Autonomous sound recording outperforms human observation for sampling birds: a systematic map and user guide

Running title: Autonomous sound recording vs. human observation

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Abstract

Autonomous sound recording techniques have gained considerable traction in the last decade, but the question remains whether they can replace human observation surveys to sample sonant animals. For birds in particular, survey methods have been tested extensively using point counts and sound recording surveys. Here, we review the latest evidence for this taxon within the frame of a systematic map. We compare sampling effectiveness of these two survey methods, the output they produce, and their practicality. When assessed against the standard of point counts, autonomous sound recording prove to be a powerful tool that samples just as many species. This technology can monitor birds in an exhaustive, standardized and verifiable way. Moreover, sound recorders give access to entire soundscapes from which new data types can be derived (vocal activity, acoustic indices…). Variables such as abundance or detection distance can be obtained to yield data sets that are comparable to and compatible with point counts. Finally, autonomous sound recorders allow investigations at high temporal and spatial resolution and coverage, which are more cost-effective and cannot be achieved by human observations alone, even though small-scale studies might be more cost-effective when carried out with point counts. Sound recorders can be deployed in many places, they are more scalable, and reliable, making them the better choice for bird surveys in an increasingly data-driven time. We also provide an overview of currently available recorders and discuss their specifications to guide future study designs.

Key-words: acoustic recording, point count, microphone, sound recorders, passive acoustic monitoring, autonomous recording units

Introduction

In the face of the current threats to global biodiversity, ecologists strive to devise efficient survey methods to measure our vanishing, under-sampled biodiversity. We need more extensive sampling coverage on temporal and spatial scales to detect trends across regions and with time (Magurran et al. 2010, Ahumada et al. 2011). We need to sample animals thoroughly to detect species at risk, implement conservation strategies, and monitor their results. Material and personal resources must be deployed with greater efficiency. To enable international cooperation and re-use of data (Wilkinson et al. 2016), a minimal bias should be attained with standardized, comparable, and repeatable sampling methods.

Vertebrates pose a particular challenge for sampling because they are mobile, often evading detection (Thompson et al. 1998). Many vertebrates are usually surveyed by direct human observation methods (e.g. point counts, transect surveys) because capture methods are inherently more intrusive and effort-demanding. Human observers rely on aural and visual detection to count animals and identify species, but given that some insects (e.g. cicadas and orthopterans) and most terrestrial vertebrates (birds, amphibians, mammals, some reptiles) commonly use sound, passive acoustic monitoring methods have recently gained more users (Shonfield and Bayne 2017).

For birds in particular, passive acoustic sampling methods have been used extensively and increasingly (Fig. 1). Many different autonomous sound recorders (Merchant et al. 2015, Whytock and Christie 2016) and software solutions for automatic species classification have been developed (Priyadarshani et al. 2018). However, human observation survey methods are still the standard, most widely-used method (Bibby et al. 2000). Although some research has compared acoustic methods with these traditional survey methods, results were controversial as some studies showed that acoustic surveys detect more bird species than point counts (Haselmayer and Quinn 2000), whereas other studies concluded the opposite (Hutto and Stutzman 2009). A recent meta-analysis found no detectable difference between both methods in terms of alpha and gamma species richness (Darras et al., 2018).

Still, many other points are yet to be discussed to determine how autonomous sound recorders match up agaisnt traditional human observation. Bird studies provide ample material for an interesting methodological comparison using a systematic map, which is an overview of the available evidence in relation to a topic of interest (James et al. 2016). Indeed, a qualitative review (Shonfield and Bayne 2017) and a commentary discussing applications and challenges of acoustic data collection in the tropics (Deichmann et al., 2018) have been published recently, and an appraisal of passive acoustic monitoring has exposed the opportunities and challenges that the technology presents

.

In the present study, we provide a more comprehensive evaluation of autonomous sound recorders, starting with the comparison with point counts in avian diversity research. We use a systematic map of studies that surveyed birds with both survey methods paired, anddiscuss the inherent advantages of either method using additional references. We focus on their sampling effectiveness, their output variables, and practicality aspects. We provide a table summarizing pros and cons succinctly to help design future studies and present different cost scenarios. We also show the latest results of our previously published meta-analysis, including three more studies, linking to a figure that will be updated as the literature body grows. Additionally, we present a guide of currently available autonomous sound recorders for prospective users, also linking to a comparison table that will be updated as new autonomous sound recorders are launched. We finally give perspectives and identify challenges and remaining knowledge gaps for realising the potential of autonomous sound recorders.

Systematic Map

Data collection

We conducted a systematic map, which is an overview of the available evidence in relation to a topic of interest (James et al., 2016). We aimed for an unbiased comparison of bird sampling methods based on autonomous sound recordings versus those based on direct human observation. However, publications about bird surveys are too numerous to review, and most survey methods used with autonomous sound recorders and human observers are not equivalent, so that separate literature searches on both topics would not be effective for our systematic map. Thus, we decided to search only for publications where comparable sampling methods were used for both humans and sound recorders for our quantitative analyses. However, we complemented this comparison with additional relevant articles to discuss more broadly how human observers perform against autonomous sound recording.

Mobile autonomous sound recording devices have not been developed yet for terrestrial habitats, consequently, the majority of studies comparing human to recorder-based surveys directly did point counts (but see Wimmer et al., 2012), where observers stay in one point – rather than transects where human samplers are moving. Point counts are written records of the birds detected aurally and visually by a human observer from a fixed position during a specified duration. Similarly, sound recorders can generate audio records of birds recorded from a fixed position during a specified time, which are then processed to obtain written records of the bird detections. Both of these bird sampling methods yield bird detections data, which are a record of the number and species of birds detected in a particular site and time (Figure 2). These data can be used to derive occupancy, density and abundance, species richness, and activity of birds.

We searched for studies comparing point counts to sound recorders and reviewed them. Scientific publications were retrieved on February 5, 2019, using the following search string combination in ISI Web of Science Core Collection (Citation Indexes) covering all years: TS=((bird* OR avian OR avifaun*) AND ("sound record*" OR "acoustic record*" OR "automated record*" OR "acoustic monitor*" OR "recording system*") AND ("point count*" OR "bird count*" OR "point survey*" OR "point-count*" OR “point transect*”)). We used the following search string for Google Scholar: “point count” AND “sound recording”, sorted by relevance, checking all search results.

We screened all articles to determine the relevance of each study for the systematic map. Only peer-reviewed references in English were considered. Studies that discussed and compared both acoustic and observational bird survey methods were included in our systematic map. Relevant full text publications were retrieved and read entirely. We found 41 studies with our Web of Science search string and 196 studies through Google scholar. We used these studies to structure our methodological comparison and complemented the discussion using references cited in these studies and with additional external, relevant articles.

Overview of recorders

For the overview of currently available autonomous recorders, we included all recorders that can currently be purchased as of February 5, 2019, and also those that are open-source and can be built with freely available instructions (Beason et al., 2018; Sethi et al., 2017; Turner, 2015; Whytock and Christie, 2016). We compiled and calculated comparable specifications for all recorders by screening technical documentation or asking manufacturers directly. We refrain from recommending any particular model as the best choice will depend on project needs and budgets. However, we explain the relevance of the technical specifications for acoustic studies.

Publication trends

We generated an overview of the publication trends with time for each sampling method. We queried ISI Web of Science on 17 September 2018, covering all years and indices: SCI-EXPANDED, SSCI. We used the search string TS=(bird* OR avifauna* OR avian OR ornitholog*) AND ((autonom* OR automat* OR unattend*) AND (sound* OR acoustic OR audio) AND (record* OR monitor*)) for autonomous sound recorders, and TS=((bird* OR avifauna* OR avian OR ornitholog*) AND ("point count*") NOT ((autonom* OR automat* OR unattend*) AND (sound* OR acoustic OR audio) AND (record* OR monitor*))) for point counts, excluding autonomous sound recorders. We retrieved the number of publications for the field of ornithology over the same time range, queried using TS=(bird* OR avifauna* OR avian OR ornitholog*), refined by the Web of Science categories of ecology, zoology, ornithology, biodiversity conservation, environmental sciences, and forestry.

