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ORIGINAL RESEARCH

Do acoustically detectable species reflect overall diversity? A case study from Australia's arid zone

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Abstract

In recent years, passive acoustic monitoring has emerged as a reliable method for monitoring soniferous fauna, with numerous studies finding estimates of species richness and community composition are comparable with estimates derived from conventional field surveys. Most of these studies compare point counts of forest bird communities with contemporaneous short-duration acoustic recordings, but several questions remain. How do these two methods compare in more open, arid ecosystems, how does applying methods optimally influence comparisons, and how do patterns in acoustically detectable species compare with overall patterns? Here we demonstrate techniques for improving sampling of acoustic data and conduct acoustic surveys to estimate species richness from ephemeral creek-lines in the Australian arid zone using a long-term passively derived acoustic dataset. We examine these results in the context of long-term observer-based transect surveys conducted along the same creek-lines to define species within the avian assemblage that are acoustically detectable or acoustically undetectable/cryptic. Our data suggest that some species were consistently missed by acoustic surveys, but most belonged to groups that are typically excluded from inventories prior to analysis including rare species, raptors, waterbirds, swallows and nocturnal birds. Further, the relative diversities of sites were well estimated by acoustic surveys, with variations between sites reflecting those estimated by observer-based field surveys. This suggests that in our study system, acoustically detectable species are reliable indicators of overall species richness. Field-based surveys will remain an important component of sampling in arid ecosystems and we highlight the value of applying acoustic and conventional field-based surveys in a complementary manner. This approach allows large, publishable datasets to be generated by exploiting the temporal reach of acoustic sensors, while also maximizing detections of acoustically cryptic species via field-based surveys. We argue that acoustic monitoring has the potential to facilitate greater research effort in largely research-deficient arid ecosystems.

Introduction

Long-duration passive acoustic monitoring has several advantages that may be desirable to both ecological researchers and environmental managers. An obvious advantage is the large volume of data that can be collected with minimal effort and ongoing expense when compared to surveys conducted by field-based observers (Thomas and Marques, 2012). This in turn allows very fine-grained temporal sampling rates. With the simultaneous deployment of multiple sensors, even greater volumes of data can be collected. This also facilitates accurate 'snapshot' style sampling, (where sampling occurs within the shortest possible timeframe) as it is possible to collect all samples at exactly the same time using passive acoustic sensors, which is typically unachievable using field-based observers. Another desirable feature of environmental recordings is that signals within them can be verified by multiple independent listeners, bringing the capacity for increased accuracy and

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verifiability, particularly where acoustic fauna inventories are archived. Acoustic monitoring is largely non-invasive and typically has no discernible negative impacts on biota. Furthermore, compared to conventional observation and capture-based sampling, acoustic monitoring is unlikely to influence animal behaviour during surveys (Darras et al. 2018b) and has minimal impact on animal welfare. Finally, acoustic recordings can be stored permanently, meaning that we can accumulate rich libraries that can be retrospectively analysed and reanalysed as acoustic processing and visualization tools are developed and refined. Concerns about the deficiency of long-term ecosystem monitoring programmes as a result of dynamic funding priorities are well documented (Lindenmayer et al. 2012; Lindenmayer et al. 2015) and passive acoustic monitoring may play an important role in addressing some of these concerns (Shonfield and Bayne, 2017; Darras et al. 2018a). Indeed, acoustic monitoring has already been effectively incorporated into long-term monitoring programmes, for example Furnas (2020).

One fundamental limitation of acoustic monitoring techniques is that they cannot detect species that are not soniferous or species that produce sounds that are not reliably identifiable. Defining those subsets of species in a given system that can and cannot be detected and identified acoustically, or that are likely and unlikely to be detected acoustically, is important for fully understanding the value of acoustic sensors for monitoring assemblages. Identifying the mechanisms that underpin their omission from inventories is also important for future application of the technique. Regardless of sampling methods, it is not known whether overall richness patterns are comparable with richness patterns of acoustically detectable and acoustically identifiable species. Our research seeks to test this in order to determine whether passive acoustic sampling techniques can be effectively used for environmental monitoring or to address ecological questions reliant on comparing species richness estimates.

Passive acoustic sensors are capable of producing very large datasets, but analysing this data is time consuming and listening to these long-duration recordings in full is rarely feasible. Aurally reviewing short samples of environmental recordings may be an effective way of addressing this big data obstacle. To determine the utility of acoustic sensors for fauna surveys, several studies have conducted comparative evaluations of passive acoustic and human-based field monitoring (Darras et al. 2018a). These are typically conducted by an aural observer reviewing soundscape recordings that were collected contemperaneously to a field-based observer (often the same observer) conducting point count (Darras et al. 2018a). The point count versus simultaneous acoustic recording approach is likely favoured in these studies as it eliminates variables such as transects or area searches by field observers sampling areas beyond the detection range of the sensor. It also eliminates different times being sampled by sensors that are deployed beyond the timeframe of the comparative survey. However, by performing comparisons in this way, the performance of one or both methodologies is constrained. Additionally, when the same observer conducts both the field survey and subsequent acoustic analyses, the comparison is systematically biased, given that the observer has detailed prior knowledge of the species present in the area, both generally and often specifically at the time of the survey. This bias can affect species identifications based on recorded vocalizations which may systematically inflate resultant richness estimates. Additionally, the presence of observers can influence bird detectability and eliminate an important advantage of acoustic surveys (Darras et al. 2018b) (although see Campbell and Francis, 2012).

Point counts are a useful survey technique for some applications, however, for others, transects or area searches are more appropriate (Verner and Ritter, 1985; Buckland 2006; Colvocoresses and Acosta, 2007). By excluding transects and area searches from methodological considerations to facilitate comparability with data from acoustic sensors, data derived from field-based observers may not be collected optimally (see Watson 2003; Watson 2004). For example in arid Australia, point counts are less effective for sampling birds than transects and area searches (Pascoe et al. 2019).

Similarly, sequential sampling may not represent the best use of long-duration acoustic data. The temporal reach of these datasets allows analysts to draw from days, weeks or months of recorded vocalizations to estimate a site's species richness, rather than being restricted to a brief window of time, as is the case with observer-based field surveys. Wimmer et al. (2013b) demonstrated that listening to 1-min clips of environmental recordings drawn randomly from dawn choruses over many days produced better estimates of species richness than listening to sequential 1-min recordings. The mechanism driving this result has not been adequately explored, but is likely because birds are highly mobile and the avian assemblage around a given point can be dynamic, showing differences in composition between days, hours and even minutes. Rather than exhaustively analysing a continuous recording, for dynamic assemblages, it may be beneficial to sample many shorter recordings (the sum of which are equivalent in length to a continuous recording) from many different times in order to increase the likelihood of encountering species that move in and out of the detectable range of the acoustic sensor. While listening to recordings sequentially (i.e. contemporaneously to data available to field observers) facilitates

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comparability, the inherent strengths of acoustic monitoring are diminished.

