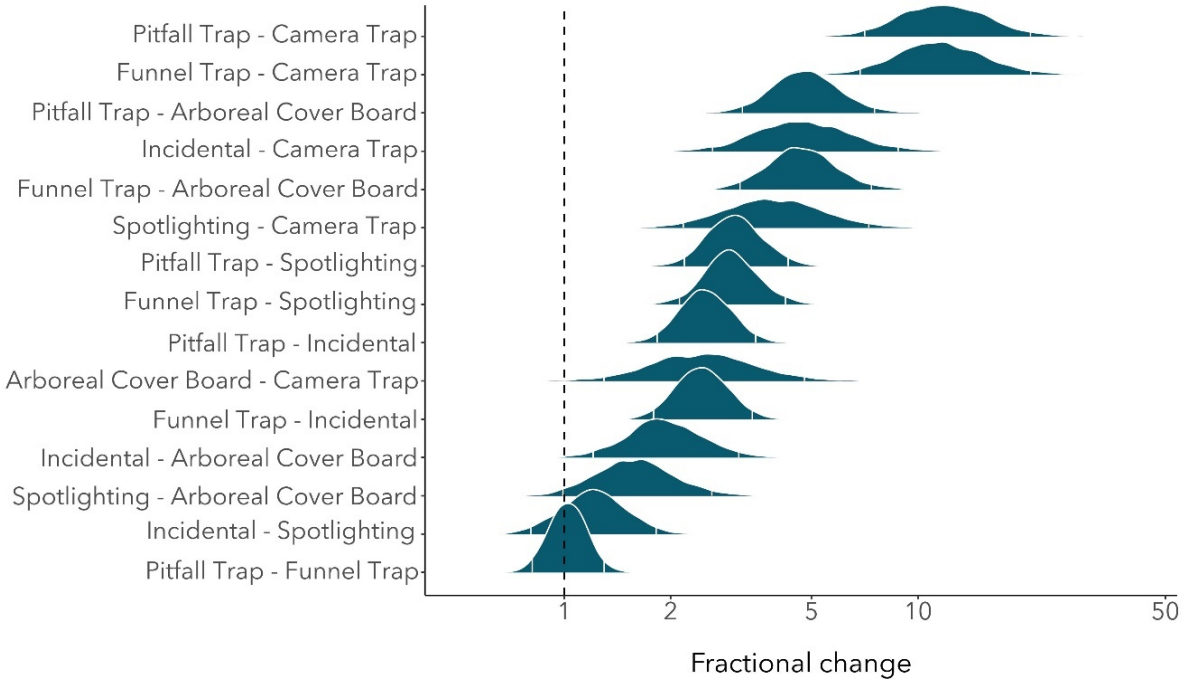

Figure 4.2. *Distribution of fractional change in species richness between survey methods across all survey sites. The ridge density plot displays the posterior distribution of the fractional change values for each pairwise comparison of survey methods (i.e., the factor by which the first method detects more species compared to the second), with gradient fill representing the density of the distribution. The x-axis is shown on a log2 scale, with a vertical dashed line*

indicating no change in species richness. The lower and upper 95% Highest Density Intervals (HDI) are depicted by the solid lines within each ridge.

Across all sites, a combination of pitfall and funnel traps recorded 87% of all species. Adding incidental encounters to that combination resulted in a detection of 95% of all species.

To control for the increase in overall species richness from south to north, I also calculated the proportion of the total number of species detected by each method at each survey site. At each survey site, pitfall and funnel traps detected the highest proportion of the total species richness, followed by incidental encounters, spotlighting, arboreal cover boards and camera traps (Figure 4.3). At the most southern site (Tarcutta), pitfall and funnel traps detected a combined 74% of the total species richness while no other method contributed more than 9%. With a decrease in latitude up to the most northern site (Rinyirru), the contribution of incidental encounters, spotlighting and arboreal cover boards to the total species richness increased, while the contribution of pitfall traps, funnel traps and camera traps decreased (Supplementary Table A4.1 for a comparison of methods for each survey site).

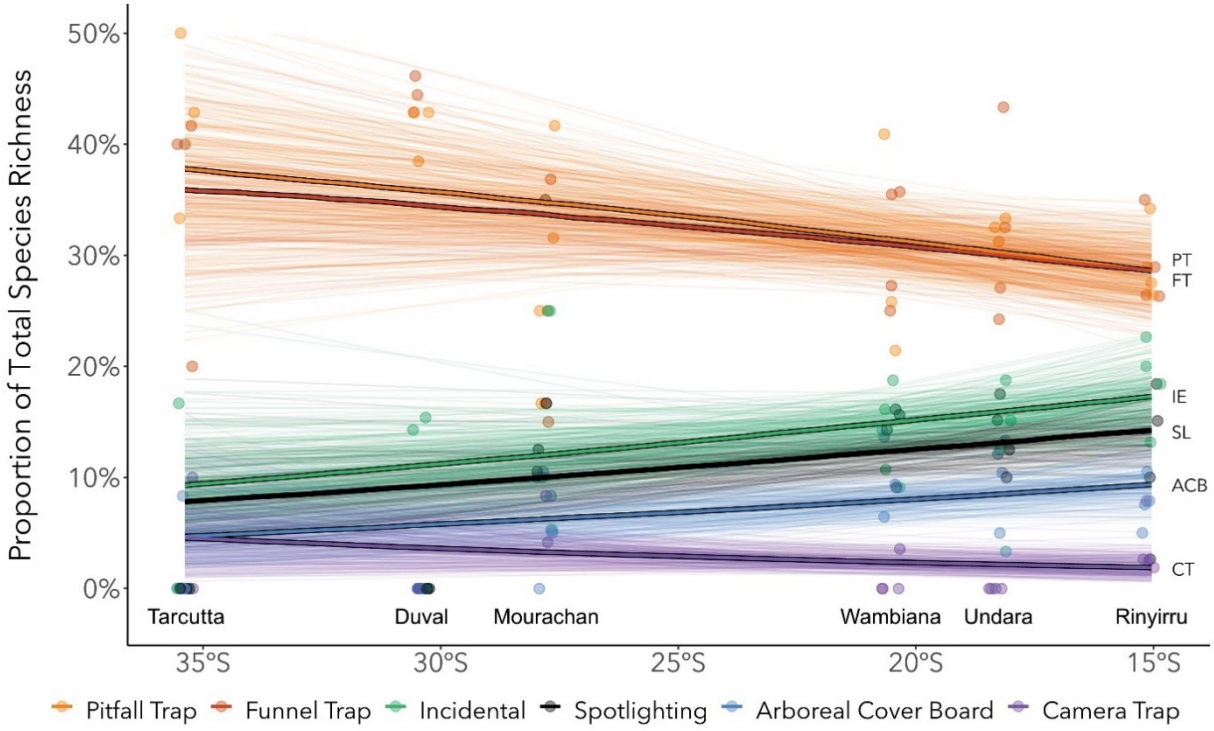

Figure 4.3. *Proportion of total species richness across latitudes for different survey methods: pitfall trap (PT), funnel trap (FT), incidental encounters (IE), spotlighting (SL), arboreal cover board (ACB), and camera trap (CT). Observed data points are represented as jittered points, while individual model simulations are shown as semi-transparent lines. The average proportions for each survey method are depicted as solid lines.*

4.3.2 Sampling effort

At all survey sites, species accumulation curves for total number of species did not reach a plateau during my survey period (Figure 4.4). Among methods, species accumulation curves for camera traps reached an asymptote at Tarcutta (after 26 d) and Mourachan (after 13 d) but did not at any other site. Curves for arboreal cover boards levelled off only at Mourachan after 20 d of sampling. No other method reached a plateau at any site. The average number of additional species detected after each 7-d survey period varied among sites (Rinyirru, 5.49, 95% CI = 5.39–5.59; Undara, 8.07, 95% CI = 7.89–8.26; Wambiana, 4.38, 95% CI = 4.29–4.47; Mourachan, 7.67, 95% CI = 7.41–7.94; Duval, 2.72, 95% CI = 2.63–2.81; Tarcutta, 2.9, 95% CI = 2.82–2.99). After 28 d (Rinyirru, Undara, Wambiana, Tarcutta) or 21 d (Mourachan, Duval) of sampling, on average 1.58 times more species had been detected than after the first 7 d of sampling across all sites (Rinyirru, 1.41; Undara, 1.54; Wambiana, 1.49; Mourachan, 1.52; Duval, 1.7; Tarcutta, 1.82). At each site, a combination of pitfall and funnel traps accumulated species more quickly than any method alone, and within 7 d, they reached over 50% of their combined total richness (i.e., total richness of pitfall and funnel traps at 28 d; Rinyirru, 0.687; Undara, 0.593; Wambiana, 0.644; Mourachan, 0.548; Duval, 0.595; Tarcutta, 0.516). At each site, pitfall traps accumulated species the quickest, but funnel traps either reached parity with or surpassed pitfall traps within the study period (Figure 4.4).

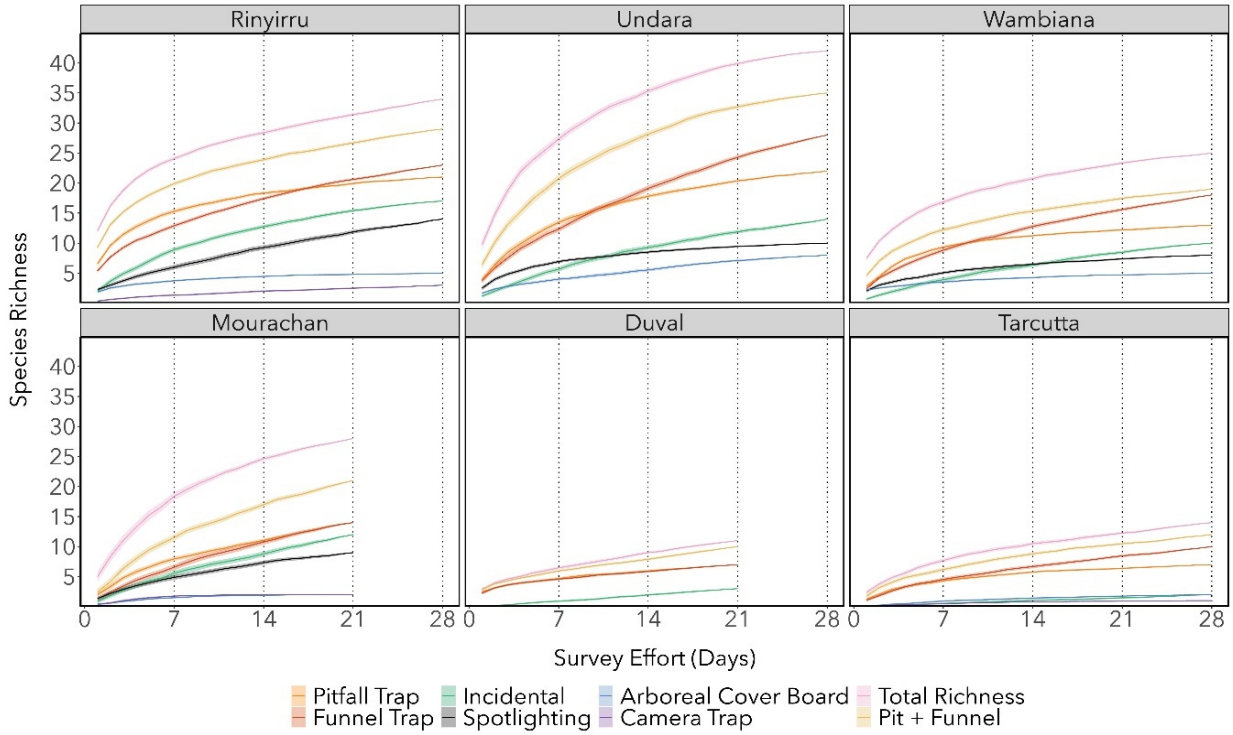

Figure 4.4. *Species accumulation curves for reptile communities across six study sites using different survey methods. The x-axis represents survey effort in days, and the y-axis shows the estimated species richness. Lines are shown for each method, as well as all methods combined (total richness [pink], and a combination of pitfall and funnel trap [yellow]). The shaded areas represent the 95% confidence intervals for each method. Vertical dotted lines indicate the cumulative effort after each survey.*

4.3.3 Community composition

Over the course of the study period, I detected reptiles across 12 families (Supplementary Table A4.3). PERMANOVA results evaluating reptile communities detected by each survey method revealed significant differences among methods, except for pitfall and funnel traps. These two methods captured highly similar species assemblages with comparable relative abundances across all sites (Jaccard, R^2 = 0.018, P = 0.617; Bray–Curtis, R^2 = 0.02, P = 0.478; Figure 4.5; Supplementary Figure A4.1). Incidental encounters and spotlighting also recorded a similar community composition but the relative abundances differed (Jaccard, R^2 = 0.04, P = 0.155; Bray–Curtis, R^2 = 0.121, P < 0.001; Supplementary Table A4.2). Variations in relative abundances were driven by incidental encounters of diurnal species, which were rarely detected through spotlighting, and much higher numbers of gecko detections via spotlighting (Supplementary Table A4.3). Pitfall traps recorded high species richness and captures of *Scincidae* (34 species; 847 captures), *Agamidae* (5 species; 39 captures), and were the only survey method to record *Typhlopidae* (3 species; 6 captures). When considering all sites

together, five species were detected only via pitfall traps (Supplementary Table A4.3). Funnel traps recorded high numbers of *Scincidae* (38 species; 810 captures), *Elapidae* (13 species; 39 captures) and *Pygopodidae* (4 species; 12 captures). Fifteen species of reptiles were recorded only in funnel traps (Supplementary Table A4.3). Spotlighting documented high numbers of *Diplodactylidae* (9 species; 148 captures) and *Gekkonidae* (2 species; 518 captures) and was the only method to detect *Pythonidae* (1 species; 2 captures). Spotlighting and incidental encounters were the only survey methods to detect *Chelidae* (one species; three captures) and *Carphodactylidae* (1 species, 10 captures). Spotlighting detected 4 unique species and incidental encounters detected 1 unique species (Supplementary Table A4.3). Arboreal cover boards produced high numbers of *Diplodactylidae* (3 species; 153 captures) and *Gekkonidae* (2 species; 217 captures). Camera traps recorded high numbers of *Varanidae* (3 species; 27 captures) and were the only method to detect *Chlamydosaurus kingii*.

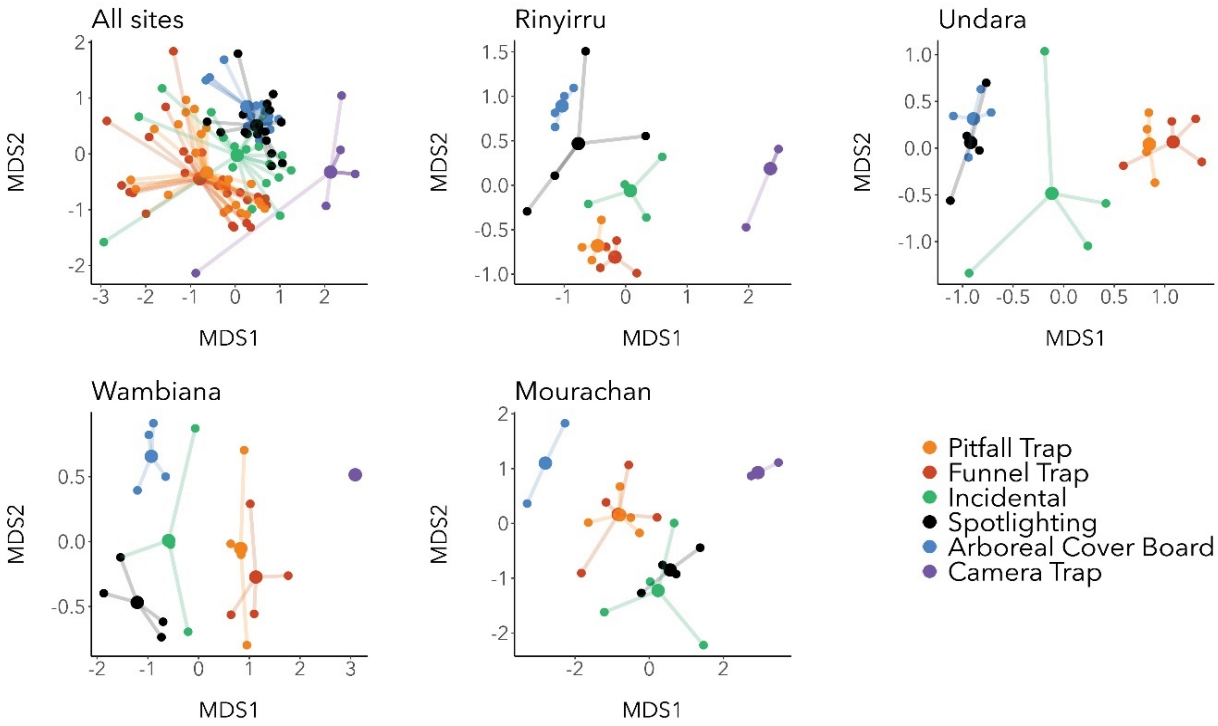

Figure 4.5. *Non-metric multidimensional scaling (NMDS) ordination of reptile communities based on Jaccard dissimilarity (presence–absence), showing the relationships among different survey methods at each survey site. Points represent individual survey plots, coloured by the survey method used. Large points indicate the centroids of each survey method, and lines connect the centroids to individual plots within each method. Camera traps failed to detect any reptiles at Undara. Tarcutta and Duval were excluded from the plot because of low samples sizes.*

4.3.4 Detectability

Overall, the average daily detection probability across all sites for each method was highest for pitfall traps (0.076), followed by funnel traps (0.069), spotlighting (0.033), arboreal cover boards (0.03), incidental encounters (0.014) and camera traps (0.003). When comparing all methods for all reptiles, pitfall traps and funnel traps were significantly more likely to detect reptiles than any other method, but did not differ significantly from each other (1.11, 95% HDI = 0.83–1.47, $P_{(0)}$ = 0.77). Spotlighting (6.81, 95% HDI = 3.64–10.69, $P_{(0)}$ = 1), arboreal cover boards (5.05, 95% HDI = 2.94–8.04, $P_{(0)}$ = 1), and incidental encounters (4.27, 95% HDI = 2.36–6.78, $P_{(0)}$ = 1) showed a significantly higher likelihood of detecting reptiles than did camera traps. Spotlighting was significantly more likely to detect reptiles compared to incidental encounters (1.59, 95% HDI = 1.07–2.3, $P_{(0)}$ = 0.99), while no significant difference was observed between arboreal cover boards and incidental encounters (1.18, 95% HDI = 0.75–1.67, $P_{(0)}$ = 0.803), or between spotlighting and arboreal cover boards (1.35, 95% HDI = 0.9–1.91, $P_{(0)}$ = 0.944).

When accounting for differences in lifestyle of reptiles, I found that pitfall and funnel traps were up to 100 times more likely to detect ground-dwelling reptiles compared to any other method, but did not differ significantly from each other (1.02, 95% HDI = 0.76–1.29, $P_{(0)}$ = 0.55; Figure 4.6). For ground-dwelling species, incidental encounters and spotlighting were significantly better than arboreal cover boards and camera traps but did not differ significantly from each other (1.23, 95% HDI = 0.81–1.78, $P_{(0)}$ = 0.839). Camera traps were significantly more likely to record ground-dwelling reptiles compared to arboreal cover boards (4.65, 95% HDI = 1.53–10.78, $P_{(0)}$ = 1). Arboreal cover boards and spotlighting were up to 62 times more likely to detect arboreal reptiles compared to any other survey method but did not differ significantly from each other (1.19, 95% HDI = 0.68–1.81, $P_{(0)}$ = 0.766; Figure 4.6). Pitfall traps produced significantly higher detectability of arboreal reptiles than funnel traps (3.85, 95% HDI = 1.7–6.62, $P_{(0)}$ = 1), incidental encounters (2.98, 95% HDI = 1.52–4.95, $P_{(0)}$ = 1), and camera traps (27.93, 95% HDI = 7.01–71.57, $P_{(0)}$ = 1), while funnel traps were only more likely to detect arboreal reptiles than camera traps (7.26, 95% HDI = 1.54–20.55, $P_{(0)}$ = 0.999) but did not differ significantly from incidental encounters (0.77, 95% HDI = 0.33–1.44, $P_{(0)}$ = 0.226). Camera traps were least likely to detect arboreal reptiles (up to 62 times less likely compared to arboreal cover boards; 61.5, 95% HDI = 16.59–162.02, $P_{(0)}$ = 1). The highest detection probabilities for any species at any plot using any method were for *Amalosia queenslandia* (89% at Undara) and *Gehyra dubia (*86% at Wambiana) using arboreal cover boards, followed by *Carlia munda* at Rinyirru using funnel traps (79%) and *Lampropholis guichenoti* at Duval using pitfall traps (76%; Supplementary Table A4.3).