Analysis of survey costs

To illustrate the costs of different studies based on autonomous sound recorders or human observers, we estimated the total costs in USD (material, travel, and labor) required for both survey methods using all possible combinations of the following parameters (R script calculator in the Supplementary Materials): recorder prices and numbers, total sampling time in minutes per site, daily sampling time per site, expert ornithologist daily wages, technician daily wages, site numbers, transport costs, and average site-to-site transport durations. Our calculation considered the number of travels required depending on the type of survey method and the autonomy of the recorder. We used a constant continuous recording autonomy of 200 minutes, which is representative of most audible sound recorders. The costs of human observers were defined as follows: (total sampling time per site × number of sites × expert wage) + (transport cost + transport time × expert wage) × (total sampling time per site / daily sampling time per site) × number of sites. The cost of using recorders was defined as follows: (recorder price × number of recorders) + (transport cost + transport time × technician wage) × (1 + ceiling(total sampling time per site / recorder autonomy)) × number of sites. We compare costs of both survey methods for four different scenarios representing different study types: conservation studies for rare species (inspired by Holmes et al. 2014), large-scale rapid assessments (inspired by Furnas and Callas 2015), and bird community surveys (in tropical versus temperate zones).

Comparison of survey methods

Firstly, we detail aspects of sampling effectiveness, which we define as the ability of either method to detect birds that are present: visual detections, the avoidance effect, overlooked birds. These aspects determine the overall performance of recorders versus humans for measuring species richness, which we show using updated results of a separate meta-analysis. We also discuss the sampling of rare species and the feasibility of hybrid approaches combining both methods. Secondly, we compare the output variables of both survey methods: number of detections, density, species richness, behavior, phenology, acoustic indices, and vocal activity. Lastly, we discuss practicality issues such as standardization, verifiability, travel time, scalability, expert labor, material and labor costs, mobility, and sampling after rain. Our results are synthesized in Table 1. Even though some of the studies from our literature search used regular sound recorders, we primarily expose the features of autonomous sound recorders, which have several additional, unique advantages due to their outdoor usability and the possibility of scheduling unattended recordings.

Sampling effectiveness

Visual detections

Point count data include visual detections, which is an undeniable advantage. Too few of the studies comparing point counts with sound recordings report the proportion of visual-only detections for a quantitative analysis. Hutto and Stutzman (2009), who had 7% visual-only detections overall (pers. comm.), showed that they were the main reason why detections within 100m of the recorder were missed in recordings. In open habitats, visual detections can be more common; however, even there point counts do not have a large advantage: In open woodland savanna, Alquezar and Machado (2015) had only 8% visual-only detections in point counts; in a mixture of open and wooded sites, Celis-Murillo et al. (2012) found 5% visual-only detections (pers. comm.) and they also argue that visual detections do not provide a great advantage, which is echoed by Hingston et al. (2018). Vold et al. (2017) showed that even in tundra bird communities, visual obstruction was not associated with detected bird abundance. In more heterogeneous montane habitats, McGrann and Furnas (2016a) only detected 1% of birds only visually and in forest, Darras et al. (2018) only detected 4% of birds only visually. Finally, visual detections mostly concern birds flying over the sampling point, which have large ranges and are relatively unrelated to the sampled location (Kułaga and Budka 2019). In habitats where vegetation obstructs the observers' sight , te low proportion of visual detections is primarily due to visual ranges being much shorter than acoustic ranges. Eventually, most birds vocalize, so that they can be detected in longer duration recordings. Also, a human avoidance effect – discussed below – might exacerbate the problem by keeping birds out of sight of the observers.

Avoidance effect

Human observers introduce an avoidance effect, especially when there is more than one (Hutto and Mosconi, 1981). Disturbance effects from observers on birds are not well documented (but see Fernández-Juricic et al., 2001). Distance-sampling approaches can show that bird detections close to the observer are lower than predicted, especially when excluding data from predominantly close range visual-only detections (Darras et al., 2018). Even clothing color influences birds' responses to human observers as seen in a reduction in detection probability when observers wear hunter-orange vests (Gutzwiller and Marcum, 1993). The calling activity of birds can also be affected by human presence (Bye et al. 2001). On the contrary, it is possible that some curious birds, which are patrolling their territory, are attracted by human presence (like some true babblers in tropical forests or Corvidae in temperate regions). Furthermore, birds can also be unaffected by human observers, as determined by locating birds with a microphone array when human observers are present or absent, even though the authors of the study were careful not to generalise their results to other bird communities (Campbell and Francis, 2012). The avoidance effect could depend on the bird community and sampling habitat: as Prabowo et al.

(2016) illustrated based on detection distances (Fig. S1), birds in disturbed systems tend to be attracted to human presence, while birds in natural systems tend to avoid it. The avoidance effect can be mitigated by camouflaged bird watching hides. Seeing that the currently available evidence is inconclusive, and the fact that distance sampling is rarely used (Buckland et al. 2008),an overall synthesis or meta-analysis of point count data based on detection distances would be helpful to determine the conditions in which the avoidance effect occurs. Overall though, humans introduce a bias in the bird observation data, and in contrast, there is no reason to believe that the smaller, immobile, odourless, dull-coloured, and silent autonomous sound recorders would affect birds.

Assuming that autonomous sound recorders lack an avoidance effect, they should yield more detections close to the survey centre. This is useful when bird surveys are carried out on small plots (homegardens, smallholdings, etc.) where human presence would affect birds in the entire plot, or even in open habitats, where human observers are too visible. The fact that the sound recordings put more weight on the centre is also convenient when environmental co-variates are measured close to it, enabling a closer linkage between these and bird community variables.

Overlooked birds

In point counts of species-rich sites, birds can be overlooked (or rather “overheard”) when they occur simultaneously or because of human error, especially during the dawn chorus or the first minutes of the study (Hutto and Stutzman, 2009). Abundance can also be underestimated for common birds (Bart and Schoultz, 1984). In contrast, sound recordings can be played back repeatedly, often leading to higher detectability for infrequently vocalizing birds (Celis-Murillo et al., 2012). Campbell and Francis (2011) showed that people simulating “blind” point counts (by listening to uninterrupted sound recordings only once) detected consistently less species than were present in the recordings. In the previous study, listeners did not visualize spectrograms (i.e. sonograms), which are routinely generated and inspected while listening to audio recordings, so that in a sense, bird calls can actually be detected both visually and aurally. Spectrograms can even be used exclusively to detect single species of interest visually, faster than by listening to the recordings (Swiston and Mennill, 2009). This further enhances detectability, especially when higher frequency hearing ability declines with age, which affects the point count data (Emlen and DeJong 1992, Gates and Mills 2005).

Species richness sampled with recorders versus point counts

There is much debate among traditional and more technology-inclined ornithologists whether sound recorders can detect as many bird species as human observers. A recent meta-analysis measured the performance of sound recorders, measured in terms of species richness, against the performance of human point counts when identical sampling durations are used and detection ranges are considered (Darras et al., 2018). It showed that the key aspects differentiating sound recorders from human point counts, namely visual detections, avoidance effects, and overlooked birds, appear to have no detectable overall negative impact on the performance of recorders versus humans. Here, we depict updated results of the same meta-analysis, which now includes two new studies and one that was previously not considered (Campbell and Francis 2011, Hingston et al. 2018, Kułaga and Budka 2019) in Figure 2. These new results reveal that recorders record a significantly higher species richness per sampling site, whereas total species richness is still statistically indistinguishable between methods.

Sampling rare species

Ecologists are debating whether sound recordings are more or less effective than point counts in detecting rare birds. Rare birds, even if they vocalise often when present, vocalise rarely overall. As Celis-Murillo et al. (2012) pointed out, point counts were more effective in some studies at detecting those (Haselmayer and Quinn, 2000; Hutto and Stutzman, 2009), possibly because visual cues allow rare birds to be identified with more certainty (Hutto and Stutzman, 2009; Leach et al., 2016). However, in the latter studies (which used identical microphone elements), the sound recorders had shorter detection ranges than the unlimited range point counts they were compared against: Hutto and Stutzman (2009) found that most detections missed by sound recorders were too distant to be recorded (52.7%). Probably, for vocalizing birds and with identical detection ranges, rare birds are not inherently more detectable with either method. Venier et al. (2012) even argue that detecting rare species is more cost-effective with autonomous sound recorders because of easily repeated, unattended sound recordings which can span much longer durations than in-person visits that are inherently more limited in time. It follows that passive acoustic monitoring systems have a greater potential for detecting rare species or confidently concluding their absence, especially when combined with automated identification algorithms, which can scan long recordings in an automated way (Tegeler et al., 2012).

