

REVIEW

A roadmap for survey designs in terrestrial acoustic monitoring

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Abstract

Passive acoustic monitoring (PAM) is increasingly popular in ecological research and conservation programs, with high-volume and long-term data collection provided by automatized acoustic sensors offering unprecedented opportunities for faunal and ecosystem surveys. Practitioners and newcomers interested in PAM can easily find technical specifications for acoustic sensors and microphones, but guidelines on how to plan survey designs are largely scattered over the literature. Here, we (i) review spatial and temporal sampling designs used in passive acoustic monitoring, (ii) provide a synthesis of the crucial aspects of PAM survey design and (iii) propose a workflow to optimize recording autonomy and recording schedules. From 1992 to 2018, most of the 460 studies applying PAM in terrestrial environments have used a single recorder per site, covered broad spatial scales and rotated recorders between sites to optimize sampling effort. Continuous recording of specific diel periods was the main recording procedure used. When recording schedules were applied, a larger number of recordings per hour was generally associated with a smaller recording length. For PAM survey design, we proposed to (i) estimate memory/battery autonomy and associated costs, (ii) assess signal detectability to optimize recording schedules in order to recover maximum biological information and (iii) evaluate cost-benefit scenarios between sampling effort and budget to address potential biases from a given PAM survey design. Establishing standards for PAM data collection will improve the quality of inferences over the broad scope of PAM research and promote essential standardization for cross-scale research to understand long-term biodiversity trends in a changing world.

Introduction

Passive acoustic monitoring (PAM) is a trending method for biological data collection, and has been increasingly employed on diverse lines of ecological research worldwide (Deichmann et al. 2018; Gibb et al. 2019; Sugai et al. 2019). Innovative audio devices capable of unattended recording allow acoustic surveys over a wide range

of environmental conditions, thereby broadening the capabilities for long-term and large-scale monitoring (Ribeiro et al. 2017; Wrege et al. 2017). PAM brings together distinct scientific areas, such as animal behavior, ecology and acoustics, meaning that the design of sampling protocols for data acquisition has to be based on multidisciplinary aspects of species, environments and sound (Laiolo 2010; Obrist et al. 2010; Blumstein et al.

2011; Sueur et al. 2012). Although, an underlying knowledge on these areas is desirable to properly conduct PAM surveys, practitioners and newcomers to PAM may lack such in-depth training (Browning et al. 2017). Thus, researchers using PAM would benefit from methodological frameworks for survey design.

PAM provides systematic data collection that allows cross-scale and long-term comparative research (Browning et al. 2017; Shonfield and Bayne 2017). Collections of PAM time-series can also be considered as historical records of ecosystem acoustic dynamics worldwide, holding a special value for areas undergoing intense changes in land use and/or climate (Krause and Farina 2016; Dena et al. 2019; Sugai and Llusia 2019). Still, these datasets require detailed recording protocols to promote repeatable surveys and research synthesis (Casey and Blackburn 2006; Gibb et al. 2019). Sampling design in PAM surveys is influenced by the researchers' knowledge and experience on target species (Gibb et al. 2019), resulting in a variety of recording protocols, not necessarily transferrable between biological groups and research goals (Darras et al. 2018a; Pérez-Granados et al. 2019).

Sampling effort in acoustic monitoring can be optimized through spatial distribution of acoustic sensors (Fig. 1) and recording schedules that determines the continuity and resolution of temporal sampling (Fig. 2). Since continuous 24-h monitoring quickly decreases the autonomy of acoustic sensors, built-in functions to pre-program recording schedules allow for longer monitoring periods and decrease maintenance requirements. Increased autonomy also promotes the investigation of biological groups that are inactive during typical temporal sampling windows for human observers (Gaston 2019, Laiolo 2010; Shonfield and Bayne 2017).

While primers on the use of microphones and recording systems are available (see Obrist et al. 2010; Blumstein et al. 2011; Browning et al. 2017), no current literature synthesizes the different practices employed in survey designs for acoustic monitoring, especially regarding automated acoustic recorders. Here, we (i) review spatial and temporal sampling designs used in terrestrial passive acoustic monitoring, (ii) provide a synthesis of the crucial aspects of PAM survey design and (iii) propose a workflow to optimize recording autonomy and recording schedules.

Literature review

We extracted information about spatial and temporal sampling from 460 research articles addressing passive acoustic monitoring in terrestrial environments compiled through a systematic literature review (Sugai et al.