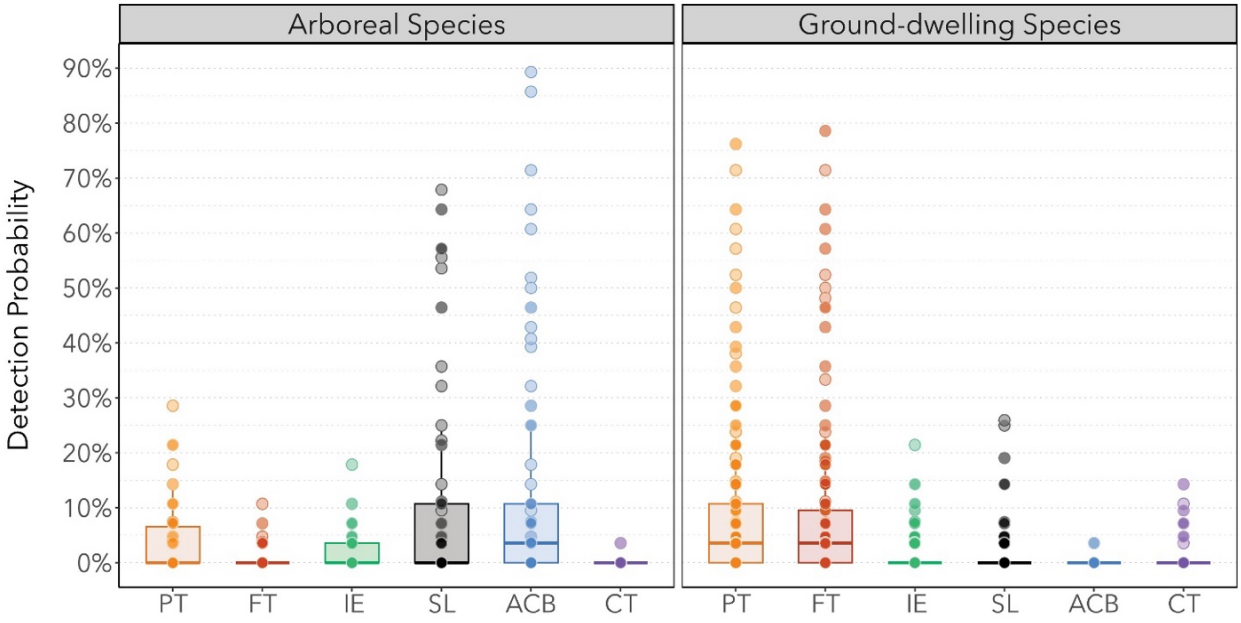

Figure 4.6. *Detection probability of arboreal and ground-dwelling reptile species using six different survey methods. The boxplots represent the distribution of detection probabilities for each survey method: pitfall trap (PT), funnel trap (FT), incidental encounters (IE), spotlighting (SL), arboreal cover board (ACB), and camera trap (CT). Individual data points are shown as circles and represent daily detection probability of a single species at a single survey plot.*

4.4 Discussion

In this study, I simultaneously compared seven survey methods—pitfall traps, funnel traps, spotlighting, arboreal cover boards, incidental encounters, camera traps, and passive acoustic monitoring (PAM)—to detect reptiles over multiple years and across an extensive spatial scale, in open eucalypt woodland across eastern Australia. Passive acoustic monitoring was ineffective for detecting Australian reptiles, leading to its removal from further analyses. I present insights into the effectiveness of each survey method in terms of species richness, sampling effort, community composition, and detectability. My results may help with the design and selection of methods for long-term reptile monitoring projects needed for the development of effective conservation and management strategies.

Across all sites, covering a broad range of latitudes, pitfall and funnels traps were the most effective methods for documenting reptiles. Both methods recorded much higher species richness, contributed the highest number of species proportionally to the total richness at each site, recorded the highest number of unique species, and had the highest detection probabilities. This is consistent with previous studies that have compared the effectiveness of pitfall and funnel traps to other sampling methods (e.g., Garden et al. 2007, McKnight et al.

2015, Baumgardt et al. 2021). Even after controlling for a general increase in species richness from south to north, pitfall and funnel traps detected the highest number of species, indicating their relative importance for observing high numbers of reptiles in a wide range of conditions (although their relative importance was greatest at the southern sites). In general, pitfall and funnel traps also had the highest daily detection probability. This was especially true for ground-dwelling species of the family *Scincidae* such as *Carlia munda*, *Lampropholis guichenoti*, *Eremiascincus pardalis pardalis*, and *Ctenotus spaldingi*.

While pitfall and funnel traps detected the highest number of species throughout my study sites, I found that the effectiveness of different survey methods varied with latitude. At the southern sites, where species richness was lower, pitfall and funnel traps were responsible for nearly all reptile detections. However, with a decrease in latitude, general species richness increased, and additional survey methods, such as arboreal cover boards and spotlighting, became necessary to adequately represent the more diverse reptile community. The different survey methods recorded vastly different assemblages of reptile communities, except for funnel and pitfall traps, highlighting the importance of using multiple methods in order to capture the true diversity of species present.

Northern sites had higher total species richness, and thus a more diverse array of reptiles, including more large and arboreal species. Previous studies have demonstrated the effectiveness of pitfall and funnel traps in detecting small to medium ground-dwelling species (e.g., Garden et al. 2007, Thompson and Thompson 2007, McKnight et al. 2015, Baumgardt et al. 2021). However, these methods may not be optimal for documenting large and arboreal reptiles and alternative methods have been suggested (Bell 2009, Nordberg and Schwarzkopf 2015). In my study, I found that pitfall and funnel traps were highly effective in detecting small to medium-sized ground-dwelling lizards, such as skinks and dragons, as well as small to medium-sized snakes, such as some species of *Colubridae* and *Elapidae*. However, these traps failed to capture medium to large snakes such as pythons, larger elapids, or large goannas, because these species would likely either never enter pitfall or funnel traps or easily escape from the trap (Thompson and Thompson 2007). Larger reptiles were more successfully documented via camera traps or incidentally. Pitfall and funnel traps were also ineffective for most arboreal species, except for three species of *Cryptoblepharus*, while arboreal cover boards and spotlighting proved substantially more effective. For example, I detected *Amalosia queenslandia* on 25 of 28 survey days using arboreal cover boards at a plot at Undara. These methods detected species of Gekkota across four families and 10 genera and achieved the highest daily detection probabilities for any species at any survey plot during my study.

Importantly, these differences in the assemblages detected suggest that my results cannot simply be explained by inherent differences in the scale of sampling effort and, instead, represent true differences in the taxa that can be sampled by each method. In other words, it could be argued that, for example, two drift fence arrays per plot represent an inherently different level of survey effort than 15 min of spotlighting per day and increasing the effort for either method (more fences or longer spotlighting periods) would have changed the results. If that was the case, however, I would expect similar taxonomic or ecological groups to be detected by each method. Additionally, the differences in species accumulation curves (Figure 4.4) are pronounced enough that increased survey effort for any one method would be unlikely to substantively change the results.

Observer-based monitoring in the field can be very costly and resources are often limited. Therefore, reptile biodiversity assessments aim to be as comprehensive as possible while keeping cost to a minimum, which can be achieved by reducing the number of simultaneously deployed methods (e.g., Garden et al. 2007, Michael et al. 2012). In my study, a combination of pitfall and funnel traps accounted for the majority of all species detected (87%). When including incidental encounters (i.e., species passively encountered while on the survey plot), the total number of species observed increased to 95% of all species. However, the only unique species documented exclusively through incidental encounters was a turtle (*Chelodina longicollis*), which was detected at night when observers would not be present on the survey plot if only deploying pitfall and funnel traps. Therefore, it is unclear how significant incidental encounters would be if only pitfall and funnel traps were used together. Previous research has highlighted the significance of incidental encounters in biodiversity assessments (McKnight et al. 2015), and although I excluded detections occurring far outside the survey plot boundaries in my analyses, I frequently encountered snake species on the roads and trails away from the plots which I did not detect during my surveys on the plots. Overall, recording incidental encounters is highly recommended, as it involves minimal additional costs and effort while potentially enhancing the overall species richness documented, particularly of cryptic species such as many snakes.

Another factor impacting the cost of biodiversity assessments is the duration of sampling. The recommended sampling duration for reptile biodiversity assessments varies depending on location, habitat, target fauna and research goal (How 1998, McDiarmid et al. 2012, Michael et al. 2012). My findings indicate that employing a combination of pitfall and funnel traps accelerates species accumulation, yielding results faster than any other method, and capturing at least 50% and has high as 69% of the total species richness within a 7-d sampling period.

However, even after 28 days of sampling, including four trips in two seasons over two years, new species continued to be detected at each site, suggesting that additional surveys or an increased number of traps for intensified sampling are required to assess the entire reptile community. In certain cases, sampling the complete community may take up to 5 yr or more (How 1998). This emphasizes the need for long-term monitoring projects to detect particularly elusive species, such as the majority of snakes in Australia.

Passive acoustic monitoring (PAM) may not be a viable method for assessing reptile biodiversity in Australia. PAM is a relatively novel monitoring method which, to my knowledge, had only been used indirectly for reptile biodiversity assessments in a single study before (McKnight et al. 2015). In my 2-yr acoustic dataset, I was also unable to detect any reptiles using species-specific call recognizers for Asian House Geckos (*Hemidactylus frenatus)*, Bynoe's Geckos (*Heteronotia binoei)*, and Dubious Dtellas (*Gehyra dubia*). Bynoe's Geckos and Dubious Dtellas have relatively quiet calls, and example calls were obtained from a laboratory environment devoid of background noise (Phongkangsananan et al. 2014). It is possible that these species were vocalising but at volumes too low to be discernible from ambient sounds. In contrast, Asian House Geckos have loud persistent calls and have been successfully detected in audio recordings previously (Marcellini 1974, Hopkins et al. 2021), and even been identified in recordings from the same type of ARU used in my study (S. Hoefer, personal observation). However, I encountered this species incidentally in the campground at Undara and Rinyirru, with only one individual detected in a funnel trap within a survey plot. This species is currently primarily associated with urban areas, and it is unlikely to be established in my survey plots. Instead, I argue that the recorders genuinely did not detect the species, because it was absent. In discussing the limitations of my study, I acknowledge that my camera trapping design could be further refined. The design I employed followed a more general setup frequently used for mammals (Claridge et al. 2010, Eyre et al. 2018, Burt et al. 2021) and could be enhanced by utilising camera trap setups specifically targeting small reptiles (Adams et al. 2017, Dundas et al. 2019, Welbourne et al. 2020). My baited camera traps, a practice highlighted in previous studies for detecting large varanids (Ariefiandy et al. 2013, Moore et al. 2020), identified some larger reptiles that were undetected by other methods, demonstrating this design's utility. However, my camera traps failed to detect any small reptiles, for which ground-facing camera trap setups are designed (Welbourne et al. 2017). Ground-facing cameras combined with small drift fences have proven useful for smaller reptiles, but their effectiveness is limited for larger species (Welbourne et al. 2015). Thus, incorporating both camera trap designs could provide a more comprehensive picture and potentially higher species richness. Future studies could

employ additional methods, such as diurnal active searches (Kutt and Colman 2023), eDNA (Kyle et al. 2022), or artificial refugia (AR) on the ground (Grant et al. 1992). While some studies have demonstrated the effectiveness of ground ARs (e.g., Engelstoft and Ovaska 2000, Kjoss and Litvaitis 2001, Seigel et al. 2002), I only used arboreal ARs in my study. After preliminarily testing corrugated iron and roof tiles at three sites for one survey trip, I detected only one unidentifiable *Carlia spp*. and decided against deploying any ground ARs. Corrugated iron and roof tiles may be less effective in northern Australia for most of the year, as temperatures can become extremely hot and humidity very high, which may lead to a decrease in reptile detections beneath ground ARs (Hoare et al. 2009, McKnight et al. 2015, Lemm and Tobler 2021). Additionally, ground ARs can require extensive effort to establish (Michael et al. 2012).

Overall, my results suggest that pitfall and funnel traps should be prioritized in reptile biodiversity assessments, especially when the primary goal is to quickly accumulate a high number of species. Nevertheless, the relative importance of these methods varies with latitude and overall species richness. In regions with high species richness, incorporating a broader array of survey methods is crucial to achieve a comprehensive assessment of reptile diversity. Furthermore, while pitfall and funnel traps proved highly effective for ground-dwelling reptiles, they were less successful in detecting arboreal species, for which arboreal cover boards and spotlighting were far superior. Employing a combination of these survey methods is likely to yield the best results and ensure a comprehensive taxonomic representation of the community.

To prevent the loss of numerous ecologically significant species, there is an urgent need to enhance our understanding of reptile diversity and habitat use worldwide. This necessitates evaluating the effectiveness of various survey techniques for documenting reptiles. Further research is required to investigate the efficiency of using multiple methods concurrently over extended periods and to compare their performance across diverse habitats.

Chapter 5. General discussion

Passive acoustic monitoring (PAM) has experienced a surge in interest over the last 30 years and can be used both to detect species and to describe their activity patterns and habitat use, which is vital for conserving and protecting species (Sugai et al. 2019). For biodiversity assessment, sound summaries in the form of acoustic indices have been used to reveal broad patterns in the soundscape, and they can serve as valuable proxies for ecosystem quality, biodiversity, and species richness (Alcocer et al. 2022, Schoeman et al. 2022, Allen-Ankins et al. 2023). However, to describe complex community structure and detect changes in species richness, the identification of individual species is essential. PAM has been effective in identifying and detecting single species across certain vertebrate groups, including threatened and invasive species (e.g., Campos-Cerqueira and Aide 2016, Hofstadter et al. 2022, Ribeiro et al. 2022), and even to estimate population metrics such as species occupancy and density (Wood et al. 2023a). However, before this study there were few examinations of the use of PAM for comprehensive vertebrate biodiversity assessments, and it was unknown whether it can replace, or should supplement, observer-based monitoring (OBM) efforts.

To quantify the effectiveness of PAM for terrestrial vertebrate biodiversity assessments, it is crucial to identify the fauna that can be reliably detected using PAM and compare these data to those obtained using traditional OBM. Such comparisons have primarily focused on birds in North America, with limited research evaluating PAM's effectiveness for other terrestrial vertebrates (**Chapter 1**). Further, the duration of audio recordings analysed significantly influences the effectiveness of PAM, and so future studies should aim to record continuously and analyse as much of the available audio data as possible, to fully utilise PAM's capabilities **(Chapter 1**)**.**

More direct PAM-OBM comparisons for a broader range of terrestrial vertebrates in other parts of the world were needed to understand how PAM can effectively be used for comprehensive biodiversity assessments. This thesis examined the value of PAM for comprehensive terrestrial vertebrate biodiversity assessments in Australia by directly comparing PAM to a wide array of simultaneously deployed OBM methods and camera trapping for mammals (**Chapter 2**), frogs (**Chapter 3**), and reptiles (**Chapter 4**). I evaluated and compared the effectiveness of PAM, OBM, and camera trapping in terms of species richness, the assemblages of species sampled by each method, and the survey effort required to reach the highest numbers of species. Additionally, I investigated the financial costs associated with

each method, one of the most prohibitive factors in large-scale, long-term biodiversity assessments.

5.1 Monitoring for terrestrial vertebrate biodiversity

Passive acoustic monitoring was highly effective in detecting a wide range of vocal mammals (**Chapter 2**) and frogs (**Chapter 3**) but failed to detect any reptiles (**Chapter 4**). By deploying automated recording units (ARUs) continuously for at least 365 days and analysing all available audio data, PAM successfully captured a higher number of vocal species than OBM or camera trapping across a large latitudinal scale. This is consistent with findings in avian studies where PAM outperformed other methods for species detection, particularly over longer monitoring periods (Klingbeil and Willig 2015, Darras et al. 2019, Kułaga and Budka 2019). However, PAM's reliance on vocalisations limits its utility for comprehensive biodiversity assessments, and thus it is essential to integrate PAM with other survey methods. For non-vocal mammals, camera trapping, spotlighting, and Elliott trapping were most effective and a combination of these three methods captured 88% of all non-vocal mammals (**Chapter 2**). For reptiles, employing a combination of funnel traps, pitfall traps, and spotlighting recorded 92% of all species (**Chapter 4**). In species-rich regions, a diverse set of monitoring techniques are necessary to adequately target ground-dwelling and arboreal species, ensuring a comprehensive assessment of non-vocal terrestrial vertebrate biodiversity (**Chapter 2**, **Chapter 4**). Notably, I detected 86% of all amphibians, mammals, and reptiles predicted by the Atlas of Living Australia (ALA) to occur across the six study sites (173 of 202 species); with OBM recording the highest species richness overall (160 species), and PAM representing the most effective remote sensing approach across taxa (54 species; Table 5.1).

Table 5.1 *Number of species predicted by the Atlas of Living Australia (ALA) and the number of species detected using observer-based monitoring (OBM), camera trapping, passive acoustic monitoring (PAM) during the survey period only, PAM with all available audio data, and the combined total of species detected in this study across six sites in eastern Australia.*

	Predicted Species Richness	Observed Species Richness				
	ALA	OBM	Camera trapping	PAM (survey period)	PAM (all audio)	Overall detected
Amphibians	34	23	1	21	34	35
Mammals	67	45	25	14	20	45
Reptiles	101	92	5	0	0	93
Overall	202	160	31	35	54	173

The greatest value of PAM lies in the fact that it can be deployed for long periods, and that it collects data on species' presence continuously. Over long periods of time, PAM always captured the highest number of vocal mammals and frogs while maintaining relatively stable costs (Figure 5.1). Although PAMs initial costs for purchasing automated recording units (ARUs), batteries, and SD cards were higher than those for camera trapping and OBM, the cost increase over two years was only 1.5-fold, compared to 4-fold for camera trapping and 21-fold for OBM. Costs can vary depending on the specific ARUs and camera traps used (Darras et al. 2019, Sugai et al. 2020, Palencia et al. 2022). Cheaper models often require more frequent battery changes and increasing maintenance costs, whereas more expensive models can reduce maintenance needs and keep costs lower over time. Both PAM and camera trapping benefit from low running costs due to their passive nature of data collection, however, PAM yielded the highest total number of species detections (**Chapter 2**, **Chapter 3**), making it the most cost-effective survey method, overall, if high species richness is the desired outcome of the survey.