Before applying non-sequential sampling protocols, it is important to consider violation of the 'closure assumption' in an occupancy-modelling context. The term closure relates to birds moving in and out of the site and requires a survey window (the period during which several surveys are conducted for occupancy analysis) be brief enough to allow the assumption that the composition of the bird assemblage remains constant. This allows the assumption to be made that if a species is detected at a site on any one survey, then it was present during all surveys, but was not detected (MacKenzie et al. 2002; MacKenzie et al. 2017). Non-sequential acoustic sampling is important in facilitating occupancy analyses of acoustic data as it is akin to repeat surveys. However, when designing sampling regimes it is important to identify whether occupancy analysis is a priority. If it is a priority, it may be necessary to limit the duration over which non-sequential samples are collected in order to minimize the risk of violating closure assumptions.

Closure is still an important consideration regardless of occupancy models. In order to define the period over which non-sequential samples should be collected where quantifying detectability is not a priority, survey protocol designers should consider the period of time that the sample is deemed to represent. If a monitoring programme surveys sites once in a season then those samples can be regarded as being representative of that season or year, despite only being collected on 1 day. As such, it is reasonable to sample acoustically derived data from throughout that season in order to best represent that season. In intensive monitoring work where sites are sampled several times within a season, a sample may represent a week and, in those cases, acoustic sampling should be restricted to that week. As long as the period that the sample is determined to represent is well defined, and an adequate buffer is left between sampling efforts to facilitate independence, then sampling of long-duration acoustic datasets from within that period should improve sample completeness.

Here, we conduct acoustic sampling surveys using a large acoustic dataset collected by sensors permanently deployed along ephemeral creek-lines in the Australian arid zone. In the process, we demonstrate methods for improving sampling of acoustic data by accurately defining the bounds of dawn choruses and randomly sampling within these bounds throughout the period that 'snapshot' style sampling by a field observer is considered to represent. We then use data derived from long-term transect surveys performed along the same creek-lines as an index against which to compare the results of the acoustic surveys. We define acoustically detectable species in the study area and reflect on mechanisms determining omissions of species known to inhabit the study area that were not detected using acoustic sensors. Having applied both acoustic sampling and transect surveys optimally we generate and compare species richness estimates and address fundamental gaps in the literature around evaluating acoustic monitoring as a method for estimating species richness.

Materials and Methods

Study site

Fieldwork was conducted in the south-eastern parts of Sturt National Park, which is located in the arid far north-western corner of New South Wales, central Australia (Fig. 1). The study sites were located along four ephemeral creek-lines within the park: Arcoola Creek, Mistletoe Creek, Stud Creek and Thompson Creek. These creeks are all located within a maximum of 10 km of each other and were selected as representative samples of the same ecosystem. However, each differs in terms of habitat type, channel structure and vegetation type, to ensure different sets of resources within the system were sampled. Arid Australian bird assemblages contain a high proportion of nomadic and irruptive species (Mac Nally et al. 2004) that respond to pulses in resources within days or weeks. Breeding events are largely dependent on rainfall rather than showing strong seasonality (Keast 1959).

Transect surveys

Transect surveys recording bird species richness have been conducted along the four creek-lines every winter since 2003 (with the exceptions of 2005 and 2013). Surveys consisted of an observer walking along a creek at a steady pace until reaching a defined end point before stopping briefly and walking back. Creek-line transects were *c.* 3 km long and extended *c.* 1.5 km in either direction from a midpoint. In each winter, each creek was surveyed once in its entirety, from one direction from the midpoint in the morning and the other direction from the midpoint in the evening of a different day. In winter, morning surveys commenced mid-morning and afternoon surveys commenced in the late afternoon, coinciding with periods of increased bird activity. Unlike temperate woodlands and forests, bird activity in the Australian arid zone does not peak at dawn and dusk, especially during winter (see Cody 1994; Watson 2004). Each of the four creek-lines were surveyed for a total of *c.* 5 h during each visit to the study site, the area being sampled determined by the extent of woody vegetation either side of the creek-line.

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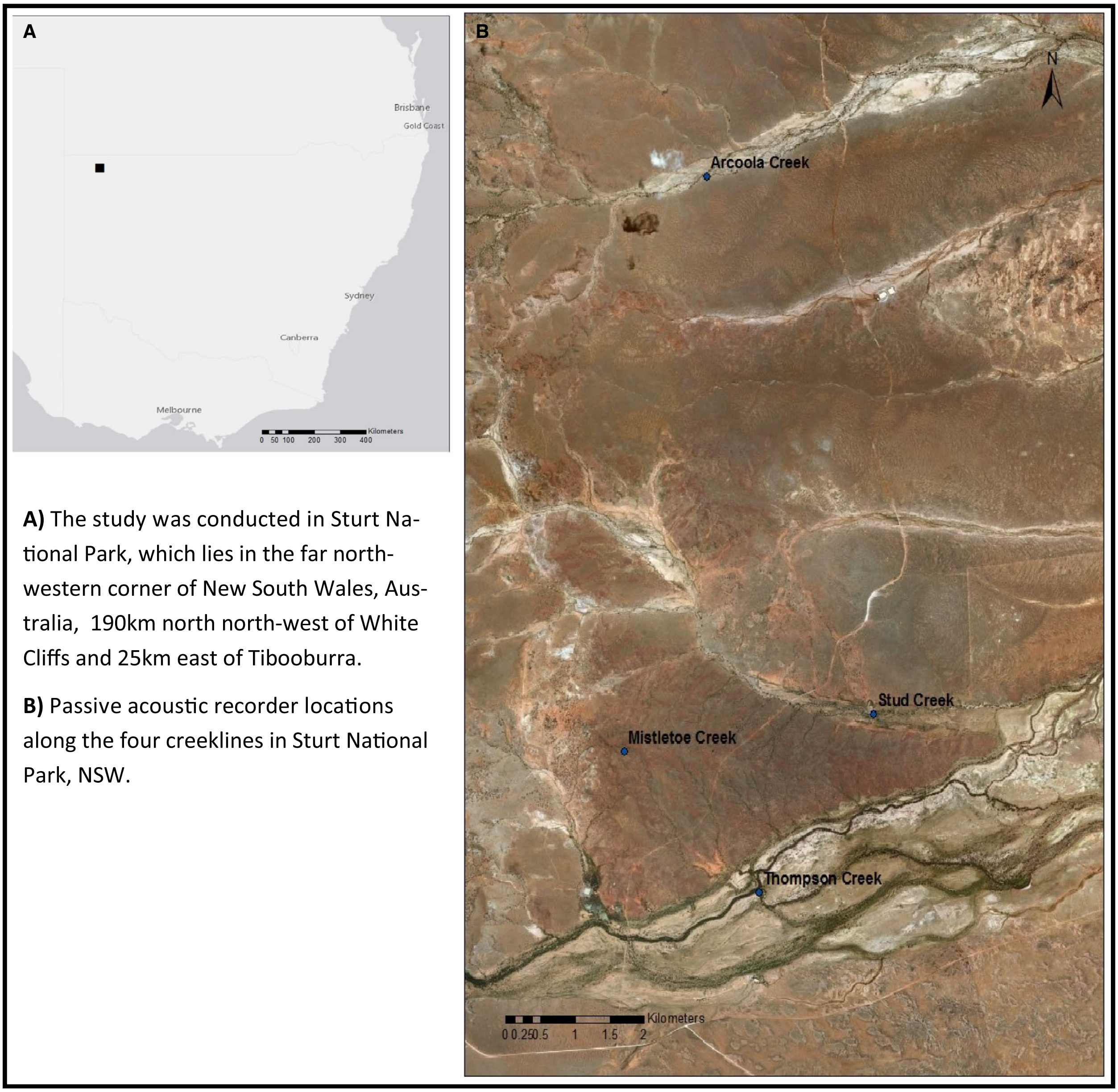

