IBIS
international journal of avian science
Ibis (2021) doi: 10.1111/ibi.12944

Review

Estimating bird density using passive acoustic monitoring: a review of methods and suggestions for further research

CRISTIAN PÉREZ-GRANADOS*[1,2,3] & JUAN TRABA[1,4]
[1]*Terrestrial Ecology Group (TEG-UAM), Department of Ecology, Universidad Autónoma de Madrid, Madrid, Spain*
[2]*National Institute for Science and Technology in Wetlands (INAU), Federal University of Mato Grosso (UFMT), Computational Bioacoustics Research Unit (CO.BRA), Cuiabá, Brazil*
[3]*Ecology Department, Alicante University, Alicante, Spain*
[4]*Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, Madrid, Spain*

Passive acoustic monitoring is a non-invasive tool for automated wildlife monitoring. This technique has several advantages and addresses many of the biases related to traditional field surveys. However, locating animal sounds using autonomous recording units (ARUs) can be technically challenging and therefore ARUs have traditionally been little employed to estimate animal density. Nonetheless, several approaches have been proposed in recent years to carry out acoustic-based bird density estimations. We conducted a literature review of studies that used ARUs for estimating bird densities or bird abundances in order to describe the applications and improve future monitoring programmes. We detected a growing interest in the use of ARUs for estimating bird density in the last 6 years (2014–19), with a total of 31 articles assessing the topic. The most common approach was to estimate the relationship between the number of vocalizations per recording time with bird density or bird abundance estimated in the field (61%). In 26 studies (79%), bird estimates obtained by human surveyors agreed with those obtained using ARUs. Some approaches have proven able to reduce biases in acoustic surveys, such as considering imperfect detection (spatially explicit capture–recapture, using microphone arrays), applying paired acoustic sampling to control for different sampling radius between humans and ARUs, or including relative sound level measurements that allow researchers to estimate bird distance to recorder. However, several studies did not include any covariates to reduce existing biases and some did not estimate the sampling radius of the recorder, which may hamper future comparisons between human and ARU surveys. Future studies should include a measurement of the sampling radius of the recorder employed to be able to obtain density estimations using ARUs. Finally, we provide some guidelines to improve the applicability of ARUs to infer bird population estimates in future studies.

Keywords: array, autonomous recording units, autonomous sound recorder, distance sampling, sonogram analyses, soundscape indices, vocal activity rate.

Estimates of wildlife population density provide valuable information for research in ecology, conservation biology, biogeography and evolution. Uncertainty in population estimates may result in

*Corresponding author.
Email: cristian.perez@ua.es
Twitter: @JuanTraba1

misleading conclusions or incorrect assignments of conservation status for threatened species. Technological advances over recent decades have provided new and non-invasive techniques for estimating wildlife density, such as the use of unmanned aerial vehicles (Nowak *et al.* 2019) and camera trapping (Burton *et al.* 2015). Among the new non-invasive techniques, the use of passive acoustic monitoring has increased in recent years (Sugai *et al.* 2019).

Passive acoustic monitoring requires the placement of autonomous recording units (ARUs) in the field, programmed to record and followed up by an interpretation of the recordings. ARUs have proven to be a suitable alternative to traditional field surveys for monitoring wildlife across many research areas (see review for terrestrial wildlife in Sugai *et al.* 2019). This technique addresses many of the problems and biases related to traditional field surveys. For example, it minimizes disturbance due to human presence, increases the spatial and temporal scale of studies and offers a great degree of standardization in data collection (Shonfield & Bayne 2017, Gibb *et al.* 2019). Another advantage is that acoustic recordings can be reanalysed and reinterpreted as new questions arise, or when looking for different species (Borker *et al.* 2014, Pérez-Granados & Schuchmann 2020a).

Despite these advantages, some shortcomings have hampered the widespread use of ARUs. Among the major obstacles for implementing ARUs in monitoring programmes are the costs associated with acquiring recorders, and the time and expertise required for recording interpretation. The recent development of low-cost recorders (Hill *et al.* 2018) and advances in computational capabilities to aid in audio interpretation may overcome these barriers (Knight *et al.* 2017, Priyadarshani *et al.* 2018), but one important shortcoming remains: it is difficult to estimate wildlife density or population numbers from sound recordings. Several years ago, Marques *et al.* (2013) reviewed methods employed for estimating animal population density using ARUs. That review included a very limited number of studies using birds as study models, the terrestrial group most often surveyed using ARUs (Sugai *et al.* 2019), but there is no consensus on how to estimate bird density using ARUs (Marques *et al.* 2013, Darras *et al.* 2018a). Indeed, several methods and statistical approaches have been implemented in recent years to infer bird densities or bird abundances around ARUs (e.g. Abrahams 2019, Orben *et al.* 2019, Yip *et al.* 2019, Pérez-Granados *et al.* 2019a, Arneill *et al.* 2020; Fig. 1).

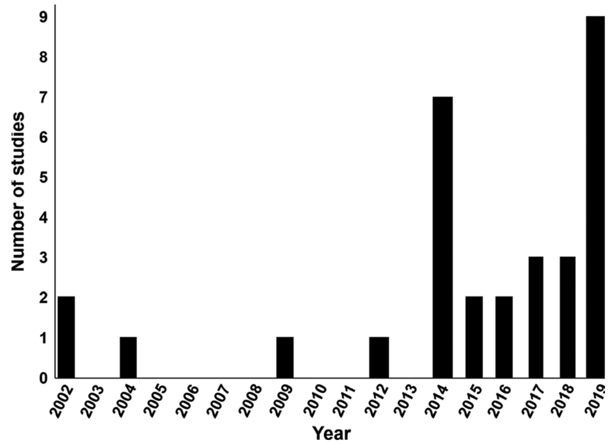

Figure 1. Change over time in the number of studies assessing the relationship between bird density and acoustic data obtained using ARUs.

A potential shortcoming of using ARUs for estimating bird densities (but also bird richness, see meta-analysis in Darras *et al.* 2018b) is that human observers and ARUs have different sampling radii (Hutto & Stutzman 2009, Van Wilgenburg *et al.* 2017), which may lead to biased density estimates if not corrected for (e.g. Van Wilgenburg *et al.* 2017, Sebastián-González *et al.* 2018, Yip *et al.* 2019). The methods used to estimate the sampling radius of ARUs vary among studies (Drake *et al.* 2016, Van Wilgenburg *et al.* 2017, Darras *et al.* 2018a) but a common approach is either to broadcast a sequence of bird vocalizations or to record vocalizations of wild birds at known distances. This procedure allows researchers to predict the detection probability of recording a bird vocalization as a function of distance while taking into account the impact of other factors (e.g. climate, wind speed or singing direction) (e.g. Drake *et al.* 2016, Turgeon *et al.* 2017, Pérez-Granados *et al.* 2019b). Once the detection probability of recording a bird vocalization has been predicted for a range of distances, the effective detection radius (EDR) of the recorder can be estimated. EDR is a common measure of the sampling radius of ARUs and is defined as the radius at which as many vocalizations are undetected within that distance as are detected beyond that distance (probability of detection of 0.5, Buckland 2001, see complete theory and application in Sólymos *et al.* 2013 and Pankratz *et al.* 2017). Other studies considered the sampling radius of the ARU as the maximum distance at which the recording device was able to record bird vocalizations (e.g. Orben *et al.* 2019, Pérez-Granados *et al.* 2019a, Arneill *et al.* 2020, Schroeder & McRae 2020). However, the latter approach might be useless under some circumstances, as it does not consider imperfect detection of vocalizations within the considered sampling radius. Another method used to truncate the sampling radius of the ARU is to include a measurement of the Sound Pressure Level (SPL) of bird vocalizations (see *Sound pressure level* section for more information) in data analyses. This method allows researchers to exclude those signals beyond the estimated distance at which the probability of detecting a bird vocalization sharply decreases (Drake *et al.* 2016, Darras *et al.* 2018a, Hedley *et al.* 2020). The sampling radius of the ARU varies among recording devices and is affected by a large number of factors, such as habitat type, background noise, vocalization directionality and species monitored (Darras *et al.* 2016, 2018a, Van Wilgenburg *et al.* 2017, Yip *et al.* 2017, Pérez-Granados *et al.* 2019b). Prior research has demonstrated that after standardizing detection ranges, bird richness values estimated using ARUs and traditional field surveys were statistically indistinguishable (Darras *et al.* 2018b), which suggests that ARUs might be also useful for estimating bird densities.

Here we review the scientific literature on the use of ARUs and the existing approaches by which bird density or bird abundance estimates can be obtained using ARUs. Our aim is to improve understanding of the different methods and statistical approaches available and the applicability of these techniques to estimate bird populations by employing passive acoustic monitoring. Finally, we also provide some recommendations about what approach could be used according to how recordings were collected, and the expertise and work effort needed for recording and for interpretation of recordings. Although our review was focused on birds, due to the rapid development of methods for this group, biases related to each method, choice of method and future considerations may all have wider applications and could be used to improve acoustic monitoring programmes for other acoustically active taxa.