Combining point counts with sound recorders

In the light of the specific advantages offered by each survey method, it appears desirable to combine point counts with autonomous sound recorders. When less vocal birds are important, combining both methods can increase the chances of detection of relatively silent birds, even though this can also be achieved by processing longer duration recordings with automated detection methods (see 4.1 in Darras et al. 2018). Using both methods has been recommended for surveying rare bird species-at-risk (Holmes et al. 2014). Presence/absence data from sound recordings can also be merged with point count data, leading to more complete assessments of the bird communities (McGrann and Furnas, 2016a). There is considerable overlap in the species detected by each method but data from both methods can be combined to detect all unique species (Leach et al., 2016). Abundance data from either survey method can also be made comparable through modelling that addresses differences in detection probability (Royle and Nichols, 2003). Even though skilled personnel is not always available to conduct point counts in these hybrid surveys, occupancy modeling can handle missing data, thus studies can even be designed with point counts conducted at a portion of the sites where sound recorders are deployed. However, the added logistical effort (when ornithologists are not available) and statistical complexity (for assessing mixed datasets of different sample numbers and survey method) of such hybrid surveys should be carefully considered.

Output variables

Number of detections

Rough abundance estimates are readily obtained from the number of detections in point counts, since it is intuitive to estimate the position of the birds and relate it to previous activity as to guess individuals' numbers. Abundance estimates are generally deemed robust, in spite of high variation at the site level (Toms et al. 2006). However, especially in dense habitats, birds are rarely seen and hard to distinguish anyway, so that we cannot know whether two non-simultaneous sightings correspond to different individuals. We recommend a more conservative estimate of abundance: the maximum number of simultaneously detected individuals of one species. It has been used in point counts (Teuscher et al. 2015) and is easily applicable to sound recordings. Still, it is also possible to count uniquely identified individuals in stereo recordings in a similar manner as in point counts because the birds' location is audible (Hedley et al., 2017). Individual birds also have unique calls which can be distinguished from another upon close analysis (Beer, 1971; Ehnes and Foote, 2015), and software solutions tackle this (Ptacek et al., 2016). Only two of the publications included in our literature search estimated abundances from sound recordings (Hobson et al. 2002, Sedláček et al. 2015), and both found that abundance estimates correlated strongly with those obtained from point counts, even though species occurring in flocks can be underestimated in sound recordings (Sedláček et al. 2015). More studies should test whether sound recordings can yield accurate abundance estimates. Indeed, it can be challenging to measure abundance from sound recordings when large groups of animals are recorded (Denes et al., 2018), but this challenge is also present in bird point counts.

Density

Going further than simple abundance estimates derived from numbers of detections, the estimation of bird densities and true abundances requires estimating detectability, which itself relies on bird detection distances (Buckland et al. 2008). The estimation of bird distances in point counts can be inaccurate (Alldredge et al., 2007). Even though the distance is measured, it is also often an estimation based on the presumed bird position, except when it can be seen. Distances to landmarks can be measured before the point count starts to be used as references in estimating distances, and sometimes, when visibility allows, laser rangefinders can also be used to measure distances accurately. When using sound recordings however, Hobson et al. (2002) previously suggested that spectrograms could be used to estimate bird call distance when the sound source level is known. Indeed, when microphones are calibrated and transmission patterns are known, it is theoretically possible to calculate a detection distance (Darras et al., 2016), even though there is much variation in acoustic directionality (Patricelli et al. 2007) or loudness of bird calls. Previously, Shonfield and Bayne, (2017) also stressed that more work is needed to estimate distances to birds in sound recordings. Recent, we showed that recording test sound sequences at measured distances can be used as a reference to estimate distances to birds reliably, enabling the use of distance sampling with sound recordings (Darras et al., 2018). In that context, simultaneous point counts can be useful to gather reference material from aural bird detection at measured distances. However, knowledge of the real-world bird vocalisation loudness is still required with this method. Alternatively, reference recordings of birds at known distances can be used to fit models of how the vocalisation loudness decreases with distance to infer detection distances (Yip et al. In press). Taking all the evidence together, bird densities can be obtained from human observer and sound recording surveys.

Species richness

Point counts and acoustic recordings can both be used to estimate species richness. For either method, naïve estimates of richness based solely on the number of species detected will be biased low if site-level detection probability is lower than one, which is frequently the case in avian studies (Bibby et al., 2000). There are a variety of analytical approaches for correcting species richness estimates from survey data including rarefaction and occupancy modeling (MacKenzie, 2006). Multispecies occupancy modeling (MSOM) is gaining acceptance as a standard technique for robustly estimating richness using a series of temporally replicated surveys over a short period of time when populations can be assumed closed (Iknayan et al., 2014). Although MSOMs have been used with both point counts and acoustic recordings (McGrann and Furnas, 2016a; Tingley et al., 2012), it is more practical to use autonomous sound recorders to obtain multiple ($\geq$3) survey replicates at comparable times of the day (Brandes, 2008). For example, Furnas and McGrann (2018) found that average detection probability of temperate forest passerines per 5-minute survey was similar for automated recorders and 50 m point counts; it was about 0.25 which suggests that 6 survey replicates would be required to achieve a site-level detection probability higher than 0.8.

Behavior

Visual point count detections can yield data about behaviour, food items, occurrence strata, sometimes even the sex and age of the bird. Such data are auxiliary and seldom used in studies designed for measuring avian diversity and community composition, as it is challenging to get a dataset large enough for statistical analysis. However, these data are useful to put results from avian studies into perspective, so we shortly discuss them here. To some degree, sound recordings can also convey information through the bird vocalisations, since they have different functions: territorial advertisement, mate attraction, and alarm calls all relate to bird behaviour. Also, distinguishing between songs – which are typically territorial – and calls can reveal whether the habitat is suitable for breeding or only visited by stray or foraging birds. It is also possible to infer habitat use by pinpointing the animals' position (Bower and Clark, 2005), and tracking moving birds with microphone arrays (Blumstein et al., 2011). Finally, miniaturised acoustic recording devices could theoretically be installed directly on birds to study physiology and behavior; this is already used for mammals (Lynch et al. 2013).

Phenology

With sound recordings spanning long time periods, temporal dynamics throughout the day, between days, and between seasons can be analysed, and phenological trends and fine-scale temporal dynamics can be assessed (Blumstein et al. 2011, Lellouch et al. 2014, Thompson et al.

2017). Acoustic recordings and point counts have been used for timing the singing phenology of birds (McGrann and Furnas, 2016b); recordings had an advantage over point counts because phenology inferences are based on the detection probability parameters, the precision of which are directly increasing with the number of survey replicates. Open-source automated detection methods also exist to process large datasets spanning thousands of hours (Potamitis et al. 2014). It is also easier to sample the same times of day at one site with sound recorders, as point count observers have to travel to the site repeatedly on different days.

Acoustic indices

Sound recordings provide continuous audio records where human observation only provides a filtered interpretation of the original audio-visual events. Using sound recordings, one can generate sound diversity indices (eg. Acoustic richness or dissimilarity, (Sueur et al., 2008)) for large datasets computationally, which can correlate well with field measures of species richness (Depraetere et al., 2012). However, there are notable differences among the indices, and some authors caution against adopting them too early or widely (Jorge et al., 2018; Mammides et al., 2017). Still, combining the most informative indices in statistical models can accurately predict terrestrial species richness ($R^2 = 0.97$) using only recordings (Buxton et al., 2018), thus bypassing the time-consuming process of identifying species from recordings manually. An added advantage is that all sonant animal taxa are included in audio recordings, allowing a more holistic biodiversity survey which would be difficult to conduct with human observers who are usually specialised on particular taxa. For example, anuran surveys are also often made by human observers, but passive acoustic monitoring is increasingly used (Koehler et al., 2017). Recording full-spectrum audio gives access to a relatively new field of research called soundscape ecology, which focuses on the entirety of biological, geophysical, or anthropogenic sounds emanating from landscapes (Pijanowski et al. 2011),

Vocal activity

Vocal activity of birds can be measured in time as an alternative to abundance. Cunningham et al. (2004) showed that vocal activity and abundance are only weakly related, meaning that it represents a different measure. The time that birds spend on calling and singing allows to weigh detections more meaningfully: very short detections of birds who are only calling once when they pass by the sampling location should not be considered equivalent to detections of continuous bird songs that span the entire survey duration. Also, detecting bird songs – as opposed to calls – implies that the singing bird is defending a territory or attracting mates, which is an important distinction that underlines the importance of the habitat in which it is detected. Bird vocal activity should correlate better with bird activity than abundance, which does not consider the duration of the bird's detection. Thus, there is potential that vocal activity represents a more relevant measure for functional analyses of bird communities. For measuring vocal activity, sound recordings are inherently better suited, as one can take the time to pinpoint the timings when birds are vocal without error. In point counts, the time of the first detection cue is commonly tracked, however, recording the end of the birds' vocalisations is much more challenging, especially when multiple individuals and species are being observed. Thus, sound recordings are better suited for measuring vocal activity than point counts.