Figure 1. (A) The study was conducted in Sturt National Park, north-western NSW, Australia. The study area is 190 km north north-west of White Cliffs and 25 km east of Tibooburra. (B) Passive acoustic recorder locations along the four creeklines in Sturt National Park, NSW.

Only bird species that were seen or heard within the creek or adjacent riparian habitat and that were below canopy height were recorded. Birds that flew overhead were not recorded unless they were deemed to be actively using the creek-line, for example a raptor flying overhead hunting along the creek-line. The results of the morning and evening surveys were compiled to generate one species list for each creek-line for each visit. All transect surveys were conducted by DMW, with full data uploaded to eBird. For all but the 'classification of rare species' component of our analysis (Table 3), we excluded transect data collected before 2014 to allow comparisons between these data and the contemporaneous acoustically derived data described next.

Acoustic surveys

Single permanent acoustic monitoring stations were installed along each of the four creek-lines in June 2014 (Fig. 2). Each station consists of a sound recorder (Wildlife Acoustics Songmeter SM2+, Maynard, MA, USA), solar panel, charge regulator and a deep cycle battery, all

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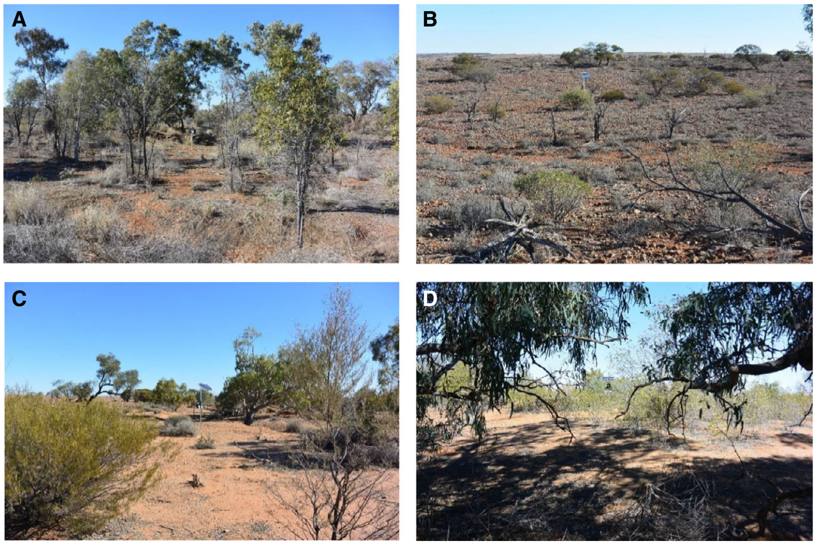

Figure 2. Images of each permanently installed acoustic sensor showing the habitat sampled. (A) Arcoola Creek, (B) Mistletoe Creek, (C) Stud Creek and (D) Thompson Creek.

mounted onto a steel pole concreted into the ground (Fig. 3). The two microphones (standard model supplied by Wildlife Acoustics with the sensor) projected from the sides of the sensor, parallel to the ground at a height of *c.* 1.5 m. These devices have been continuously recording acoustic data since deployment (with the exception of periods where sensors have malfunctioned). Audio was collected as 22 050 Hz, 16-bit WAAC (.wac) files, which were stored on high capacity SD cards. SD cards were collected and replaced annually during transect surveys. Recordings were then converted to 22 050 Hz, 16-bit WAVE files and imported into *Ecosounds* (https://www.ecosounds.org), an online platform designed for storing, annotating and analysing long-duration environmental recordings (Wimmer et al. 2013a).

Microphones were replaced in winter 2017 and we conducted distance trials at this time to ensure detection range remained constant. Trials were conducted at Arcoola and Thompson Creeks whereby calls of Pied Honeyeaters *Certhionyx variegatus* were played at a fixed volume at distances of 10, 25, 50 and 100 m from the sensor (playback was also conducted at 200 m from the sensor at Arcoola Creek). This playback routine was repeated four times at each creek-line; 2 with microphones that were 3 years old played once through open country and once through vegetation and then 2 with replacement microphones again once through open country and once through vegetation. We then prepared spectrograms for each playback event and made visual and aural comparisons.

These trials revealed no observable difference in attenuation between old microphones and new microphones.

Figure 3. The acoustic monitoring station from Thompson Creek in Sturt National Park. The black panel at the top of the station is the solar panel, the green box is the Wildlife Acoustics Songmeter SM2+ and the white box is a weatherproof case that holds the deep cycle battery and charge regulator

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There was also no observable difference in attenuation according to vegetation structure suggesting that the vegetation along the creek-lines where distance trials were carried out was not structurally complex enough to influence recordings. In general, attenuation over distance was intuitive and signals gradually became weaker with distance from the sensor. At greater distances, wind appeared to influence the ability of the sensors to detect playback. This was not due to microphones clipping, but to turbulence limiting the ability of the air to propagate sound. Even at 200 m between speaker and sensor, signals were detectable, but often only parts of calls could be heard and seen in spectrograms. This suggests that between gusts, sounds were able to reach the sensor, but during gusts they were interrupted. These results confirm that detection range remained constant throughout this experiment even after microphones were replaced. Given that vegetation structure had no observable effect, it is likely that detection range remained constant between creek-lines.