METHODS

We conducted a systematic review of methods employed for estimating bird density or bird abundance using ARUs by performing a literature search in the Web of Science (Science Citation Index Expanded) and Google Scholar platforms on 1 January 2020 spanning all years. We performed the search using the following keyword combination: (((bird OR avian) AND ('automated recorder' OR ARU OR 'acoustic monitoring')) AND (population OR density OR estimate))). The initial literature search resulted in more than 11 000 articles. We then excluded those articles not in English and those monitoring non-avian taxa. We also excluded articles that did not use ARUs and that did not compare bird density (or abundance) estimated by both ARUs and observational bird surveys.

Some studies estimated bird abundance around recorders, whereas others estimated bird density. However, we have considered both types of studies in our review based on the assumption that if an approach is able to count accurately the number of birds around recorders, then bird density could potentially be estimated (see Marques *et al.* 2013). To facilitate reading we have employed the term bird density throughout the text, although for each specific approach we have detailed which population metric has been estimated (e.g. bird abundance, relative abundance, bird density). We decided to include those articles using bird abundance simulations (e.g. Drake *et al.* 2016). Although bird behaviour may differ between simulations and actual scenarios, we considered it interesting to include these studies for a wider spectrum of possible methods to be applied to reduce biases among ARU data and human surveys. Our initial set for assessment included 31 studies (Data S1).

For each article considered, we extracted the following information: publication year, location of monitoring data, journal of publication, monitored taxa, recording equipment employed (recorder and type of microphone), method employed for recording interpretation and main approach used to compare acoustic data with field bird population estimate. The use of these approaches is not exclusive. Indeed, some of the methods are used together to obtain more reliable density estimation (e.g. Dawson & Efford 2009, Sebastián-González *et al.* 2018). In such cases, we considered the main approach employed. Three publications (Williams *et al.* 2018, Orben *et al.* 2019, Arneill *et al.* 2020) reported independent assessments for two different approaches in the same study. In these cases, we considered the approaches evaluated as independent case studies, as the authors provided an independent evaluation for each approach. Our final data therefore comprised 34 case studies. The methods employed for estimating field bird abundance or bird density greatly differed among studies, although point counts (PC hereinafter) was the counting method most often employed (15 of 34 cases, see method employed for each study in Tables 1 and 2). To facilitate reading, we will use the term 'traditional field surveys' hereafter to refer to the different methods employed. However, in a few cases we detail the specific field method employed. For each article we also reported whether bird estimates obtained with acoustic data were similar to those estimated by traditional field surveys, according to the main statistical analyses of the study, which mainly estimated Pearson's correlation between acoustic data and bird density (nine of 34 cases) or assessed the relationship between these variables through generalized linear models (nine of 34 cases) (see analyses employed on each study in Tables 1 and 2).

RESULTS

Overview of the use of ARUs for estimating bird abundance

The number of studies published on the use of ARUs for estimating bird abundance has been increasing since the first publication in 2002. This increase is especially marked for the last 6-year period (2014–19), when > 84% of the articles were published. The year 2019, the last year considered in our review, was the most productive one (Fig. 1), in agreement with the increase in interest among researchers in using ARUs for monitoring terrestrial wildlife (Sugai *et al.* 2019). Most of the studies were carried out in North America (19 studies, 61% of the total), Europe (seven studies, 23%) and Oceania (three studies, 10%); only one study each took place in Asia and Africa (3% each). The number of studies per country is given in Figure S1.

Most studies focused on a single species (18 studies, 58%) (Tables 1 and 2) and up to 14 of the 28 avian Orders were considered among the taxa analysed (Table S1). The number of articles published per journal is given in Table S2.

Recording equipment, settings and recording interpretation

The Wildlife Acoustics Song Meter recorders were the ARUs most commonly employed (20 studies, 60.6%), followed by ARUs built by the researchers themselves (six times, 18.2%) (see Table S3 for a complete list). Omnidirectional microphones were used in 26 of the 31 papers found (83.9%); the other five studies (17.1%) used directional microphones. Recordings were analysed manually, by visualizing or listening to the recordings, in 16 of the papers reviewed. Automated signal recognition software was also used in 16 papers (the list with the number of times that each automated signal recognition software was employed is provided in Table S4).

Methods to estimate bird abundance

We identified a total of eight approaches to estimate bird density using ARUs (Table 3). Below we present a detailed description of the reasoning and how to employ each method, the number of studies that used the method and their main results. Methods that require multiple microphones are described first, followed by those approaches that can be performed using a single recorder mounted with a single microphone.

Multiple microphones

Microphone arrays

The deployment of spatially dispersed groups of microphones (microphone arrays, Blumstein *et al.* 2011) enables researchers to study signal directionality based on the location of vocalizing animals. The basic assumption is that recordings made using an array of microphones can be used to infer the position of vocalizing individuals on the basis of the time delay for the arrival of the signals at different microphones (Dawson & Efford 2009, see review in Blumstein *et al.* 2011) (Fig. 2). This approach allows researchers to apply the spatially explicit capture–recapture (SECR) method (Borchers & Efford 2008). SECR is a statistical methodology able to deal with imperfect detection of birds and adjust for the area sampled. By

Table 1. Summary table of studies testing the relationship between bird abundance estimated using ARUs and that estimated using traditional field surveys.

Method	Taxa	Sites (recordings)	Bird abundance	Statistical analyses	Agreement	Simultaneous surveys	Reference
Microphone array	Ovenbird *Seiurus aurocapilla*	1	Mist-net	95% CI comparison	YES	NO	Dawson and Efford (2009)
Microphone array	Eurasian Bittern *Botaurus stellaris*	1	Birds detected	Basic comparison	None provided	NO	Frommolt and Tauchert (2014)
Stereo recordings	Multi-species	1 (51)	PC	*t*-test	YES (10 out of 10)	YES	Hobson *et al.* (2002)
Stereo recordings	Australasian Bittern *Botaurus poiciloptilus*	1 (57)	PC	Spearman rank correlation	YES	NO	Williams *et al.* (2018)
Paired acoustic sampling	Multi-species	105 (363)	PC	95% CI comparison	YES (33 out of 35)	YES	Van Wilgenburg *et al.* (2017)
Paired acoustic sampling	Multi-species	6 (280)	PC	95% CI comparison	YES (9 out of 13)	YES	Bombaci and Pejchar (2019)
Sound pressure level	Multi-species	1	Test	83% CI comparison	YES (2 out of 2)	YES	Yip *et al.* (2019)
Sonogram analyses	Yellow Rail *Coturnicops noveboracensis*	1	Simulation	95% CI comparison	YES	[a]	Drake *et al.* (2016)
Sonogram analyses	Multi-species	59	PC	Generalized linear model	NO	YES	Vold *et al.* (2017)
Sonogram analyses	Multi-species	28 (33)	PC	Wilcoxon test	YES/NO	YES	Darras *et al.* (2018a)
Soundscape indices	Manx Shearwater *Puffinus puffinus*	12 (24)	Tape-playbacks	Generalized linear model	NO	NO	Arneill *et al.* (2020)
Soundscape indices	Leach's Storm Petrel *Oceanodroma leucorhoa*	2 (13)	Nest abundance	Pearson's correlation	NO	NO	Orben *et al.* (2019)
Cue counting	Bell Miner *Manorina melanophrys*	26	PC	Generalized linear mixed model	NO[b]	YES	Lambert and McDonald (2014)
Cue counting + SPL	Hawaii Amakihi *Chlorodrepanis virens*	2	PC	95% CI comparison	YES	NO	Sebastián-González *et al.* (2018)

This table excludes studies using the detected vocal activity rate (Table 2). The table information includes: Type of estimation of bird abundance: PC = point-counts; type of statistical analyses carried out to compare field and acoustic bird abundance; and the main result of that comparison (in parentheses is shown, when possible, the number of species with respect to the total of species monitored for which there was agreement between traditional and acoustic-based surveys). Simultaneous surveys means whether traditional field surveys were carried out at the same (YES) or different time (NO) as recordings. A complete list of references can be found in Data S1. CI, confidence interval; SPL, sound pressure level. [a]Bird abundance was simulated by creating recording samples with a known number of calling individuals. [b]Bird density estimated using ARUs was greater than with PC.

mounting an array of microphones, it is possible to estimate the probability that at least one of the microphones detects a given bird. The probability is modelled by combining detector probabilities, each of which is assumed to be a decreasing function of distance from the source. Bird density can then be estimated using an array of detectors by maximizing the appropriate likelihood. Complete theory and application of SECR to sound recordings is described in Dawson and Efford (2009). SECR has been applied only once for estimating Ovenbird *Seiurus aurocapilla* density (using an array of 75 ARUs equipped with four microphones each; Dawson & Efford 2009, Table 1). That study found that estimates of Ovenbird density obtained using SECR were consistent with estimates

Table 2. Summary table of studies testing the relationship between the detected vocal activity rate and bird density estimated using traditional field surveys.