Practicality

We depict and compare the data collection and entry procedure when doing point counts versus using autonomous sound recorders in Figure 2 and detail it here. Recommendations have been made for conducting point counts (Bibby et al., 2000), during which an observer stands in the middle of the sampling site and counts birds heard or observed for a specific duration. Field notes serve as a basis for entering data into digital spreadsheets later. Sometimes, audio recordings are made to assist with identification later, and doubtful aural detections can be re-checked. Binoculars routinely support the identification of visual detections and in rare cases, photographic data may complement the survey.

Standard recommendations exist for using autonomous sound recorders (Darras et al., 2018). Recording schedules are programmed before installing recorders. On-site, recorders should be installed on a support at a constant recording height. The recorders' function can be shortly checked. Test sound recordings from different distances are recommended to estimate detection distances for distance sampling (Darras et al., 2018). Recorders will start recording at their programmed time, and they are retrieved after the program ends. Typically, batteries are swapped, data are checked and backed up, and after this, recorders can be installed again. Finally, the retrieved data can be processed in different ways: The recordings can either be analysed directly for computing soundscape-level acoustic diversity indices, or they can be processed with automated classification software or manual identification using spectrograms and sound playback.

Standardization

We discuss standardization by assessing the features of either method that enable unbiased comparisons of biodiversity estimates (richness, abundance, composition) between studies and sampling sites. Point counts suffer from a trade-off between a time and sampler bias: with an increasing number of observers, more simultaneous – and thus temporally unbiased – data points can be obtained, but the number of observer-specific – thus observer biased – data points increases. The observer bias is commonly recognised (Sauer et al. 1994) and it can lead to an under- or overestimation of the actual number of species present (from 81% to 132%, Simons et al., 2007), and it also has been quantified by comparing interpretations of single observers to completely annotated and multiply checked sound recordings as a reference (Campbell and Francis, 2011). In contrast, sound recorders incur no sampler bias in the raw audio data when the equipment and settings are identical. Their microphones are manufactured within given signal-to-noise ratio tolerances, but it may change with time, due to environmental stress (rainfall, temperature variations, mechanical shocks, etc.), thus requiring regular calibration (Turgeon et al., 2017). However, the raw audio data should be processed by the same interpreter to avoid an observer bias. Even though the bias between observers can be relatively low when using multiple interpreters (Rempel et al. 2005), crucially, it can be quantified thereafter by verifying the recordings.

Verifiability and updatability

Verifiability and updatability aspects concern features of the survey methods which allow respectively to confirm the quality of the data, or to correct the data themselves (mainly species identifications) as to eliminate possible biases. The verifiability of point counts is low as we are depending on the identification skills, current physical state, and memory of a single observer. Especially in tropical regions, the many species vocalizing simultaneously makes correct identification of all individuals a challenging task. Moreover, auditory detections are sometimes uncertain (Mortimer and Greene, 2017). When point count observations have corresponding photographic or audio evidence material, the observer bias can be lessened, but this is rarely done. The bias can also be corrected with high numbers of replicates, expertise checks, and observer shifts in one site (Lindenmayer et al., 2009). With sound recordings, audio evidence is available at no additional cost, and interpretation of recordings can be carried out whenever it is convenient, even by a single person. Venier et al. (2012) showed how sound recordings can be re-interpreted to correct the initial species identifications. Even when sound recordings are processed by different people, the result can be reviewed and standardized by one person, which is helpful in long-term monitoring projects.

Travel time

Observers carrying out point counts need only one visit per survey replicate. In contrast, sound recorders need to be installed before they start recording and must be picked up for collecting the data or recharging batteries (but see Aide et al., 2013 for remote data collection and continuous power supply). However, it is also possible to install them, leave the sampling site, record sound, and take them back with one travel, in cases when human presence is known to affect birds, or when ornithologists are not available, or even when only few recorders are available. When recorders are installed and picked up by ornithologists, this can be combined with a point count (McGrann and Furnas, 2016b), which can yield useful reference data for distance estimation (Darras et al., 2018). Depending on the study design, either one of the survey methods could be more practical: if sampling replicates on consecutive days at the same site are needed, sound recorders will prove handy. If the number of sampling sites is high and replicate visits are few, either many recorders or frequent travels will be needed. Our cost analysis considers these aspects in the calculation.

Scalability

Temporal coverage is easily increased with autonomous sound recorders and this is one of the main advantages of these devices. Usually, the duration of point counts needs to be optimised so that all sites can be reached within the birds’ activity window and sampled long enough, as there is only a limited number of sites that can be reached within one day. Acoustic surveys, however, allow for greater flexibility in scaling up sampling effort. Provided multiple recorders are available, multiple sites can be sampled simultaneously. It is straightforward to record for long durations or multiple days only at the expense of data storage, energy supply, and data transfer time, all of which are cheap compared with specialised ornithological labour. Currently available recorders can record continuously for 5 to 33 days (Table 2). Some recorders have even higher autonomy by relying on solar panels for their energy supply. Transmitting data automatically through wireless networks enables sampling for even longer durations (Aide et al., 2013). Interestingly, choosing intermittent parts from long recordings enables to detect more species than a single continuous recording of the same duration would yield (Cook and Hartley, 2018; Klingbeil and Willig, 2015), due to temporal species turnover. In species occupancy modelling, the increased number of replicates also considerably improves site-level detectability, and overall accuracy and precision of state variables such as richness. For example, additional acoustic survey replicates doubled the alpha richness estimate of montane avian communities through occupancy modelling (McGrann and Furnas, 2016a), which was not possible previously with point counts only (McGrann et al., 2014).

Spatial coverage is also easily increased as recorders become more affordable. However, when recorders are scheduled for multiple repeated recordings, they cannot be used elsewhere except after an additional transportation. This potentially leads to a trade-off between increasing temporal coverage and spatial coverage but this issue is offset by the recent, lowest price point of

50 USD at which autonomous sound recorders can be purchased (Audiomoth). For a given budget, 40 times more units can be purchased, and even though the sound detection spaces should be smaller, these more numerous units would cover a much larger sampling area than possible when using the most expensive recorders. In some cases, large coverages were achieved with the help of citizen scientists (Jeliazkov et al., 2016). It also becomes feasible to conduct linear acoustic transects, analogous to the common line transect surveys conducted by human observers, but with all transect points sampled simultaneously. However, any spatial arrangement can be used. Random placement of recorders would allow sampling sites more independently, which simplifies statistical analysis and removes bias in spatial upscaling. With sufficient numbers of recorders, even a complete, full-time coverage of a given territory can be achieved, leading to an enhanced version of territory mappings that are conducted by humans.

Expert labor

It is costly to hire ornithologists for field surveys; demand is high during the short breeding season, and in some regions (e.g. the tropics) experts may be unavailable. Passive acoustic monitoring systems, however, can be installed and picked up by technical staff to assign experts to the interpretation of recordings only (Rempel et al. 2005). The units can be set up as quickly as humans need time for getting ready for a point count. Scheduling sound recorders also usually does not require programming experience, and programs can sometimes be saved onto storage media to be loaded by technical staff (e.g. Song Meters of Wildlife Acoustics). Some custom open-source solutions do require some command-line input (e.g. Solo recorder, Whytock and Christie, (2016). Thus, by following simple protocols, it is possible to gather raw audio data without the help of ornithologists; for analysing these data however, experts are still required.