Sampling

We took two steps to improve the efficiency of acoustic sampling; accurately defining dawn choruses and sampling over long periods within these defined dawn choruses. False-colour spectrograms (Towsey et al. 2014), visualizations that display acoustic data using complementary acoustic indices to emphasize features of interest within soundscapes, were used to define bounds of dawn choruses to direct sampling to periods of maximum acoustic activity (Fig. 4). The acoustic indices we used to produce false-colour spectrograms are defined and described in Table 1. We visually scanned images that depicted 24 h soundscapes over several years and made note of the shifts in dawn choruses between seasons and creek-lines. For each creek-line and month, we determined the window of time that the dawn chorus typically fell within. Dawn choruses varied between creeks and months, but sampling never began before 0630 or finished after 1030. It is important to note that even though peak periods did not always commence at dawn, we continue to refer to them as dawn choruses. All acoustic sampling targeted dawn choruses as false-colour spectrograms consistently showed these periods to be much more acoustically complex than other periods. By accurately defining periods of peak acoustic activity, we were able to strictly constrain our sampling effort to these periods. This was an attempt to minimize the chances of encountering samples that contained no bird song, which we deemed to be an important consideration in a relatively sparse soundscape.

Wimmer et al. (2013b) found that when sampling long-duration environmental recordings using a fixed number of 1-min samples, selecting these samples randomly rather than in a sequential block produced greater estimates of bird species richness. Following these findings, we sampled 30 $\times$ 2 min recordings selected randomly from within dawn choruses (as defined by false-colour spectrogram analysis) within the Austral winter months of June, July and August. Where data had not been collected due to sensor malfunction, we generated samples from the remaining winter dawn choruses for that year and creek. In 2017, the sensor on Stud Creek failed, so the survey was not able to be conducted for that creek-line (Table 2).

We drew data from this 3-month time period, rather than a shorter sample window, for example a week either side of the transect survey, as a result of the frequency at which transect surveys were routinely conducted. Typically, each creek-line is surveyed once every year in winter. Thus, the questions that these surveys are able to inform are based upon the birds that are present at the study sites in that particular year or season, rather than in that month, week or day.

Our approach of non-sequential sampling was a way for us to justify comparing transects to recordings from a fixed point. This is because the temporal reach of the sensor should offset the lack of spatial reach compared to transects (see Zwart et al. 2014), although we did not seek to quantify to what extent. Another factor that justifies comparing disparate geographic areas (transects vs. fixed sensors) is that most point counts are intended to be representative of the broader area beyond the detectable range of a sensor or field observer.

Acoustic analysis

Recordings were analysed in *Ecosounds* (Wimmer et al. 2013a) by simultaneously listening to and viewing accompanying real-time greyscale spectrograms that displayed 30 sec of data at a time. Sony MDR10R headphones were used in acoustic analysis. We compiled inventories for each creek in each winter from 2014 to 2017 by recording every species detected within 30 $\times$ 2 min samples. Each survey of 30 $\times$ 2 min samples took no more than 2 h to complete, which constituted less than half the survey effort of each 5-h transect survey.

Acoustic recordings were exclusively analysed by DGS, an experienced field ecologist with considerable field experience in the study area. He was familiar with the sites and was present for the transect surveys in summer 2015 and winter 2016, confirming comparability of observer skills with DMW. Data from 2015 were not included in these comparative analyses. It was important that our acoustic observer was independent and not familiar with the outcome of the majority of transect surveys, but not entirely naive to the sites, equipment and the avian assemblage.

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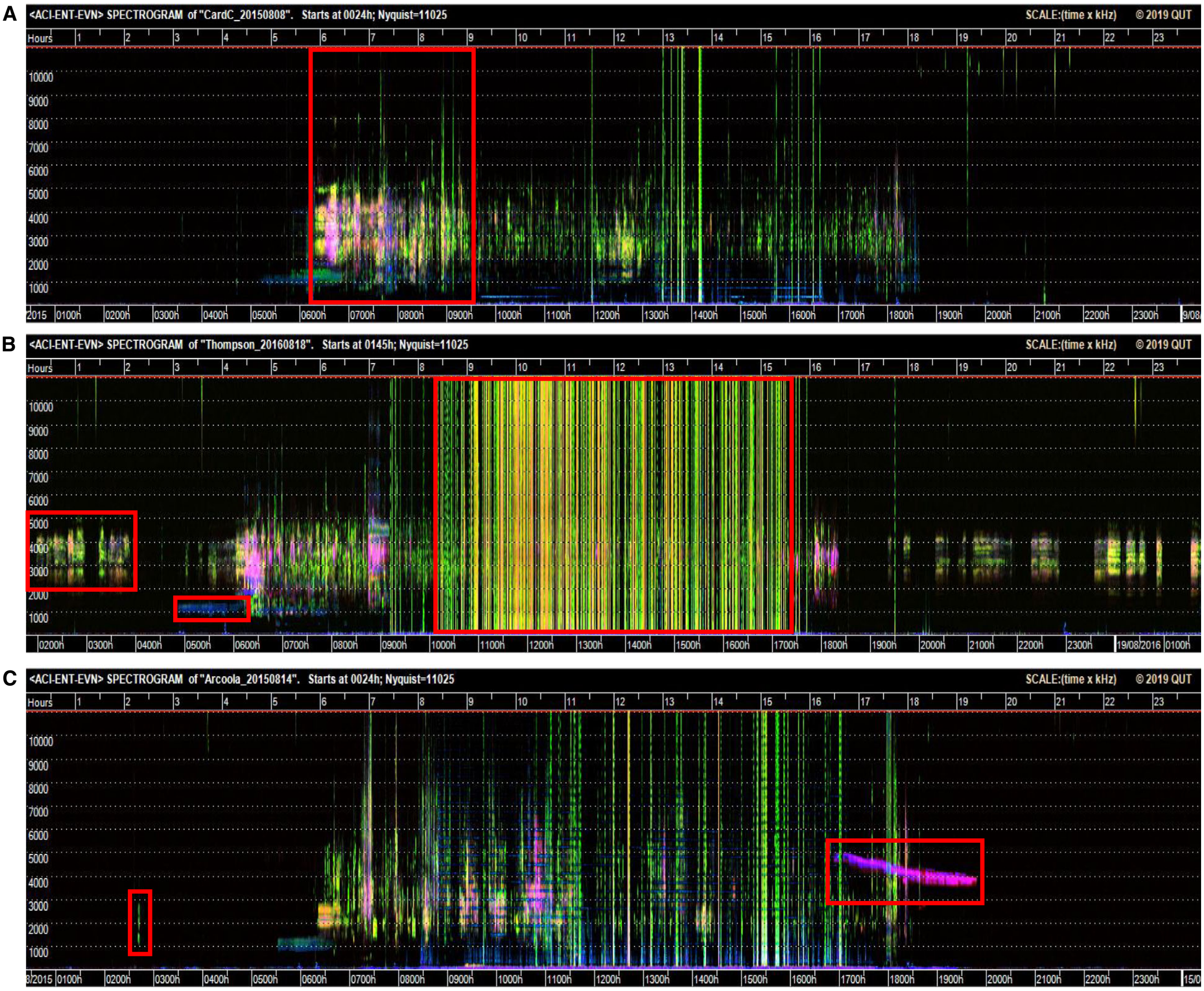