Taxa	Sites (recordings)	Bird abundance	Statistical analyses	Agreement	Reference
Dickcissel *Spiza americana*	9 (511)	Radar	Spearman rank correlation	YES/NO	Larkin *et al.* (2002)
General bird abundance	2 (555)	Radar	Regression analyses	YES	Farnsworth *et al.* (2004)
General bird abundance	10 (220)	PC	ANOVA	NO	Venier *et al.* (2012)
Forster's Tern *Sterna forsteri*	12	Nest abundance	Generalized linear mixed model	YES	Borker *et al.* (2014)
Cory's Shearwater *Calonectris borealis*	9	Nest abundance	Pearson's correlation	YES	Oppel *et al.* (2014)
Multi-species	7 (76)	Mist-net	Pearson's correlation	YES	Sanders and Mennill (2014)
European Nightjar *Caprimulgus europaeus*	6 (22)	LT	Generalized linear mixed model	NO	Zwart *et al.* (2014)
Marbled Murrelet *Brachyramphus marmoratus*	7	Field detections	Pearson's correlation	YES	Borker *et al.* (2015)
Multi-species	16 (48)	PC	Pearson's correlation	YES	Sedláček *et al.* (2015)
Marbled Murrelet	6 (18)	Radar and field detections	*t*-test	YES	Cragg *et al.* (2016)
Multi-species	3 (18)	PC, LT & MM	Negative binomial mixed model	YES (3 out of 4)	Prevost (2016)
Multi-species	1 (351)	PC	Generalized linear mixed model	YES (8 out of 10)	Pankratz *et al.* (2017)
Australasian Bittern	1 (123)	PC	Spearman rank correlation	YES	Williams *et al.* (2018)
Western Capercaillie *Tetrao urogallus*	10 (19)	Lek counts	Spearman rank correlation	YES	Abrahams (2019)
American Woodcock *Scolopax minor*	3 (35)	PC	Pearson's correlation	YES	Buck (2019)
Leach's Storm Petrel	2 (13)	Nest abundance	Pearson's correlation	YES	Orben *et al.* (2019)
Multi-species	27–35	PC – LT	Pearson's correlation	YES (2 out of 2)	Pérez-Granados *et al.* (2019a)
Dupont's Lark *Chersophilus duponti*	5	LT	Pearson's correlation	YES	Pérez-Granados *et al.* (2019b)
Manx Shearwater	12 (24)	Tape-playbacks	Zero-inflated negative binomial mixed model	NO	Arneill *et al.* (2020)
King Rail *Rallus elegans*	10	Callback survey	Generalized linear mixed model	YES	Schroeder and McRae (2020)

Table information includes: Type of estimation of bird abundance: PC = point-counts, LT = line transect, MM = mapping method; type of statistical analyses carried out to compare field abundance and acoustic data; and the main result of the comparison (in parentheses is shown, when possible, the number of species with respect to the total of species monitored for which there was agreement between traditional and acoustic-based surveys). A complete list of references can be found in Data S1. ANOVA, analysis of variance.

obtained by traditional field surveys (Table 1). A second study also used an array of four ARUs and counted the number of Eurasian Bitterns *Botaurus stellaris* in a restored wetland based on the location of vocalizing birds (Frommolt & Tauchert 2014). Although a fair comparison among methods was not included in that case, the authors stated that microphone arrays provided more reliable information than traditional field surveys.

Stereo recordings

Theoretically, recordings made using a single recorder but equipped with several microphones may allow researchers to determine bird density around recorders (Fig. 2). Two studies have already employed stereo configuration (one ARU with two microphones) to estimate bird abundance of a given species around ARUs (Hobson *et al.* 2002, Table 1) and in both cases the authors

Table 3. Population metrics already estimated (compared for the detected vocal activity rate and soundscape indices), and principal advantages and disadvantages of approaches available for estimating bird population metrics using ARUs.

Method	Population metrics	Principle	Advantages	Disadvantages
Microphone array	Bird density, bird abundance	Multiple microphones or ARUs can be used to determine the location of calling birds according to time-of-detection and direction of arrival	(1) Bird location can be estimated with error < 1 m; (2) allows using spatially explicit capture-recapture method; (3) can cover large areas.	(1) Microphone arrays can be costly and logistically difficult; (2) time and effort needed for recording interpretation is multiplied with the number of recordings; (3) there might be variation in the quality among microphones employed
Stereo recordings	Bird abundance	Birds vocalizing in stereo recordings can be estimated according to the direction the call came from and signal volume or separation between calls	(1) Covers a larger area than using a single microphone.	(1) Number of detected males is limited by the number of channels and criteria employed; (2) time for data analyses is twice that using a single microphone; (3) might be useless for bird species with large mobility while singing; (4) recording quality has to be high
Detected vocal activity rate	Bird density, bird abundance, colony size, nest density, nest occupancy	Bird vocal activity is density-dependent, and thus number of calls detected per recording can be used to estimate number of birds around ARUs	(1) Easy and fast to estimate; (2) allows estimates of species-specific or general bird abundance; (3) previous studies provide a good background for future studies.	(1) Several sampling sites need to be monitored to estimate a reliable relationship between DVAR and bird density; (2) long recording periods may be needed to obtain a low-error DVAR; (3) density estimated by acoustic data is related to other sites, (4) vocal activity may vary among and within days
Paired acoustic sampling	Bird density	A factor correction can be applied to correct for differential sampling radius of ARUs and human surveys	(1) Easy reduction of the biases in acoustic surveys; (2) allows a direct and fairer comparison between the two methods (human and ARUs)	(1) Human and acoustic data need to be collected synchronously; (2) bird distance to recorder has to be estimated with accuracy; (3) specific formulae need to be developed for each bird species; (4) difficulty in estimating the sampling radius for shy/rare species
Sound pressure level	Bird density	Distance of vocalizing birds to the recorder can be predicted measuring sound level of recorded bird songs, through a logarithmic relationship with distance. Later, bird density can be estimated following the distance sampling framework	(1) Greatly reduces the biases in acoustic surveys; (2) can be fully automated; (3) allows use of distance sampling procedure; (4) a library of recorded songs at different distances can be used	(1) Requires calibration recordings for establishing the relationship between distance and SL; (2) difficult to estimate such a relationship for shy/rare species; (3) bird movements while recording may make it difficult to use the index; (4) birds may change their vocal intensity according to, for example, singing direction, seasonality or weather

(continued)

Table 3. (continued)

Method	Population metrics	Principle	Advantages	Disadvantages
Sonogram analyses	Bird density, bird abundance	Bird abundance can be estimated by visually inspecting the sonograms (similar to stereo recordings)	(1) Estimates a minimum number of birds per recording; (2) can consider specific vocal behaviour of monitored species, allows application of distance sampling techniques (see Darras *et al.* 2018a)	(1) Can be logistically difficult for long-term monitoring programmes; (2) does not take into account imperfect detection or bird distance; (3) reference sounds at different frequencies are required
Soundscape indices	Nest density, nest occupancy	Large number of individuals will produce more complex and energetic recordings	(1) Easy method for scanning large datasets of recordings; (2) fully automated	(1) Several sampling sites need to be monitored to estimate a reliable relationship between soundscape indices and bird density; (2) effectiveness will be reduced with the presence of non-target species, (3) species with constant vocal repertoire will not produce more complex recordings
Cue counting	Bird density	Number of birds can be estimated by dividing the total number of calls recorded by the cue rate at which individuals vocalize	(1) Deep background applying cue counting to PC data; (2) easy and fast to estimate	(1) An unbiased average cue rate of the species is required; (2) long recording periods may be needed to obtain a low error of vocalization counts; (3) vocalization counts and cue rate may vary among and within days

found agreement between bird abundance estimated from sound recordings and bird abundance estimated in the field (Table 2). In both cases the researchers heard the stereo recordings and estimated bird abundance based on the direction the call came from (left/right channel), and volume or temporal separation between multiple calls. In that way, Williams *et al.* (2018) counted the number of Australasian Bitterns *Botaurus poiciloptilus* around the ARU and classified a call as belonging to a new individual if the combination of volume and direction differed from calls previously catalogued. The authors stated that audible analyses of stereo recordings were promising for counting the species and found a strong correlation between the number of Bitterns detected in the field and those identified from the recordings (rho = 0.76, $P < 0.01$, Williams *et al.* 2018). Hobson *et al.* (2002) also declared that abundance estimates for the 10 most abundant species obtained through audible analyses of stereo recordings were also similar to those obtained through traditional field surveys.