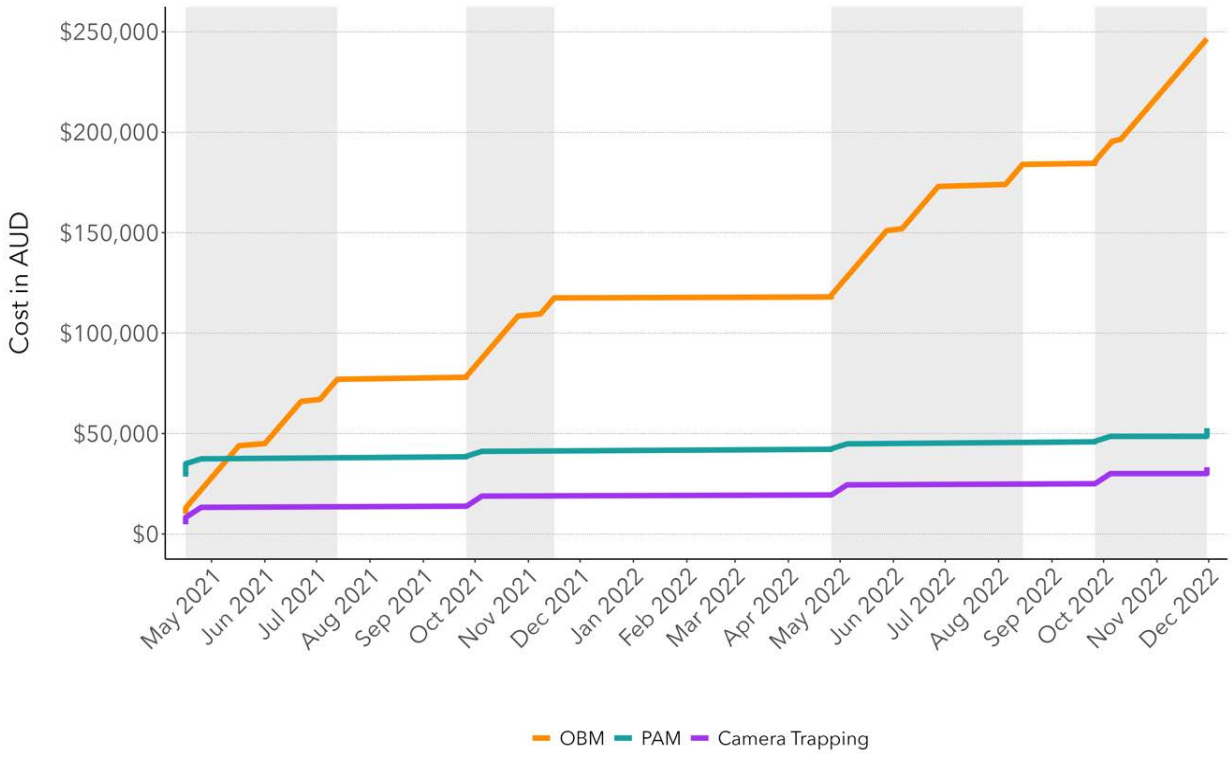

Figure 5.1 *The rate of increase in total cost in Australian Dollar (AUD) for observer-based monitoring (OBM – orange), passive acoustic monitoring (PAM – green), and camera trapping (purple) over the duration of this research. Costs includes initial equipment purchases, deployment and fieldwork expenses (accommodation, transportation, salary, food), and compensation of staff for data analysis and validation for PAM and camera trapping. The grey bands represent the four survey periods during this research.*

If long-term PAM is not feasible, targeting breeding seasons to detect animals is a viable alternative for many species (e.g., Crowley et al. 2014, Frommolt 2017, Riegert 2022, Appel et al. 2023). For frogs, breeding and vocal activity are closely linked to rain events (Hauselberger and Alford 2005, Xie et al. 2017, Brodie et al. 2021), and I found that frogs were most effectively sampled in spring and summer when these rain events and breeding activities are more prevalent (**Chapter 3**). However, while some vocal mammals, such as koalas and deer, may call more frequently during breeding seasons (Ellis et al. 2011, Bocci et al. 2013, Hagens et al. 2018, Law et al. 2020), other species, such as dingoes, possums, and gliders, use vocalisations for non-reproductive purposes and may vocalise throughout the year (Déaux and Clarke 2013, Rosenfeld and Hoffmann 2021, Whisson et al. 2021). Consequently, restricting the recording period for mammals could risk missing some species, especially those that vocalise

infrequently, like pigs and cats. Therefore, continuously recording throughout the year should remain the goal to ensure comprehensive detection of all vocal species.

5.2 Limitations

One inherent limitation of PAM is its inability to detect non-vocal animals, leading to incomplete assessments of vertebrate diversity. This limitation is well-documented across various studies, emphasising the restriction of PAM to vocalising species (e.g., Haselmayer and Quinn 2000, Farmer et al. 2009, Hutto and Stutzman 2009, Alquezar and Machado 2015). While this is an obvious drawback of PAM, it is important to recognise that all monitoring methods have inherent constraints. For example, observer-based monitoring, which relies on field-based human observers, is limited by logistical challenges, financial resources, and the availability of experts, often making it impractical over extensive spatial and temporal scales (Darras et al. 2019, Kitzes and Schricker 2019, Rhinehart et al. 2020). Similarly, camera trapping, although effective in capturing non-vocal fauna, is restricted by its limited field of view, and typically targets ground-dwelling species. Furthermore, some studies have found a positive correlation between the species richness of vocal and non-vocal species (**Chapter 2**, Alcocer et al. 2022, Allen-Ankins et al. 2023, Botero-Cañola et al. 2024), suggesting that detecting all species, including non-vocal ones, may not be necessary to estimate overall species richness. Consequently, changes in vocal species richness could serve as indicators of shifts in overall species diversity.

Automated recording units allow continuous data collection over extended periods without human presence, which is especially beneficial during or after extreme weather events, when accessing field sites may not be possible (Darras et al. 2019). However, much like camera traps, this also makes ARUs susceptible to theft and vandalism, which can sometimes be mitigated with the use of safety locks, camouflage, and secure mounting techniques (Meek et al. 2019). Additionally, technological failures in ARUs can pose substantial challenges. Given that these devices are often deployed in remote locations and monitored only periodically, any malfunction due to battery depletion, memory card failure, or environmental damage can result in significant data loss until the next scheduled maintenance visit. In fact, this project experienced significant data loss at some sites due to corrupted SD cards and unexpected battery depletion or malfunction. Furthermore, ARUs are limited to sampling within a single location and microhabitat, whereas field observers can move and assess multiple habitats during a survey. To achieve similar coverage across diverse habitats with PAM, a greater number of audio recorders would be necessary, which would significantly increase costs. Alternatively,

deployment lengths could be reduced, and devices rotated between sites to balance coverage and cost efficiency, though this approach would sacrifice the continuity of data collection.

It is possible that the presence of bait at camera traps within each survey plot attracted species to the area, leading to their detection by the audio recorders and potentially boosting PAM performance. However, given that the ARUs were deployed continuously and over the long term, and that animals would need to have been nearby to detect the bait, it is highly likely that these species would have been detected by the ARUs even in the absence of bait.

I acknowledge that my acoustic analyses were conducted in a High Performance Computing environment (HPC) providing enhanced computational resources over conventional local machines. Therefore, analyses attempting to handle similar volumes of audio data and species example calls on conventional computers will require an increased time investment.

I also recognise that many species have a large repertoire of vocalisations, and more call examples could have been considered for each species, potentially enhancing detection. Therefore, my findings on the performance of PAM for terrestrial vertebrate biodiversity assessments, compared to OBM and camera trapping, are likely conservative. These results may be further improved as additional call examples become available with the increased deployment of acoustic sensors. Similarly, the methods used to analyse PAM data for reptiles differed from those used for mammals (**Chapter 2**) and frogs (**Chapter 3**) and detecting vocal reptiles may be possible with improved techniques such as deep-learning models.

5.3 Conclusions and future directions

Long-term PAM combined with BirdNET feature embeddings was highly effective for detecting vocal mammals and frogs in Australia. This approach enabled the analysis of over 300,000 hours (equivalent to more than 36 years) of continuous audio data from six sites across eastern Australia, requiring as little as a single example call per target species. PAM provides extensive, permanently stored information with comparatively low time and financial investments. These permanent audio recordings offer valuable insights into biodiversity and vocalising species, including species richness and community composition (**Chapter 2**, **Chapter 3**), and can be reanalysed as acoustic analysis techniques advance. Additionally, the audio data can be repurposed or used to search for other species in the future. Audio data collected for a specific purpose can serve diverse applications at any point in the future and can even act as a time capsule that offers insights into past biodiversity (Sugai and Llusia 2019). Furthermore, long-term PAM enables a deeper understanding of calling patterns across a wide range of species, helping to identify optimal periods for targeted monitoring efforts.

Advancements in technology will continue to enhance the capabilities of PAM for terrestrial biodiversity assessments. For example, real-time data processing and wireless data transfer are developing quickly and can help mitigate data loss and reduce maintenance requirements, thereby increasing the autonomy of audio recorders (e.g., Aide et al. 2013, Mohaimenuzzaman et al. 2022, 2023, Wood et al. 2024). Similarly, improvements in battery and storage technology will enable collection of more audio data across broader frequency ranges, allowing for detection of a wider array of species, including those with ultrasonic vocalisations. Additionally, recorders equipped with an array of time-synchronised microphones can capture more detailed spatial information about vocalisations, enhancing individual recognition and abundance estimates (Rhinehart et al. 2020, Heath et al. 2024), although moderately accurate abundance estimates can be made using calling activity alone (Pérez-Granados and Traba 2021).

Automated acoustic analyses are crucial for advancing the effectiveness of large-scale, long-term passive acoustic monitoring. While PAM combined with BirdNET embeddings requires manual validation, this validated data can be used to build and train robust deep-learning models such as Convolutional Neural Network (CNN) species recognisers (Ghani et al. 2023, McGinn et al. 2023). My approach focused on surveying a broad range of species rather than targeting specific ones. Although building CNN recognisers for each species is possible, it is time-consuming. Therefore, I opted for a quicker method more suited to broad surveying, focusing on detecting daily presence rather than detailed species vocal activity. While detecting an overall presence of species would have required even less manual validation, finer-scale analyses of calling activity would necessitate the development and use of reliable species recognisers. As more advanced recognisers are developed for a wider array of species and locations, PAM's ability to detect species will be enhanced. This will enable more reliable detection of both species that are currently difficult to distinguish and commonly vocalising species, making PAM even more effective at estimating species richness with minimal validation required.

By collecting call examples from diverse locations and times of year, CNN recognisers can significantly enhance the speed and accuracy of acoustic analyses (Sethi et al. 2024). These advanced deep learning models can differentiate between similar-sounding species (Allen-Ankins et al. 2024), reducing the need to group or omit species due to difficulties in call differentiating during validation. Despite the steep learning curve associated with analysing acoustic data using deep learning models, these tools are becoming increasingly user-friendly, with simple user interfaces and clear instruction manuals (Wood et al. 2022, 2023a, Pérez-

Granados et al. 2023). Over time, they will become more accessible, enabling a wide variety of users, including researchers, practitioners, and citizen scientists, to apply them to audio recordings and gain valuable information about vocalising species.

However, regardless of how advanced automated analyses of acoustic data become, PAM will never be able to detect non-vocal species. Therefore, a multifaceted approach, using PAM to detect vocal species in conjunction with targeted observer-based monitoring or remote sensing methods (e.g., camera traps, drones, satellite) for vocally inaccessible fauna, will provide the most comprehensive and cost-effective solution for large-scale, long-term assessments of terrestrial vertebrate biodiversity.

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Appendices

Appendix A. Supplementary materials for Chapter 1

Supplementary Table A1.1. *ANOVA examining the factors affecting the performance of passive acoustic monitoring (PAM) relative to observer-based monitoring (OBM).*

	Chi-squared	df	P-value
Vertebrate class	0.6397	3	0.8872
Region	16.275	4	0.0027
Recording period	15.3031	2	0.0005
Acoustic analysis	0.0645	1	0.7995
Longer sampling duration	6.9148	3	0.0747

Supplementary Table A1.2. *Tukey post hoc pairwise comparisons for Vertebrate class, Region, Recording period, Acoustic analysis and Longer sampling duration to examine which factors affect the magnitude of difference between passive acoustic monitoring (PAM) and observer-based monitoring (OBM).*

	estimate	SE	df	95% CI low	95% CI high	P-value
Vertebrate class						
Amphibians - Birds	0.0314	0.0790	13	-0.2004	0.2633	0.9778
Amphibians - Flying mammals	0.0589	0.0741	13	-0.1587	0.2764	0.8558
Amphibians - (Non-flying mammals)	0.0297	0.0870	13	-0.2255	0.2850	0.9856
Birds - Flying mammals	0.0274	0.0689	13	-0.1749	0.2298	0.9777
Birds - (Non-flying mammals)	-0.0017	0.0832	13	-0.2459	0.2425	1.0000
Flying mammals - (Non-flying mammals)	-0.0291	0.0843	13	-0.2765	0.2182	0.9852
Region						
Africa - Europe	0.3607	0.1363	13	-0.0684	0.7897	0.1182
Africa - North America	0.1793	0.0851	13	-0.0887	0.4474	0.2742
Africa - Oceania	-0.0086	0.1137	13	-0.3665	0.3493	1.0000
Africa - South America	0.2677	0.0988	13	-0.0433	0.5788	0.1064
Europe - North America	-0.1813	0.1122	13	-0.5346	0.1719	0.5131
Europe - Oceania	-0.3693	0.1230	13	-0.7566	0.0181	0.0647
Europe - South America	-0.0929	0.1225	13	-0.4786	0.2928	0.9380
North America - Oceania	-0.1879	0.0836	13	-0.4510	0.0752	0.2223
North America - South America	0.0884	0.0718	13	-0.1378	0.3146	0.7348
Oceania - South America	0.2763	0.1062	13	-0.0580	0.6107	0.1272
Recording period						
Continuous - Simultaneous	0.1797	0.0785	13	-0.0275	0.3870	0.0930
Continuous - Targeted	0.3261	0.0898	13	0.0889	0.5633	0.0080
Simultaneous - Targeted	0.1463	0.1041	13	-0.1285	0.4212	0.3667
Acoustic analysis						
Automated - Manual	-0.0283	0.1116	13	-0.2693	0.2127	0.8035
Longer sampling duration						
Equal - OBM	-0.1813	0.1225	13	-0.5410	0.1783	0.4761
Equal - PAM	0.1041	0.0751	13	-0.1165	0.3246	0.5294
OBM - PAM	0.2854	0.1494	13	-0.1532	0.7240	0.2710

Appendix B. Supplementary materials for Chapter 2

Supplementary Table A2.1. *Overview of the number and source of the 46 example calls for 17 Australian vocal mammal species used in this study.*

Common Name	Scientific Name	Example Call	Source
Black Flying-fox	*Pteropus alecto*	fruitbat_01	A2O Recordings (https://data.acousticobservatory.org/)
Grey-headed Flying-fox	*Pteropus poliocephalus*	fruitbat_02	Wild Ambience (https://wildambience.com/about/)
Little Red Flying-fox	*Pteropus scapulatus*	fruitbat_03	Wild Ambience (https://wildambience.com/about/)
Cat	*Felis catus*	cat_01	Wild Ambience (https://wildambience.com/about/)
Cat	*Felis catus*	cat_02	Wild Ambience (https://wildambience.com/about/)
Cat	*Felis catus*	cat_03	Wild Ambience (https://wildambience.com/about/)
Common Brushtail Possum	*Trichosurus vulpecula*	brushie_01	Wild Ambience (https://wildambience.com/about/)
Common Brushtail Possum	*Trichosurus vulpecula*	brushie_02	Wild Ambience (https://wildambience.com/about/)
Common Brushtail Possum	*Trichosurus vulpecula*	brushie_03	Wild Ambience (https://wildambience.com/about/)
Common Ringtail Possum	*Pseudocheirus peregrinus*	ringtail_01	Wild Ambience (https://wildambience.com/about/)
Common Ringtail Possum	*Pseudocheirus peregrinus*	ringtail_02	Wild Ambience (https://wildambience.com/about/)
Common Ringtail Possum	*Pseudocheirus peregrinus*	ringtail_03	Wild Ambience (https://wildambience.com/about/)
Eastern Grey Kangaroo	*Macropus giganteus*	macropod_01	A2O Recordings (https://data.acousticobservatory.org/)
Eastern Grey Kangaroo	*Macropus giganteus*	macropod_02	A2O Recordings (https://data.acousticobservatory.org/)
Common Wallaroo	*Osphranter robustus*	macropod_03	Macaulay Library (https://macaulaylibrary.org/asset/232881)
Bare-nosed Wombat	*Vombatus ursinus*	wombat_01	Wild Ambience (https://wildambience.com/about/)
Bare-nosed Wombat	*Vombatus ursinus*	wombat_02	A2O Recordings (https://data.acousticobservatory.org/)
Bare-nosed Wombat	*Vombatus ursinus*	wombat_03	Wild Ambience (https://wildambience.com/about/)
Cow	*Bos taurus*	cow_01	A2O Recordings (https://data.acousticobservatory.org/)
Cow	*Bos taurus*	cow_02	A2O Recordings (https://data.acousticobservatory.org/)
Dingo	*Canis familiaris*	dingo_01	A2O Recordings (https://data.acousticobservatory.org/)
Dingo	*Canis familiaris*	dingo_02	Wild Ambience (https://wildambience.com/about/)
Dingo	*Canis familiaris*	dingo_03	A2O Recordings (https://data.acousticobservatory.org/)
Dromedary	*Camelus dromedarius*	dromedary_01	A2O Recordings (https://data.acousticobservatory.org/)
Dromedary	*Camelus dromedarius*	dromedary_02	Macaulay Library (https://macaulaylibrary.org/asset/96255)
Dromedary	*Camelus dromedarius*	dromedary_03	A2O Recordings (https://data.acousticobservatory.org/)
Fallow Deer	*Dama dama*	deer_01	iNaturalist (https://www.inaturalist.org/observations/96822240)
Fallow Deer	*Dama dama*	deer_02	YouTube (https://www.youtube.com/watch?v=SkDKbmsn3HQ)
Koala	*Phascolarctos cinereus*	koala_01	Wild Ambience (https://wildambience.com/about/)
Koala	*Phascolarctos cinereus*	koala_02	Wild Ambience (https://wildambience.com/about/)
Koala	*Phascolarctos cinereus*	koala_03	Wild Ambience (https://wildambience.com/about/)
Pig	*Sus scrofa*	pig_01	A2O Recordings (https://data.acousticobservatory.org/)
Pig	*Sus scrofa*	pig_03	Wild Ambience (https://wildambience.com/about/)
Red Fox	*Vulpes vulpes*	fox_01	A2O Recordings (https://data.acousticobservatory.org/)
Red Fox	*Vulpes vulpes*	fox_02	A2O Recordings (https://data.acousticobservatory.org/)
Red Fox	*Vulpes vulpes*	fox_03	A2O Recordings (https://data.acousticobservatory.org/)
Sheep	*Ovis aries*	sheep_01	Macaulay Library (https://macaulaylibrary.org/asset/126289)
Sheep	*Ovis aries*	sheep_02	Macaulay Library (https://macaulaylibrary.org/asset/126289)
Squirrel Glider	*Petaurus norfolcensis*	squirrel_01	Wild Ambience (https://wildambience.com/about/)
Squirrel Glider	*Petaurus norfolcensis*	squirrel_02	Wild Ambience (https://wildambience.com/about/)
Squirrel Glider	*Petaurus norfolcensis*	squirrel_03	Wild Ambience (https://wildambience.com/about/)
Sugar Glider	*Petaurus breviceps*	sugar_01	Wild Ambience (https://wildambience.com/about/)
Sugar Glider	*Petaurus breviceps*	sugar_02	Wild Ambience (https://wildambience.com/about/)
Sugar Glider	*Petaurus breviceps*	sugar_03	Wild Ambience (https://wildambience.com/about/)
White-striped Freetail-bat	*Austronomus australis*	wsftbat_01	A2O Recordings (https://data.acousticobservatory.org/)
White-striped Freetail-bat	*Austronomus australis*	wsftbat_02	A2O Recordings (https://data.acousticobservatory.org/)

Supplementary Table A2.2. *Detailed summary of the survey dates, acoustic recording hours, and camera trapping days (summed for all four camera traps) at a survey plot level across the six study sites.*

Site	Plot	First survey			Second survey			Third survey			Fourth survey			Total survey days	Total camera trapping days	Total acoustic data (survey period) in hours	Total acoustic data (all audio) in hours
		Dates	Acoustic data (hours)	Camera trapping days	Dates	Acoustic data (hours)	Camera trapping days	Dates	Acoustic data (hours)	Camera trapping days	Dates	Acoustic data (hours)	Camera trapping days				
Tarcutta	Dry A	29/4/2021 – 6/5/2021	167	28	18/10/2021 – 25/10/2021	168	14	8/5/2022 – 15/5/2022	154	28	22/11/2022 – 29/11/2022	160	28	28	98	649	18600
Tarcutta	Dry B	29/4/2021 – 6/5/2021	167	28	18/10/2021 – 25/10/2021	168	28	8/5/2022 – 15/5/2022	166	28	22/11/2022 – 29/11/2022	158	28	28	112	659	22356
Tarcutta	Wet A	29/4/2021 – 6/5/2021	163	28	18/10/2021 – 25/10/2021	168	28	8/5/2022 – 15/5/2022	164	28	22/11/2022 – 29/11/2022	158	28	28	112	653	8605
Tarcutta	Wet B	29/4/2021 – 6/5/2021	167	28	18/10/2021 – 25/10/2021	168	28	8/5/2022 – 15/5/2022	163	28	22/11/2022 – 29/11/2022	158	28	28	112	656	20289
Duval	Dry A	18/4/2021 – 25/4/2021	167	28	NA	NA	NA	28/4/2022 – 5/5/2022	166	28	12/11/2022 – 19/11/2022	129	28	21	84	462	11397
Duval	Dry B	18/4/2021 – 25/4/2021	168	28	NA	NA	NA	NA	NA	NA	12/11/2022 – 19/11/2022	144	28	14	56	312	16209
Duval	Wet A	18/4/2021 – 25/4/2021	167	28	NA	NA	NA	28/4/2022 – 5/5/2022	163	28	12/11/2022 – 19/11/2022	148	28	21	84	478	12402
Duval	Wet B	18/4/2021 – 25/4/2021	168	21	NA	NA	NA	NA	NA	NA	12/11/2022 – 19/11/2022	133	28	14	49	301	10921
Mourachan	Dry A	9/5/2021 – 16/5/2021	167	28	NA	NA	NA	19/6/2022 – 26/6/2022	167	28	2/11/2022 – 9/11/2022	167	28	21	84	501	14894
Mourachan	Dry B	9/5/2021 – 16/5/2021	8	28	NA	NA	NA	19/6/2022 – 26/6/2022	1	28	2/11/2022 – 9/11/2022	166	28	21	84	175	10667