Figure 4. Long-duration false-colour spectrograms displaying 24 h of acoustic data from Thompson (A, B) and Arcoola (C) Creeks in Sturt National park. The *Y* axis displays frequency in kHz and the *X* axis displays time in Australian eastern daylight time. The acoustic complexity index (ACI) is displayed in red, temporal entropy in green and acoustic events per second in blue (see Table 2). Note that the values can mix to produce composite colours, for example mixing red with blue makes purple, which means the purple at 07:45 is a combination of ACI and ENT. (A) In this image, there is a visible concentration of acoustic activity and complexity between 06:15 and 09:30 and this was considered to be the bounds of the dawn chorus from which samples were randomly selected (as marked by the red box). (B) From left to right in this image, the first red box shows a signal from nocturnal singing of Willie wagtail (a diurnal bird that calls at night during the breeding season [Higgins et al. 2006]). The second box is a signal from an Australian magpie, which begins pre-dawn and continues into the dawn chorus. Care was taken to exclude nocturnal vocalisations such as these from dawn chorus mapping. The third box in this image demonstrates the effect that wind can have on acoustic data and visualisations of such data. There has been a significant amount of clipping in this recording and the valuable data that the recording contains is obscured by wind noise. Where noise obscured visualisation of dawn choruses, these days were excluded from the dawn chorus mapping process. (C) In this image, the first box highlights a signal from the Australian owlet-nightjar, a nocturnal species. Care was taken to exclude nocturnal calls of nocturnal birds in the same way they were for nocturnal calls of diurnal birds. The second box in this image highlights a trace left by a chorus of insects. These sometimes occurred pre-dawn and care was taken to identify these traces as non-avian and ignore them when defining bounds of dawn choruses.

While the acoustic observer was present for the winter 2016 transect surveys, the nature of our acoustic sampling regime, which drew random samples from long periods of time, means that any biases derived from his recollection of birds present 3 years earlier would be negligible.

Data analysis

For both acoustic monitoring and transect data, we treated each year's survey as a single sample for each creekline and used EstimateS (Colwell 2005) to calculate

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Table 1. Summary of the spectral indices applied in order to generate the long-duration false-colour spectrograms used in this research.

Index	Purpose	Reference
Acoustic complexity index (ACI)	Quantifies the relative change in acoustic intensity in each frequency range (bin) of the amplitude spectrogram. ACI is widely used as a measure of biophony (sound produced by living organisms) in environmental recordings. It should be noted that our spectral ACI returns a spectrum of ACI values rather than aggregating values to return a single scalar value	Pieretti et al. (2011), Farina et al. (2013), Farina et al. (2014)
Temporal entropy (ENT)	A measure of the acoustic energy concentration in each frequency bin. Used to highlight brief sound events in long periods of silence	Sueur et al. (2008), Sueur et al. (2014), Towsey et al. (2014)
Acoustic events per second (EVN)	A measure of the number of acoustic events per second, averaged over the same 1-min segment	Towsey (2017)

Table 2. Summary of sensor malfunctions during the course of the study period.

Creek	Stopped recording	Commenced recording	Days offline
Stud	30/01/2015	8/07/2015	159
Stud	29/06/2016	15/07/2016	16
Stud	13/02/2017	26/06/2017	133
Thompson	13/09/2014	1/10/2014	18
Thompson	5/12/2014	9/07/2015	216

Sensors were offline for a total of 542 days, compared to 3744 days in which they were online.

predicted species richness estimates using the Chao 2 estimator for each creek-line and method. We also calculated the Chao 2 log-linear confidence interval lower and upper bounds to 95%. We then removed raptors, nocturnal birds and waterbirds (all species that would ordinarily be removed before analysis of transect data; after Watson [2010]) and recalculated predicted species richness estimates along with upper and lower bounds in the same way.

To test for differences between acoustic surveys and transect surveys, we adopted the difference between transect and acoustic Chao 2 richness as our test statistic (null hypothesis = no difference between survey methods). We used parametric bootstrapping (B = 100 000) to calculate means for four groups; transect and acoustic surveys where no species were excluded and transect and acoustic surveys where raptors, nocturnal birds and waterbirds were excluded. We then found the difference between means for each survey method, both where all species were included and where raptors, nocturnal birds and waterbirds were excluded. We then computed 95% confidence intervals for the difference in means (both for all species and where raptors, nocturnal birds and waterbirds were excluded) using the percentile method. Where this interval included 0, we did not reject the null hypothesis.

We elected not to use multi-species occupancy modelling (Iknayan et al. 2014). This technique is infrequently used for these sorts of studies (four of 225 studies comparing terrestrial bird diversity reviewed by Watson [2017]), and would rely on different detectability estimates for field surveys versus acoustic surveys. To maximize comparability of our estimates, we used richness estimation that is widely employed in inventory-based studies and can be equally applied to both datasets.

Results

Acoustic monitoring and transect surveys detected a combined total of 79 species from 2014 to 2017 (Appendix A1). We detected 57 species during acoustic monitoring surveys and 76 species were detected during the transect surveys. Of the 79 species detected by both methods combined, acoustic monitoring did not detect 22 species (Table 3) and transect surveys did not detect three species. The three species identified by acoustic monitoring that were not detected by transect surveys were Fan-tailed Cuckoo, Black Honeyeater and Crested Bellbird. Fan-tailed Cuckoos are rare in the study area having only been detected once during transect surveys since 2003.

At Arcoola, Stud and Thompson Creeks, transect-derived measures of species richness produced greater predicted richness estimates than acoustically derived data (Fig. 5). However, at Mistletoe Creek, both methods detected the same number of species and acoustic monitoring yielded greater predicted richness estimates than transect-derived data. The detected and predicted species richness estimated by acoustic monitoring each broadly reflect those of the transect surveys in that Thompson Creek has the greatest species richness, followed by Arcoola, Stud and Mistletoe Creeks. We found no significant difference between transect and acoustic surveys where no species were excluded (95% confidence interval for the difference in means was −7.88 to 31.18).