2019). These articles were filtered from more than 10 000 articles returned by searches on Thomson Reuters Web of Science and Google Scholar from 1900–2018, using distinct combinations of 35 keywords (Sugai et al. 2019). We screened articles for information describing the spatial sampling, including (i) spatial scale (maximum distance between monitored sites), (ii) total number of recorders used, (iii) spatial distribution of recorders per site (single or multiple –distributed randomly, over transects or over grids–), (iv) use of between-site recorder displacement (i.e. if recorders were rotated over distinct sites) and (v) use of within-site recorder displacement during the recording sessions (e.g. mobile transects; Fig. 1). To describe temporal sampling, we compiled (i) if recording schedules covered the entire 24-h day or specific diel periods, (ii) if recordings were continuous or discontinuous (e.g. starting at regular intervals), (iii) the length of each recording and (iv) the number of recordings taken per hour (Fig. 2)

Spatial Sampling

Spatial sampling in the literature

Over three decades of research using PAM in terrestrial environments (1992–2018), studies have been mostly focused on macro spatial scales (64%), followed by meso (22.1%) and micro (14%) scales (Figs. 1 and 3A), with some investigations spanning entire countries (e.g. Frey-Ehrenbold et al., 2013). Most studies used between one and three acoustic recorders (50.1%), with only 13.5% using more than 10 recorders (Fig. 3B). The main spatial distribution of devices was a single recorder per site (70.8%), with less studies using a random assignment (15.5%) and a minority using transects, grids, or a mix of both (9.6%, 2.5% and 1.6% respectively, Fig. 3C).

Between-site recorder displacement prevailed among the studies (67%; Fig. 3D), especially when few recorders were used (75%; Fig. 1; Fig. 3E). Within-site recorder displacement was reported for only 9.3% of the studies, whereas the vast majority used static recorders during the recording sessions (85.6%; Fig. 3F). Only 53.7% of all studies described their sampling designs with all five reviewed features of spatial sampling, characterizing an important shortfall in current practices for documenting protocols.

Overview of spatial sampling in PAM

Passive acoustics use sound recordings from multiple sources at a given time and place through automated acoustic sensors, in contrast with traditional targeted

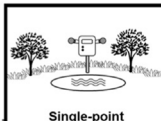
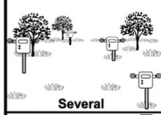
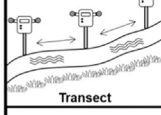
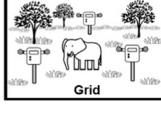
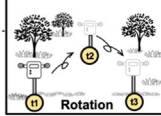

| Item | Definition | Categories | Examples |
|-------------------------------------|--|--|--|
| Spatial scale | Maximum distance between two monitored sites | Micro: < 1 km and single-site studies Meso: 1 – 20 km Macro: > 20 km | Towsey <i>et al.</i> (2019) Piel (2018) Torrent <i>et al.</i> (2018) |
| Total number of recorders | | Low: < 2 Medium: 3 – 10 High: > 10 | Priyadarshani <i>et al.</i> , (2018) Oliver <i>et al.</i> (2018) Ribeiro <i>et al.</i> (2018) |
| Spatial distribution of recorders | Arrangement of the acoustic sensors in each study site | Single: one recorder per site Severai: random distribution of recorders Transect: recorders distributed along a path Grid: regular distribution of recorders Single and transect (si. & tr.): recorders distributed as single or along transects in different locations Single and severai (si. & se.): recorders distributed as single or multiple (randomly) in different locations |  Single-point Bridges and Dorcas, (2000) Munro <i>et al.</i> (2018)  Severai Estrada-Villegas <i>et al.</i> , (2018) Deichman <i>et al.</i> (2017)  Transect Abrahams and Deny, (2018)  Grid |
| Between-site recorders displacement | Whether acoustic sensors are displaced between the monitored sites | Fixed: recorders remains in a single site throughout the monitoring period Rotating: recorders are rotated between diferent sites |  Rotation Phillips <i>et al.</i> (2018) Ross <i>et al.</i> (2018) |
| Within-site recorders displacement | Whether acoustic sensors are displaced within a monitored sites | Static: recorders are static during a recording session Traveling: recorders are moved by an operator during recording session Static and traveling (st. & tr.): use of static and traveling recorders in different sites |  Traveling McCracken <i>et al.</i> (2018) D'Accunto <i>et al.</i> (2018) Winter <i>et al.</i> (2017) |

Figure 1. Spatial sampling components extracted from articles using passive acoustic monitoring. Items are described with respective categories and examples for its use.

recording techniques used in bioacoustic surveys (e.g. Laiolo 2010). When focused on particular species, spatial sampling relies on the home range, habitat use and calling behavior of focal taxa. Nonetheless, research on soundscapes often deploy recorders according to the spatial configuration of environmental factors (e.g. landscape structure and urbanization level; Depraetere et al. 2012; Fuller et al., 2015). Generally, single recording stations are broadly used to monitor populations and communities with clumped distribution patterns, such as lekking and chorusing species (Bridges and Dorcas 2000; Oseen and Wassersug 2002; Frommolt 2017). Long-term acoustic monitoring allows the investigation of broad aspects of seasonal activity and population dynamics (Sugai et al.

2019). A standalone recorder per site along an ecological gradient or over different habitat types can be employed to account for environmental heterogeneity (Wrege et al. 2010; Llusia et al. 2013a; Figueira et al. 2015), for instance, to determine the influence of spatially structured environmental factors on soundscapes, diversity patterns, occupancy models, or behavioral changes across species ranges (Campos-Cerqueira et al. 2019; Depraetere et al. 2012; Llusia et al. 2013b; Gil et al. 2015). However, more than a single recorder within a site may be required to properly detect a target species or to characterize spatial variation in soundscapes. For example several recorders may be desirable to study populations with low densities (Haselmayer and Quinn 2000; Pérez-Granados et al.