Site	Plot	First survey			Second survey			Third survey			Fourth survey			Total survey days	Total camera trapping days	Total acoustic data (survey period) in hours	Total acoustic data (all audio) in hours
		Dates	Acoustic data (hours)	Camera trapping days	Dates	Acoustic data (hours)	Camera trapping days	Dates	Acoustic data (hours)	Camera trapping days	Dates	Acoustic data (hours)	Camera trapping days				
Mourachan	Wet A	9/5/2021 – 16/5/2021	118	28	NA	NA	NA	19/6/2022 – 26/6/2022	4	28	2/11/2022 – 9/11/2022	166	28	21	84	288	13299
Mourachan	Wet B	9/5/2021 – 16/5/2021	158	28	NA	NA	NA	19/6/2022 – 26/6/2022	165	28	2/11/2022 – 9/11/2022	166	28	21	84	489	8083
Wambiana	Dry A	5/7/2021 – 12/7/2021	165	28	10/11/2021 – 17/11/2021	16	28	12/6/2022 – 19/6/2022	165	28	28/9/2022 – 5/10/2022	166	28	28	112	512	27108
Wambiana	Dry B	5/7/2021 – 12/7/2021	164	28	10/11/2021 – 17/11/2021	163	28	12/6/2022 – 19/6/2022	166	28	28/9/2022 – 5/10/2022	3	28	28	112	496	15323
Wambiana	Wet A	5/7/2021 – 12/7/2021	166	28	10/11/2021 – 17/11/2021	166	28	12/6/2022 – 19/6/2022	164	28	28/9/2022 – 5/10/2022	166	28	28	112	662	15108
Wambiana	Wet B	5/7/2021 – 12/7/2021	164	28	10/11/2021 – 17/11/2021	158	28	12/6/2022 – 19/6/2022	161	28	28/9/2022 – 5/10/2022	167	28	28	112	650	21185
Undara	Dry A	3/6/2021 – 10/06/2021	164	28	29/9/2021 – 6/10/2021	164	28	8/5/2022 – 15/5/2022	146	28	13/10/2022 – 20/10/2022	160	28	28	112	634	11971
Undara	Dry B	3/6/2021 – 10/06/2021	161	28	29/9/2021 – 6/10/2021	155	28	8/5/2022 – 15/5/2022	151	28	13/10/2022 – 20/10/2022	163	28	28	112	630	12280
Undara	Wet A	3/6/2021 – 10/06/2021	159	28	29/9/2021 – 6/10/2021	41	28	8/5/2022 – 15/5/2022	NA	28	13/10/2022 – 20/10/2022	NA	28	27	112	200	4382
Undara	Wet B	3/6/2021 – 10/06/2021	165	28	29/9/2021 – 6/10/2021	95	28	8/5/2022 – 15/5/2022	133	28	13/10/2022 – 20/10/2022	158	28	27	112	551	11212
Rinyirru	Dry A	14/6/2021 – 21/6/2021	166	21	8/10/2021 – 15/10/2021	145	28	7/8/2022 – 14/8/2022	137	28	23/10/2022 – 30/10/2022	130	28	28	105	578	8548
Rinyirru	Dry B	14/6/2021 – 21/6/2021	159	28	8/10/2021 – 15/10/2021	110	28	7/8/2022 – 14/8/2022	161	28	23/10/2022 – 30/10/2022	160	28	28	112	590	10495

Appendices

Site	Plot	First survey			Second survey			Third survey			Fourth survey			Total survey days	Total camera trapping days	Total acoustic data (survey period) in hours	Total acoustic data (all audio) in hours
		Dates	Acoustic data (hours)	Camera trapping days	Dates	Acoustic data (hours)	Camera trapping days	Dates	Acoustic data (hours)	Camera trapping days	Dates	Acoustic data (hours)	Camera trapping days				
Rinyirru	Wet A	14/6/2021 – 21/6/2021	158	28	8/10/2021 – 15/10/2021	142	28	7/8/2022 – 14/8/2022	146	28	23/10/2022 – 30/10/2022	135	28	28	112	581	5898
Rinyirru	Wet B	14/6/2021 – 21/6/2021	161	28	8/10/2021 – 15/10/2021	144	28	7/8/2022 – 14/8/2022	141	28	23/10/2022 – 30/10/2022	150	28	28	112	596	6178

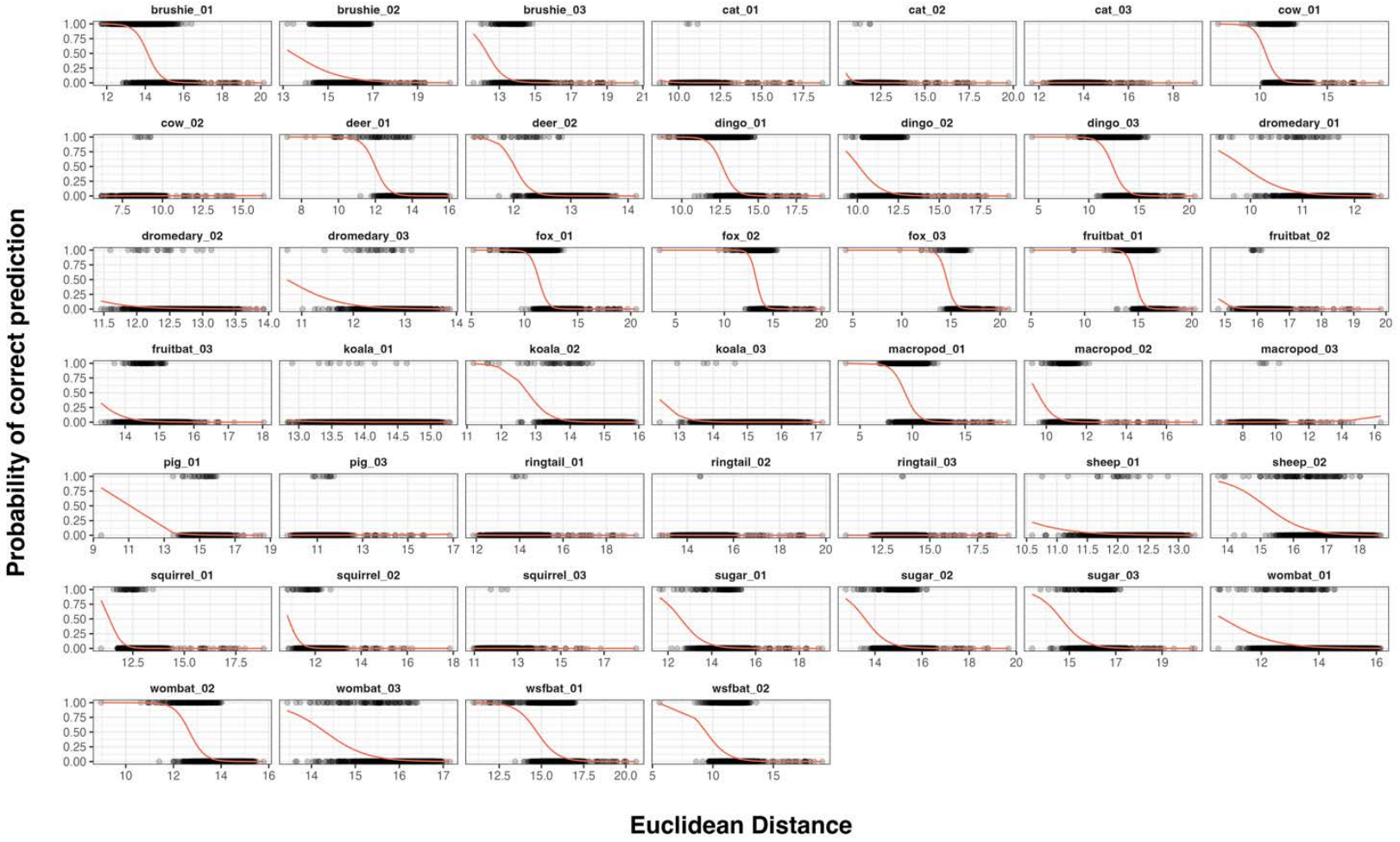
Supplementary Table A2.3. *Mammal species detected via Observer-based monitoring (OBM) through pitfall traps, funnel traps, Elliott traps, cage traps, spotlighting, and incidental encounters; camera trapping; and passive acoustic monitoring (PAM) for both matching only the survey period, and all available audio data. The numbers for each species represent instances of detection rather than abundances. Species are categorised by their conservation status according to the EPBC Act List of Threatened Fauna, divided into "Threatened Fauna" and "Non-threatened Fauna", as well as "Alien Fauna". "Vocal" mammals, defined as those vocalising within the human audible range with available example calls, are indicated in red.*

Common name	Scientific name	Observer-based monitoring (OBM)						Camera trapping	Passive acoustic monitoring (PAM)	
		PT	FT	ET	CT	SL	IE	Camera traps	Survey period	All audio
Threatened species										
Koala	*Phascolarctos cinereus*						1	1		64
Grey-headed flying-fox	*Pteropus poliocephalus*					12	1			
Fruit bat	*Pteropus alecto/ Pteropus poliocephalus/ Pteropus scapulatus*					28	2		16	312
Southern greater glider	*Petauroides volans*					37	1			
Alien species										
Cow	*Bos taurus*					77	140		6	276
Sheep	*Ovis aries*						26	4	3	123
Dromedary	*Camelus dromedarius*					49	36	49	1	96
Red fox	*Vulpes vulpes*					4	4	86	26	648
Cat	*Felis catus*					1	5	31		7
Pig	*Sus scrofa*					2	7	31		39
Fallow deer	*Dama dama*						5	15	1	104
House mouse	*Mus musculus*	193	36	676	1	167		124		
Black rat	*Rattus rattus*	1		25		4		26		
European rabbit	*Oryctolagus cuniculus*					1	2	2		
Brown hare	*Lepus europaeus*					4	4	13		
Non-threatened species										
Eastern grey kangaroo	*Macropus giganteus*					87	119	158		
Common wallaroo	*Osphranter robustus*					1	2	6		
Macropod	*Macropus giganteus/ Osphranter robustus*					88	121	164	27	752
Black flying-fox	*Pteropus alecto*					29				
Little red flying-fox	*Pteropus scapulatus*					7	1			
Inland broad-nosed bat	*Scotorepens balstoni*					1				
Yellow-bellied sheathtail-bat	*Saccolaimus flaviventris*					16	1			
White-striped freetail-bat	*Austronomus australis*					19			36	857
Dingo	*Canis familiaris*					14	49	11	92	1720
Bare-nosed wombat	*Vombatus ursinus*					1	1	14	14	369
Short-beaked echidna	*Tachyglossus aculeatus*						1	23		
Antilopine wallaroo	*Osphranter antilopinus*					1		4		
Red-necked wallaby	*Notamacropus rufogriseus*					39	19	31		
Swamp wallaby	*Wallabia bicolor*					16	16	66		
Whiptail wallaby	*Notamacropus parryi*						1			
Agile wallaby	*Notamacropus agilis*					39	40	59		
Rufous bettong	*Aepyprymnus rufescens*				30	13	3	30		
Northern brown bandicoot	*Isoodon macrourus*				8		1	46		
Common brushtail possum	*Trichosurus vulpecula*			1	130	198	13	363	59	1545
Common ringtail possum	*Pseudocheirus peregrinus*					65	8			9
Sugar glider	*Petaurus breviceps*					30	2		32	387
Squirrel glider	*Petaurus norfolcensis*					18	1		10	84
Feathertail glider	*Acrobates pygmaeus*					1	1			
Yellow-footed antechinus	*Antechinus flavipes*		1	82		5	4	20		

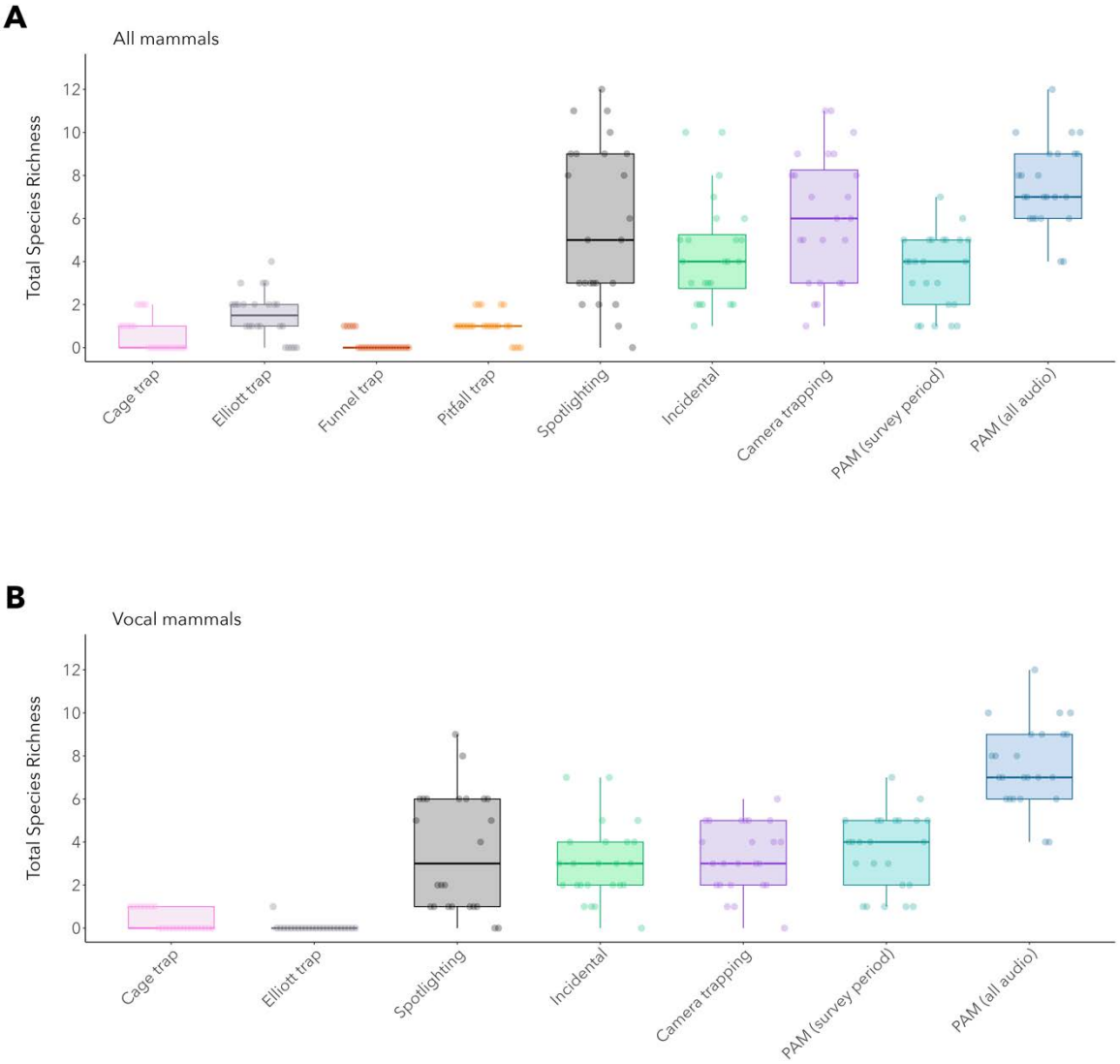
Common name	Scientific name	Observer-based monitoring (OBM)						Camera trapping	Passive acoustic monitoring (PAM)	
		PT	FT	ET	CT	SL	IE	Camera traps	Survey period	All audio
Common planigale	*Planigale maculata*	1								
Long-tailed planigale	*Planigale ingrami*	3								
Common dunnart	*Sminthopsis murina*			4				5		
Rakali	*Hydromys chrysogaster*					1				
Canefield rat	*Rattus sordidus*			1						
Bush rat	*Rattus fuscipes*			2						
Lakeland-downs mouse	*Leggadina lakedownensis*	7		10						
Delicate mouse	*Pseudomys delicatulus*	6	1	7		1	1			
Total species richness		6	3	9	4	33	32	25	13	17
Total vocal species richness		0	0	0	1	15	16	11	13	17
Total threatened species richness		0	0	0	0	2	3	1	1	2
Total alien species richness		2	1	2	1	9	9	10	5	7
Total non-threatened richness		4	2	7	3	22	20	14	7	8

Supplementary Table A2.4. *Overall and "Per day" time investment (in hours) to produce species lists via passive acoustic monitoring (PAM), observer-based monitoring (OBM), and camera trapping, as well as the time investment required per species detection for each method.*

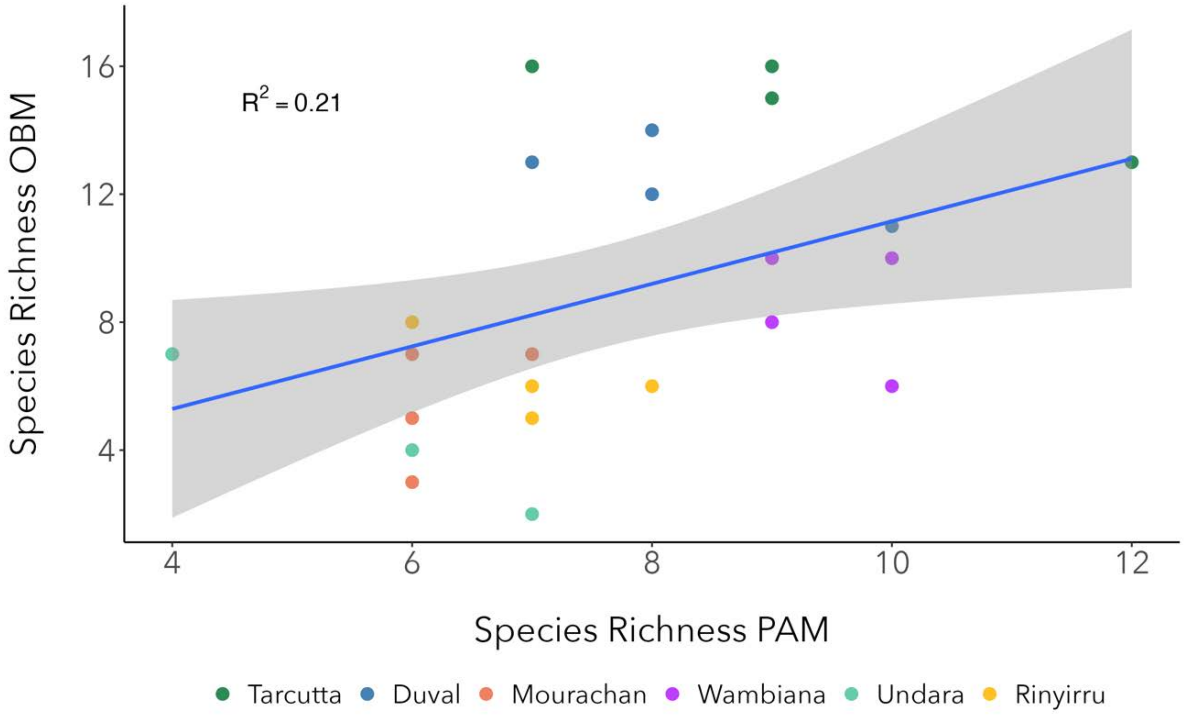
Activity	Time Investment (hours)		
	PAM (317,410 hours)	OBM (168 survey days)	Camera Trapping (~100,000 images)
Data analysis	252		49
Data validation	35		68
Fieldwork + data entry	12	4,032	64
Per day	0.02	24	0.7
Per species detection	17	90	5
Overall	299	4032	181