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Table 3. Species that were detected during transect surveys from 2014 to 2017, but not by acoustic monitoring surveys

Scientific name	Common name	Raptor	Nocturnal	Rare	Detected opportunistically?
Geopelia cuneata	Diamond dove				Y
Eurostopodus argus	Spotted nightjar		Y	Y (4)	
Anhinga novaehollandiae	Australasian darter			Y (1)	
Aquila audax	Wedge-tailed eagle	Y			
Hieraaetus morphnoides	Little eagle	Y		Y (2)	
Circus assimilis	Spotted harrier	Y			
Accipiter cirrocephalus	Collared sparrowhawk	Y			
Haliastur sphenurus	Whistling kite	Y			
Ninox boobook	Southern boobook	Y	Y	Y (4)	Y
Falco cenchroides	Nankeen Kestrel	Y			
Falco berigora	Brown falcon	Y			
Falco hypoleucos	Grey falcon	Y		Y (4)	
Psephotus haematonotus	Red-rumped parrot			Y (1)	
Neopsephotus bourkii	Bourke's parrot				
Climacteris picumnus	Brown treecreeper			Y (3)	
Ashbyia lovensis	Gibberbird			Y (1)	
Coracina maxima	Ground cuckoo-shrike			Y (2)	Y
Artamus cyanopterus	Dusky woodswallow			Y (2)	
Artamus leucorynchus	White-breasted woodswallow			Y (1)	
Cheramoeca leucosterna	White-backed swallow				
Petrochelidon nigricans	Tree martin				
Hirundo neoxena	Welcome swallow				

Numerals in the rare column indicate the number of times they have been detected since 2003 in the long-term dataset (n = 72 surveys). Species detected on <5 occasions were considered to be rare. Detected opportunistically indicates whether the species was detected while exploring acoustic data outside of formal sampling.

When raptors, nocturnal birds and waterbirds were excluded (after Watson 2010; Fig. 3), disparities between richness estimates predicted by the two datasets were reduced at Arcoola, Stud and Thompson Creeks, increased in favour of acoustic monitoring at Mistletoe Creek (Fig. 6), and still reflected overall differences between species assemblages at each creek. We found no significant difference between transect and acoustic surveys where raptors, nocturnal birds and waterbirds were excluded (95% confidence interval for the difference in means was -10.47 to 20.25).

Discussion

In this work we demonstrate techniques for improving sampling efficiency to review acoustic data, including accurately defining dawn choruses in order to guide sampling of long-duration acoustic recordings and sampling these recordings using short-duration samples over long periods of time. We then conducted acoustic surveys applying these techniques and compared the results with transect surveys conducted by a field-based observer. The acoustic surveys produced species richness estimates that broadly reflected the same variation between creek-lines as observer-based field surveys and we were unable to find a statistically significant difference between the two methods. When raptors, nocturnal birds and waterbirds were excluded from analyses and estimators of predicted richness were applied, the results of each method were even more similar and again we found no significant difference between the two methods, demonstrating that acoustically detectable species are reliable estimators of overall bird species richness.

This work is the first evaluation to compare passive acoustic monitoring with field-based observers using a multi-year dataset, although (Furnas and McGrann, 2018) estimated detection probabilities for each method over 3 years. This is important because it allowed us to compare estimates of species richness and composition in varying climatic conditions, giving us a more robust understanding of the merits of each methodology. Additionally, as far as we are aware, this is the first published work to sample avian communities in the Australian arid zone using passive acoustic sensors and one of few in arid zones internationally (see Rich et al. 2019). Our study sites are open habitats in which birds are often seen relatively easily. Hence, our study area represents an ideal place to test passive acoustic monitoring against field-based observers as it challenges acoustic monitoring techniques more than in closed/dense habitats where birds are more often heard than seen.

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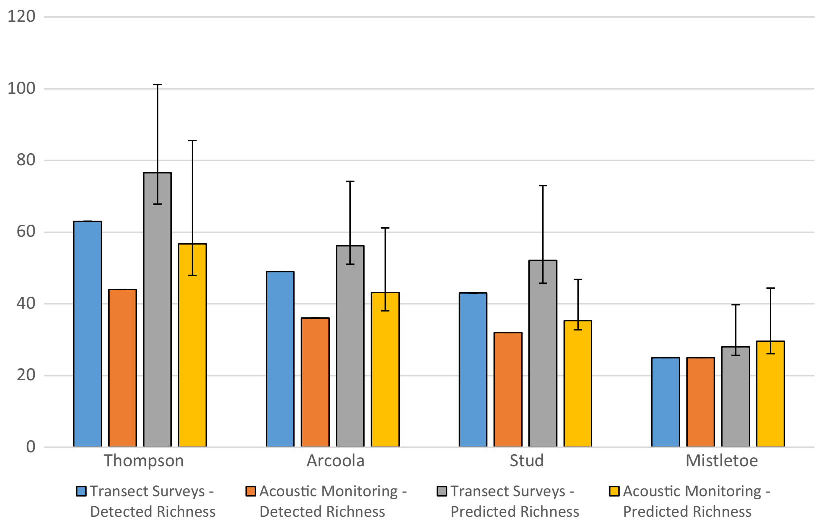

Figure 5. Species richness estimated for each creek-line and method for the entire bird assemblage. Predicted richness estimates are included for each method. Error bars on predicted richness estimates represent Chao 2 log-linear confidence interval lower and upper bounds to 95%.

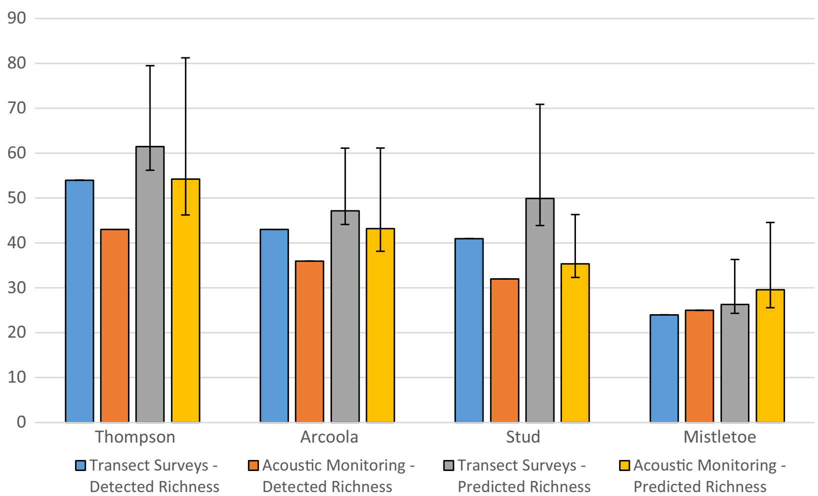

Figure 6. Species richness estimated for each creek-line and method after excluding raptors, nocturnal birds and waterbirds. Predicted richness estimates are included for each method. Error bars on predicted richness estimates represent Chao 2 log-linear confidence interval lower and upper bounds to 95%.