Autonomous sound recorders allow for a more efficient use of expert ornithologists. When ornithologists are required to design and start new avian surveys in the field, they can carry out initial point counts to gather data about non-vocal species, as well as reference recordings for estimating bird detection distances more accurately (Darras et al. 2018). Funds for taxonomic experts can be minimized to assign them only to processing or reviewing recordings, or even postpone that until funds become available. Even non-experts can attain high accuracy levels when using automated species classification methods (Goyette et al., 2011), and sound recordings are easier to process for surveyors with little ornithological (Kułaga and Budka 2019). Moreover, data can be sent to ornithologists or accessed online from anywhere (see for example http://soundefforts.uni-goettingen.de/). Even citizen scientists have been mobilised to successfully sample Orthopterans to subsequently automatically detect focal species (Jeliazkov et al., 2016). It is often stated that identifying birds inside sound recordings is a time-consuming process, but the processing time can be halved by filtering out sections without bird vocalisations (Eichinski and Roe, 2017; Zhang et al., 2015) and in some cases the “search space” - or the number of recordings that need to be screened – can be reduced by 94% (Potamitis et al. 2014). In analyses of selected species, acoustic recordings also require less time in the field and the lab (Holmes et al., 2014). It is also possible to listen to a recording without interruption, thereby simulating a “blind” point count (Campbell and Francis, 2011; Venier et al., 2012) of the same duration. Such a procedure incurs the same labour cost as for a point count, or even less when considering that data can be entered directly in an electronic format. Altogether, we argue that the labor cost of processing audio data from autonomous sound recorders is entirely dependent on the researchers' needs and decisions. On the one hand, minimal sampling intensity and labor cost can be achieved that is identical with point counts. On the other hand, the full potential can be realised with maximal sampling intensity to find every single vocalisation. Any other processing option in between is possible, but only automonous sound recorders offer this choice. The trade-off of higher sampling intensities lies in the increased processing effort, which can be minimised with automated detection methods.

Automation

Automated species identification is possible only with sound recordings; this procedure diminishes reliance on expert workforce and allows to process large datasets in much shorter time than would be possible using human labor. Different open-source and commercial solutions for automated detection exist and it is widely recognised that automated analysis is the only practical solution to realize the full potential of long-duration field recordings, as it allows to process longer recordings in an unattended way to increase detection chances. Usually, the focus has been on single species can be detected with a measurable probability and accuracy (Brandes 2008). The field of automated species detection is burgeoning and has been reviewed recently (Priyadarshani et al. 2018). In this review, “recall” measures for automated detection are emphasized, as they describe the true positive rate of a particular method; recall rates reported by the publications had a median of 85%. The tested methods are usually deemed to perform very accurately, and some disadvantage that they might have compared to manual identification can be made up by processing larger data sets. Species counts from manual processing can be expanded by the addition of automated detections from longer recordings (Tegeler et al. 2012). Night birds have been preferably detected with automated methods (Shonfield et al., 2018), presumably because it is easier to detect calls in the typically lower and more constant ambient sound. However, the recordings used for benchmarking are sometimes not representative of real-world, noisier conditions (Priyadarshani et al. 2018). The efficiency of automated species detection methods also depends on the method used, the quality of the recordings, and the target species: efficiency compared to manual processing is sometimes equivalent or lower (Digby et al. 2013, Joshi et al. 2017). Rapid progress is being made and it is also possible to rely only on the vocalisations contained within the field recordings to generate classifiers (Ovaskainen et al., 2018). The number of species that can be reliably identified computationally will undoubtedly increase, but it is still challenging to handle complex song structures, noisy field conditions or distant calls (both resulting in low signal-to-noise ratios of the target vocalisations), overlapping calls of non-target species, and large song repertoires (Bardeli et al. 2010, Priyadarshani et al. 2018). So far, there are no fully automated methods allowing to identify all species of an entire bird community, even the most "intelligent" automated methods like machine learning still require initial input and final checks from human experts. Even as online audio bird databases such as Xeno-Canto (www.xeno-canto.org) are available, it is impossible to rely entirely as reference recordings for classifiers (such as in Araya-Salas and Smith-Vidaurre 2017) or on their birding community for identifying unknown bird species: Experts should always be accounted for when planning acoustic avian studies.

Material and labor costs

Autonomous sound recorders generally entail higher material costs, while point counts entail higher labor costs. Point counts usually only require binoculars and field gear, and directional microphones are optional. It is difficult to hire the same ornithologists throughout in long-term studies. Sound recorders however, are purchased once and typically last for years if maintained properly, until irreparably broken or stolen, greatly facilitating long-term data compatibility. Autonomous sound recorders can be costly, but a variety of products exist (Table 2), from budget constructions (Maina et al., 2016; Whytock and Christie, 2016) to commercial products (e.g. Wildlife Acoustics), spanning a price range of fifty to thousands of USD. Still, it is important to plan for replacement costs of batteries, and especially microphones, which are exposed to the elements and which can degrade significantly over time. Microphones are also the most expensive components of recorders, but they can be assembled with open-source designs (Darras et al. 2018). Altogether, the total costs of each survey method (for both labor and materials) is highly context-dependent, but we estimated them for four different study types (Figure 4). We tried to keep the estimation simple and robust while accounting for the most important parameters, as the complexity of such calculations is not bounded by any objective criteria.

Mobility

Some wilderness sites in forest, at high elevations, or unexplored regions can be difficult to reach. For point counts, the observer preferably has to be present on-site at dawn, which is often impossible or dangerous in inaccessible or unsafe areas. In contrast, placing autonomous sound recorders in such challenging conditions is easier:transport can occur any time without rush when conditions are best (during daylight), and the devices are usually weatherproof so that they can safely stay there for long periods of time. Autonomous sound recorders can reliably meet the programmed schedule as long as they are installed before recording. Furthermore, Prevost (2016) showed that sound recorders were amenable to installation on hot air balloons, due to their low size and weight. Also, deployment to inaccessible areas with unmanned aerial vehicles is feasible (Wilson et al., 2017), and installation on cars can also be envisaged (Jeliazkov et al. 2016). In the future, large geographical scales could also be sampled using autonomous wireless recorder networks that collect and transmit data wirelessly (Collins et al., 2006).

Sampling after rain

Autonomous sound recorders suffer from a drawback when it is raining: many microphones are not or waterproof and foam screens are commonly used for protection against water and wind. After rain, windscreens are soaked with water, which results in a loss of sensitivity and can take several hours to dry. This is a clear disadvantage and a technical challenge waiting for a solution. In wind-still regions, using acoustic vents with high water ingress protection ratings is a sensible alternative to the use of foam windscreens (Darras et al. 2018).

Overview of autonomous sound recorders and their technical specifications

We provide an overview of the currently available recorders in Table 2. The technical specifications essentially determine the suitability for a particular study or application and are discussed below.

Commercial versus open-source solutions

Budget and time constraints determine whether solutions that work out of the box should be purchased or specially tailored recorders should be built. Even commercial recorders can have a steep learning curve, but building recorders from different components usually requires good technical and basic programming skills. Support or warranties are usually not available for non-commercial solutions, as they cost roughly an order of magnitude less. On the other side, custom-built solutions are more flexible, easily repaired or upgraded to meet the desired specifications. Both commercial and open-source solutions suffer from restricted product lifespans, as they get replaced by successor models (as governed by marketing strategy), or when their components become unavailable or discontinued.

Audio quality

Audio quality is mainly determined by the number of microphones or recording channels, the signal-to-noise ratio of the microphones, and their height (Darras et al., 2018), the latter being independent from the recorder itself. All but one of the recorders (Audiomoth) presented here can be used with cables to install microphones in the desired location, if necessary. However, the number of microphones cannot be changed and at least two microphones are necessary to record binaural cues, which give a more accurate spatial representation of the soundscape when listening.

The microphone itself is a crucial element as it is transducing sound energy into electrical energy. Its signal-to-noise ratio, which is equivalent to its self-noise level, describes how faithfully and cleanly it is recording sound, and it is an inherent characteristic of the microphone model (within tolerances). Basically, the higher the signal-to-noise ratio, the higher the sound quality, even though signal amplifiers also affect the final sound quality slightly. Commercial vendors sometimes do not disclose which microphones are used so that you have little knowledge or control over them. However, the acoustic ports are usually standard parts available through electronic retailers, so that cheaper, custom-built solutions also work (Darras et al. 2018).

The sampling frequency, when divided by two, indicates what maximum sound frequency can be recorded. All of the presented recorders are able to record sound at a sampling frequency of 44.1 kHz, which enables to record all audible sound. Some of them however can use higher sampling frequencies, which allows them to be used as ultrasound sampling devices for surveying bats, for instance, as long as suitable full-spectrum microphones are used (Darras et al. 2018).