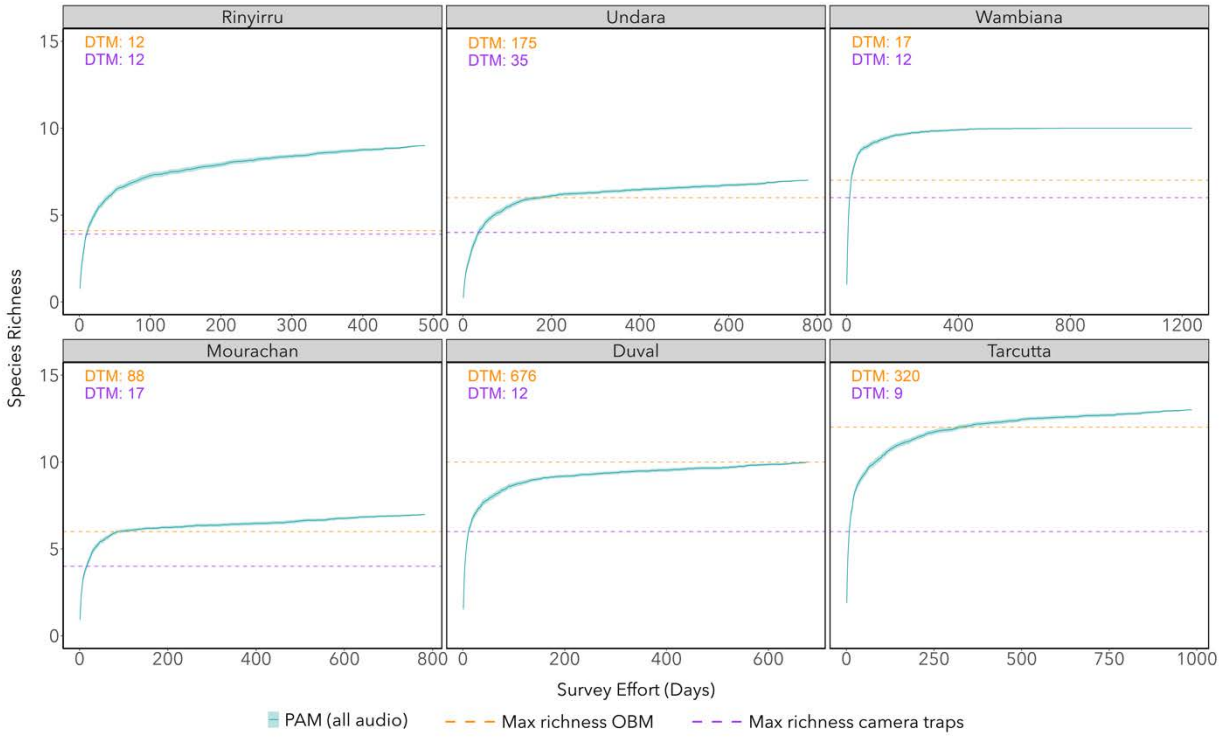
Supplementary Figure A2.1. *Probability of correctly predicting true positive detections based on the Euclidean distance for each of the 46 example calls, analysed for the 17 vocal mammal species used in this study. Note that true positives were predicted by lower Euclidean distances, suggesting that extracting the lowest daily distance should lead to species detections when present.*



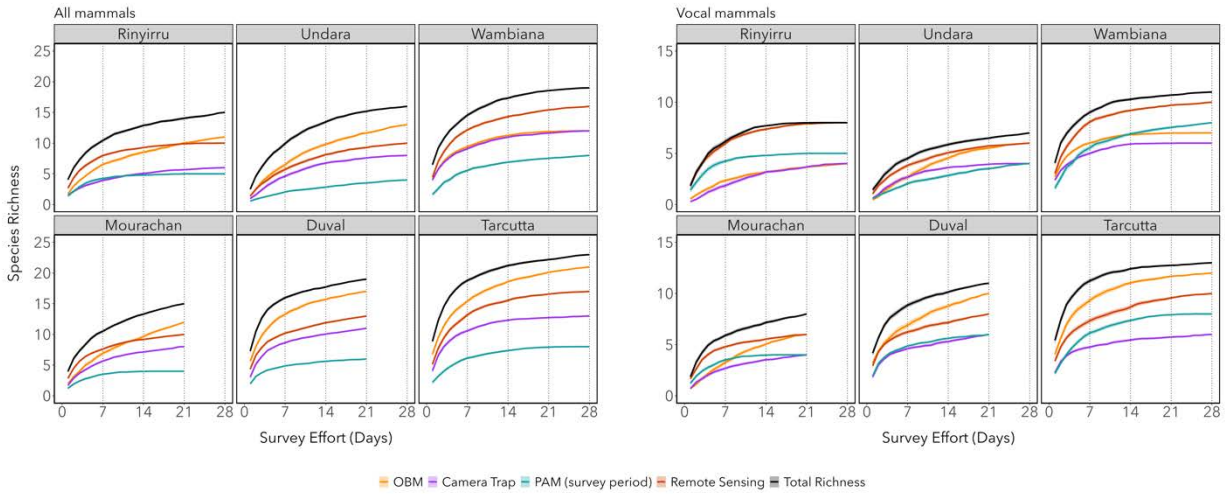
Supplementary Figure A2.2. *Total species richness of mammal communities (all mammals [A] and vocal mammals only [B]) for each survey plot at each site detected by each survey method: cage trap (pink), Elliott trap (light grey), funnel trap (red), pitfall trap (orange), spotlighting (black), incidental encounters (green), camera trapping (purple), passive acoustic monitoring using only audio data matching the survey period (teal), and passive acoustic monitoring using all available audio data (blue).*



Supplementary Figure A2.3. *Relationship between species richness via PAM (passive acoustic monitoring) and species richness via OBM (observer-based monitoring) across six different study sites. Each point represents a sampling site, colour-coded by location. The blue line indicates the linear regression fit, with the grey shaded area representing the 95% confidence interval.*



Supplementary Figure A2.4. *Species accumulation curves for passive acoustic monitoring (PAM) using all audio data available at six survey sites. Intersections between the green accumulation curves and dashed lines indicate the points where PAM's species richness equals the total vocal mammal richness identified by observer-based monitoring (OBM - orange) and camera trapping (purple). The numbers highlighted in the top left corner of each plot represent the "Days to Match" (DTM), indicating the time it took for PAM to match the maximum total species richness recorded by either OBM or camera traps at each site.*



Supplementary Figure A2.5. *Species accumulation curves for mammal communities (all mammals [left] and vocal mammals only [right]) at six survey sites for each assessment method over up to 28 survey days. Lines represent the different assessment methods, as well as a combination of passive acoustic monitoring (PAM) for the survey period and camera traps (denoted as "Remote Sensing" in red) and all methods combined (total richness [black]). Shaded areas around each line corresponds to the 95% confidence intervals and dotted vertical lines mark the cumulative effort after each survey. This graph shows the differences in rate of species accumulation at each site for each method. Note that observer-based monitoring (OBM) accumulates species most effectively at most sites, but "Remote Sensing" is more effective at some sites particularly for vocal mammals.*

Appendix C. Supplementary materials for Chapter 3

Supplementary Table A3.1. *Overview of the number and source of the 115 example calls for 50 Australian frog species used in this study.*

Common Name	Scientific Name	Example Call	Source
Bufonidae			
Cane Toad	*Rhinella marina*	RhinellaMarina_01	David Stewart
Cane Toad	*Rhinella marina*	RhinellaMarina_02	David Stewart
Hylidae			
Green-striped Frog	*Cyclorana alboguttata*	CycloranaAlboguttata_01	David Stewart
Superb Collared Frog	*Cyclorana brevipes*	CycloranaBrevipes_01	David Stewart
Knife-footed Frog	*Cyclorana cultripes*	CycloranaCultripes_01	David Stewart
Knife-footed Frog	*Cyclorana cultripes*	CycloranaCultripes_02	David Stewart
Eastern Snapping Frog	*Cyclorana novaehollandiae*	CycloranaNovaehollandiae_01	David Stewart
Eastern Water-holding Frog	*Cyclorana platycephala*	CycloranaPlatycephala_01	FrogID
Eastern Water-holding Frog	*Cyclorana platycephala*	CycloranaPlatycephala_02	FrogID
Rough Collared Frog	*Cyclorana verrucosa*	CycloranaVerruscosa_01	David Stewart
Northern Sedge Frog	*Litoria bicolor*	LitoriaBicolor_01	David Stewart
Northern Sedge Frog	*Litoria bicolor*	LitoriaBicolor_02	David Stewart
Booroolong Frog	*Litoria booroolongensis*	LitoriaBooroolongensis_01	Michael Mahony
Booroolong Frog	*Litoria booroolongensis*	LitoriaBooroolongensis_02	Michael Mahony
Booroolong Frog	*Litoria booroolongensis*	LitoriaBooroolongensis_03	Michael Mahony
Green Treefrog	*Litoria caerulea*	LitoriaCaerulea_01	David Stewart
Green Treefrog	*Litoria caerulea*	LitoriaCaerulea_02	David Stewart
Green Treefrog	*Litoria caerulea*	LitoriaCaerulea_03	David Stewart
Bleating Tree Frog	*Litoria dentata*	LitoriaDentata_01	David Stewart
Bleating Tree Frog	*Litoria dentata*	LitoriaDentata_02	David Stewart
Southern Brown Tree Frog	*Litoria ewingii*	LitoriaEwingii_01	FrogID
Southern Brown Tree Frog	*Litoria ewingii*	LitoriaEwingii_02	FrogID
Southern Brown Tree Frog	*Litoria ewingii*	LitoriaEwingii_03	FrogID
Eastern Sedge Frog	*Litoria fallax*	LitoriaFallax_01	David Stewart
Eastern Sedge Frog	*Litoria fallax*	LitoriaFallax_02	David Stewart
Eastern Sedge Frog	*Litoria fallax*	LitoriaFallax_03	David Stewart
Eastern Sedge Frog	*Litoria fallax*	LitoriaFallax_04	David Stewart
Bumpy Rocket Frog	*Litoria inermis*	LitoriaInermis_01	David Stewart
Bumpy Rocket Frog	*Litoria inermis*	LitoriaInermis_02	David Stewart
Broad-palmed Rocket Frog	*Litoria latopalmata*	LitoriaLatopalmata_01	David Stewart
Broad-palmed Rocket Frog	*Litoria latopalmata*	LitoriaLatopalmata_02	David Stewart
Broad-palmed Rocket Frog	*Litoria latopalmata*	LitoriaLatopalmata_03	David Stewart
Jevelin Frog	*Litoria microbelos*	LitoriaMicrobelos_01	David Stewart
Jevelin Frog	*Litoria microbelos*	LitoriaMicrobelos_02	David Stewart
Striped Rocket Frog	*Litoria nasuta*	LitoriaNasuta_01	David Stewart
Striped Rocket Frog	*Litoria nasuta*	LitoriaNasuta_02	David Stewart
Striped Rocket Frog	*Litoria nasuta*	LitoriaNasuta_03	David Stewart
Tawney Rocket Frog	*Litoria nigrofrenata*	LitoriaNigrofrenata_01	David Stewart
Pallid Rocket Frog	*Litoria pallida*	LitoriaPallida_01	David Stewart
Pallid Rocket Frog	*Litoria pallida*	LitoriaPallida_02	David Stewart
Emerald-spotted Tree Frog	*Litoria peronii*	LitoriaPeronii_01	David Stewart
Emerald-spotted Tree Frog	*Litoria peronii*	LitoriaPeronii_02	David Stewart
Emerald-spotted Tree Frog	*Litoria peronii*	LitoriaPeronii_03	David Stewart
Southern Bell Frog	*Litoria raniformis*	LitoriaRaniformis_01	Sarah Talbot
Southern Bell Frog	*Litoria raniformis*	LitoriaRaniformis_02	Sarah Talbot
Northern Laughing Tree Frog	*Litoria rothii*	LitoriaRothii_01	David Stewart
Northern Laughing Tree Frog	*Litoria rothii*	LitoriaRothii_02	David Stewart
Northern Laughing Tree Frog	*Litoria rothii*	LitoriaRothii_03	David Stewart
Little Red Tree Frog	*Litoria rubella*	LitoriaRubella_01	David Stewart
Little Red Tree Frog	*Litoria rubella*	LitoriaRubella_02	David Stewart
Little Red Tree Frog	*Litoria rubella*	LitoriaRubella_03	David Stewart
Tyler's Tree Frog	*Litoria tyleri*	LitoriaTyleri_01	David Stewart
Tyler's Tree Frog	*Litoria tyleri*	LitoriaTyleri_02	David Stewart
Whistling Tree Frog	*Litoria verreauxii verreauxii*	LitoriaVerreaixiiVereauxii_01	David Stewart
Whistling Tree Frog	*Litoria verreauxii verreauxii*	LitoriaVerreaixiiVereauxii_02	David Stewart

Common Name	Scientific Name	Example Call	Source
Limnodynastidae			
Tusked Frog	*Adelotus brevis*	AdelotusBrevis_01	David Stewart
Tusked Frog	*Adelotus brevis*	AdelotusBrevis_02	David Stewart
Tusked Frog	*Adelotus brevis*	AdelotusBrevis_03	David Stewart
Tusked Frog	*Adelotus brevis*	AdelotusBrevis_04	David Stewart
Marbled Frog	*Limnodynastes convexiusculus*	LimnodynastesConvexiusculus_01	David Stewart
Marbled Frog	*Limnodynastes convexiusculus*	LimnodynastesConvexiusculus_02	David Stewart
Marbled Frog	*Limnodynastes convexiusculus*	LimnodynastesConvexiusculus_03	David Stewart
Marbled Frog	*Limnodynastes convexiusculus*	LimnodynastesConvexiusculus_04	David Stewart
Eastern Banjo Frog	*Limnodynastes dumerilii dumerilii*	LimnodynastesDumeriliiDumerilli_01	David Stewart
Eastern Banjo Frog	*Limnodynastes dumerilii dumerilii*	LimnodynastesDumeriliiDumerilli_02	David Stewart
Eastern Banjo Frog	*Limnodynastes dumerilii dumerilii*	LimnodynastesDumeriliiDumerilli_03	David Stewart
Barking Frog	*Limnodynastes fletcheri*	LimnodynastesFletcheri_01	David Stewart
Giant Banjo Frog	*Limnodynastes interioris*	LimnodynastesInterioris_01	Sarah Talbot
Giant Banjo Frog	*Limnodynastes interioris*	LimnodynastesInterioris_02	Sarah Talbot
Giant Banjo Frog	*Limnodynastes interioris*	LimnodynastesInterioris_03	Sarah Talbot
Striped Marsh Frog	*Limnodynastes peronii*	LimnodynastesPeronii_01	David Stewart
Striped Marsh Frog	*Limnodynastes peronii*	LimnodynastesPeronii_02	David Stewart
Salmon-striped Frog	*Limnodynastes salmini*	LimnodynastesSalmini_01	David Stewart
Salmon-striped Frog	*Limnodynastes salmini*	LimnodynastesSalmini_02	David Stewart
Spotted Marsh Frog	*Limnodynastes tasmaniensis*	LimnodynastesTasmaniensis_01	David Stewart
Spotted Marsh Frog	*Limnodynastes tasmaniensis*	LimnodynastesTasmaniensis_02	David Stewart
Spotted Marsh Frog	*Limnodynastes tasmaniensis*	LimnodynastesTasmaniensis_03	David Stewart
Superb Banjo Frog	*Limnodynastes terraereginae*	LimnodynastesTerraereginae_01	David Stewart
Superb Banjo Frog	*Limnodynastes terraereginae*	LimnodynastesTerraereginae_02	David Stewart
Sudell's Frog	*Neobatrachus sudellae*	NeobatrachisSudelli_01	Dale Roberts
Holy Cross Frog	*Notaden bennettii*	NotadenBennettii_01	David Stewart
Holy Cross Frog	*Notaden bennettii*	NotadenBennettii_02	David Stewart
Northern Spadefoot	*Notaden melanoscaphus*	NotadenMelanoscaphus_01	David Stewart
Ornate Burrowing Frog	*Platyplectrum ornatum*	PlatyplectrumOrnatum_01	David Stewart
Ornate Burrowing Frog	*Platyplectrum ornatum*	PlatyplectrumOrnatum_02	David Stewart
Ornate Burrowing Frog	*Platyplectrum ornatum*	PlatyplectrumOrnatum_03	David Stewart
Myobatrachidae			
Desert Froglet	*Crinia deserticola*	CriniaDeserticola_01	David Stewart
Desert Froglet	*Crinia deserticola*	CriniaDeserticola_02	David Stewart
Desert Froglet	*Crinia deserticola*	CriniaDeserticola_03	David Stewart
Desert Froglet	*Crinia deserticola*	CriniaDeserticola_04	David Stewart
Beeping Froglet	*Crinia parinsignifera*	CriniaParinsignifera_01	David Stewart
Beeping Froglet	*Crinia parinsignifera*	CriniaParinsignifera_02	David Stewart
Beeping Froglet	*Crinia parinsignifera*	CriniaParinsignifera_03	David Stewart
Beeping Froglet	*Crinia parinsignifera*	CriniaParinsignifera_04	David Stewart
Northern Froglet	*Crinia remota*	CriniaRemota_01	David Stewart
Northern Froglet	*Crinia remota*	CriniaRemota_02	David Stewart
Clicking Froglet	*Crinia signifera*	CriniaSignifera_01	David Stewart
Clicking Froglet	*Crinia signifera*	CriniaSignifera_02	David Stewart
Clicking Froglet	*Crinia signifera*	CriniaSignifera_03	David Stewart
Clicking Froglet	*Crinia signifera*	CriniaSignifera_04	David Stewart
Sloane's Froglet	*Crinia sloanei*	CriniaSloanei_01	Alexandra Knight
Sloane's Froglet	*Crinia sloanei*	CriniaSloanei_02	Alexandra Knight
Sloane's Froglet	*Crinia sloanei*	CriniaSloanei_02	Alexandra Knight
Brown Toadlet	*Pseudophryne bibronii*	PseudophryneBibronii_01	David Stewart
Brown Toadlet	*Pseudophryne bibronii*	PseudophryneBibronii_02	David Stewart
Smooth Toadlet	*Uperoleia laevigata*	UperoleiaLaevigata_01	David Stewart
Smooth Toadlet	*Uperoleia laevigata*	UperoleiaLaevigata_02	David Stewart
Smooth Toadlet	*Uperoleia laevigata*	UperoleiaLaevigata_03	David Stewart
Stonemason Toadlet	*Uperoleia lithomoda*	UperoleiaLithomoda_01	David Stewart
Stonemason Toadlet	*Uperoleia lithomoda*	UperoleiaLithomoda_02	David Stewart
Einasleigh Toadlet	*Uperoleia littlejohni*	UperoleiaLittlejohni_01	David Stewart
Einasleigh Toadlet	*Uperoleia littlejohni*	UperoleiaLittlejohni_02	David Stewart
Mimic Toadlet	*Uperoleia mimula*	UperoleiaMimula_01	David Stewart
Chubby Toadlet	*Uperoleia rugosa*	UperoleiaRugosa_01	David Stewart
Chubby Toadlet	*Uperoleia rugosa*	UperoleiaRugosa_02	David Stewart

Supplementary Table A3.2. *Frog species detected via observer-based monitoring (OBM) through pitfall traps (PF), funnel traps (FT), arboreal cover boards (ACB), spotlighting (SL), and incidental encounters (IE); and passive acoustic monitoring (PAM) for both matching only the survey period, and all available audio data. The numbers for each species represent instances of detection rather than abundances.*