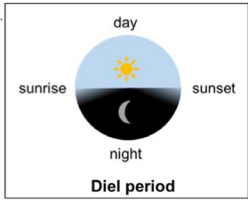
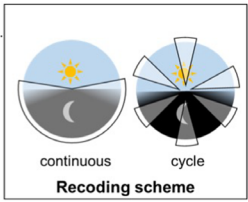
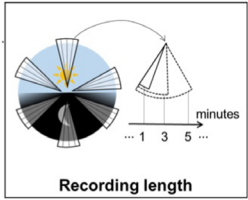
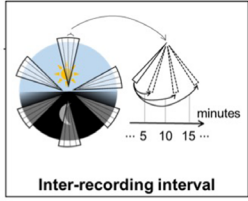
| Item | Definition | Examples |
|--------------------------|--|---|
| Diel period | Specific periods of the day which acoustic monitoring takes place. Usually associated with the highest activity levels of the studied organism |  <p>24 h (Astaras <i>et al.</i>, 2017), Dawn (Buxton <i>et al.</i>, 2016)</p> |
| Recording scheme | Whether the onset and end of a recording session is continuous or scheduled to distinct periods |  <p>Continuous through the night (Torrent <i>et al.</i>, 2018), regular samples through the day (Campos-Cerqueira and Aide, 2016)</p> |
| Recording length | Whitin a recording session, the amount of minutes of each single recording event |  <p>One minute (Schalk and Saenz, 2016), 30 min (Burivalova <i>et al.</i>, 2018)</p> |
| Inter-recording interval | Whitin a recording session, the interval separating single recording events |  <p>One recording each 10 minutes (Aide <i>et al.</i>, 2017)</p> |

Figure 2. Temporal sampling components from articles using passive acoustic monitoring. Items are described with respective examples for its use.

2018). Additionally, the physical nature of each habitat alters species detectability, with increased detection reported for non-forested areas (Enari et al. 2017) and flat riparian habitats (Ribeiro et al. 2018). Therefore, specific spatial arrangements with multiple recorders as random assignments of recorders (Munro et al. 2018) or replicates along horizontal or vertical transects and grids (Rodriguez et al. 2014; Kalan et al. 2015) can be used to increase spatial replicates and species detectability (Pollock et al. 2002). These spatial sampling designs are particularly suitable to monitor species with less predictable

distribution patterns, such as highly mobile species, solitary animals, moving flocks, species with explosive activity patterns and low-density populations (e.g. Brooke et al. 2000; Pieretti et al. 2011; Hagens et al. 2018).

Although sampling over multiple locations is often essential to increase sound detection and to address the effect of environmental factors on biodiversity (Skalak et al. 2012; Wood et al. 2019), animal behavior (Gil et al. 2015; Ulloa et al. 2019), or soundscape dynamics (Fuller et al., 2015), it requires a higher number of automated recorders, which may be a limiting factor for researchers.