Most existing comparative studies of acoustic sampling and more conventional observation-based sampling use the same approach to standardize sampling for both methods (Darras et al. 2018a). That is, they prioritize neat experimental designs over applying survey techniques in order to maximize their potential for detecting species. For the acoustic component of comparative studies, no previous research has sampled non-sequentially from long-duration acoustic data and the work of Wimmer et al. (2013b) suggests that this is more effective than sequential sampling. Studies that structure comparative trials by constraining both techniques can reveal useful and relevant insights about what can and cannot be detected using microphones versus the human ear. They also advance our understanding of the advantages of observer-based field surveys (e.g. the ability for observers to detect species using visual cues and habitat context, and track down unfamiliar calls to visually confirm a species identity) compared to the advantages of acoustic sampling (e.g. ability to re-listen and boost faint or brief signals, and share unfamiliar signals with other skilled observers to confirm an identity). However, where the performance of a technique is systematically restricted to adhere to an experimental design, comparative insights drawn from such studies related to the overall performance of each methodology should be regarded as

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provisional. Additionally, the outcomes of research that compares these two survey methodologies using the same analysis to conduct field and acoustic surveys may be affected by bias as the observer has prior knowledge of what to expect during acoustic surveys.

Although we recognize our inferences are limited to four creek-lines over 4 years, our approach was unique in that we applied each method optimally, that is in a way that maximized their potential for detecting bird species in our given system (as one would in the absence of a comparative evaluation). The transect survey protocol was developed prior to the conception of acoustic monitoring, so it is clear that this protocol was considered the best way to sample our sites. Subsequently, we designed a methodology for acoustic sampling to maximize species richness estimates. This included some novel methods including defining dawn choruses using false-colour spectrograms and sampling non-sequentially to allow temporal variation to compensate for reduced spatial coverage compared to transect surveys. We suggest that this sets a framework for a more useful comparison of methods, because each method is designed to exploit the strengths of that method rather than designed to be a 'balanced', but potentially unrepresentative comparison. We also decided to use independent observers for each methodology. Using independent observers minimizes observer bias derived from prior knowledge of survey results and allows a level of objectivity that is not achieved in most similar studies. [This approach does introduce the potential for inter-observer biases, however, the ability to share unfamiliar calls with other skilled observers virtually eliminates this effect; although in practice, sharing of calls was rarely necessary.]

Acoustically detectable species

Of the 77 species detected in the study period using transect surveys, we detected 54 plus an additional 3 that were not detected by transect surveys. There were 22 species that were not detected by acoustic monitoring (Table 3) and 9 of these species were diurnal raptors (no raptors were detected during the acoustic monitoring survey effort), one was a waterbird (Australasian Darter) and two were nocturnal (Southern Boobook and Spotted Nightjar). These three groups would be excluded from any analysis of transect data as the surveys were not designed in a way that would detect them reliably. Of the diurnal raptors, 2 (Little Eagle and Grey Falcon) were rarely detected in the long-term dataset as were both nocturnal species and the waterbird.

The omission of diurnal raptors from the species list derived from acoustic data is not entirely unexpected as many Australian diurnal raptors rarely vocalize (Marchant and Higgins, 1993). Whistling Kites, Nankeen Kestrels and Brown Falcons vocalize relatively frequently (Marchant and Higgins, 1993) and we expected to detect these species during the course of the acoustic surveys. Nankeen Kestrels were detected several times during transect surveys, so it is possible that their omission was a result of the limited scope of these surveys, possibly reflecting diel variation in their calling behaviour. However, Whistling Kites were only detected once during transect surveys and Brown Falcons only twice so they may have occurred in the study area infrequently during the study period. Wedge-tailed Eagles, Spotted Harriers, Collared Sparrowhawks and Grey Falcons are likely to be poorly monitored by acoustic sensors. We expect many other arid zone raptors not detected here would also very rarely be identifiable in environmental recordings. The ability to record raptors during field-based surveys may be an important advantage of such methods, particularly where raptors are assessed to be actively using the site (as is the case with our transect surveys). Many birds have 'aerial' or 'hawk' alarm calls that are performed in response to predatory birds in flight (Marler 1955). One potential solution to this problem could be to eavesdrop and use these referential calls as a proxy indicator of predatory species in an area. Further investigations could be made into how specific these alarm calls are, that is do alarm calls identify predators to species level or are they more generic? Some research on Noisy Miners *Manorina melanocephala* has determined different alarm calls are elicited by different groups of predators, suggesting this may be possible retrospectively (Cunningham and Magrath, 2017; Holt et al. 2017).

There were two nocturnal species detected during transect surveys that were not detected by acoustic surveys. These were Southern Boobook and Spotted Nightjar. Both were rarely detected in the long-term dataset, in all cases being flushed as observers walked along the creek-line. However, even with greater effort, the current methodology is unlikely to detect these species. Both very rarely vocalize during the day, but have distinctive vocalizations that can be heard readily at night. With an altered sampling regime, we expect these species to both be sufficiently detectable using acoustic monitoring where nocturnal data are sampled. Similarly, Bourke's Parrots are largely crepuscular and vocalize mostly after dusk and before dawn when moving to water sources (Higgins 1999). Again, acoustic sampling did not occur during those times and as such, the omission of this species is not unexpected. Had sampling schedules incorporated these times, these species are likely to have been acoustically detectable. It is important to highlight the flexibility that acoustic monitoring provides around sampling at different times of day. Sampling regimes can be easily

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customized to include birds that sample outside dawn and dusk choruses, including at night. In arid Australia, nocturnal birds would benefit from favourable signal-to-noise ratios as wind is typically strongest during daylight hours.

In addition to those discussed above, there was a suite of species from various taxonomic groups that were not detected acoustically, but were also rare in the long-term dataset. The majority of these species are soniferous and produce vocalizations that should be detectable and uniquely identifiable in soundscape recordings. Among these species was the Ground Cuckoo-shrike, which we opportunistically detected on several separate occasions within environmental recordings from Sturt National Park. It is likely that these species were not detected during acoustic surveys as a result of their rarity in the study area rather than a result of them being acoustically cryptic. Conversely, Diamond Doves are common in the study site, having been detected on 20 of 72 surveys on the creek-lines since 2003. However, they were only detected once by transect surveys from 2014 to 2017 suggesting that they were rare during the time that acoustic sensors were deployed.

One of the most interesting omissions from the list of acoustically detectable species derived from the acoustic monitoring efforts were the members of the Hirundinidae —the Swallows and Martins. There are four Hirundinidae species present in Sturt National Park: Welcome Swallow, White-backed Swallow, Tree Martin and Fairy Martin. All but Fairy Martins were detected during transect surveys in the study period and they are all well represented in the long-term dataset. The reason these species were not detected acoustically is unclear. It may be that they typically inhabit only certain sections of the creek-lines that are beyond the range of the sensors. It is possible they do not vocalize frequently and/or loudly meaning that they are detected by sensors less often than other species and our sampling effort was insufficient to detect them. This may be exacerbated by the position of the microphones, parallel to the ground, therefore less able to receive acoustic signals from directly above. Alternatively, as these three species are highly visually detectable and are often observed hawking insects in the open, it may be that field observers typically rely on these visual cues to detect these species. While our observer is familiar with their vocalizations and can readily identify them all by calls, they may not be as acutely attuned to detecting these vocalizations as they are for calls of species that are more visually cryptic. It is worth noting that swallows (and other aerial foragers such as swifts) are routinely excluded from analyses of conventional bird surveys (Watson 2010). Our data suggest that where these species cannot be detected reliably by an acoustic observer who is aware of the complexities of their acoustic detectability, and thus absences of detections in acoustic dataset should not be used to infer actual absences, these species should also be excluded from acoustic surveys.