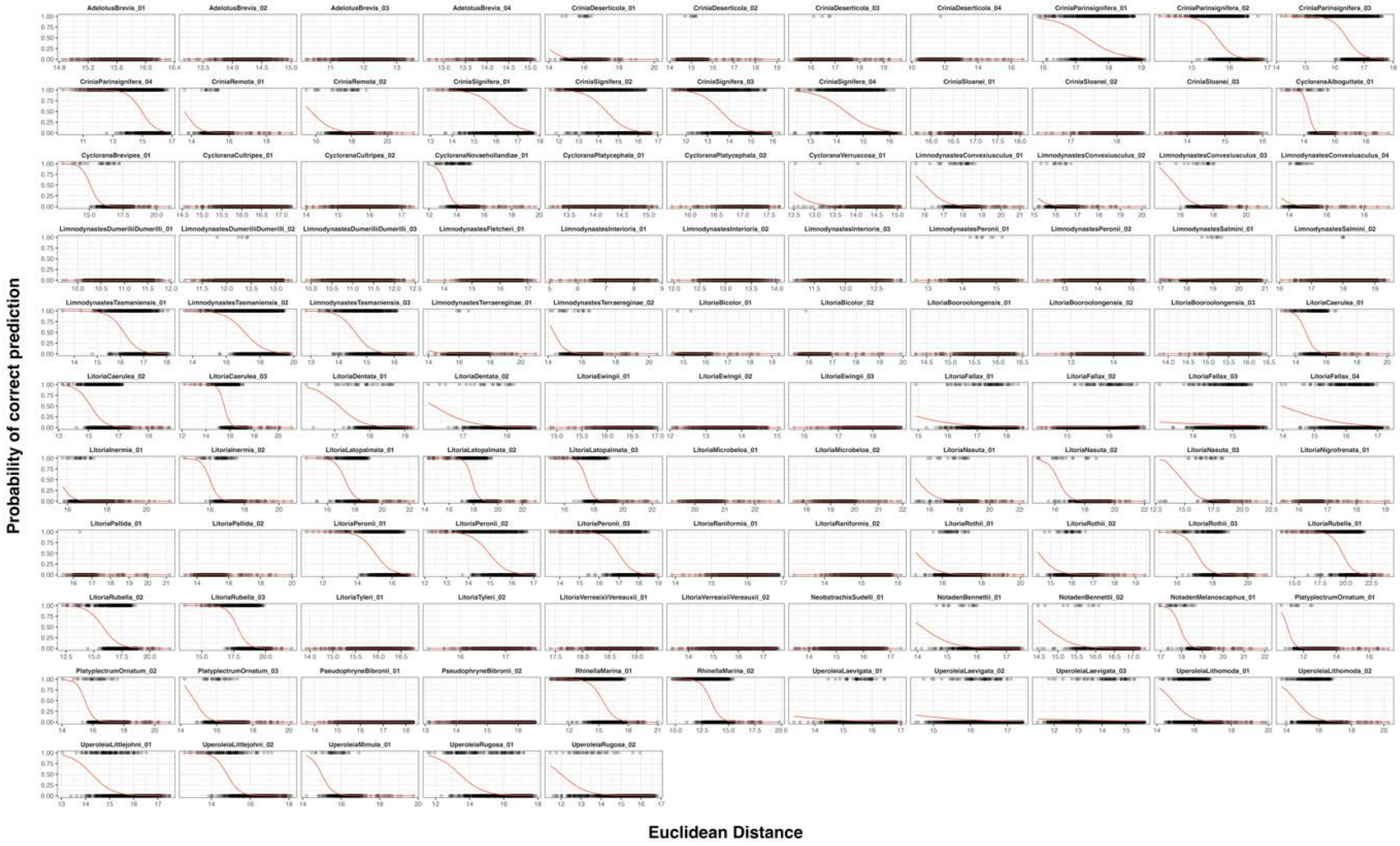
Common name	Scientific name	Observer-based monitoring (OBM)					Passive acoustic monitoring (PAM)	
		PT	FT	ACB	SL	IE	Survey period	All audio
Bufonidae								
Cane Toad	*Rhinella marina*	143	119		321	19	65	1547
Hylidae								
Green-striped Frog	*Cyclorana alboguttata*							33
Superb Collared Frog	*Cyclorana brevipes*							25
Eastern Snapping Frog	*Cyclorana novaehollandiae*		2		8	8	3	67
Rough Collared Frog	*Cyclorana verrucosa*							3
Northern Sedge Frog	*Litoria bicolor*							3
Green Tree Frog	*Litoria caerulea*	4	2		52	19	35	717
Bleating Tree Frog	*Litoria dentata*							56
Eastern Sedge Frog	*Litoria fallax*				82	4	19	446
Bumpy Rocket Frog	*Litoria inermis*	1	9		40		1	76
Broad-palmed Rocket Frog	*Litoria latopalmata*	4	7		187	27	50	582
Striped Rocket Frog	*Litoria nasuta*	8	4		1	1	1	57
Pallid Rocket Frog	*Litoria pallida*							1
Emerald-spotted Tree Frog	*Litoria peronii*				276	10	54	1164
Northern Laughing Tree Frog	*Litoria rothii*					1	1	184
Little Red Tree Frog	*Litoria rubella*	26	6	2	107	16	26	1108
Limnodynastidae								
Marbled Frog	*Limnodynastes convexiusculus*	4	1				1	75
Eastern Banjo Frog	*Limnodynastes dumerilii dumerilii*	1			33	11	1	5
Scarlet-sided Banjo Frog	*Limnodynastes grayi*	6	4		5	2	8	21
Striped Marsh Frog	*Limnodynastes peronii*	1						8
Salmon-Striped Frog	*Limnodynastes salmini*							11
Spotted Marsh Frog	*Limnodynastes tasmaniensis*	54	10		160	9	53	1413
Superb Banjo Frog	*Limnodynastes terraereginae*	2	3					
Holy Cross Frog	*Notaden bennettii*	3			5	1		28
Northern Spadefoot	*Notaden melanoscaphus*	23	4		15	2		26
Ornate Burrowing Frog	*Platyplectrum ornatum*	95	22	1	4	6		65
Myobatrachidae								
Desert Froglet	*Crinia deserticola*						2	26
Beeping Froglet	*Crinia parinsignifera*	11	8		603	65	86	2298
Northern Froglet	*Crinia remota*				1		9	44
Clicking Froglet	*Crinia signifera*	20	7		208	62	92	2612
Smooth Toadlet	*Uperoleia laevigata*							166
Stonemason Toadlet	*Uperoleia lithomoda*						17	323
Einasleigh Toadlet	*Uperoleia littlejohni*						3	210
Mimic Toadlet	*Uperoleia mimula*							33
Chubby Toadlet	*Uperoleia rugosa*	13	2		47		13	144
Total number of species		18	16	2	19	17	21	34

Supplementary Table A3.3. *Total frog species richness detected via observer-based monitoring (OBM), passive acoustic monitoring (PAM) for both matching only the survey period, and all available audio data, and all methods combined.*

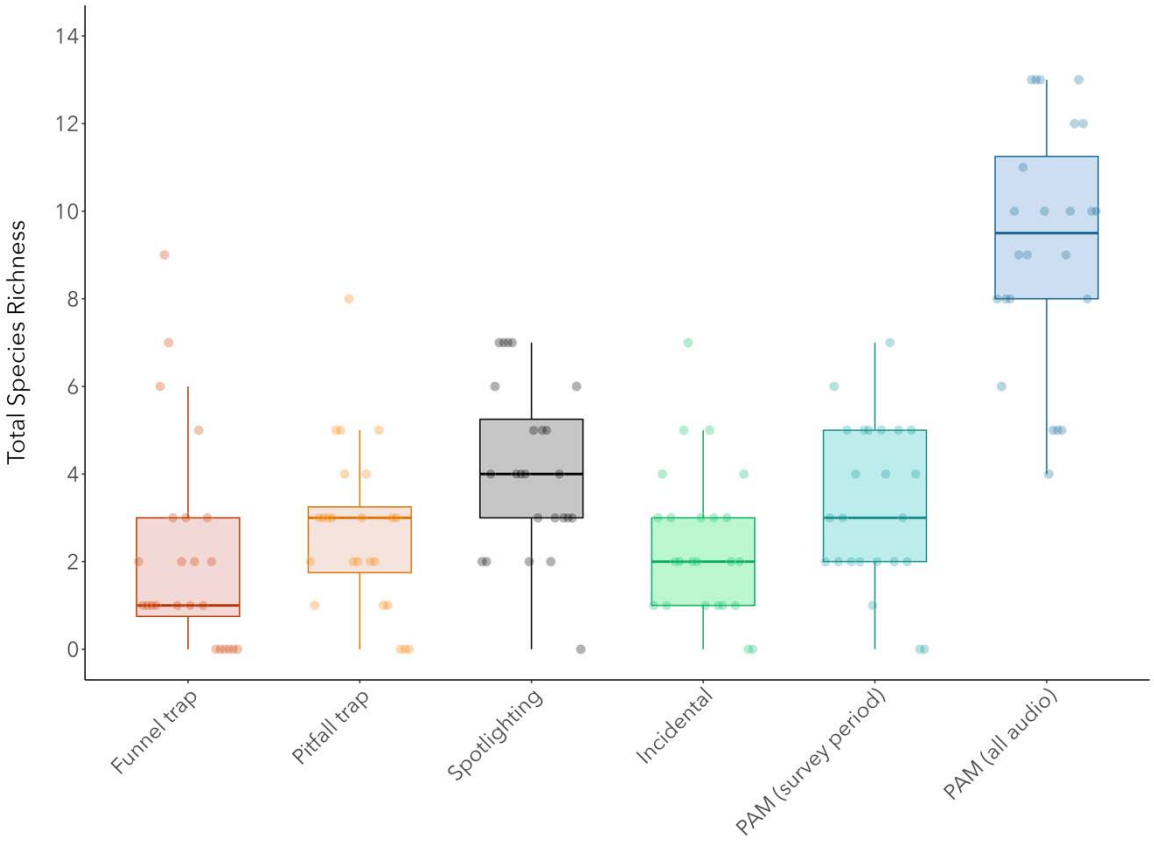
	Total species richness			
	OBM	PAM (survey period)	PAM (all audio)	All methods combined
Tarcutta	6	5	6	6
Duval	6	7	10	10
Mourachan	9	8	13	13
Wambiana	7	6	12	12
Undara	9	10	15	15
Rinyirru	12	8	16	19

Supplementary Table A3.4. *Overview of the number and source of the 115 example calls for 50 Australian frog species used in this study.*

	Days to match OBM species richness				
	PAM spring	PAM summer	PAM autumn	PAM winter	PAM total
Tarcutta	–	–	–	–	495
Duval	5	5	35	64	7
Mourachan	23	37	–	–	42
Wambiana	36	9	38	60	19
Undara	64	13	–	–	35
Rinyirru	–	39	–	–	68



Supplementary Figure A3.1. *Probability of correctly predicting true positive detections based on the Euclidean distance for each of the 115 example calls, analysed for the 50 frog species used in this study. Note that true positives were predicted by lower Euclidean distances, suggesting that extracting the lowest daily distance should lead to species detections when present.*



Supplementary Figure A3.2. *Total species richness of frogs for each survey plot at each site detected by each survey method: funnel trap (red), pitfall trap (orange), spotlighting (black), incidental encounters (green), passive acoustic monitoring using only audio data matching the survey period (teal), and passive acoustic monitoring using all available audio data (blue).*

Appendix D. Supplementary materials for Chapter 4

Supplementary Table A4.1. *Pairwise comparisons of survey methods for species richness at each survey site. The table presents the average fractional change (i.e., the factor by which one method detects more species compared to the other), lower and upper bounds of the highest density interval (HDI), and the probability that one method is more effective than the other. These summary statistics are based on the posterior draws from the Bayesian regression model.*

	Average fractional change	Lower HDI	Upper HDI	$P_{(0)}$
All Sites				
Pitfall Trap - Funnel Trap	1.02	0.8	1.27	0.588
Pitfall Trap - Incidental	2.49	1.79	3.4	1
Pitfall Trap - Spotlighting	3.04	2.13	4.18	1
Pitfall Trap - Arboreal Cover Board	4.8	3.09	7.12	1
Pitfall Trap - Camera Trap	11.89	6.39	20.14	1
Funnel Trap - Incidental	2.45	1.76	3.35	1
Funnel Trap - Spotlighting	2.96	2.07	4.09	1
Funnel Trap - Arboreal Cover Board	4.69	2.94	6.98	1
Funnel Trap - Camera Trap	11.56	6.36	19.96	1
Incidental - Spotlighting	1.21	0.79	1.81	0.812
Incidental - Arboreal Cover Board	1.93	1.11	2.97	0.997
Incidental - Camera Trap	4.74	2.52	8.61	1
Spotlighting - Arboreal Cover Board	1.58	0.94	2.56	0.966
Spotlighting - Camera Trap	3.94	1.89	6.73	1
Arboreal Cover Board - Camera Trap	2.48	1.14	4.38	0.998
Tarcutta				
Pitfall Trap - Funnel Trap	1.05	0.62	1.71	0.578
Pitfall Trap - Incidental	4.04	1.64	7.72	0.999
Pitfall Trap - Spotlighting	4.81	2.03	9.65	1
Pitfall Trap - Arboreal Cover Board	8.03	2.53	18.67	1
Pitfall Trap - Camera Trap	8.42	1.79	24.04	1
Funnel Trap - Incidental	3.79	1.59	7.34	1
Funnel Trap - Spotlighting	4.55	1.67	8.83	1
Funnel Trap - Arboreal Cover Board	7.58	2.35	17.77	1
Funnel Trap - Camera Trap	8.03	1.96	23.57	1
Incidental - Spotlighting	1.19	0.36	2.65	0.658
Incidental - Arboreal Cover Board	1.99	0.53	5.23	0.903
Incidental - Camera Trap	2.12	0.41	6.44	0.879
Spotlighting - Arboreal Cover Board	1.64	0.36	4.39	0.817
Spotlighting - Camera Trap	1.76	0.32	5.7	0.808
Arboreal Cover Board - Camera Trap	1.06	0.13	3.59	0.529
Duval				
Pitfall Trap - Funnel Trap	1.04	0.7	1.47	0.585
Pitfall Trap - Incidental	3.25	1.72	5.17	1

	Average fractional change	Lower HDI	Upper HDI	$P_{(0)}$
Pitfall Trap - Spotlighting	3.88	2.1	6.49	1
Pitfall Trap - Arboreal Cover Board	6.32	2.74	11.69	1
Pitfall Trap - Camera Trap	9.87	3.73	20.51	1
Funnel Trap - Incidental	3.11	1.61	4.94	1
Funnel Trap - Spotlighting	3.73	1.96	6.18	1
Funnel Trap - Arboreal Cover Board	6.03	2.67	11.19	1
Funnel Trap - Camera Trap	9.48	3.27	19.94	1
Incidental - Spotlighting	1.21	0.56	2.17	0.712
Incidental - Arboreal Cover Board	1.93	0.77	3.95	0.954
Incidental - Camera Trap	3.03	0.89	6.79	0.995
Spotlighting - Arboreal Cover Board	1.61	0.6	3.33	0.884
Spotlighting - Camera Trap	2.52	0.77	5.83	0.98
Arboreal Cover Board - Camera Trap	1.57	0.38	3.75	0.81
Mourachan				
Pitfall Trap - Funnel Trap	1.03	0.74	1.36	0.587
Pitfall Trap - Incidental	2.9	1.8	4.28	1
Pitfall Trap - Spotlighting	3.47	2.18	5.34	1
Pitfall Trap - Arboreal Cover Board	5.58	3.05	9.47	1
Pitfall Trap - Camera Trap	10.76	5	19.46	1
Funnel Trap - Incidental	2.8	1.8	4.19	1
Funnel Trap - Spotlighting	3.36	2.05	5.14	1
Funnel Trap - Arboreal Cover Board	5.38	2.95	9.09	1
Funnel Trap - Camera Trap	10.31	4.57	19.22	1
Incidental - Spotlighting	1.21	0.67	1.95	0.763
Incidental - Arboreal Cover Board	1.92	0.92	3.47	0.98
Incidental - Camera Trap	3.69	1.43	7.11	1
Spotlighting - Arboreal Cover Board	1.6	0.72	2.88	0.928
Spotlighting - Camera Trap	3.08	1.32	6.1	1
Arboreal Cover Board - Camera Trap	1.91	0.71	4.04	0.943
Wambiana				
Pitfall Trap - Funnel Trap	1.01	0.81	1.22	0.546
Pitfall Trap - Incidental	2.09	1.66	2.68	1
Pitfall Trap - Spotlighting	2.54	1.96	3.4	1
Pitfall Trap - Arboreal Cover Board	3.97	2.68	5.3	1
Pitfall Trap - Camera Trap	13.25	7.02	21.87	1
Funnel Trap - Incidental	2.08	1.58	2.64	1
Funnel Trap - Spotlighting	2.51	1.89	3.26	1
Funnel Trap - Arboreal Cover Board	3.91	2.79	5.34	1
Funnel Trap - Camera Trap	13.06	7.23	22.43	1
Incidental - Spotlighting	1.21	0.89	1.64	0.89
Incidental - Arboreal Cover Board	1.89	1.29	2.66	1
Incidental - Camera Trap	6.3	3.19	10.73	1
Spotlighting - Arboreal Cover Board	1.55	0.99	2.12	0.995
Spotlighting - Camera Trap	5.17	2.81	9.06	1
Arboreal Cover Board - Camera Trap	3.32	1.73	5.89	1

	Average fractional change	Lower HDI	Upper HDI	$P_{(0)}$
Undara				
Pitfall Trap - Funnel Trap	1.01	0.79	1.24	0.53
Pitfall Trap - Incidental	1.9	1.43	2.43	1
Pitfall Trap - Spotlighting	2.31	1.67	3.02	1
Pitfall Trap - Arboreal Cover Board	3.54	2.5	4.87	1
Pitfall Trap - Camera Trap	13.95	6.65	25.47	1
Funnel Trap - Incidental	1.89	1.41	2.4	1
Funnel Trap - Spotlighting	2.29	1.69	2.99	1
Funnel Trap - Arboreal Cover Board	3.54	2.41	4.78	1
Funnel Trap - Camera Trap	14.02	6.76	25.42	1
Incidental - Spotlighting	1.21	0.83	1.64	0.874
Incidental - Arboreal Cover Board	1.86	1.29	2.65	1
Incidental - Camera Trap	7.38	3.47	13.71	1
Spotlighting - Arboreal Cover Board	1.54	1.01	2.18	0.988
Spotlighting - Camera Trap	6.09	2.83	11.22	1
Arboreal Cover Board - Camera Trap	3.93	1.87	7.6	1
Rinyirru				
Pitfall Trap - Funnel Trap	1	0.73	1.29	0.5
Pitfall Trap - Incidental	1.64	1.13	2.28	0.998
Pitfall Trap - Spotlighting	2.01	1.37	2.88	1
Pitfall Trap - Arboreal Cover Board	3.04	2.01	4.66	1
Pitfall Trap - Camera Trap	15.4	6.71	33.59	1
Funnel Trap - Incidental	1.65	1.15	2.26	0.998
Funnel Trap - Spotlighting	2	1.34	2.82	1
Funnel Trap - Arboreal Cover Board	3.06	1.86	4.46	1
Funnel Trap - Camera Trap	15.38	5.91	33.34	1
Incidental - Spotlighting	1.22	0.77	1.81	0.815
Incidental - Arboreal Cover Board	1.83	1.17	2.9	0.995
Incidental - Camera Trap	9.3	3.55	20.44	1
Spotlighting - Arboreal Cover Board	1.52	0.83	2.33	0.952
Spotlighting - Camera Trap	7.69	2.82	16.58	1
Arboreal Cover Board - Camera Trap	4.98	1.88	11.42	1

Supplementary Table A4.2. *Pairwise PERMANOVA comparison of survey methods using ADONIS for Jaccard (presence-absence) and Bray-Curtis dissimilarities (relative abundance) across all sites. The table displays P-values (adjusted for multiple comparisons), effect sizes (R^2), sums of squares (SumsOfSqs), mean squares (MeanSqs), and F-statistics (F.Model) for each comparison.*