Storage and power

All recorders are autonomous only as far as storage is not full and batteries are not depleted. Fully autonomous solutions (power- and storage-wise) do exist (Aide et al., 2013), but they are usually expensive, complicated to set up, and not for sale, so they are not covered here. Thus, we provided an estimate of the run time in approximately equivalent conditions without being able to test actual units in the field. Run time is determined by the batteries' capacity and the power consumption of the device, which is dependent on many factors (mainly the sampling rate and recording schedule).

All recorders record sound in WAV format, which is an uncompressed, qualitatively lossless audio format. Some have proprietary lossless and lossy compressed audio formats (Wildlife acoustics), and proprietary software can be required for conversion or playback, and only one uses an open-source lossless compression format (FLAC, Bioacoustic Recorder). Compression can reduce or increase power consumption, depending on whether the processor or the storage-writing hardware is more efficient, but will always result in storage space savings, which can be crucial.

Physical specifications and options

The size and weight obviously affects how transportable the units are, and also how sturdy their support has to be. All units considered here are portable, but smaller recorders can be transported in greater quantities in simple backpacks and also strapped to tree branches, drones or animals. Depending on their number, bulky recorders however can make it necessary to use cars for transporting them.

Some units have integrated geopositioning sensors, which are especially useful when recorders are used as mobile units in transects. Spatial coordinates also help ascertain the location where the recording took place. Finally, from all the units presented here, only one (Audiomoth) is currently not weatherproof, but a weatherproof case is being developed.

Challenges, perspectives, and knowledge gaps

Currently, autonomous sound recorders are still used in variable ways, as there is no widely accepted standard, although best practice recommendations have been made for maximum compatibility and comparability with point counts (Darras et al., 2018). On the one hand, the wide range of available hardware solutions reflects the varied needs and possibilities of that technology. On the other hand, comparisons of studies that use different recorders are not straightforward as different recording systems likely have different detection ranges (Darras et al., 2018). Luckily, they can be standardised when estimating detection distances (Darras et al., 2018). For the moment however, no standard survey protocols are used (Gibb et al. 2018), and very few studies standardise detection spaces, although they are considerably affected by the sampling sites themselves (Darras et al., 2016). Similarly, for processing audio recordings, there are no widely accepted standards for assessing the performance of recognisers (Knight et al., 2017), which hampers a unified benchmarking of the software for automated species identification, even though some benchmark datasets are available (Priyadarshani et al. 2018).

Covering large spatio-temporal scales is an important challenge that has been tackled with acoustic surveys (Furnas and Callas, 2015). However, it is still hampered by bottlenecks: limited power autonomy, limited storage capacity, and labour-intensive transport and installation of recorders. Even though almost fully autonomous systems have been developed (Aide et al., 2013), there are no easily-implemented solutions available yet. Power limitations are being released gradually through the use of solar-panels (most recorders can be connected to those) and power-efficient components (Audiomoth). Storage issues are still costly to circumvent. Some recorders can transmit little data packages through the mobile network (Song Meters), but no attempt has been made yet to use multiple recorders to transmit data locally in networks, at the only expense of power, like has been done with other sensors (Collins et al., 2006). Transmitting data via low-orbit satellites can be envisioned too ("ICARUS Initiative," n.d.). Lastly, deploying acoustic recorders on large scales with drones would significantly improve the reach of such systems into little-explored areas.

For the moment, autonomous sound recorders inherently – and obviously – generate only aural detections. In the future, it is imaginable to combine them with photographic sensors similar to camera traps, to design devices that make maximal use of all visible and audible events around them. Camera traps can already be set up to take pictures at specific times and some models also record audio while making videos. It is conceivable to create hybrid devices which would entirely mimic a human observer by yielding both visual and audio detections. This would enable detecting not only sonant animals but also larger, seldom vocalising animals, and it would also complement the audio data by giving pictures of the sampled animals to support species identification.

Conclusion

For identical sampling durations, sound recorders are on par with human observers to sample birds, and if used properly, they can surpass them. Autonomous sound recorders are more practical, scalable, consistent, and deliver verifiable results, but their main advantage lies in their potential to collect many more data than human observers. Identification algorithms for species-specific automated detection are developed at a rapid pace and tackle these growing amounts of data(Priyadarshani et al. 2018), which present new challenges to store and document them (Gaunt et al., 2005), even thoughstandard solutions have been proposed for manage these (Roch et al., 2016). Considering the largely context-specific costs of avian studies, recorders are probably more efficient for conservation-focused work and large-scale assessments, while small bird community surveys can be relatively more efficient with human observers. Even so, at the time of writing, machines do not replace humans yet quite. One might worry that sound recording devices put ornithologists out of a job, but it is more likely that ornithologists will just be able to redirect their time to less repetitive activities. Still, all audio data should ultimately be vetted by experts before conclusions are published, and as bird survey data collection becomes easier and relies more on “citizen scientists” and other non-experts to acquire, the demand for experts could actually increase. Technology could also provide ornithologists greater work flexibility as audio data can be analysed at any time, from anywhere. Ornithologists will continue to fulfil an indispensable function in the field and in the office observing bird behaviour in the field and habitats, designing studies, improving our understanding of avian ecology and evolution, and developing strategies for effective conservation.

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Tables

Table 1: Comparison of strengths and weaknesses between point count and automated sound recording methods for surveying birds. Asterisks denote criteria for which regular sound recorders deliver the same results as autonomous sound recorders.

Criteria	Autonomous sound recordings	Point counts	Justification
Visual detections*		+	sound recordings are audio only
Avoidance effect	+		humans disturb birds
Missed detections*	+		recordings can be played back
Rare species	+		rare species easily detected with longer recordings
Abundance*		+	abundance easier to measure in point counts
Species richness	+		Recorders gather more data to yield more accurate true richness
Detection distances	=	=	distances can be estimated
Behavior*		+	no visual data for sound recorders
Phenology	+		Long periods of time easily sampled with recorders
Acoustic indices	+		measurable with sound recorders
Vocal activity*	+		measurable with sound recorders
Standardization*	+		identical sampling possible with multiple recorders
Verifiability*	+		audio evidence always available

Travel time*	+		recorders superior when there are three or more visits per site
Scalability	+		sound recorders can sample almost anytime
Expert workforce*	+		sound recorders rely less on human expertise
Material and labor costs	=	=	context-dependent
Transportability	+		recorders can be deployed in inaccessible locations and can be rapidly set up
Sampling after rain		+	Wet microphone windscreens block sound

Table 2: Overview of the currently available autonomous sound recorders that can sample the audible frequency range, along with their specifications. A regularly updated version with more details is available here.

*: with microphones, converted to US dollars on 19 Jul 2018

**: with batteries

***: technical support exists

Model	**Manufacturer**	**Channels**	**Price ($)***	**Power autonomy**	**Weight****	**Dimensions (cm)**	**Warranty (years)**
Audiomoth	Open Acoustic Devices (open-source)	1	50	187	80	5.8 × 4.8 × 1.5	no
BAR	Frontier Labs	1 or 2	602	222	360	11 × 13 × 7	1
BAR-LT		2	811		890	11 × 16 × 7	1
SM4	Wildlife Acoustics	2	849	205	1300	21.8 × 18.6 × 7.8	3
SM3Bat		2	2187	161	3200	32.4 × 20 × 6.5	3
SM2Bat+		2	1169	120	680	20.3 × 20.3 × 2.3	no

Solo, ARUPI, Sethi et al., AURITA	Raspberry-Pi based open-source recorders	2	160-296	variable	~600	20 × 8 × 9.5	no
Swift	Cornell University (non-profit)	1	250-300	550	1088-2494	20.3 × 12.7 × 10.2 - 21.6 × 17.1 × 10.2	no***