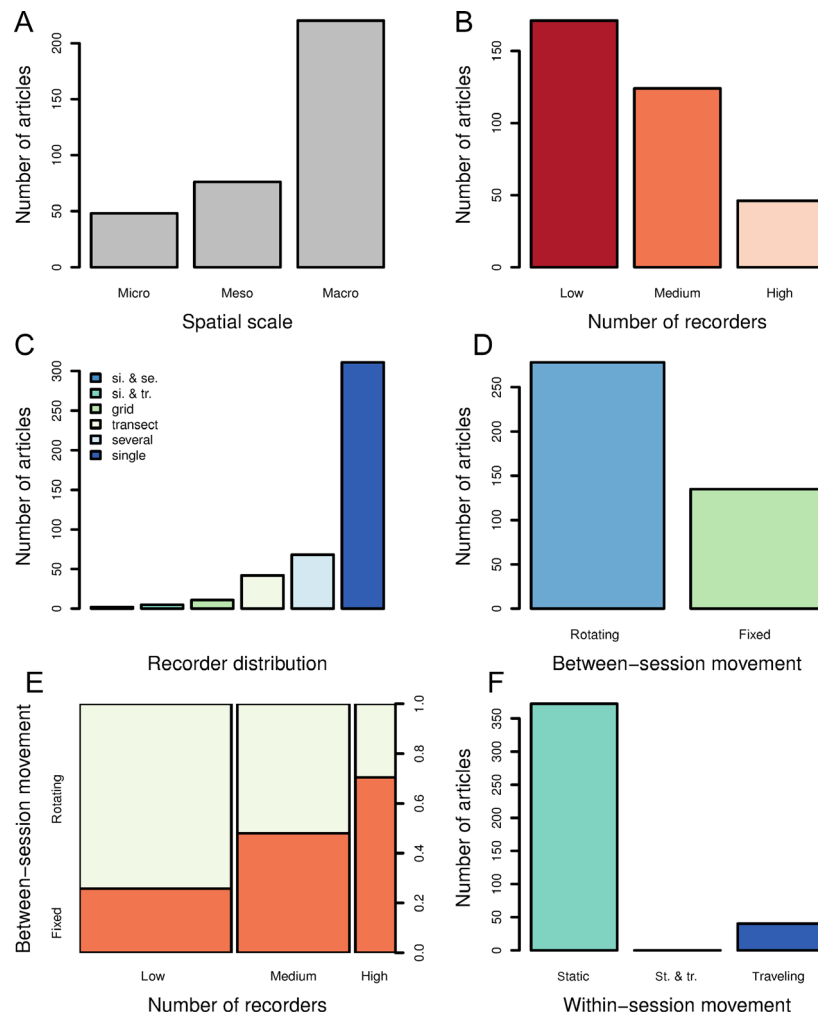


Figure 3. Spatial characteristics in articles employing passive acoustic monitoring in terrestrial environments (1992–2018): (A) spatial scale of published studies based on passive acoustic monitoring (micro: <1 km; meso: 1–20 km; macro: >20 km); (B) number of recorders per study (low: <3; medium: 3–10; high: >10); (C) recorder distribution within each study site (“si. & tr.”: both single point and transect; “si. & se.”: both single point and several); (D) between-site recorder displacement; (E) between-site recorder displacement in function of the number of recorders; (F) within-session recorder displacement (“st. & tr.”: both static and traveling recorders).

As an alternative, protocols based on recorders rotation can be used to cover a higher number of sampling sites (Gil et al. 2015; Machado et al. 2017). However, this method has two main drawbacks: (i) rotation procedures precludes simultaneous recording across sampling sites, potentially introducing bias from seasonal or weather changes, which must be accounted for; (ii) the number of monitoring days before rotating will influence species detectability, especially for rare species. Monitoring for more than a single day per site is thus recommended to ensure adequate detectability (Skalak et al. 2012; Ribeiro et al. 2017; Pérez-Granados et al. 2019). Additionally, recent development of low cost and versatile acoustic devices as alternatives to costly commercial automated

units (Farina et al. 2014; Whytock and Christie 2017; Hill et al. 2018) may allow researchers to employ at least one stationary acoustic sensor at each monitoring site (Whytock and Christie 2017).

Within-site recorder displacement is usually performed by an operator walking, riding a bike or driving a car along a transect or road and aims to increase spatial coverage (Schmidt et al. 2013; Mendes et al. 2017; D’Acunto et al. 2018). As it requires an operator, long-term data collection is challenging (but see citizen science-based approaches and car-based techniques; Newson et al. 2015; Whitby et al. 2014). Although this practice is usual for surveys of bat activity, its efficiency to capture activity patterns is lower when compared with designs using

several stationary automated sensors (Stahlschmidt and Brühl 2012, Braun de Torrez et al. 2017).

Considerations about detection space

The area within which a particular signal is detected by an acoustic sensor (i.e. the *detection space*) strongly influences species detectability and is key to standardize sampling efforts in PAM (Darras et al., 2016, Llusia et al. 2011). Thus, measurement of detection space should be required to define the number of recorders per site or to estimate population densities, but it is often absent from studies as it is a labor-intensive task under field conditions (Merchant et al., 2015, Obrist et al. 2010). Estimates of detection areas can be achieved using focal signals played back at varying distances and directions from the recorder (Llusia et al. 2011; Hagens et al. 2018), allowing standardization of detectability among recorders (Yip et al. 2017; Hagens et al. 2018) and leading to better detection rates than point-count methods (Darras et al. 2018b). Recent efforts in combining playback tests and models of sound transmission provide robust estimates of species-specific detection distances (Sebastián-González et al. 2018; Yip et al. 2019), and together with models of sound attenuation over heterogeneous environments (Royle 2018), they should support the standardizing of spatial sampling efforts in PAM.

Temporal Sampling

Temporal sampling in the literature

Our review unveiled that 76.9% of the studies on terrestrial passive acoustic monitoring used continuous recordings, whereas 69.5% monitored specific diel periods (Figs. 2 and 4). Discontinuous recordings (i.e. regular sampling) were used in only 23.1% of the studies, within which monitoring of specific diel periods or 24 h occurred in similar proportions (52.4% and 47.6%, respectively; Fig. 4A). Recording schedules were highly diverse across studies, although a larger number of recordings per hour were generally associated with a smaller recording length (Fig. 4B–C). Moreover, studies tended to either use a few recordings per hour with small recording lengths when recorded 24 h, or larger recording lengths for monitoring specific diel periods (Fig. 4B–C). Particularly, most studies using discontinuous recordings over 24 h (Fig. 4B) used a single recording per hour (46.9%), either up to 3 min (59%) or between 3 and 10 min (31.8%). The remaining studies used 2, 4, or 6 recordings per hour. Among this type of studies targeting specific diel periods (Fig. 4C), 51% had a single recording per hour of 10 to 30 min length (48%), or 2.5 min or less (32%).