Single recorder

Detected vocal activity rate

The basic assumption of this method is that bird vocal activity is density-dependent, and thus detected vocal activity rate (DVAR, number of vocalizations detected per unit area per unit time of recording) among sites should be correlated with the abundance of a bird population (Larkin *et al.* 2002, Borker *et al.* 2014). Therefore, once the relationship between DVAR and bird abundance for a target species is known, it can be used to predict bird density around recorders in sites of unknown population density (see application in Oppel *et al.* 2014). DVAR has been the approach most often applied (20 studies found in this

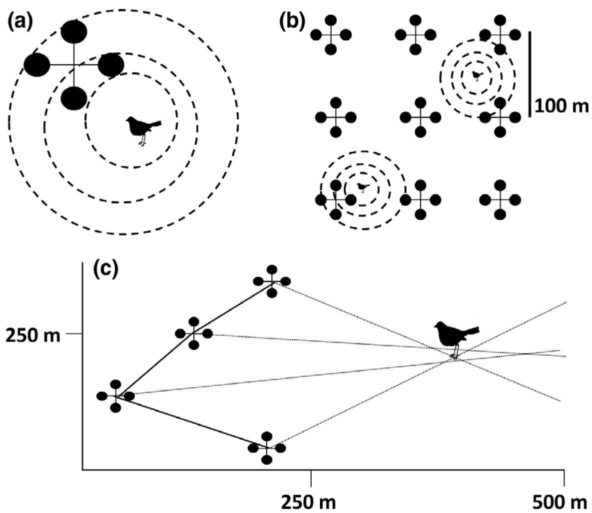

Figure 2. Method of acoustic location of birds using multiple (four in our examples) microphones (circles) and variable number of ARUs. (a) Sound waves of bird songs reach each of the four microphones of the recorder at different times, allowing bird location, similar to the way in which bird density is estimated in stereo recording. (b) Example of a microphone array for estimating bird density using four microphones at nine recording positions. This method allows more detailed analyses and improves sound location. (c) Four recorders equipped with four microphones separated in space. Bird positions can be determined at the centre of the intersection of estimated directions of each recorder. This type of array enables greater spatial coverage but reduces location accuracy. It can be especially well suited to species whose vocalizations can be heard at long distances (Frommolt & Tauchert 2014).

review) as an indicator of both general (Farnsworth *et al.* 2004) and species-specific bird abundance (Borker *et al.* 2014, Pérez-Granados *et al.* 2019a). In 17 of the 20 studies (84.2%) the authors found a significant relationship between DVAR and bird population metrics (Tables 2 and 3).

Paired acoustic sampling

Van Wilgenburg *et al.* (2017) designed an analytical approach able to calibrate counts from ARUs with traditional point counts (PC) to make comparable bird densities estimated with traditional and acoustic-based surveys. This approach was developed to account for imperfect detection and species availability. Observers should perform paired sampling, with recordings being collected when human observers perform PC, noting the estimated distance to detected birds and time-of-detection. Paired acoustic sampling assumes that the number of individuals of a bird species in the surveyed area is equal for both methods, and thus differences between human and ARU counts should be due to differences in the area sampled by the two methods (Bombaci & Pejchar 2019). It is then possible to estimate statistical offsets that account for the differences in sampling radius among humans and ARUs; these offsets can therefore be used to reduce biases in count data collected by ARUs and thus to obtain non-biased, and comparable, population densities (Van Wilgenburg *et al.* 2017). This approach has been employed in two studies, and in both cases the application of the paired acoustic sampling significantly reduced the biases in acoustic surveys and derived similar densities between PC and ARUs (Table 1).

Sound pressure level

An alternative method for correcting biases in acoustic surveys is to measure the sound pressure level (SPL) of bird songs, which is a measure, usually in decibels, of the energy of a sound signal. The SPL of an acoustic signal in audio recordings can be predicted through a logarithmic decline with distance and therefore can be used as a proxy of individual distance for estimating bird density in a distance sampling framework. Distance sampling is a common method to estimate bird population density using traditional field surveys by accounting for imperfect detection of individuals with increasing distance from an observer (Buckland *et al.* 2001). Bird distance to the observer needs to be measured with no or low error (Yip *et al.* 2019). SPL estimation requires calibration recordings to establish the relationship between SPL and bird distance, as well as to determine the source level (Yip *et al.* 2019). Three studies included a measurement of the SPL in their analyses. In two studies the authors measured the SPL of bird vocalizations and followed the distance sampling framework; in one of them the authors simulated different bird densities and evaluated the effectiveness of this technique to estimate bird densities without including other covariates (Yip *et al.* 2019, see also Sebastián-González *et al.* 2018). In the third study, the known relationship between SPL and distance of vocalizing Bell Miners *Manorina melanophrys* allowed the authors to choose only those vocalizations uttered within a 50-m radius of the recorder, and therefore to estimate the density of the species within that radius (Lambert & McDonald 2014). All three studies including a measurement of SPL in their analyses found that ARUs performed as well as or better than traditional field surveys for detecting bird abundance when measuring SPL in recordings (Table 1).

Sonogram analyses

Visual and aural inspection of sonograms have allowed researchers to estimate the number of birds vocalizing based on species-specific vocal behaviour (Drake *et al.* 2016) or to estimate bird density after estimating the distances of recorded birds in sound recordings using a reference recording of test sounds emitted from known distances at different frequencies (Darras *et al.* 2018a). The inspection of sonograms was used in three studies and in two of them there was agreement between acoustic data and bird data estimated using traditional field surveys (Table 1). Methods employed for estimating bird abundance using inspection of sonograms greatly differed among studies and thus we provide a more detailed explanation.

Drake *et al.* (2016) estimated Yellow Rail *Coturnicops noveboracensis* abundance in a recording by counting the number of birds calling within the estimated minimum separation between calls for a single individual. The number of males around ARUs was estimated as the number of calls detected within that minimum separation between calls of a single male. Therefore, if three calls were detected within the selected time frame, three males were consequently estimated to be around the sampling radius of the recorder. In another study, Vold *et al.* (2017) estimated the maximum number of birds of each distinguishable species by counting the number of individuals vocalizing simultaneously in the recording. Vold *et al.* (2017) found that, on average, the number of birds detected by ARUs was lower than the number of birds detected by PC. Vold *et al.* (2017) highlighted that differences found between methods could largely be attributed to the different sampling radius of human and ARUs, as well as the conservative protocol followed during the study (non-overlapping songs were considered the same individual).

Darras *et al.* (2018a) also manually inspected sonograms but they devised a new method that consisted of the use of reference sounds broadcasted at known distances and different frequencies for calibrating the estimation of bird detection distances from sound recordings collected using ARUs. This approach allowed the standardization of data collected from ARUs and the estimation of bird density by the application of distance sampling techniques (see *Sound pressure level* section for more information about distance sampling). These authors found similar bird abundance estimated using ARUs, in comparison with PC, when using either an unlimited or a fixed radius, but ARUs detected more birds when using distance sampling. They hypothesized that this was related to a flushing effect due to human presence while performing PC, supported by the fact that most recorder detections were made at short distances (< 30 m), and almost no birds closer than 10 m were detected during PC.

Soundscape indices

Soundscape indices are used based on the assumption that the acoustic complexity of a soundscape is a direct surrogate for the number of species around recorders (Pieretti *et al.* 2011) and have been commonly employed using bird communities as a study model. Following a similar reasoning, the relationship between soundscape indices and number of individuals around recorders might be used to infer the density of a bird species around ARUs if soundscape indices and bird abundance are correlated. Two studies have already measured the relationship between three soundscape indices and the density of two bird species estimated by traditional field surveys (Table 4), although neither of the two studies found a significant relationship between the soundscape indices obtained per recording and bird densities around ARUs. In the first study, Orben *et al.* (2019) assessed the relationship between the Acoustic Energy Index (an index related to the amount of energy within a determined band of frequency, see Table 4) and the burrow occupancy of Leach's Storm Petrel *Oceanodroma leucorhoa*, which although marginally non-significant, explained a large proportion of the burrow occupancy ($R^2 = 0.41$, $P = 0.051$, Orben *et al.* 2019). In the second study, Arneill *et al.* (2020) tested the relationship between the Acoustic Complexity Index and the Bioacoustic Index (see definitions in Table 4) and the burrow occupancy of the Manx Shearwater *Puffinus puffinus*; in both the cases, the relationships found were non-significant ($P > 0.5$ in both cases; Arneill *et al.* 2020).

Table 4. Summary of principles and application of soundscape indices employed for assessing the relationship between soundscape indices and bird abundance.

Index	Principle	Species tested	Application
ACI	ACI captures the dynamic changes in soundscape recordings. It is calculated as the average absolute fractional change in spectral amplitude, averaged over all frequency bins for entire recordings (Pieretti *et al.* 2011)	*Puffinus puffinus*	Arneill *et al.* (2020) estimated the ACI and BIO indices per recording within the frequency limits 1500–8000 Hz. They reduced the lower frequency band of setting defaults (2 kHz) to ensure the range of the *P. puffinus* call was included in the analyses. They assumed that variations in these indices between recordings reflect variation in the number vocalizations
BIO	BIO provides a measure of both the spectral amplitude and the number of frequency bands used in a recording. It is calculated as the area under the mean frequency spectrum (Boelman *et al.* 2007)		
AEI	Bird calls are band-limited. AEI characterizes the relative amount of energy within a determined band of frequency	*Oceanodroma leucorhoa*	Orben *et al.* (2019) measured mean relative energy in 187 43-Hz frequency bins for every 2 s of recordings. They employed mean relative energy on the bins from 1376 to 1462 Hz (greatest amount of energy for *O. leucorhoa*) as an index of species density

ACI, Acoustic Complexity Index; AEI, Acoustic Energy Index; BIO, Bioacoustic Index.