	Sums OfSqs	Mean Sqs	F.Model	R^2	P-value	P-value (adjusted)
Jaccard (presence-absence)						
Camera Trap - Arboreal Cover Board	3.037	3.037	10.376	0.293	0.000999	0.001249
Camera Trap - Funnel Trap	2.627	2.627	7.045	0.180	0.000999	0.001249
Camera Trap - Incidental	2.359	2.359	6.543	0.201	0.000999	0.001249
Camera Trap - Pitfall Trap	2.765	2.765	7.618	0.192	0.000999	0.001249
Camera Trap - Spotlighting	2.838	2.838	9.268	0.279	0.000999	0.001249
Arboreal Cover Board - Funnel Trap	2.617	2.617	6.801	0.148	0.000999	0.001249
Arboreal Cover Board - Incidental	1.356	1.356	3.595	0.098	0.000999	0.001249
Arboreal Cover Board - Pitfall Trap	2.394	2.394	6.357	0.140	0.000999	0.001249
Arboreal Cover Board - Spotlighting	1.186	1.186	3.528	0.102	0.000999	0.001249
Funnel Trap - Incidental	1.004	1.004	2.353	0.056	0.001998	0.002305
Funnel Trap - Pitfall Trap	0.350	0.350	0.835	0.018	0.617383	0.617383
Funnel Trap - Spotlighting	2.060	2.060	5.205	0.120	0.000999	0.001249
Incidental - Pitfall Trap	1.130	1.130	2.700	0.063	0.000999	0.001249
Incidental - Spotlighting	0.519	0.519	1.331	0.040	0.154845	0.165906
Pitfall Trap - Spotlighting	2.123	2.123	5.480	0.126	0.000999	0.001249
Bray-Curtis (relative abundance)						
Camera Trap - Arboreal Cover Board	2.888	2.888	9.363	0.272	0.000999	0.001153
Camera Trap - Funnel Trap	2.733	2.733	7.546	0.191	0.000999	0.001153
Camera Trap - Incidental	2.404	2.404	6.830	0.208	0.000999	0.001153
Camera Trap - Pitfall Trap	2.740	2.740	7.498	0.190	0.000999	0.001153
Camera Trap - Spotlighting	3.110	3.110	11.249	0.319	0.000999	0.001153
Arboreal Cover Board - Funnel Trap	2.672	2.672	6.930	0.151	0.000999	0.001153
Arboreal Cover Board - Incidental	1.552	1.552	4.066	0.110	0.000999	0.001153
Arboreal Cover Board - Pitfall Trap	2.287	2.287	5.890	0.131	0.000999	0.001153
Arboreal Cover Board - Spotlighting	1.072	1.072	3.295	0.096	0.001998	0.002141
Funnel Trap - Incidental	1.530	1.530	3.713	0.085	0.000999	0.001153
Funnel Trap - Pitfall Trap	0.380	0.380	0.920	0.020	0.477522	0.477522
Funnel Trap - Spotlighting	2.804	2.804	7.632	0.167	0.000999	0.001153
Incidental - Pitfall Trap	1.465	1.465	3.534	0.081	0.000999	0.001153
Incidental - Spotlighting	1.585	1.585	4.402	0.121	0.000999	0.001153
Pitfall Trap - Spotlighting	2.709	2.709	7.316	0.161	0.000999	0.001153

Supplementary Table A4.3. *Summary of all reptile species detected via each of the six survey methods (excluding passive acoustic monitoring due to its inability to detect any reptiles) for each survey plot within the respective study sites. This table includes all recaptures; therefore, the numbers represent observations not individuals. Numbers in brackets represent the daily detectability. PT = pitfall trap, FT = funnel trap, IE = incidental encounter, SL = spotlighting, ACB = arboreal cover board, CT = camera trap. Total number of unique species represents the sum of all unique species per survey site.*

Species	Site	Plot	Survey Methods					
			PT	FT	IE	SL	ACB	CT
Lacertilia								
Agamidae								
Amphibolurus muricatus	Duval	DryA	0 (0)	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)
Chlamydosaurus kingii	Rinyirru	WetA	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.036)
Diporiphora australis	Undara	DryA	2 (0.071)	1 (0.036)	2 (0.071)	0 (0)	0 (0)	0 (0)
Diporiphora australis	Undara	DryB	3 (0.111)	5 (0.148)	2 (0.074)	0 (0)	0 (0)	0 (0)
Diporiphora australis	Rinyirru	DryA	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Diporiphora bilineata	Rinyirru	DryA	12 (0.214)	4 (0.107)	2 (0.036)	0 (0)	0 (0)	0 (0)
Diporiphora bilineata	Rinyirru	DryB	6 (0.179)	3 (0.107)	3 (0.107)	0 (0)	0 (0)	0 (0)
Diporiphora bilineata	Rinyirru	WetA	7 (0.214)	9 (0.286)	0 (0)	0 (0)	0 (0)	0 (0)
Diporiphora bilineata	Rinyirru	WetB	5 (0.179)	1 (0.036)	1 (0.036)	1 (0.036)	0 (0)	0 (0)
Diporiphora nobbi	Mourachan	DryB	1 (0.048)	0 (0)	2 (0.048)	0 (0)	0 (0)	0 (0)
Pogona barbata	Mourachan	DryB	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Tympanocryptis sp. Einasleigh Uplands	Undara	DryA	1 (0.036)	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)
Tympanocryptis sp. Einasleigh Uplands	Undara	DryB	1 (0.037)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Carphodactylidae								
Nephrurus asper	Undara	DryA	0 (0)	0 (0)	3 (0.071)	9 (0.25)	0 (0)	0 (0)
Nephrurus asper	Undara	WetA	0 (0)	0 (0)	1 (0.036)	1 (0.036)	0 (0)	0 (0)
Diplodactylidae								
Amalosia queenslandia	Undara	DryA	1 (0.036)	1 (0.036)	0 (0)	3 (0.107)	25 (0.464)	0 (0)
Amalosia queenslandia	Undara	DryB	0 (0)	0 (0)	0 (0)	10 (0.111)	31 (0.519)	0 (0)
Amalosia queenslandia	Undara	WetA	0 (0)	0 (0)	0 (0)	14 (0.357)	86 (0.893)	0 (0)
Amalosia queenslandia	Undara	WetB	0 (0)	0 (0)	0 (0)	0 (0)	2 (0.074)	0 (0)
Amalosia queenslandia	Rinyirru	DryB	0 (0)	0 (0)	1 (0.036)	2 (0.071)	3 (0.107)	0 (0)
Amalosia queenslandia	Rinyirru	WetA	0 (0)	0 (0)	0 (0)	0 (0)	2 (0.071)	0 (0)
Diplodactylus platyurus	Undara	DryA	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Diplodactylus platyurus	Undara	DryB	4 (0.148)	0 (0)	1 (0.037)	3 (0.074)	0 (0)	0 (0)
Diplodactylus platyurus	Undara	WetA	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Diplodactylus platyurus	Undara	WetB	1 (0.037)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Diplodactylus vittatus	Tarcutta	WetA	4 (0.071)	2 (0.071)	1 (0.036)	0 (0)	0 (0)	0 (0)
Diplodactylus vittatus	Mourachan	DryA	1 (0.048)	0 (0)	1 (0.048)	1 (0.048)	0 (0)	0 (0)
Diplodactylus vittatus	Mourachan	DryB	0 (0)	0 (0)	1 (0.048)	0 (0)	0 (0)	0 (0)
Diplodactylus vittatus	Mourachan	WetA	0 (0)	0 (0)	0 (0)	2 (0.095)	0 (0)	0 (0)
Lucasium steindachneri	Wambiana	DryA	2 (0.071)	2 (0.071)	1 (0.036)	2 (0.071)	0 (0)	0 (0)
Lucasium steindachneri	Wambiana	DryB	5 (0.143)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Lucasium steindachneri	Wambiana	WetB	1 (0.036)	0 (0)	0 (0)	2 (0.036)	0 (0)	0 (0)
Lucasium steindachneri	Undara	DryB	2 (0.074)	0 (0)	1 (0.037)	0 (0)	0 (0)	0 (0)
Lucasium steindachneri	Mourachan	DryA	0 (0)	0 (0)	0 (0)	3 (0.143)	0 (0)	0 (0)
Lucasium steindachneri	Mourachan	DryB	1 (0.048)	0 (0)	1 (0.048)	1 (0.048)	0 (0)	0 (0)
Lucasium steindachneri	Mourachan	WetA	2 (0.095)	1 (0.048)	4 (0.143)	6 (0.19)	0 (0)	0 (0)
Lucasium steindachneri	Mourachan	WetB	2 (0.095)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Oedura castelnaui	Wambiana	WetB	0 (0)	0 (0)	1 (0.036)	6 (0.107)	0 (0)	0 (0)
Oedura castelnaui	Undara	DryB	0 (0)	0 (0)	0 (0)	1 (0.037)	0 (0)	0 (0)
Oedura castelnaui	Undara	WetA	0 (0)	0 (0)	1 (0.036)	3 (0.107)	1 (0.036)	0 (0)
Oedura castelnaui	Rinyirru	DryA	0 (0)	0 (0)	0 (0)	5 (0.071)	0 (0)	0 (0)
Oedura castelnaui	Rinyirru	DryB	0 (0)	0 (0)	3 (0.071)	20 (0.571)	0 (0)	0 (0)
Oedura coggeri	Undara	DryA	0 (0)	0 (0)	0 (0)	5 (0.143)	0 (0)	0 (0)
Oedura coggeri	Undara	DryB	0 (0)	0 (0)	0 (0)	4 (0.111)	0 (0)	0 (0)
Oedura monilis	Mourachan	DryA	0 (0)	0 (0)	0 (0)	1 (0.048)	0 (0)	0 (0)

Species	Site	Plot	Survey Methods					
			PT	FT	IE	SL	ACB	CT
Rhynchoedura ormsbyi	Mourachan	DryA	0 (0)	0 (0)	0 (0)	2 (0.048)	0 (0)	0 (0)
Rhynchoedura ormsbyi	Mourachan	DryB	6 (0.286)	0 (0)	2 (0.095)	5 (0.19)	0 (0)	0 (0)
Rhynchoedura ormsbyi	Mourachan	WetA	4 (0.095)	3 (0.095)	1 (0.048)	8 (0.143)	0 (0)	0 (0)
Rhynchoedura ormsbyi	Mourachan	WetB	0 (0)	0 (0)	0 (0)	1 (0.048)	0 (0)	0 (0)
Strophurus williamsi	Wambiana	DryA	0 (0)	0 (0)	0 (0)	7 (0.214)	0 (0)	0 (0)
Strophurus williamsi	Wambiana	DryB	0 (0)	0 (0)	1 (0.036)	28 (0.464)	3 (0.107)	0 (0)
Strophurus williamsi	Wambiana	WetA	0 (0)	0 (0)	0 (0)	1 (0.036)	0 (0)	0 (0)
Strophurus williamsi	Wambiana	WetB	0 (0)	0 (0)	0 (0)	1 (0.036)	0 (0)	0 (0)
Strophurus williamsi	Mourachan	DryA	0 (0)	0 (0)	0 (0)	1 (0.048)	0 (0)	0 (0)
Strophurus williamsi	Mourachan	DryB	0 (0)	0 (0)	1 (0.048)	0 (0)	0 (0)	0 (0)
Gekkonidae								
Christinus marmoratus	Tarcutta	DryB	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Gehyra dubia	Wambiana	DryA	0 (0)	0 (0)	3 (0.107)	66 (0.643)	13 (0.464)	0 (0)
Gehyra dubia	Wambiana	DryB	0 (0)	0 (0)	5 (0.036)	60 (0.643)	42 (0.714)	0 (0)
Gehyra dubia	Wambiana	WetA	0 (0)	0 (0)	4 (0.107)	85 (0.464)	53 (0.857)	0 (0)
Gehyra dubia	Wambiana	WetB	0 (0)	0 (0)	1 (0.036)	72 (0.571)	22 (0.286)	0 (0)
Gehyra dubia	Undara	DryA	0 (0)	0 (0)	0 (0)	28 (0.536)	8 (0.25)	0 (0)
Gehyra dubia	Undara	DryB	0 (0)	0 (0)	0 (0)	12 (0.222)	2 (0.074)	0 (0)
Gehyra dubia	Undara	WetA	0 (0)	0 (0)	2 (0.071)	12 (0.321)	1 (0.036)	0 (0)
Gehyra dubia	Undara	WetB	0 (0)	0 (0)	0 (0)	56 (0.556)	14 (0.407)	0 (0)
Gehyra dubia	Rinyirru	DryA	0 (0)	0 (0)	0 (0)	13 (0.214)	7 (0.25)	0 (0)
Gehyra dubia	Rinyirru	DryB	1 (0.036)	0 (0)	6 (0.179)	52 (0.679)	15 (0.429)	0 (0)
Gehyra dubia	Rinyirru	WetA	0 (0)	0 (0)	2 (0.071)	8 (0.25)	22 (0.607)	0 (0)
Gehyra dubia	Rinyirru	WetB	0 (0)	0 (0)	1 (0.036)	28 (0.571)	15 (0.393)	0 (0)
Gehyra dubia	Mourachan	DryB	0 (0)	0 (0)	0 (0)	1 (0.048)	0 (0)	0 (0)
Gehyra dubia	Mourachan	WetB	0 (0)	0 (0)	1 (0.048)	0 (0)	0 (0)	0 (0)
Hemidactylus frenatus	Rinyirru	WetA	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Heteronotia binoei	Wambiana	DryA	5 (0.107)	9 (0.25)	1 (0.036)	1 (0.036)	0 (0)	0 (0)
Heteronotia binoei	Wambiana	DryB	8 (0.179)	8 (0.179)	0 (0)	0 (0)	0 (0)	0 (0)
Heteronotia binoei	Wambiana	WetA	0 (0)	2 (0.071)	1 (0.036)	0 (0)	1 (0.036)	0 (0)
Heteronotia binoei	Wambiana	WetB	1 (0.036)	0 (0)	0 (0)	6 (0.143)	0 (0)	0 (0)
Heteronotia binoei	Undara	DryA	0 (0)	1 (0.036)	2 (0.071)	4 (0.143)	1 (0.036)	0 (0)
Heteronotia binoei	Undara	DryB	0 (0)	0 (0)	2 (0.037)	3 (0.074)	0 (0)	0 (0)
Heteronotia binoei	Undara	WetB	0 (0)	0 (0)	1 (0.037)	9 (0.259)	0 (0)	0 (0)
Heteronotia binoei	Rinyirru	DryA	0 (0)	4 (0.143)	0 (0)	1 (0.036)	1 (0.036)	0 (0)
Heteronotia binoei	Rinyirru	DryB	2 (0.071)	3 (0.107)	0 (0)	0 (0)	0 (0)	0 (0)
Heteronotia binoei	Rinyirru	WetA	2 (0.071)	6 (0.214)	0 (0)	0 (0)	0 (0)	0 (0)
Heteronotia binoei	Rinyirru	WetB	0 (0)	4 (0.143)	0 (0)	0 (0)	0 (0)	0 (0)
Heteronotia binoei	Mourachan	DryA	0 (0)	0 (0)	0 (0)	1 (0.048)	0 (0)	0 (0)
Heteronotia binoei	Mourachan	WetA	0 (0)	0 (0)	1 (0.048)	0 (0)	0 (0)	0 (0)
Pygopodidae								
Delma tincta	Undara	DryA	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Delma tincta	Undara	WetA	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Delma tincta	Undara	WetB	1 (0.037)	1 (0.037)	0 (0)	0 (0)	0 (0)	0 (0)
Lialis burtonis	Wambiana	WetA	0 (0)	2 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)
Lialis burtonis	Undara	DryB	0 (0)	2 (0.074)	0 (0)	0 (0)	0 (0)	0 (0)
Lialis burtonis	Rinyirru	DryA	0 (0)	0 (0)	0 (0)	1 (0.036)	0 (0)	0 (0)
Lialis burtonis	Rinyirru	DryB	0 (0)	2 (0.071)	1 (0.036)	0 (0)	0 (0)	0 (0)
Lialis burtonis	Rinyirru	WetA	2 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Lialis burtonis	Rinyirru	WetB	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Lialis burtonis	Mourachan	WetA	0 (0)	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)
Pygopus schraderi	Undara	WetA	0 (0)	2 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)
Pygopus steelescotti	Rinyirru	WetB	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Scincidae								
Carlia jarnoldae	Undara	DryA	3 (0.107)	4 (0.143)	8 (0.143)	0 (0)	0 (0)	0 (0)
Carlia jarnoldae	Undara	DryB	2 (0.074)	2 (0.074)	1 (0.037)	0 (0)	0 (0)	0 (0)
Carlia jarnoldae	Undara	WetA	2 (0.036)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Carlia jarnoldae	Undara	WetB	1 (0.037)	4 (0.148)	0 (0)	0 (0)	0 (0)	0 (0)
Carlia munda	Wambiana	DryA	3 (0.107)	7 (0.214)	1 (0.036)	0 (0)	0 (0)	0 (0)
Carlia munda	Wambiana	DryB	1 (0.036)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Carlia munda	Wambiana	WetA	8 (0.214)	27 (0.464)	0 (0)	0 (0)	0 (0)	0 (0)
Carlia munda	Wambiana	WetB	15 (0.429)	26 (0.571)	1 (0.036)	0 (0)	0 (0)	0 (0)
Carlia munda	Undara	DryA	17 (0.393)	40 (0.607)	1 (0.036)	0 (0)	0 (0)	0 (0)
Carlia munda	Undara	DryB	1 (0.037)	17 (0.481)	0 (0)	0 (0)	0 (0)	0 (0)
Carlia munda	Undara	WetA	9 (0.25)	43 (0.571)	0 (0)	0 (0)	0 (0)	0 (0)
Carlia munda	Undara	WetB	1 (0.037)	4 (0.111)	0 (0)	0 (0)	0 (0)	0 (0)
Carlia munda	Rinyirru	DryA	45 (0.714)	55 (0.786)	3 (0.107)	0 (0)	0 (0)	0 (0)