Overview of temporal sampling in PAM

PAM offers a wide variety of temporal sampling protocols that can be selected according research goals, study groups and equipment. Continuous monitoring over 24 h and over large periods are preferable to increase the

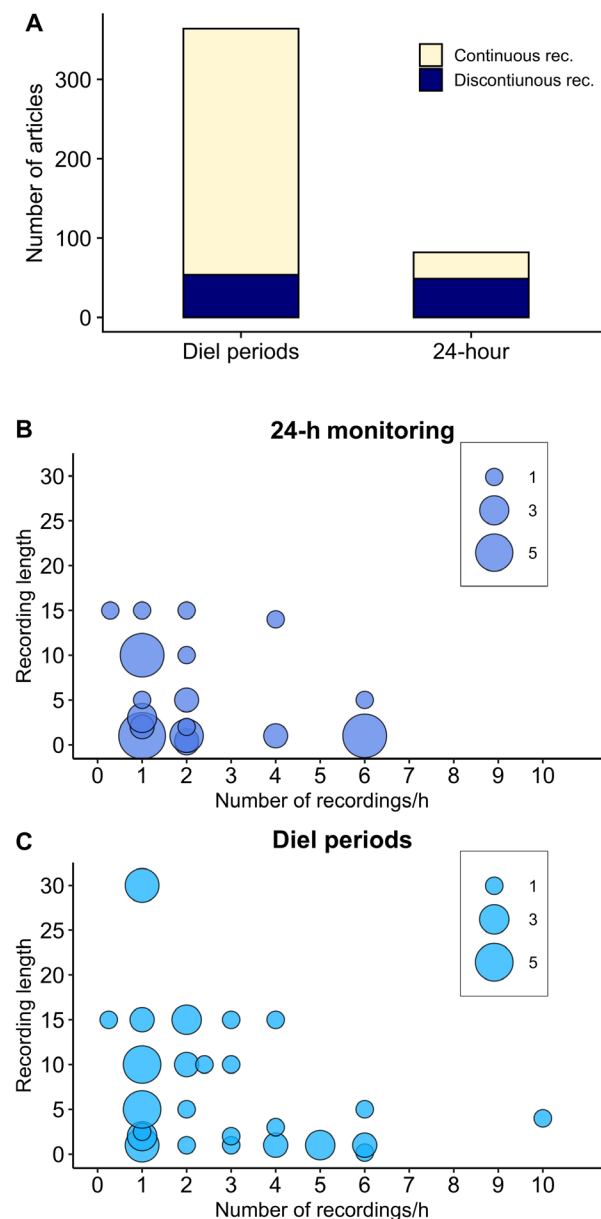


Figure 4. Recording schedules used in articles employing passive acoustic monitoring in terrestrial environments (1992–2018): (A) number of articles that used 24-h or diel monitoring periods and employed continuous (white) or discontinuous recordings (blue); and (B) recording lengths (vertical axis) in relation to number of recording events per hour (horizontal axis) used in articles that employed discontinuous recordings over 24-h or (C) at a specific diel period.

likelihood of recording sounds within a site, and is especially necessary to investigate the temporal activity of rare or cryptic species (Astaras et al. 2017; Wrege et al. 2017). However, it requires larger storage space and power supply. Equipment autonomy can be increased by powering the system with solar panels and by using wireless networks for data transfer (Aide et al. 2013; Kasnesis et al. 2019), which can be added to the motherboard of customizable acoustic sensors (Whytock and Christie 2017). Additionally, data storage can also be reduced with recordings set to be triggered only when sound level reaches a certain threshold (usually employed for bats and katydids, Andreassen et al. 2014; Jeliaskov et al. 2016). This, however, can result in missed detection of signals emitted at low levels, from long distances, or in noisy environments.

Conversely, the autonomy of acoustic sensors is often optimized by scheduling recordings within specific diel periods coinciding with high activity levels of the target species (Gibb et al. 2019). Thus, continuous recording at specific periods is the most common monitoring practice found in the literature, with night, dusk and dawn being the most investigated diel periods for bats, birds and anurans (Sugai et al. 2019). Focusing on continuous diel periods can provide higher estimates of species diversity when compared with discontinuous 24-h monitoring (Wimmer et al. 2013; La and Nudds 2016; Pérez-Granados et al. 2018), as detection probabilities usually decrease after the daily activity peak (e.g. sunset for bats, Skalak et al. 2012). Furthermore, extending monitoring periods on long-term studies is required to properly capture seasonal variations in species activity (Shearin et al. 2012; Hagens et al. 2018), as for species influenced by light intensity and lunar phases (e.g. bats and katydids, Lang et al. 2006; e.g. anurans, Onorati and Vignoli 2017; Underhill and Höbel 2018), or species with variable activity associated with seasonal phenology, such as the bimodal daily activity peak during summer reported for bats (Skalak et al. 2012).

Additionally, a greater autonomy can also be achieved by scheduling recordings at regular intervals (Browning et al. 2017). As a starting point, protocols of point counts and other traditional acoustic surveys can offer guidance to determine recording lengths for PAM, as they can provide comparable biological data with PAM methods to estimate alpha and gamma diversity (Darras et al. 2018a), community composition (Alquezar and Machado 2015), population trends of cryptic species (Digby et al. 2013; Hagens et al. 2018), and to discriminate individual calls (Ehnes and Foote 2015). Point counts surveys have been widely used in avian (Rosenstock et al. 2002; Matsuoka et al. 2014) and amphibian research (Pierce and Gutzwiller 2004; Dorcas et al. 2009). For long-term monitoring of amphibian population

trends, call surveys with three to 5-min lengths per hour have shown to be adequate for most species (Shirose et al. 1997; Dorcas et al. 2009), whereas for birds shorter lengths may increase false negatives, and studies have often used lengths of five to 20 min (Bonthoux and Balent 2012, Table 1). Overall, longer surveys increase detection probabilities and produce better estimates of species diversity, but still acceptable levels of accuracy can be obtained for the same metrics by using shorter time windows (Table 1), without affecting the overall scientific conclusions (Hagens et al. 2018).