Passive cue counting

The rationale for passive cue counting (cue counting hereinafter) is that animal density around recorders can be estimated by dividing the number of cues recorded using ARUs (e.g. number of bird songs per unit area per unit time of recording) by an estimate of the average rate at which individuals of the target species vocalize (average number of bird songs per unit time, in this example) (Hiby & Ward 1986, Marques *et al.* 2013). Two studies have employed cue counting, but including also an estimate of the distance of the vocalizing birds to the ARU (Lambert & McDonald 2014), and in both cases, density estimates obtained by the cue counting approach were similar or even higher to those estimates obtained by traditional field surveys (Table 1 and see Pérez-Granados *et al.* in press). In the first case study, Lambert and McDonald (2014) estimated the density of the Bell Miner around recorders by dividing the number of vocalizations recorded within a limited radius (according to SPL of the recorded signals) by the average cue rate of the species. Lambert and McDonald (2014) concluded that cue counting was able to detect more birds, and therefore estimated higher densities, than were traditional field surveys, despite being a less expensive protocol. Similarly, Sebastián-González *et al.* (2018) estimated the density of the Hawaii Amakihi *Chlorodrepanis virens* by applying cue counting, and including as covariates the probability of detecting a vocalization within the detection area of the recorder and an estimate of the distance of the vocalizing individuals to the recorder (by measuring the SPL of the signals recorded).

DISCUSSION

We provide some recommendations for scientists and managers aiming to select methods for estimating bird density with ARUs, according to their devices, needs, knowledge and statistical skills. These recommendations may also apply to inform their decision on what ARUs to use or what methods can be used for estimating bird densities from archived recordings. The approaches described are complementary and used together to obtain more reliable density estimations (e.g. Dawson & Efford, 2009). The choice of method for estimating bird density around ARUs depends on several factors. Among the most important are: (1) the number and type of ARUs, (2) the proven effectiveness and applicability of the method, (3) whether traditional field surveys are required before or at the time of recording for calibration, and (4) the work and expertise required for interpreting recordings. Practical guidelines regarding the best equipment to use and the settings and recording methods can be found in Gibb *et al.* (2019), Darras *et al.* (2018b) and Sugai *et al.* (2020).

Number and type of devices

All the approaches described can be applied when recording with a single ARU equipped with one microphone, with the exception of pinpointing birds' location using stereo recordings or on the basis of the time delay for arrival of the signals to different microphones, for which one ARU with multiple microphones or a microphone array, respectively, are required. The use of microphone arrays also allows researchers to apply any of the methods described above, and a reduced number of channels and recordings may be selected for data analyses. However, budget can be limiting for projects aimed at performing long-term monitoring based on the use of microphone arrays (though see low-cost devices such as Audiomoth; Hill *et al.* 2018). The creation of an array with several ARUs and microphones requires greater financial investment, especially because ARUs must be equipped with GPS devices and recording must be synchronized (Van Wilgenburg *et al.* 2017). However, this high sampling effort may reduce spatial coverage when employing microphone arrays (but see Frommolt & Tauchert 2014; Fig. 2). Recording quality (e.g. signal-to-noise ratio of the microphone, sampling rate, recording format) may also have an impact on the effectiveness of the approach employed. This impact may be lower for those studies that estimate the sampling radius of the ARU employed, but will be greater for studies that do not control for differential sampling radius among ARUs and human observers. Finally, a low recording quality may reduce the effectiveness of those approaches that require extraction of information about vocalization characteristics, such as SPL.

Effectiveness and applicability

DVAR is the only approach whose effectiveness has been evaluated in a (relatively) large number of species and under different recording conditions (Table 2). Nonetheless, paired acoustic sampling has also demonstrated its value for estimating bird density in many bird species. The other seven approaches have been tested only a few times (maximum two) using a small number of species as study models, and more research is needed before making any generalizations about their effectiveness. Future studies comparing the effectiveness of different methods using the same acoustic dataset may be useful to provide more reliable comparisons among approaches. The lack of studies using ARUs to estimate bird density in tropical areas is a crucial gap that should be addressed (Scarpelli *et al.* 2019), especially because ARUs could be extremely useful in the tropics, where the dominant vegetation is usually tall and dense and the logistics of human access are difficult (Pérez-Granados & Schuchmann 2020b). However, some of the methods reviewed here (e.g. soundscape indices) may be less effective in tropical areas due to the larger number of vocal species and background noise (Eldridge *et al.* 2018). A disadvantage of using soundscape indices for estimating bird densities at the species level is that they include non-target sounds (e.g. other birds, rain, wind) within their summarized indices. Indeed, Arneill *et al.* (2020) and Orben *et al.* (2019) used soundscape indices with contradictory results, partially as a result of using different frequency limits (Table 4). They also tested different soundscape indices, thus precluding direct comparisons. For example, Orben *et al.* (2019) measured the Acoustic Energy Index in a very narrow frequency band (1376–1462 Hz), where most of the energy of the call of their target species (Leach's Storm Petrel) was concentrated, reducing as much as possible the presence of non-target species. However, Arneill *et al.* (2020) used a wide frequency band (1500–8000 Hz) and therefore included most of the vocalizations of other taxa in their measurements of the soundscape. Thus, the lack of a relationship between soundscape indices and abundance of the Manx Shearwater obtained by Arneill *et al.* (2020) may be linked to the wide frequency band considered in their study. A reasonable solution to partly resolve this problem in future species-specific studies aiming to use soundscape indices for estimating species' density around ARUs might be to narrow the bandwidth of the sound frequencies to be analysed as much as possible.

Prior knowledge about the vocal behaviour of the target species could also be a limiting factor, because some of the approaches described here require prior calibration or previous knowledge about the vocal behaviour of the target species for estimating bird densities using ARUs. For example, to predict bird abundance or bird densities using either DVAR or soundscape indices, it is necessary to have previously estimated a regression of observed bird density as a function of the selected acoustically derived estimate index. A regression framework could then be used to predict relative density around recorders deployed in sites with unknown numbers of individuals. Although little is known about the number of independent sites needed to estimate the relationship between DVAR and bird abundance, previous studies have suggested that a minimum number of 20–30 sites is required (Pérez-Granados *et al.* 2019c). Similarly, for before applying cue counting, researchers should have previously estimated an unbiased average cue rate at which individuals vocalize (Buckland 2006, Lambert & McDonald 2014). This will in turn require sampling of a representative number of vocalizing individuals (Lambert & McDonald 2014, Sebastián-González *et al.* 2018). Likewise, to include the measurement of SPL of received signals in the analyses also requires prior knowledge of the relationship between SPL and bird distance to the recorder, and the paired acoustic sampling approach also requires previously estimated statistical offsets to correct for different sampling radius of the recorder for each species monitored. In contrast, some approaches can be used to infer bird density from sound recordings without prior calibration or previous knowledge of the vocal behaviour of the target species. For example, bird density can be estimated using reference sound recordings to estimate bird detection distances to the recorder (Darras *et al.* 2018a) or based on the direction and time-of-detection when placing microphone arrays or recording in stereo.

Birds tend to move while vocalizing, which may in most cases make the estimation of bird densities using ARUs difficult. However, the impact of birds' mobility on the performance of some methods may be low (e.g. soundscape indices and those applying distance sampling, if only the first detection of a bird species at a location is used), but it is a serious limitation for other methods. Among the methods more affected by bird movements is the use of stereo recordings, because the maximum number of vocalizing individuals detected is limited by the number of channels and criteria employed (Hobson *et al.* 2002, Williams *et al.* 2018). Moreover, the process of deciding the direction and the volume of the received signal to distinguish calls from individuals can be subjective and may require high levels of expertise and concentration (Williams *et al.* 2018). Thus, stereo recordings may be useful for monitoring birds living in low densities (e.g. bitterns, some rails, owls) but would be ineffective for monitoring birds living in higher densities. However, in some other approaches, such as when using microphone arrays, birds' movements between recorders should have low or no impact on bird estimates, as bird location can be described according to the direction-of-arrival and time of detection of the signal to each recorder. For microphone arrays, one of the major components of variance might be microphone variability, due to the large number of microphones involved (Marques *et al.* 2013). In general, microphones should be standardized prior to sampling whatever method is being used (Turgeon *et al.* 2017).