Figures

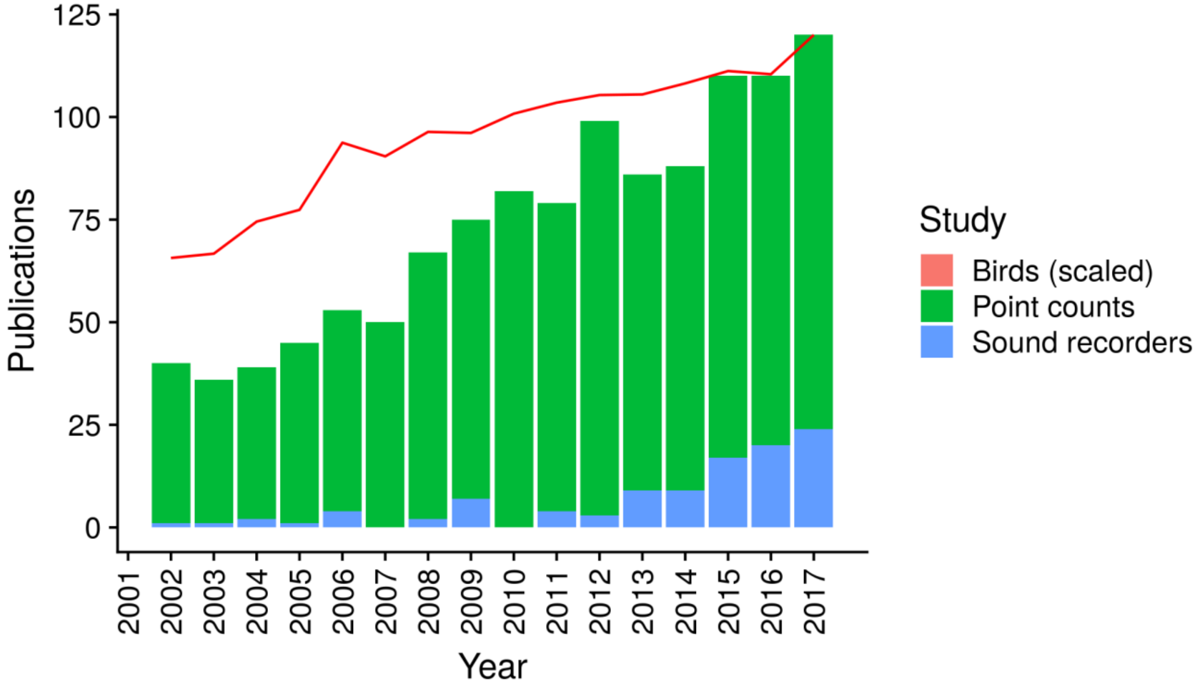
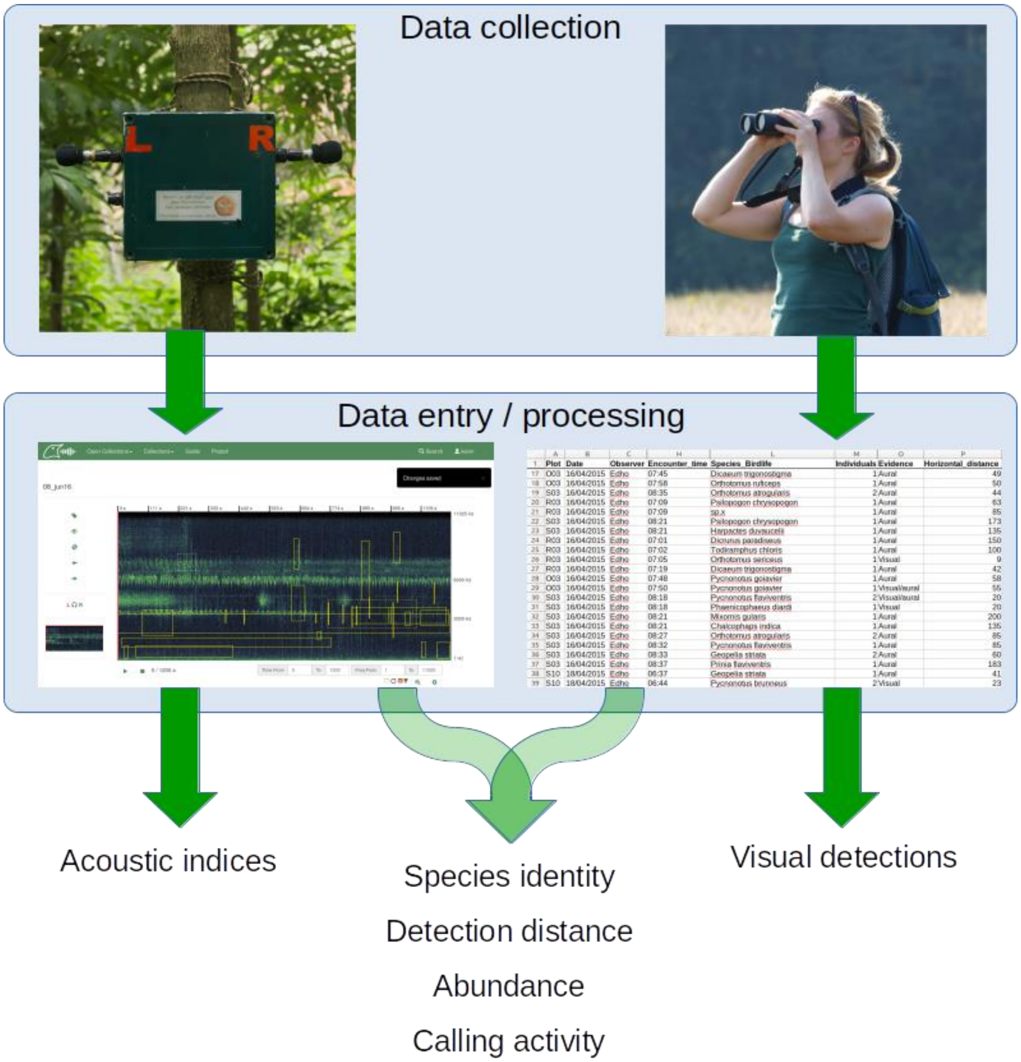


Figure 1: Number of publications per year mentioning autonomous sound recorders or point counts (excluding recorders). Records start with the first occurrence of recorders in 2002. The red line shows the trend in the number of publications in ornithology, scaled by the maximum number of publications shown in the bars.



	A	B	C	H	L	M	O	P
1	Plot	Date	Observer	Encounter_time	Species_Birdlife	Individuals	Evidence	Horizontal_distance
17	O03	16/04/2015	Edho	07:45	Dicaeum trigonostigma	1	Aural	49
18	O03	16/04/2015	Edho	07:58	Orthotomus ruficeps	1	Aural	50
19	S03	16/04/2015	Edho	08:35	Orthotomus atrogularis	2	Aural	44
20	R03	16/04/2015	Edho	07:09	Psilopogon chrysopogon	1	Aural	63
21	R03	16/04/2015	Edho	07:09	sp.x	1	Aural	85
22	S03	16/04/2015	Edho	08:21	Psilopogon chrysopogon	1	Aural	173
23	S03	16/04/2015	Edho	08:21	Harpactes duvaucelii	1	Aural	135
24	R03	16/04/2015	Edho	07:01	Dicrurus paradiseus	1	Aural	150
25	R03	16/04/2015	Edho	07:02	Todiramphus chloris	1	Aural	100
26	R03	16/04/2015	Edho	07:05	Orthotomus sericeus	1	Visual	9
27	R03	16/04/2015	Edho	07:19	Dicaeum trigonostigma	1	Aural	42
28	O03	16/04/2015	Edho	07:48	Pycnonotus goiavier	1	Aural	58
29	O03	16/04/2015	Edho	07:50	Pycnonotus goiavier	1	Visual/aural	55
30	S03	16/04/2015	Edho	08:18	Pycnonotus flaviventris	2	Visual/aural	20
31	S03	16/04/2015	Edho	08:18	Phaenicophaeus diardi	1	Visual	20
32	S03	16/04/2015	Edho	08:21	Mixornis gularis	1	Aural	200
33	S03	16/04/2015	Edho	08:21	Chalcophaps indica	1	Aural	135
34	S03	16/04/2015	Edho	08:27	Orthotomus atrogularis	2	Aural	85
35	S03	16/04/2015	Edho	08:32	Pycnonotus flaviventris	1	Aural	85
36	S03	16/04/2015	Edho	08:33	Geopelia striata	2	Aural	60
37	S03	16/04/2015	Edho	08:37	Prinia flaviventris	1	Aural	183
38	S10	18/04/2015	Edho	06:37	Geopelia striata	1	Aural	41
39	S10	18/04/2015	Edho	06:44	Pycnonotus brunneus	2	Visual	23

Figure 2: Overview of the data collection and processing workflow for point counts and autonomous sound recorders. Recorder photo: Patrick Diaz. Point counts photo: Summer 2017 by Joachim Rutschke, Calcareous grassland in Ehra-Lessin, Landkreis Gifhorn. Screenshot of spectrogram from Biosounds (http://soundefforts.uni-goettingen.de/)