Sound-producing invertebrates (e.g. crickets and katydids) have been less studied using PAM, but still produce species-specific signals (Riede 2018) that can be reliably monitored by acoustic sensors (Diwakar et al. 2007). Low temporal partitioning among sound-producing insects seems to be pervasive across communities (Schmidt et al. 2013), allowing acoustic monitoring to rely on fewer short-length recordings per night (e.g. 3-min recordings every 30 min, Thompson et al. 2019). Remarkably, orthopterans are one of the most targeted group for large-scale citizen science PAM studies, where recordings are taken continuously along a circuit and standardized based on speed instead of time (Penone et al. 2013; Jeliaskov et al. 2016).

The frequency of recordings taken during monitoring determines the temporal data resolution and also influences target species detection. Shorter inter-recording intervals from 24-h monitoring provide better estimates of temporal acoustic dynamics than larger intervals (Bradfer-Lawrence et al. 2019), although the performance varies over habitat types (Pieretti et al. 2015). Additionally, extending the number of monitored days leads to higher detection probabilities (Pérez-Granados et al. 2019; Skalak et al. 2012, but see Thompson et al. 2019), and may also increase the statistical power for detecting meaningful effects over temporal trends (Wood et al. 2019). As distinct combinations of recording length and number of scheduled recordings influence how well total acoustic activity is captured, a critical appraisal of the sampling effort is required to set appropriate temporal PAM designs. In this sense, pilot studies can provide initial estimates of the efficiency of distinct recording schedules for a given goal (Wimmer et al. 2013; Hagens et al. 2018; Bradfer-Lawrence et al. 2019).

Considerations about audio settings

The selection of audio settings on acoustic sensors determines the quality of the recordings of PAM programs (Obrist et al. 2010; Villanueva-Rivera et al., 2011). Here, we highlight here essential audio settings that must be considered, and common standards used in PAM.

Table 1. Examples of recommendations of calling survey length (also point counts or other acoustic surveys) from literature that addressed the effect of distinct survey techniques on diversity patterns

| Biological group | Duration | Reasoning | Reference |
|------------------|----------|--|------------------------------|
| Anurans | 3 | Adequate to sample species occurrence and calling intensity for most species. In most cases, all species were identified in the first minute of survey. | Shirose et al. (1997) |
| | 5 | Sufficient to detect 94% of all species | Gooch et al. (2006) |
| | 5–15 | Higher detection probability on 5-min calling survey for large populations during peak breeding | Williams et al. (2013) |
| | 10 | Higher detection probability to detect all species | Crouch and Peter (2002) |
| | 15 | Sufficient to detect 90% of all species | Pierce and Gutzwiller (2004) |
| Birds | 5 | Other lengths (10, 15 and 20) improve moderately explanation of community structure and prediction of species distribution | Bonthoux |
| | 5 | Detection increase with larger survey duration only for few species | Thompson et al. (2002) |
| | 5 to 10 | Better performance of species-habitat models | Dettmers et al. (1999) |
| | 10 | Larger duration did not produced better richness estimates | Gutzwiller (1991) |
| | 2–10 | Density estimates from 2 min are only 13% lower than 10-min count | Lee and Marsden (2008) |
| | | Suggestion of group-specific count period: 4 min for omnivores 6 min for nectarivores and upperstory gleaning insectivores 8 min for understory insectivores and canopy frugivores 10 min for sallying insectivores, ground-dwellers, carnivores and coucals/koels | |

Sampling rate is the number of sound amplitude measures captured per second by a microphone (in Hz). The sampling rate must be at least twice the maximum intended frequency to be recorded (Nyquist–Shannon sampling theorem) to ensure a proper recording of the signal. A broad range of vocalizations from most terrestrial vertebrates and some invertebrates can be recorded with standard microphones sensible to the human-ear frequency range (20 Hz–20 kHz) using 44.1 or 48 kHz sampling rates. Conversely, bats, some mammals (e.g. rodents) and most invertebrates demand ultrasonic microphones recording at higher sampling rates (e.g. 96–192 kHz). As larger sampling rates produce larger file sizes, an alternative to enhance sensor autonomy is to identify the frequency of the highest-pitched sound of the target species (e.g. 7 kHz), double it ($2 \times 7 = 14$ kHz) and set the sampling rate a few kHz higher to avoid missing signals at slightly higher frequencies. In the example of a 7 kHz signal, a sampling rate of 20 kHz would be high enough to capture the intended signal and would produce files that are about 50% smaller than files produced from sampling rates of 48 or 44.1 kHz.