Bird vocal activity differs within the day and among days for both exogenous and endogenous reasons (Catchpole & Slater 2008). Moreover, vocal activity of the same species may vary spatially and affect comparisons among sites (Marques *et al.* 2013). It is therefore important to control for factors that alter the vocal behaviour and the detectability of a species' vocalization for obtaining unbiased density estimations. The variable vocal behaviour of birds may have an impact on every approach but might be more influential for those approaches using vocalization counts as variable response (e.g. DVAR and cue counting); in the worst case, vocalization counts may only be useful to estimate bird densities in the monitored area, allowing no wider generalization. A solution for reducing the impact of both exogenous and endogenous factors on the number of recorded vocalizations might be to record over several days and use the average number of vocalizations counted over this period as the variable response (see reduction of the coefficient of variation of the mean DVAR for three bird species as a function of consecutive recording days in Pérez-Granados *et al.* 2019c and Pérez-Granados & Schuchmann 2020b). A similar solution may apply for estimating a reliable average cue rate, which is needed to apply cue counting successfully. The time period for which each individual is monitored should therefore be long enough to ensure that the average estimate is representative of the survey period, including any periods during which monitored birds are silent (Pérez-Granados et al. in press). Similarly, a representative sample of birds should be monitored to estimate the average cue rate for the target species (Buckland 2006, Sebastián-González *et al.* 2018).

Fieldwork at recording time

Some methods can be applied without the need to collect data during recording (microphone arrays, sonogram analyses, soundscape indices), while other approaches require trained observers to collect additional information while recording (Table 5). One such method is paired acoustic sampling, because the estimated statistical offsets to account for the differences in sampling radius among humans and ARUs are species-specific and must be estimated for each species separately. This may reduce their applicability to shy or threatened birds. Moreover, paired acoustic sampling requires observers accurately to estimate their distance from detected birds as well as the time-of-detection, which can be difficult for some species and situations (Bombaci & Pejchar 2019) and may require extra training for observers to meet analytical assumptions (Van Wilgenburg *et al.* 2017).

Another method that requires additional work while recording is the measurement of SPL for estimating bird detection distances from sound recordings. For example, Yip *et al.* (2019) found that a calibration dataset of approximately 300 vocalizations was needed to minimize error in bird distance prediction by SPL. However, these studies have proven the value of including measurements of SPL to predict bird distances from sound recordings. For example, Yip *et al.* (2019) found that error from all SPL-predicted distances was less than estimated human error extracted from the literature. Similarly, Sebastián-González *et al.* (2018) found that measured and predicted distances were significantly related. Moreover, the measured statistical offsets by paired acoustic sampling and the relationship between SPL and birds' predicted distances may vary among species, recorders, habitat type or birds' singing direction, and therefore more research is still required (Darras *et al.* 2016, Sebastián-González *et al.* 2018, Pérez-Granados *et al.* 2019b, Yip *et al.* 2019). In this sense, the use of reference sound recordings would be an optimal solution for estimating bird detection distances in sound recordings, when reference recordings of birds have not been collected or are difficult to obtain. Indeed, Darras *et al.* (2018a) have already demonstrated that estimated bird distances from sound recordings can be similar to actual distances of the birds estimated in the field. The creation of sound libraries cataloguing bird vocalizations recorded or broadcasted at known distances may therefore be useful for future bioacoustics studies aiming to estimate bird densities using ARUs. Nonetheless, whenever possible it would be desirable to estimate detectability for the species and the conditions (habitat type, ARU employed) of the survey rather than using reference sound recordings, as the applicability of sound libraries is likely to be lower when compared with specific tests for the species and ARU of the survey.

Time and expertise needed for interpreting recordings

The time required for recording analyses is multiplied when using microphone arrays or stereo recordings because of the larger number of recordings collected. Among the approaches available for estimating bird densities with a single ARU, DVAR, cue counting and use of soundscape indices are among those requiring less effort and expertise for recording interpretation, because the variable response (vocalizations counts or acoustic index) can easily be estimated (Table 5). Similarly, the effort required for interpreting recordings using the paired acoustic sampling approach is low, because once the statistical offset has been estimated, its application is similar to that described above for DVAR and cue counting. However, the measurement of SPL of acoustic signals can be laborious, because sounds must be isolated, measured (using reference recordings of birds made at different distances), and bird detection distances estimated through specific functions (Yip *et al.* 2019). Visual and aural inspection of sonograms is costly in time and expertise required for interpreting recordings, and its use may be limited for long-term monitoring programmes (Table 5).

CONCLUSIONS

- Passive acoustic monitoring has the potential to reliably estimate bird population density around ARUs.
- Future studies aiming to use ARUs for estimating bird densities should estimate the sampling

Table 5. The number and type of ARUs required, work needed at the time of recording, time cost for interpreting recordings and knowledge required to apply each method (once recordings have been analysed) for estimating bird density using ARUs.

Method	Minimum number of devices required	Fieldwork at recording time	Time cost and expertise for recording interpretation	Expertise required for estimating bird density
Microphone array	Spatially dispersed groups of microphones	Low (although large number of ARUs may need to be deployed, increasing working effort)	Very high (multiple recordings must be analysed accounting for time stamps and ARU location).	Medium (bird density is estimated based on the estimated location of vocalizing birds; specific formulae considering recording location and time stamps are required to do so)
Stereo recordings	A single recorder with two microphones	Low (no need to collect data while recording)	High (recordings need to be checked accounting for time stamps, channel of the signal and volume)	Low (number of birds equals number of different birds identified in sound recordings)
Detected vocal activity rate	A single recorder with one microphone	Medium (it is necessary to record on multiple sites to estimate the relationship between DVAR and bird density. Accuracy is greater when recording during longer periods)	Low (count the number of vocalizations per recording and the relationship between bird density and detected bird vocal activity rate)	Low (bird density can be predicted using the known relationship between bird density and soundscape indices, see application in Oppel *et al*. 2014)
Paired acoustic sampling	A single recorder with one microphone	Very high (paired sampling, observers need to record distance to birds detected and time of detections)	Low (count the number of vocalizations per recording)	High (statistical offsets have to be estimated for each bird species and for each ARU using specific functions)
Sound pressure level	A single recorder with one microphone	High (observers need to annotate distance to birds detected, species-specific studies are needed, although playback tests and referenced sounds can be used)	High (bird vocalizations must be isolated and measured)	High (the relationship between SPL and bird distance to the recorder needs to be estimated and specific models, such as distance sampling, are required to obtain bird densities from sound recordings)
Sonogram analyses	A single recorder with one microphone	Medium (it is necessary to study the vocal behaviour of the target species or record reference sounds of different frequencies at variable distances, see Darras *et al*. 2018a)	High (visual inspection of sonograms considering the vocal behaviour of the species monitored or estimating bird distances according to signal intensity based on reference sounds)	Medium (bird population size can be directly estimated from visual inspection, but complex statistical models, including distance sampling, might be required for estimating bird densities from sound recordings using reference sounds, see Darras *et al*. 2018a)
Soundscape indices	A single recorder with one microphone	Medium (it is necessary to record on many sites to estimate the relationship between the selected soundscape index and bird density)	Medium (estimation of soundscape indices can be automated, for example using specific R packages; it is also necessary to assess the relationship between bird density and the selected soundscape index)	Low (bird density can be predicted using the known relationship between bird density and soundscape indices)
Cue counting	A single recorder with one microphone	High (it is necessary to know the average cue rate of individuals of the target species)	Low (count the number of vocalizations per recording)	Low (bird density is estimated dividing the number of vocalizations per recording by the average cue rate of individuals of the target species).

radius of the ARU employed for the target species in the habitat type of the survey and, whenever possible, control for imperfect detection (e.g. estimate the probability of detecting a bird vocalization within the sampling radius considered). This is the only way to estimate bird density and will allow more fair comparisons among studies.