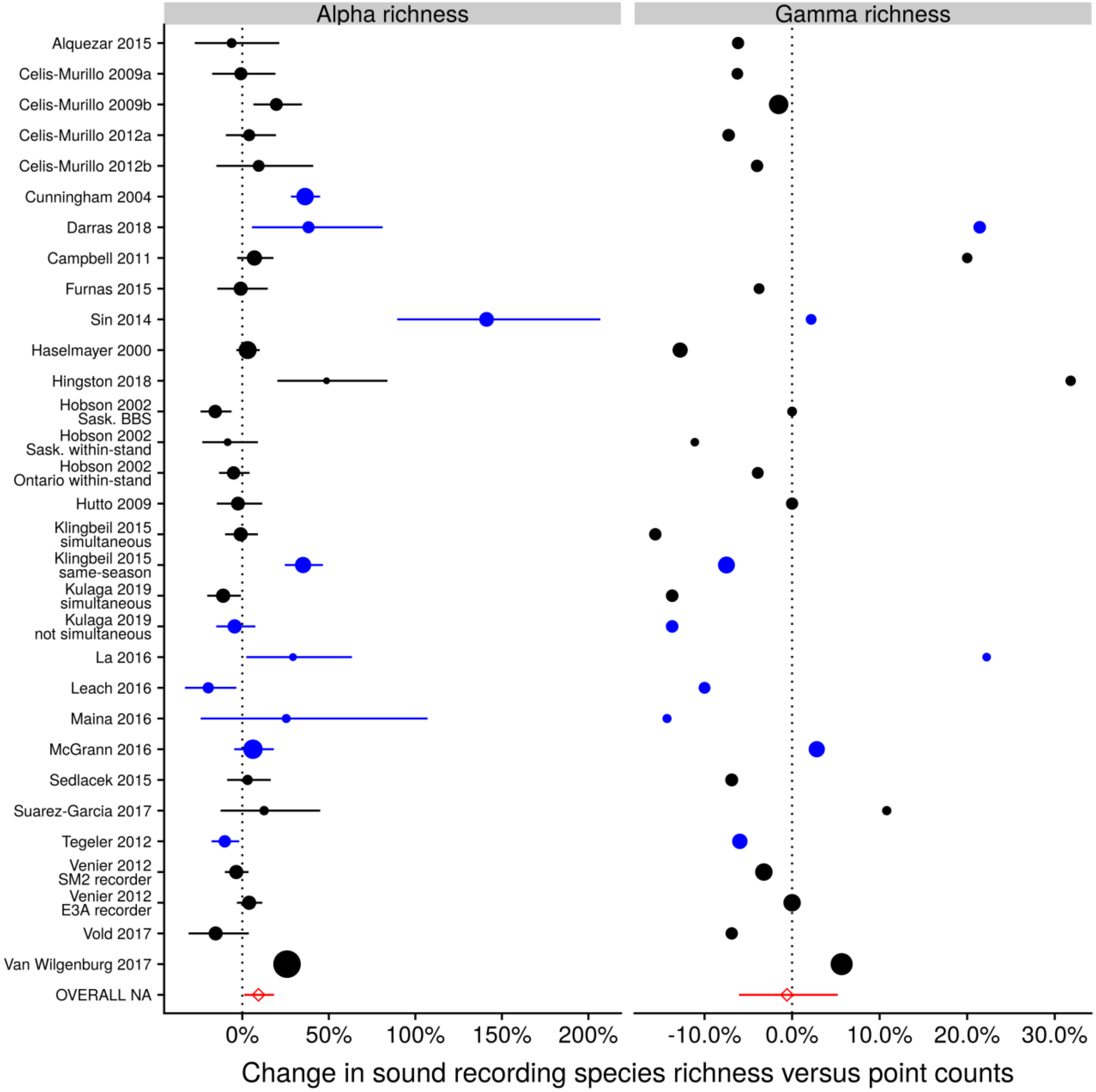


Figure 3: Response ratios of bird species richness sampled by automated sound recorders compared to point counts with equal sampling durations. Alpha richness is the number of species per site, gamma richness is the number of species overall. The error bars display 95% confidence intervals, and indicate a significant ($p < 0.05$) difference to the control (point counts) when they do not overlap the zero value marked by the dotted line. The dot size and study weight are

proportional to the number of sites for alpha richness and total survey time for gamma richness. Blue dots represent studies in which sound recordings were not simultaneous with point counts. Red diamonds represent the overall effect. Reproduced in an updated version with permission from Darras et al., (2018)

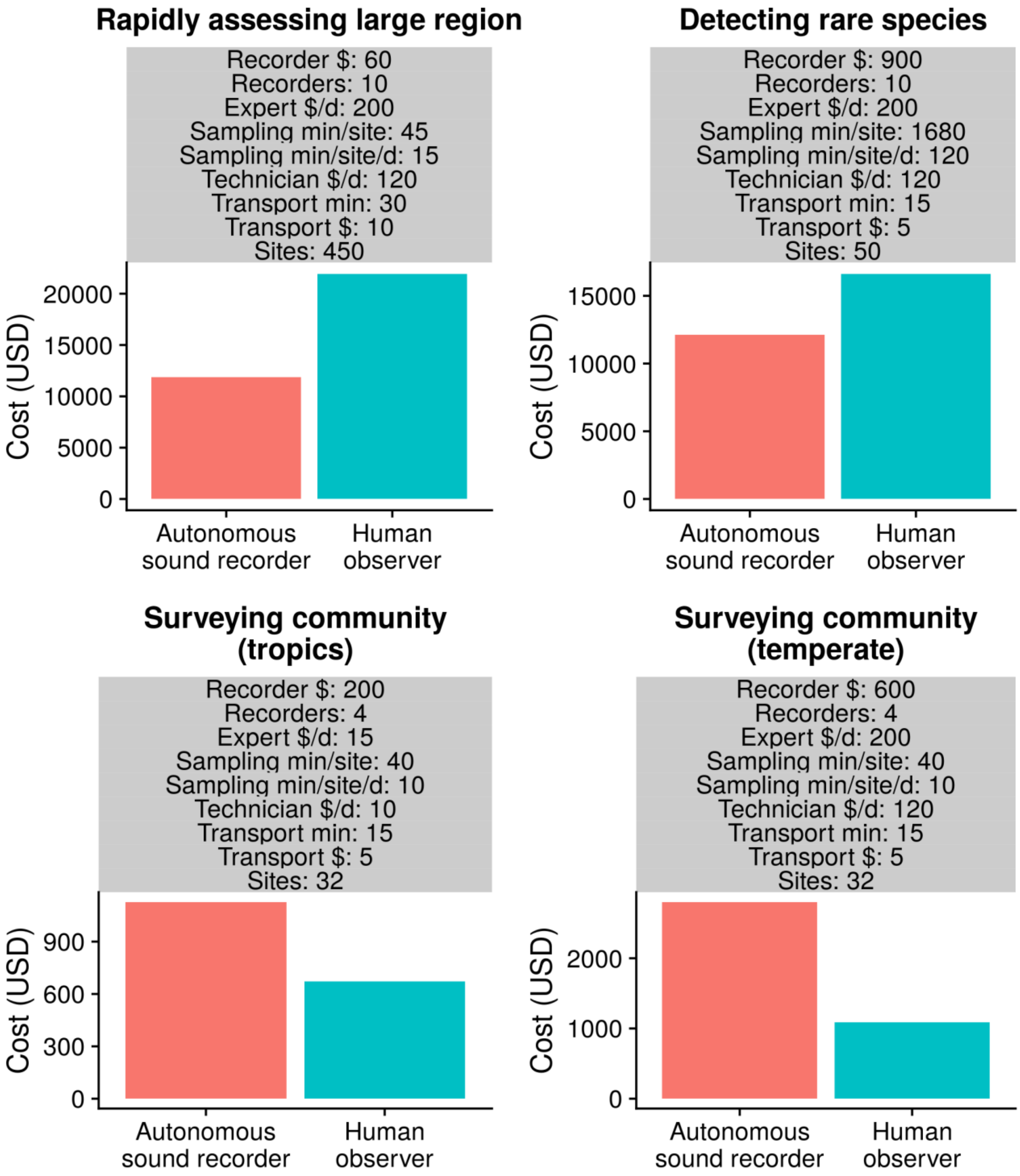


Figure 4: Total costs (material, travel, and labor) for each survey method for different combinations of cost parameters characterising four typical avian study types.