Audio gain modulates the sound amplitude of the recorded signal by amplifying or attenuating it by a constant rate. Higher gain increases the likelihood of recording a distant or weak sound and consequently the detection space. However, it also amplifies background noise and increased the chance of audio clipping (i.e. amplitudes that exceed the maximum range of the device), resulting in distortions that can compromise further analysis (Obrist et al. 2010). In most automated

recording units, gain is pre-set and remains fixed within the temporal extent of monitoring, unlike manual focal recording where gain can be adjusted by the operator according to acoustic conditions. Undertaking pilot tests over varying conditions can thus help optimize this parameter. Alternatively, stereo recordings with distinct gains for each channel can be used for long-term acoustic monitoring where changing sound levels are expected. However, while different gain levels have negligible impacts on sensor autonomy, stereo recordings double the amount of collected data and increase power consumption for high sampling rates (above 44.1 kHz).

When more than one microphone is available, *stereo/multichannel mode* can be used to place microphones in different locations with extension cables to monitor different habitats or strata using a single acoustic device, or to guarantee a suitable record (from at least one channel) in case of microphone malfunction (Digby et al. 2013; Rodriguez et al. 2014). Other common standards in audio settings are (i) a minimum of 16-bit audio *bit depths* and (ii) the use of uncompressed (WAVE or AIFF) or lossless compressed *audio formats*. Lossy compression formats such as MP3 or AAC can alter the acoustic parameters in recordings and decrease the performance of automated analysis of acoustic data (Araya-Salas et al., 2019). Still, compressed audio recordings have proven useful for analyses based on aural recognition (Villanueva-Rivera et al., 2011) and can yield similar estimates of acoustic diversity provided by uncompressed files, with the benefit of optimizing memory usage (Linke & Deretic, 2019).

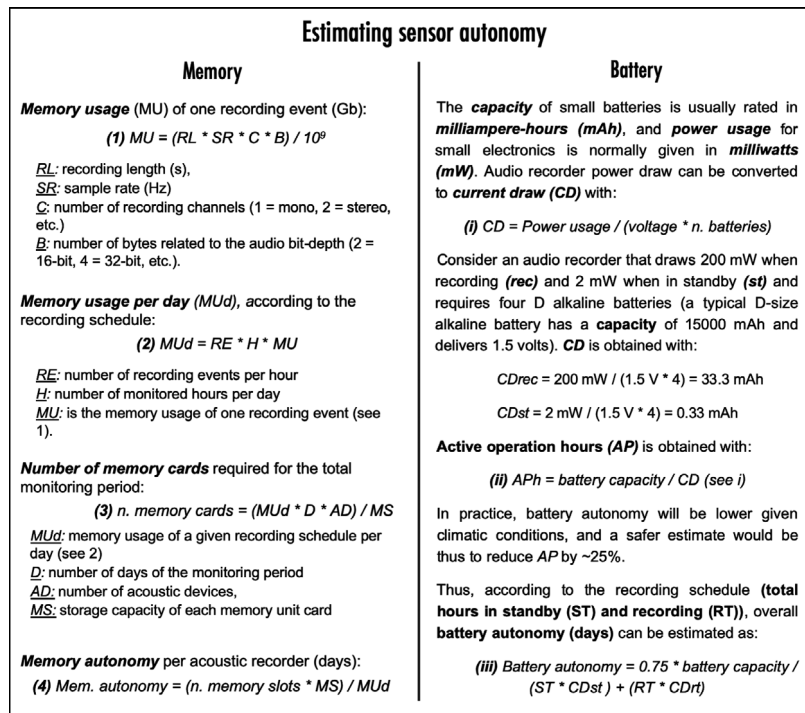


Figure 5. Estimating sensor autonomy by calculating memory and battery usage given audio settings, recording schedule and electrical calculations.

Autonomy estimation

The autonomy of acoustic sensors is determined by (i) memory usage, considering audio settings and the capacity of storage units (e.g. memory cards) and (ii) battery usage, considering the electrical aspects of battery cells and acoustic sensors (Fig. 5). To illustrate how different recording schedules and audio settings can influence sensor autonomy, we explore memory and battery usage using a SM4 (Wildlife Acoustics Inc.) with default settings (stereo recording powered by size 4D alkaline batteries and stored in .WAV format) for recording (i) continuous 24-h, 5 h per day (e.g. dawn and dusk), and 2 h per day (e.g. only dawn or dusk); (ii) recording lengths of 1, 3 and 5 min; (iii) regular recording intervals from one to six recordings per hour and (iv) sampling rates of 24 and 48 kHz (Fig. 6).

As expected, memory and battery autonomy decrease with longer monitoring periods, recording lengths and sampling rate. For schedules containing a higher number of recordings per hour, memory consumption sharply increases with larger sampling rates and recording lengths (Fig. 6). For instance, negligible differences in memory consumption are observed for one and two recordings per hour, whereas memory consumption changes considerably among five and six recordings per hour.

Overall, short recording lengths provide greater autonomy for schedules of discontinuous recordings through the day. Conversely, monitoring specific diel periods allows increased recording lengths and/or number of recordings per hour with less impact on autonomy when compared with the minimum scheduling settings for 24-h monitoring (Fig. 6).