- Some of the approaches described here might be useful to reduce biases in every acoustic survey, and therefore to improve the estimation of bird density using ARUs. Among these approaches, we highlight: (i) paired acoustic sampling to estimate the different sampling radius among ARUs and human observers and (ii) including a measurement of the SPL of the received signal, which may allow for estimating bird densities but also truncation of the sampling radius of the ARU to a sensible threshold beyond which the probability of detection sharply decreases for ARUs. This will allow better application of distance sampling to obtain more accurate bird density estimates (e.g. Yip *et al.* 2019). However, for those studies unable to estimate the relationship between SPL and bird distance to the recorder, the use of reference sound recordings of different frequencies and uttered at known distances might be an alternative aid to applying distance sampling (Darras *et al.* 2018a).
- Microphone arrays enable researchers to determine the position of vocalizing individuals with high accuracy and to apply any of the methods described, but also to use sophisticated methods to control for imperfect detection of birds and the sampling radius of the recorder, such as SECR. Using arrays could therefore be a recommended approach for future surveys aiming to estimate bird densities using ARUs. However, the high cost of acquiring multiple microphones (and ARUs), together with greater time needed for data analyses, might be a limitation for some studies.
- Estimating bird density from stereo recordings could be a good solution to increase the area sampled with a single recording. However, the criteria previously employed for counting birds from recordings have been subjective and therefore further research recording in stereo and including some of the approaches to reduce biases among ARUs and human observers (e.g. measurement of SPL, paired acoustic sampling) is required to improve our knowledge about whether recording in stereo does improve acoustic survey efficiency. Similarly, estimating bird densities directly by visual inspection of recordings might be useless for most circumstances and it might be better to use some of the approaches already available that have proven their effectiveness across multiple bird species.
- DVAR and cue counting are based on vocalization counts. Thus, researchers should be aware that vocal activity at the population and individual level (cue rate) vary over time and space, but also depend on many endogenous and exogenous factors, so that direct comparisons across time or space may be biased. However, both methods may be a feasible solution to predict bird density under difficult circumstances for traditional surveys, such as inaccessible cliff locations (Oppel *et al.* 2014) or when monitoring cryptic birds living in canopy forest (Lambert & McDonald 2014).
- The possible use of soundscape indices may require narrowing as much as possible the bandwidth of the vocalization selected for recording analyses to reduce the presence of non-target species within the selected frequencies. Soundscape indices may perform better in areas with low numbers of species around ARUs, but further research is needed.
- To increase our understanding about the species and circumstances in which the use of ARUs can be useful for estimating bird densities, further research should evaluate the effectiveness of the described approaches in tropical areas and report outcomes, including when there is no agreement between traditional field and acoustic-based surveys.

The authors wish to thank several projects that have financed their studies in bioacoustics. Special thanks to the Research and Conservation Program of Zoo de Barcelona, within the project 'Nuevas tecnologías para viejos trabajos. Uso de grabadores automáticos para la detección y censo de especies raras y amenazadas. El caso de la alondra ricotí en Lleida y otras poblaciones pequeñas'; the LIFE-Ricotí-project (LIFE15-NAT-ES-000802), granted by the European Commission; and the project BBVA-Ricotí granted by the BBVA Foundation. This is a contribution to the Excellence Network REMEDINAL TE-CM (P2018/EMT- 4338), supported by Comunidad de Madrid. We thank Kevin Darras, Carlos Abrahams, Esther Sebastián-González and three anonymous reviewers whose comments helped to improve the manuscript.

AUTHOR CONTRIBUTION

Cristian Pérez-Granados: Conceptualization (supporting); Data curation (equal); Formal analysis (lead); Funding acquisition (equal); Investigation (equal); Methodology (lead); Project administration (equal); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing-original draft (lead); Writing-review & editing (equal). **Juan Traba:** Conceptualization (lead); Data curation (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (equal); Methodology (supporting); Project administration (equal); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing-original draft (supporting); Writing-review & editing (equal).

Data Availability Statement

All references included in the review are provided as Data S1.

REFERENCES

Abrahams, C. 2019. Comparison between lek counts and bioacoustic recording for monitoring Western Capercaillie (*Tetrao urogallus* L.). *J. Ornithol.* **19**: 685–697.

Arneill, G.E., Critchley, E.J., Wischnewski, S., Jessopp, M.J. & Quinn, J.L. 2020. Acoustic activity across a seabird colony reflects patterns of within-colony flight rather than nest density. *Ibis* **162**: 416–428.

Blumstein, D.T., Mennill, D.J., Clemins, P., Girod, L., Yao, K., Patricelli, G., Deppe, J.L., Krakauer, A.H., Clark, C., Cortopassi, K.A., Hanser, S.F., McCowan, B., Ali, A.M & Kirschel, A.N.G. 2011. Acoustic monitoring in terrestrial environments using microphone arrays: applications, technological considerations and prospectus. *J. Appl. Ecol.* **48**: 758–767.

Boelman, N.T., Asner, G.P., Hart, P.J. & Martin, R.E. 2007. Multi-trophic invasion resistance in Hawaii: bioacoustics, field surveys, and airborne remote sensing. *Ecol. Appl.* **17**: 2137–2144.

Bombaci, S.P. & Pejchar, L. 2019. Using paired acoustic sampling to enhance population monitoring of New Zealand's forest birds. *N. Z. J. Ecol.* **43**: 3356.

Borchers, D.L. & Efford, M.G. 2008. Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics* **64**: 377–385.

Borker, A.L., Halbert, P., Mckown, M.W., Tershy, B.R., & Croll, D.A. 2015. A comparison of automated and traditional monitoring techniques for marbled murrelets using passive acoustic sensors. *Wildlife Soc. Bull.* **39**: 813–818.

Borker, A.L., McKown, M.W., Ackerman, J.T., Eagles-Smith, C.A., Tershy, B.R. & Croll, D.A. 2014. Vocal activity as a low cost and scalable index of seabird colony size. *Conserv. Biol.* **28**: 1100–1108.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford: Oxford University Press.

Buckland, S.T. 2006. Point-transect surveys for songbirds: robust methodologies. *Auk* **123**: 345–357.

Buck, E. 2019. *Acoustic monitoring of American Woodcok (Scolopax minor)*. Chancellors Honors Program Senior Thesis, University of Tennessee.

Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E. & Boutin, S. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *J. Appl. Ecol.* **52**: 675–685.

Catchpole, C.K. & Slater, P.J. 2008. *Bird Song: Biological Themes and Variation*, 2nd edn. Cambridge: Cambridge University Press.

Cragg, J.L., Burger, A.E. & Piatt, J.F. 2016. Techniques for monitoring Brachyramphus murrelets: a comparison of radar, autonomous acoustic recording and audio-visual surveys. *Wildlife Soc. Bull.* **40**: 130–139.

Darras, K., Batáry, P., Furnas, B., Celis-Murillo, A., Van Wilgenburg, S.L., Mulyani, Y.A. & Tscharntke, T. 2018b. Comparing the sampling performance of sound recorders versus point counts in bird surveys: a meta-analysis. *J. Appl. Ecol.* **55**: 2575–2586.

Darras, K., Furnas, B., Fitriawan, I., Mulyani, Y. & Tscharntke, T. 2018a. Estimating bird detection distances in sound recordings for standardizing detection ranges and distance sampling. *Meth. Ecol. Evol.* **9**: 1928–1938.

Darras, K., Pütz, P., Rembold, K. & Tscharntke, T. 2016. Measuring sound detection spaces for acoustic animal sampling and monitoring. *Biol. Conserv.* **201**: 29–37.

Dawson, D.K. & Efford, M.G. 2009. Bird population density estimated from acoustic signals. *J. Appl. Ecol.* **46**: 1201–1209.

Drake, K.L., Frey, M., Hogan, D. & Hedley, R. 2016. Using digital recordings and sonogram analysis to obtain counts of Yellow Rails. *Wildl. Soc. Bull.* **40**: 346–354.

Eldridge, A., Guyot, P., Moscoso, P., Johnston, A., Eyre-Walker, Y. & Peck, M. 2018. Sounding out ecoacoustic metrics: avian species richness is predicted by acoustic indices in temperate but not tropical habitats. *Ecol. Ind.* **95**: 939–952.

Farnsworth, A., Gauthreaux, S.A., Jr & Blaricom, D.V. 2004. A comparison of nocturnal call counts of migrating birds and reflectivity measurements on Doppler radar. *J. Avian Biol.* **35**: 365–369.

Frommolt, K.H. & Tauchert, K.H. 2014. Applying bioacoustic methods for long-term monitoring of a nocturnal wetland bird. *Ecol. Inf.* **21**: 4–12.

Gibb, R., Browning, E., Glover-Kapfer, P. & Jones, K.E. 2019. Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. *Methods Ecol. Evol.* **10**: 169–185.

Hedley, R.W., Wilson, S.J., Yip, D.A., Li, K. & Bayne, E.M. 2020. Distance truncation via sound level for bioacoustic surveys in patchy habitat. *Bioacoustics*. 1–21. https://doi.org/10.1080/09524622.2020.1730240