Detection rates

The species that showed the greatest disparity in detection rates in favour of acoustic monitoring were Budgerigars, Little Crows and Australian Ravens (Appendix A1). These species are commonly seen and heard flying overhead while conducting creek-line surveys in the field and it is likely that these were commonly detected and recorded during acoustic surveys when they would be ruled to be outside of the survey area by a field observer and not recorded. This raises another interesting challenge for acoustic monitoring in that it is more difficult to assign species to distance categories or determine whether the signal is from an individual that is within or beyond the bounds of a defined site. Recent research has demonstrated that determining distance and direction from sensors is achievable when stereo microphones are used (Darras et al. 2018b) or when multi-sensor arrays are used (Blumstein et al. 2011; Yip et al. 2019). Still, the ability to assess how an organism is interacting with a site is likely to be an important advantage of surveys conducted by field-based observers, for example where a decision needs to be made as to whether a bird overhead is actively using the site or simply flying past.

Species richness estimates

The species richness estimates predicted by transect survey data were greater than those produced using acoustic data. By removing groups that were not considered to be core creek-line bird species (raptors, nocturnal birds and waterbirds), the disparity between richness estimates of transect data and acoustic data, both detected and predicted, was reduced (Fig. 6). At Mistletoe Creek, acoustic monitoring produced greater species richness estimates than transect surveys. Mistletoe Creek consistently produced the lowest species richness estimates. We expect the reason acoustic monitoring was slightly more effective at Mistletoe Creek, while being less effective at other creeks, was due to the survey effort. A total sampling effort of 60 min may have been sufficient for Mistletoe Creek, whereas other creeks that support greater bird species richness require a greater survey effort. It is worth noting that sites with lower species richness do not always require less survey effort, and can actually require greater effort to be adequately sampled (Watson 2004). A useful additional step in the design of acoustic sampling methods could be to use species accumulation curves to

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estimate survey completeness and accurately define optimal survey effort for each site.

The species richness estimates derived from acoustic monitoring were broadly reflective of the different avian assemblages at each creek-line, demonstrating that richness estimates of acoustically detectable species are broadly reflective of overall bird diversity. Thompson Creek was found by both methods to be the most species rich followed by Arcoola, Stud and then Mistletoe Creeks. Differences in species richness between creeks were even more apparent when raptors, nocturnal birds and waterbirds were excluded from analysis. These results are promising for the broader application of acoustic monitoring in the Australian arid zone and pave the way for using acoustic monitoring to track diversity at greater spatiotemporal scales.

Implications

Arid zone bird species and assemblages are research deficient compared to species that occupy coastal areas of temperate regions (Clarke 1997; Ducatez and Lefebvre, 2014; Yarwood et al. 2019). Clarke (1997) makes a compelling argument that the mechanism behind this pervasive bias is the relative ease at which large, publishable datasets can be generated. The spatiotemporal reach of passive acoustic monitoring means that these sensors have tremendous potential to facilitate data collection in remote areas and greatly improve our ability to detect population declines and identify and manage threatening processes for species that occupy these systems. It is possible to use acoustically derived data to complement field-based monitoring, and this may frequently be logistically advantageous (Darras et al. 2018a), given that the use of acoustic sensors minimally necessitates two site visits; deployment and retrieval. Furnas and McGrann (2018) demonstrated this well by combining field surveys with acoustic surveys and using the resultant data to produce multi-species occupancy models. By combining methods, species not detected reliably by acoustic sensors can be sampled more effectively and included in analyses.

Furthermore, our research demonstrates the utility of long-term deployments of passive acoustic sensors and we suggest these devices may play an important role in addressing challenges related to funding long-term monitoring programmes. Passive acoustic sensors are increasingly affordable and given that devices and accessories are typically one-off purchases, accounting for them in budgets is simple. As automation of analytical processes for environmental recordings advances, staffing costs are likely to be even further reduced.

This work demonstrates that acoustic sensors can be deployed permanently and that high-quality acoustic datasets can be gathered cost effectively and with relative ease. While the prospect of remotely gathering datasets of very high spatiotemporal resolution in remote areas is exciting and provides accessibility to address a suite of previously unanswerable questions, it is still critical that acoustic monitoring is not seen as a comprehensive replacement for other survey methods. There are considerable limitations to acoustically derived data, some of which we have explored here. Rather than treating acoustic monitoring as a panacea, researchers and land managers should seek to incorporate the technique as a means of complementing other components of monitoring protocols and filling in the spatiotemporal gaps that these other methods leave. Acoustic sensors are tools for ecologists to operate rather than an alternative to field effort and skills. We still need field ecologists regularly interacting with ecosystems and learning from them in an immersive way. Skilled field ecologists are key to acoustic monitoring, both when designing monitoring protocols and determining sites for deployment and when reviewing and interpreting acoustically derived data. Additionally, many important questions arise when curious and observant ecological minds are immersed in ecosystems and the value of this should not be underestimated.

Conclusion

By applying acoustic monitoring in a considered and optimized way, we calculated species richness estimates that broadly reflected the same variations between creek-lines as transect surveys, even with less than a quarter of effective survey effort. Species composition of acoustically detectable species can also be measured with comparable accuracy, however, a suite of species that are acoustically undetectable/cryptic will be overlooked. It is important to recognize species that are acoustically undetectable/cryptic and account for this when designing monitoring and survey protocols and in subsequent analyses. We defined acoustically detectable and undetectable/cryptic species and found that the latter were overwhelmingly species that were not targeted by our transect survey design, meaning that most would be excluded from any subsequent analyses. Where researchers are seeking to sample entire bird communities, our results suggest it may be beneficial to use observer-based field surveys in combination with acoustic surveys in order to capture these additional data, particularly in remote and inaccessible areas. Our research also yielded insight into the ways that field observers may perceive and prioritize visual and acoustic cues based on species behavioural traits during a survey. While this is not necessarily a limiting factor for acoustic monitoring, it does suggest that field observers should be aware of such biases before undertaking acoustic surveys.

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Having demonstrated that acoustic surveys can be a way of addressing many of the challenges of monitoring bird assemblages in inaccessible locations such as arid Australia, we hope to encourage others to invest more research effort into these largely research-deficient landscapes.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix A1. Species detected during transect and acoustic monitoring surveys.

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