Species	Site	Plot	Survey Methods					
			PT	FT	IE	SL	ACB	CT
Carlia munda	Rinyirru	DryB	27 (0.429)	77 (0.786)	8 (0.214)	2 (0.036)	0 (0)	0 (0)
Carlia munda	Rinyirru	WetA	2 (0.071)	3 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)
Carlia munda	Rinyirru	WetB	2 (0.071)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Carlia rubigo	Wambiana	DryB	1 (0.036)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Carlia rubigo	Wambiana	WetA	6 (0.214)	5 (0.179)	0 (0)	0 (0)	0 (0)	0 (0)
Carlia rubigo	Wambiana	WetB	6 (0.143)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Carlia schmeltzii	Wambiana	DryB	2 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Carlia schmeltzii	Wambiana	WetA	1 (0.036)	1 (0.036)	1 (0.036)	0 (0)	0 (0)	0 (0)
Carlia schmeltzii	Wambiana	WetB	4 (0.143)	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)
Carlia schmeltzii	Undara	DryA	8 (0.25)	1 (0.036)	2 (0.071)	0 (0)	0 (0)	0 (0)
Carlia schmeltzii	Undara	DryB	0 (0)	2 (0.074)	0 (0)	0 (0)	0 (0)	0 (0)
Carlia schmeltzii	Undara	WetA	0 (0)	3 (0.107)	1 (0.036)	0 (0)	0 (0)	0 (0)
Carlia schmeltzii	Undara	WetB	4 (0.111)	5 (0.185)	0 (0)	0 (0)	0 (0)	0 (0)
Carlia schmeltzii	Rinyirru	DryB	1 (0.036)	2 (0.071)	1 (0.036)	0 (0)	0 (0)	0 (0)
Carlia schmeltzii	Rinyirru	WetA	1 (0.036)	4 (0.143)	2 (0.071)	0 (0)	0 (0)	0 (0)
Carlia schmeltzii	Rinyirru	WetB	0 (0)	7 (0.25)	0 (0)	1 (0.036)	0 (0)	0 (0)
Carlia tetradactyla	Tarcutta	WetA	5 (0.179)	4 (0.143)	0 (0)	0 (0)	0 (0)	0 (0)
Carlia tetradactyla	Tarcutta	WetB	8 (0.214)	12 (0.286)	0 (0)	0 (0)	0 (0)	0 (0)
Carlia vivax	Undara	DryB	0 (0)	2 (0.074)	0 (0)	0 (0)	0 (0)	0 (0)
Cryptoblepharus adamsi	Wambiana	DryA	0 (0)	0 (0)	0 (0)	0 (0)	2 (0.071)	0 (0)
Cryptoblepharus adamsi	Wambiana	DryB	2 (0.071)	0 (0)	0 (0)	0 (0)	4 (0.107)	0 (0)
Cryptoblepharus adamsi	Wambiana	WetA	9 (0.286)	1 (0.036)	0 (0)	0 (0)	41 (0.643)	0 (0)
Cryptoblepharus adamsi	Wambiana	WetB	4 (0.143)	0 (0)	2 (0.071)	0 (0)	19 (0.5)	0 (0)
Cryptoblepharus adamsi	Undara	DryA	0 (0)	0 (0)	0 (0)	0 (0)	2 (0.071)	0 (0)
Cryptoblepharus australis	Wambiana	DryA	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Cryptoblepharus australis	Wambiana	WetA	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.036)	0 (0)
Cryptoblepharus australis	Wambiana	WetB	0 (0)	0 (0)	0 (0)	0 (0)	2 (0.071)	0 (0)
Cryptoblepharus australis	Tarcutta	DryA	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.036)	0 (0)
Cryptoblepharus australis	Mourachan	DryA	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Cryptoblepharus australis	Mourachan	WetA	0 (0)	0 (0)	0 (0)	0 (0)	4 (0.095)	0 (0)
Cryptoblepharus australis	Mourachan	WetB	0 (0)	0 (0)	0 (0)	0 (0)	5 (0.143)	0 (0)
Cryptoblepharus metallicus	Undara	WetB	2 (0.074)	1 (0.037)	0 (0)	0 (0)	1 (0.037)	0 (0)
Cryptoblepharus metallicus	Rinyirru	DryA	4 (0.107)	1 (0.036)	0 (0)	0 (0)	14 (0.321)	0 (0)
Cryptoblepharus metallicus	Rinyirru	DryB	5 (0.107)	1 (0.036)	1 (0.036)	1 (0.036)	10 (0.25)	0 (0)
Cryptoblepharus metallicus	Rinyirru	WetA	7 (0.179)	2 (0.071)	0 (0)	0 (0)	12 (0.286)	0 (0)
Cryptoblepharus metallicus	Rinyirru	WetB	8 (0.214)	0 (0)	1 (0.036)	0 (0)	9 (0.179)	0 (0)
Cryptoblepharus pannosus	Undara	DryA	0 (0)	1 (0.036)	0 (0)	0 (0)	1 (0.036)	0 (0)
Cryptoblepharus pannosus	Undara	WetA	3 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Cryptoblepharus pannosus	Undara	WetB	1 (0.037)	0 (0)	0 (0)	0 (0)	1 (0.037)	0 (0)
Cryptoblepharus pannosus	Tarcutta	DryA	2 (0.071)	0 (0)	0 (0)	0 (0)	1 (0.036)	0 (0)
Cryptoblepharus pannosus	Tarcutta	DryB	2 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Cryptoblepharus pannosus	Tarcutta	WetA	2 (0.071)	0 (0)	0 (0)	0 (0)	5 (0.107)	0 (0)
Cryptoblepharus pannosus	Mourachan	DryA	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.048)	0 (0)
Cryptoblepharus pannosus	Mourachan	WetA	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.048)	0 (0)
Cryptoblepharus pannosus	Mourachan	WetB	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Cryptoblepharus virgatus	Rinyirru	DryA	9 (0.214)	0 (0)	0 (0)	0 (0)	3 (0.107)	0 (0)
Cryptoblepharus virgatus	Rinyirru	DryB	4 (0.107)	0 (0)	1 (0.036)	1 (0.036)	2 (0.036)	0 (0)
Cryptoblepharus virgatus	Rinyirru	WetA	2 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus allotropis	Mourachan	DryA	3 (0.143)	2 (0.095)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus allotropis	Mourachan	DryB	8 (0.143)	2 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus allotropis	Mourachan	WetA	12 (0.238)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus allotropis	Mourachan	WetB	3 (0.143)	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus brevipes	Rinyirru	DryA	7 (0.214)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus brevipes	Rinyirru	DryB	3 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus eutaenius	Undara	DryA	1 (0.036)	2 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus eutaenius	Undara	DryB	1 (0.037)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus ingrami	Mourachan	WetA	0 (0)	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus robustus	Wambiana	DryA	2 (0.071)	2 (0.071)	1 (0.036)	0 (0)	0 (0)	0 (0)
Ctenotus robustus	Wambiana	DryB	2 (0.071)	2 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus robustus	Wambiana	WetA	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus robustus	Wambiana	WetB	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus robustus	Tarcutta	DryB	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus robustus	Rinyirru	DryB	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus robustus	Mourachan	DryB	1 (0.048)	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus robustus	Mourachan	WetA	0 (0)	4 (0.19)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus robustus	Mourachan	WetB	0 (0)	3 (0.143)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus robustus	Duval	WetA	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus spaldingi	Undara	DryA	3 (0.071)	8 (0.214)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus spaldingi	Undara	DryB	1 (0.037)	5 (0.185)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus spaldingi	Undara	WetA	4 (0.143)	6 (0.214)	1 (0.036)	0 (0)	0 (0)	0 (0)

Species	Site	Plot	Survey Methods					
			PT	FT	IE	SL	ACB	CT
Ctenotus spaldingi	Undara	WetB	0 (0)	2 (0.074)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus spaldingi	Rinyirru	DryA	5 (0.107)	12 (0.357)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus spaldingi	Rinyirru	DryB	5 (0.179)	26 (0.607)	1 (0.036)	0 (0)	0 (0)	0 (0)
Ctenotus spaldingi	Rinyirru	WetA	0 (0)	3 (0.107)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus spaldingi	Rinyirru	WetB	4 (0.107)	4 (0.143)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus taeniolatus	Undara	DryB	0 (0)	2 (0.074)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus taeniolatus	Rinyirru	DryA	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus taeniolatus	Duval	WetA	0 (0)	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)
Ctenotus zebrilla	Undara	WetA	5 (0.179)	2 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)
Egernia striolata	Tarcutta	DryA	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Egernia striolata	Tarcutta	DryB	4 (0.143)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Egernia striolata	Tarcutta	WetB	3 (0.071)	3 (0.107)	0 (0)	0 (0)	0 (0)	0 (0)
Egernia striolata	Duval	DryB	1 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Eremiascincus isolepis	Undara	DryA	0 (0)	2 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)
Eremiascincus pardalis pardalis	Rinyirru	DryA	12 (0.286)	2 (0.071)	1 (0.036)	0 (0)	0 (0)	0 (0)
Eremiascincus pardalis pardalis	Rinyirru	DryB	17 (0.464)	21 (0.464)	2 (0.071)	0 (0)	0 (0)	0 (0)
Eremiascincus pardalis pardalis	Rinyirru	WetA	22 (0.571)	23 (0.464)	4 (0.143)	0 (0)	0 (0)	0 (0)
Eremiascincus pardalis pardalis	Rinyirru	WetB	39 (0.643)	37 (0.643)	2 (0.071)	3 (0.071)	0 (0)	0 (0)
Eremiascincus richardsonii	Mourachan	DryB	0 (0)	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)
Glaphyromorphus cracens	Undara	DryA	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Hemiergis talbingoensis talbingoensis	Duval	DryB	2 (0.143)	1 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)
Hemiergis talbingoensis talbingoensis	Duval	WetA	0 (0)	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)
Hemiergis talbingoensis talbingoensis	Duval	WetB	0 (0)	1 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)
Lampropholis delicata	Duval	DryA	15 (0.381)	15 (0.429)	0 (0)	0 (0)	0 (0)	0 (0)
Lampropholis delicata	Duval	DryB	12 (0.357)	2 (0.143)	0 (0)	0 (0)	0 (0)	0 (0)
Lampropholis delicata	Duval	WetA	20 (0.524)	14 (0.333)	1 (0.048)	0 (0)	0 (0)	0 (0)
Lampropholis delicata	Duval	WetB	10 (0.5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Lampropholis guichenoti	Tarcutta	WetA	0 (0)	0 (0)	2 (0.036)	0 (0)	0 (0)	0 (0)
Lampropholis guichenoti	Tarcutta	WetB	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Lampropholis guichenoti	Duval	DryA	32 (0.762)	30 (0.524)	0 (0)	0 (0)	0 (0)	0 (0)
Lampropholis guichenoti	Duval	DryB	30 (0.5)	26 (0.643)	0 (0)	0 (0)	0 (0)	0 (0)
Lampropholis guichenoti	Duval	WetA	33 (0.762)	38 (0.714)	0 (0)	0 (0)	0 (0)	0 (0)
Lampropholis guichenoti	Duval	WetB	28 (0.643)	10 (0.357)	0 (0)	0 (0)	0 (0)	0 (0)
Lerista bougainvillii	Tarcutta	DryB	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Lerista bougainvillii	Tarcutta	WetA	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Lerista punctatovittata	Mourachan	DryA	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Lerista timida	Mourachan	DryA	0 (0)	1 (0.048)	1 (0.048)	1 (0.048)	0 (0)	0 (0)
Lerista timida	Mourachan	DryB	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Lerista zonulata	Undara	DryA	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Lerista zonulata	Undara	WetA	3 (0.107)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Lerista zonulata	Rinyirru	WetA	32 (0.607)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Lerista zonulata	Rinyirru	WetB	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Liburnascincus mundivensis	Undara	DryA	0 (0)	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)
Liburnascincus mundivensis	Undara	DryB	1 (0.037)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Lygisaurus aeratus	Rinyirru	DryA	18 (0.321)	8 (0.179)	3 (0.107)	1 (0.036)	0 (0)	0 (0)
Lygisaurus aeratus	Rinyirru	DryB	7 (0.179)	8 (0.214)	0 (0)	2 (0.036)	0 (0)	0 (0)
Lygisaurus aeratus	Rinyirru	WetA	15 (0.393)	5 (0.179)	1 (0.036)	0 (0)	0 (0)	0 (0)
Lygisaurus aeratus	Rinyirru	WetB	13 (0.357)	5 (0.143)	1 (0.036)	0 (0)	0 (0)	0 (0)
Lygisaurus foliorum	Mourachan	DryB	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Lygisaurus foliorum	Mourachan	WetB	4 (0.19)	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)
Lygisaurus rococo	Undara	WetB	0 (0)	2 (0.074)	0 (0)	0 (0)	0 (0)	0 (0)
Menetia greyii	Wambiana	DryA	5 (0.143)	3 (0.107)	0 (0)	0 (0)	0 (0)	0 (0)
Menetia greyii	Wambiana	DryB	7 (0.143)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Menetia greyii	Wambiana	WetB	1 (0.036)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Menetia greyii	Undara	DryA	2 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Menetia greyii	Undara	DryB	1 (0.037)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Menetia greyii	Undara	WetA	4 (0.143)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Menetia greyii	Rinyirru	DryA	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Menetia greyii	Mourachan	DryB	2 (0.095)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Menetia greyii	Mourachan	WetB	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Morethia boulengeri	Tarcutta	DryA	6 (0.179)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Morethia boulengeri	Tarcutta	DryB	2 (0.071)	2 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)

Species	Site	Plot	Survey Methods					
			PT	FT	IE	SL	ACB	CT
Morethia boulengeri	Tarcutta	WetA	13 (0.25)	6 (0.179)	0 (0)	0 (0)	0 (0)	0 (0)
Morethia boulengeri	Tarcutta	WetB	3 (0.071)	2 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)
Morethia boulengeri	Mourachan	DryA	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Morethia boulengeri	Mourachan	DryB	2 (0.095)	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)
Morethia boulengeri	Mourachan	WetA	3 (0.095)	4 (0.095)	1 (0.048)	0 (0)	0 (0)	0 (0)
Morethia boulengeri	Mourachan	WetB	1 (0.048)	2 (0.095)	0 (0)	0 (0)	0 (0)	0 (0)
Morethia taeniopleura	Wambiana	DryA	3 (0.107)	4 (0.143)	0 (0)	0 (0)	0 (0)	0 (0)
Morethia taeniopleura	Wambiana	DryB	0 (0)	3 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)
Morethia taeniopleura	Wambiana	WetA	1 (0.036)	3 (0.107)	0 (0)	0 (0)	0 (0)	0 (0)
Morethia taeniopleura	Wambiana	WetB	2 (0.071)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Morethia taeniopleura	Undara	DryA	6 (0.179)	3 (0.107)	0 (0)	0 (0)	0 (0)	0 (0)
Morethia taeniopleura	Undara	DryB	2 (0.074)	1 (0.037)	0 (0)	0 (0)	0 (0)	0 (0)
Morethia taeniopleura	Undara	WetA	2 (0.071)	3 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)
Morethia taeniopleura	Undara	WetB	5 (0.148)	4 (0.148)	0 (0)	0 (0)	0 (0)	0 (0)
Morethia taeniopleura	Rinyirru	WetA	11 (0.321)	2 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)
Morethia taeniopleura	Rinyirru	WetB	2 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Proablepharus tenuis	Wambiana	DryA	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Proablepharus tenuis	Wambiana	WetB	1 (0.036)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Proablepharus tenuis	Undara	DryA	6 (0.214)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Proablepharus tenuis	Undara	DryB	1 (0.037)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Proablepharus tenuis	Undara	WetA	3 (0.107)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Proablepharus tenuis	Undara	WetB	2 (0.074)	1 (0.037)	0 (0)	0 (0)	0 (0)	0 (0)
Pygmaeascincus timlowi	Wambiana	DryA	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Pygmaeascincus timlowi	Wambiana	WetA	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Saproscincus mustelinus	Duval	DryA	9 (0.286)	8 (0.19)	0 (0)	0 (0)	0 (0)	0 (0)
Saproscincus mustelinus	Duval	DryB	14 (0.286)	9 (0.5)	0 (0)	0 (0)	0 (0)	0 (0)
Saproscincus mustelinus	Duval	WetA	4 (0.143)	10 (0.238)	0 (0)	0 (0)	0 (0)	0 (0)
Saproscincus mustelinus	Duval	WetB	11 (0.286)	8 (0.429)	0 (0)	0 (0)	0 (0)	0 (0)
Varanidae								
Varanus panoptes panoptes	Rinyirru	DryA	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (0.071)
Varanus panoptes panoptes	Rinyirru	DryB	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (0.071)
Varanus panoptes panoptes	Rinyirru	WetA	0 (0)	0 (0)	2 (0.071)	0 (0)	0 (0)	3 (0.107)
Varanus panoptes panoptes	Rinyirru	WetB	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (0.071)
Varanus panoptes panoptes	Mourachan	DryA	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.048)
Varanus panoptes panoptes	Mourachan	DryB	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	4 (0.143)
Varanus panoptes panoptes	Mourachan	WetA	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (0.095)
Varanus panoptes panoptes	Mourachan	WetB	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.048)
Varanus scalaris	Rinyirru	DryA	3 (0.107)	0 (0)	0 (0)	2 (0.071)	0 (0)	0 (0)
Varanus scalaris	Rinyirru	DryB	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Varanus scalaris	Rinyirru	WetB	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Varanus storri	Undara	DryB	1 (0.037)	1 (0.037)	0 (0)	0 (0)	0 (0)	0 (0)
Varanus tristis	Rinyirru	DryB	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Varanus tristis	Rinyirru	WetA	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.036)
Varanus tristis	Rinyirru	WetB	6 (0.214)	1 (0.036)	1 (0.036)	0 (0)	0 (0)	0 (0)
Varanus tristis	Mourachan	WetB	0 (0)	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)
Varanus varius	Tarcutta	DryB	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (0.071)
Varanus varius	Mourachan	DryA	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (0.095)
Varanus varius	Mourachan	WetA	0 (0)	0 (0)	1 (0.048)	0 (0)	0 (0)	4 (0.143)
Varanus varius	Mourachan	WetB	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.048)
Serpentes								
Colubridae								
Boiga irregularis	Wambiana	DryA	0 (0)	0 (0)	0 (0)	1 (0.036)	0 (0)	0 (0)
Tropidonophis mairii mairii	Wambiana	DryA	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Tropidonophis mairii mairii	Wambiana	WetA	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Tropidonophis mairii mairii	Rinyirru	DryB	2 (0.071)	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)
Tropidonophis mairii mairii	Rinyirru	WetA	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Tropidonophis mairii mairii	Rinyirru	WetB	6 (0.071)	1 (0.036)	1 (0.036)	0 (0)	0 (0)	0 (0)
Elapidae								
Brachyurophis australis	Wambiana	DryA	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Brachyurophis australis	Undara	DryA	1 (0.036)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Brachyurophis campbelli	Undara	DryB	0 (0)	1 (0.037)	0 (0)	0 (0)	0 (0)	0 (0)
Brachyurophis campbelli	Rinyirru	WetA	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Cryptophis boschmai	Wambiana	DryA	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Cryptophis boschmai	Wambiana	WetB	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Cryptophis boschmai	Undara	DryB	0 (0)	1 (0.037)	0 (0)	0 (0)	0 (0)	0 (0)

Species	Site	Plot	Survey Methods					
			PT	FT	IE	SL	ACB	CT
Cryptophis boschmai	Undara	WetB	0 (0)	1 (0.037)	0 (0)	0 (0)	0 (0)	0 (0)
Cryptophis nigrostriatus	Undara	WetB	0 (0)	2 (0.037)	0 (0)	0 (0)	0 (0)	0 (0)
Cryptophis nigrostriatus	Rinyirru	DryB	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Demansia vestigiata	Wambiana	WetB	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Demansia vestigiata	Rinyirru	DryA	0 (0)	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)
Demansia vestigiata	Rinyirru	DryB	0 (0)	2 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)
Demansia vestigiata	Rinyirru	WetA	0 (0)	0 (0)	2 (0.036)	0 (0)	0 (0)	0 (0)
Demansia vestigiata	Rinyirru	WetB	0 (0)	11 (0.214)	1 (0.036)	0 (0)	0 (0)	0 (0)
Furina diadema	Mourachan	WetB	0 (0)	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)
Furina ornata	Wambiana	DryB	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Furina ornata	Wambiana	WetB	0 (0)	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)
Furina ornata	Undara	DryB	0 (0)	0 (0)	0 (0)	1 (0.037)	0 (0)	0 (0)
Furina ornata	Undara	WetB	0 (0)	0 (0)	0 (0)	2 (0.074)	0 (0)	0 (0)
Furina ornata	Rinyirru	DryA	0 (0)	0 (0)	0 (0)	1 (0.036)	0 (0)	0 (0)
Furina ornata	Rinyirru	DryB	0 (0)	1 (0.036)	0 (0)	1 (0.036)	0 (0)	0 (0)
Furina ornata	Rinyirru	WetA	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Hoplocephalus bitorquatus	Undara	DryA	0 (0)	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)
Hoplocephalus bitorquatus	Undara	WetA	1 (0.036)	0 (0)	0 (0)	1 (0.036)	2 (0.071)	0 (0)
Oxyuranus scutellatus scutellatus	Rinyirru	WetB	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Pseudechis porphyriacus	Duval	WetA	0 (0)	1 (0.048)	1 (0.048)	0 (0)	0 (0)	0 (0)
Pseudonaja nuchalis	Undara	DryB	0 (0)	1 (0.037)	0 (0)	0 (0)	0 (0)	0 (0)
Pseudonaja nuchalis	Undara	WetB	0 (0)	1 (0.037)	0 (0)	0 (0)	0 (0)	0 (0)
Pseudonaja nuchalis	Rinyirru	WetA	0 (0)	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)
Pseudonaja textilis	Wambiana	DryA	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Pseudonaja textilis	Wambiana	WetA	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	1 (0.036)
Pseudonaja textilis	Wambiana	WetB	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Pseudonaja textilis	Undara	WetB	0 (0)	1 (0.037)	0 (0)	0 (0)	0 (0)	0 (0)
Pseudonaja textilis	Tarcutta	DryB	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Suta dwyeri	Tarcutta	WetA	0 (0)	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)
Suta dwyeri	Mourachan	WetA	0 (0)	0 (0)	0 (0)	1 (0.048)	0 (0)	0 (0)
Suta dwyeri	Mourachan	WetB	0 (0)	1 (0.048)	0 (0)	1 (0.048)	0 (0)	0 (0)
Vermicella annulata	Mourachan	DryA	0 (0)	2 (0.095)	0 (0)	0 (0)	0 (0)	0 (0)
Vermicella annulata	Mourachan	DryB	0 (0)	0 (0)	1 (0.048)	0 (0)	0 (0)	0 (0)
Pythonidae								
Antaresia maculosa	Wambiana	WetA	0 (0)	0 (0)	0 (0)	1 (0.036)	0 (0)	0 (0)
Antaresia maculosa	Undara	DryA	0 (0)	0 (0)	0 (0)	1 (0.036)	0 (0)	0 (0)
Typhlopidae								
Anilios broomi	Rinyirru	DryA	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Anilios broomi	Rinyirru	DryB	2 (0.071)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Anilios broomi	Rinyirru	WetB	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Anilios nigrescens	Duval	WetA	1 (0.048)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Anilios proximus	Tarcutta	DryB	1 (0.036)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Testudines								
Chelidae								
Chelodina longicollis	Duval	WetB	0 (0)	0 (0)	1 (0.071)	0 (0)	0 (0)	0 (0)
Emydura macquarii	Wambiana	WetA	0 (0)	0 (0)	0 (0)	3 (0.071)	0 (0)	0 (0)
Emydura macquarii	Mourachan	WetA	0 (0)	0 (0)	4 (0.095)	0 (0)	0 (0)	0 (0)
Total number of species			60	69	42	28	11	5
Total number of unique species			13	33	3	7	2	3
Total number of observations			978	944	152	706	514	29
Average detection probability			0.076	0.069	0.014	0.033	0.03	0.003