Hiby, A.R. & Ward, A.J. 1986. Analysis of cue-counting and blow rate estimation experiments carried out during the 1984/85 IDCR minke whale assessment cruise. *Report of the International Whaling Commission* **36**: 473–476.
Hill, A.P., Prince, P., Piña Covarrubias, E., Doncaster, C.P., Snaddon, J.L. & Rogers, A. 2018. AudioMoth: evaluation of a smart open acoustic device for monitoring biodiversity and the environment. *Methods Ecol. Evol.* **9**: 1199–1211.
Hobson, K.A., Rempel, R.S., Greenwood, H., Turnbull, B. & Van Wilgenburg, S.L. 2002. Acoustic surveys of birds using electronic recordings: new potential from an omnidirectional microphone system. *Wildl. Soc. Bull.* **30**: 709–720.
Hutto, R.L. & Stutzman, R.J. 2009. Humans versus autonomous recording units: a comparison of point-count results. *J. Field Ornithol.* **80**: 387–398.
Knight, E., Hannah, K., Foley, G., Scott, C., Brigham, R. & Bayne, E. 2017. Recommendations for acoustic recognizer performance assessment with application to five common automated signal recognition programs. *Avian Conserv. Ecol.* **12**: 2.
Lambert, K.T. & McDonald, P.G. 2014. A low-cost, yet simple and highly repeatable system for acoustically surveying cryptic species. *Austral Ecol.* **39**: 779–785.
Larkin, R.P., Evans, W.R. & Diehl, R.H. 2002. Nocturnal flight calls of Dickcissels and Doppler radar echoes over south Texas in spring. *J. Field Ornithol.* **73**: 2–9.
Marques, T.A., Thomas, L., Martin, S.W., Mellinger, D.K., Ward, J.A., Moretti, D.J., Harris, D. & Tyack, P.L. 2013. Estimating animal population density using passive acoustics. *Biol. Rev.* **88**: 287–309.
Nowak, M.M., Dziób, K. & Bogawski, P. 2019. Unmanned Aerial Vehicles (UAVs) in environmental biology: a review. *Eur. J. Ecol.* **4**: 56–74.
Oppel, S., Hervias, S., Oliveira, N., Pipa, T., Silva, C., Geraldes, P., Goh, M., Immler, E. & McKown, M. 2014. Estimating population size of a nocturnal burrow-nesting seabird using acoustic monitoring and habitat mapping. *Nat. Conserv.* **7**: 1–13.
Orben, R.A., Fleishman, A.B., Borker, A.L., Bridgeland, W., Gladics, A.J., Porquez, J., Sanzenbacher, P., Stephensen, S.W., Swift, R., McKown, M.W. & Suryan, R.M. 2019. Comparing imaging, acoustics, and radar to monitor Leach's Storm-petrel colonies. *PeerJ* **7**: e6721.
Pankratz, R.F., Hache, S., Sólymos, P. & Bayne, E.M. 2017. Potential benefits of augmenting road-based breeding bird surveys with autonomous recordings. *Avian Conserv. Ecol.* **12**: 18.
Pérez-Granados, C., Bota, G., Giralt, D., Albarracín, J. & Traba, J. 2019b. Cost-effectiveness assessment of five audio recording systems for wildlife monitoring: differences between recording distances and singing direction. *Ardeola* **66**: 311–325.
Pérez-Granados, C., Bota, G., Giralt, D., Barrero, A., Gómez-Catasús, J., Bustillo-de la Rosa, D. & Traba, J. 2019a. Vocal Activity Rate index: a useful method to infer terrestrial bird abundance with acoustic monitoring. *Ibis* **161**: 901–907.
Pérez-Granados, C., Gómez-Catasús, J., Bustillo-de la Rosa, D., Barrero, A., Reverter, M. & Traba, J. 2019c. Effort needed to accurately estimate Vocal Activity Rate index using acoustic monitoring: a case study with dawn-time singing passerine. *Ecol. Ind.* **107**: 105608.
Pérez-Granados, C. & Schuchmann, K.-L. 2020a. Monitoring the annual vocal activity of two enigmatic Neotropical birds: the Common Potoo (*Nyctibius griseus*) and the Great Potoo (*Nyctibius grandis*). *J. Ornithol.* **161**: 1129–1141.
Pérez-Granados, C. & Schuchmann, K.L. 2020b. Illuminating the nightlife of two Neotropical nightjars: vocal behavior over a year and monitoring recommendations. *Ethol. Ecol. Evol.* **32**: 466–480.
Pérez-Granados, C., Barrero, A., Reverter, M., Gómez-Catasús, J., Bustillo-de la Rosa, D. & Traba, J. 2021. Assessment of cue counting for estimating bird density using passive acoustic monitoring: recommendations for estimating a reliable cue rate. *Avian Conservation and Ecology*. In press.
Pieretti, N., Farina, A. & Morri, D. 2011. A new methodology to infer the singing activity of an avian community: the Acoustic Complexity Index (ACI). *Ecol. Ind.* **11**: 868–873.
Prevost, S.C. 2016. *Estimating Avian Populations with Passive Acoustic Technology and Song Behavior*. Master's Thesis, University of Tennessee.
Priyadarshani, N., Masland, S. & Castro, I. 2018. Automated birdsong recognition in complex acoustic environments: a review. *J. Avian Biol.* **49**: jav-01447.
Sanders, C.E. & Mennill, D.J. 2014. Acoustic monitoring of nocturnally migrating birds accurately assesses the timing and magnitude of migration through the Great Lakes. *The Condor* **116**: 371–383.
Scarpelli, M.D., Ribeiro, M.C., Teixeira, F.Z., Young, R.J. & Teixeira, C.P. 2019. Gaps in terrestrial soundscape research: it's time to focus on tropical wildlife. *Sci. Tot. Environm.* **707**: 135403.
Schroeder, K.M. & Mcrae, S.B. 2020. Automated auditory detection of a rare, secretive marsh bird with infrequent and acoustically indistinct vocalizations. *Ibis* **162**: 1033–1046.
Sebastián-González, E., Camp, R.J., Tanimoto, A.M., De Oliveira, P.M., Lima, B.B., Marques, T.A. & Hart, P.J. 2018. Density estimation of sound-producing terrestrial animals using single automatic acoustic recorders and distance sampling. *Avian Conserv. Ecol.* **13**: 7.
Sedláček, O., Vokurková, J., Ferenc, M., Djomo, E.N., Albrecht, T. & Hořák, D. 2015. A comparison of point counts with a new acoustic sampling method: a case study of a bird community from the montane forests of Mount Cameroon. *Ostrich* **86**: 213–220.
Shonfield, J. & Bayne, E.M. 2017. Autonomous recording units in avian ecological research: current use and future applications. *Avian Conser. Ecol.* **12**: 14.
Sólymos, P., Matsuoka, S.M., Bayne, E.M., Lele, S.R., Fontaine, P., Cumming, S.G., Stralberg, D., Schmiegelow, F.K.A. & Song, S.J. 2013. Calibrating indices of avian density from non-standardized survey data: making the most of a messy situation. *Methods Ecol. Evol.* **4**: 1047–1058.
Sugai, L.S.M., Desjonquères, C., Silva, T.S.F. & Llusia, D. 2020. A roadmap for survey designs in terrestrial acoustic monitoring. *Remote Sensing Ecol. Conserv.* **6**: 220–235.
Sugai, L.S.M., Silva, T.S.F., Ribeiro, J.W., Jr & Llusia, D. 2019. Terrestrial passive acoustic monitoring: review and perspectives. *Bioscience* **69**: 15–25.

Turgeon, P., Van Wilgenburg, S. & Drake, K. 2017. Microphone variability and degradation: implications for monitoring programs employing autonomous recording units. *Avian Conserv. Ecol.* **12**: 9.

Van Wilgenburg, S., Sólymos, P., Kardynal, K. & Frey, M. 2017. Paired sampling standardizes point count data from humans and acoustic recorders. *Avian Conserv. Ecol.* **12**: 13.

Venier, L.A., Holmes, S.B., Holborn, G.W., Mcilwrick, K.A. & Brown, G. 2012. Evaluation of an automated recording device for monitoring forest birds. *Wildlife Soc. Bull.* **36**: 30–39.

Vold, S.T., Handel, C.M. & McNew, L.B. 2017. Comparison of acoustic recorders and field observers for monitoring tundra bird communities. *Wildl. Soc. Bull.* **41**: 566–576.

Williams, E.M., O'Donnell, C.F. & Armstrong, D.P. 2018. Cost-benefit analysis of acoustic recorders as a solution to sampling challenges experienced monitoring cryptic species. *Ecol. Evol.* **8**: 6839–6848.

Yip, D.A., Knight, E.C., Haave-Audet, E., Wilson, S.J., Charchuk, C., Scott, C.D., Sólymos, P. & Bayne, E.M. 2019. Sound level measurements from audio recordings provide objective distance estimates for distance sampling wildlife populations. *Remote Sensing Ecol. Conserv.* **6**: 301–315.

Yip, D., Leston, L., Bayne, E., Sólymos, P. & Grover, A. 2017. Experimentally derived detection distances from audio recordings and human observers enable integrated analysis of point count data. *Avian Conserv. Ecol.* **12**: 11.

Zwart, M.C., Baker, A., McGowan, P.J. & Whittingham, M.J. 2014. The use of automated bioacoustic recorders to replace human wildlife surveys: an example using nightjars. *PLoS One* **9**: e102770.

Received 13 May 2020;
revision accepted 31 January 2021.
Associate Editor: Esther Sebastián-González

SUPPORTING INFORMATION

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

Data S1. List of references included in the review.

Figure S1. Number of studies by location of monitoring data assessing the relationship between bird abundance and acoustic data obtained using Autonomous Recording Units.

Table S1. Number of times that each bird Order was considered among the taxa analysed.

Table S2. Number of papers published by journal.

Table S3. Number of times that different Autonomous Recording Units were used.

Table S4. Number of times that different automated signal recognition software has been employed for recording analyses.