Rewinding the tape: trade-offs between sampling efficiency and cost

Based on our assessment of the current literature, we suggest the following workflow to optimize spatial and temporal sampling designs for passive acoustic monitoring (Fig. 7):

1 Design spatial effort over the study area to properly address the extent of the spatial scale studied (Pollock et al. 2002; Wood et al. 2019). If the number of available recorders is low, consider employing rotation procedures, lower cost recorders or more microphones. Whenever possible, undertake pilot tests to estimate the detection space (or distance) of sensors over the range of monitoring habitats, while also optimizing gain levels (Llusia et al. 2011; Enari et al. 2017; Darras et al. 2018b; Pérez-Granados et al. 2019; Yip et al. 2019).

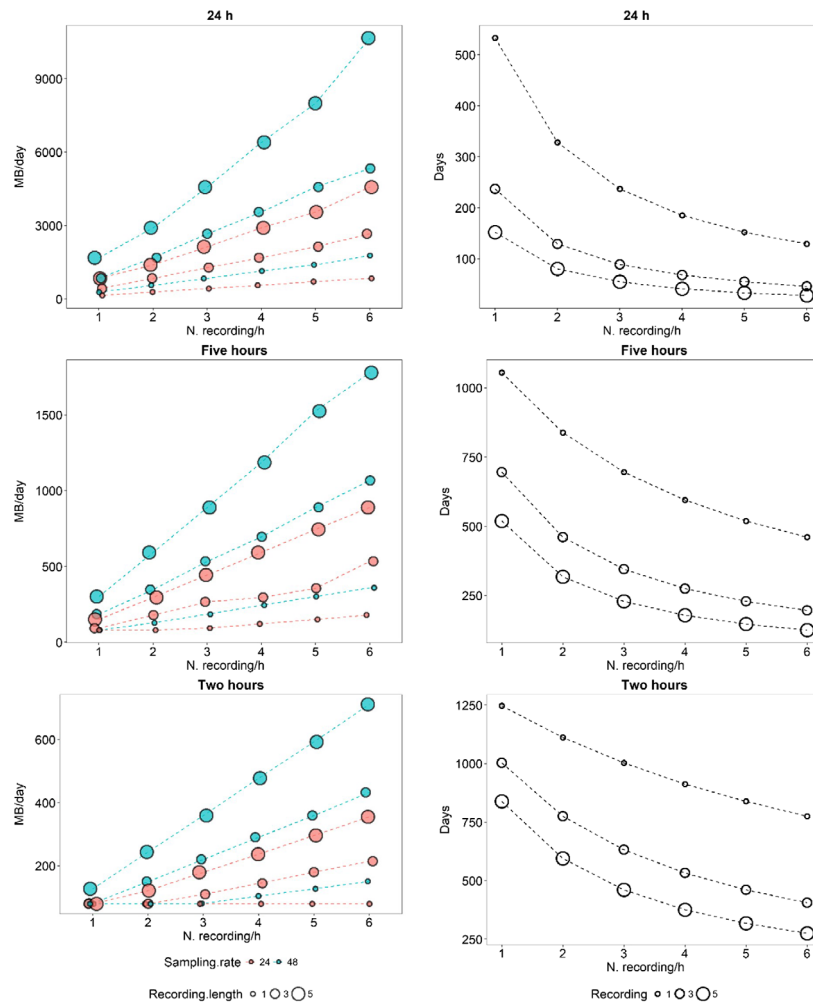


Figure 6. Memory (left) and battery (right) usages for a combination of recording schedules and audio settings based on distinct (i) recording periods (continuous 24-h, 5 h and 2 h), (ii) sample rates (24 and 48 kHz), (iii) recording lengths (1, 3 and 5 min) and (iv) recording intervals (one to six recordings per hour).

Use this information to determine the appropriate distance among sampling sites.

- 2 Make a list of potential recording schedules based on behavioral and ecological aspects of focal taxa and research goal. Prioritize larger diel periods and continuous recordings. When employing discontinuous recordings, include a wide range of distinct recording lengths, supported by previous recording protocols (Table 1), and number of recordings per hour (i.e. inter-recording interval).
- 3 Conduct continuous 24-h audio recordings prior to start monitoring and estimate species detectability or other biological parameters of interest (e.g. species richness, community composition; Hagens et al. 2018) for the previously listed recording schedules (see point 2). Conversely, when monitoring is already on course and scheduled following given standards, consider conducting continuous recordings for a subset of sites during

specific days. Evaluate the congruence of information obtained from the different recording schedules with the information obtained from 24-h recordings. For instance, use species accumulation or rarefaction curves and non-parametric estimates of species diversity (Gotelli and Colwell 2001; Brose et al. 2003), cumulative standard errors of mean estimates (Bradfer-Lawrence et al. 2019), coefficient of variance of acoustic activity indices (Pérez-Granados et al. 2019), or procrustes superimposition for compositional similarities (Saito et al. 2015). Alternatively, resort to modeling techniques to estimate species detection probabilities and occupancy rates that include imperfect detection when estimating biological parameters such as species richness (Dorazio et al. 2006; Celis-Murillo et al. 2012; Hagens et al. 2018; Ribeiro et al. 2018). This procedure can support choosing among distinct recording schedules prior to start

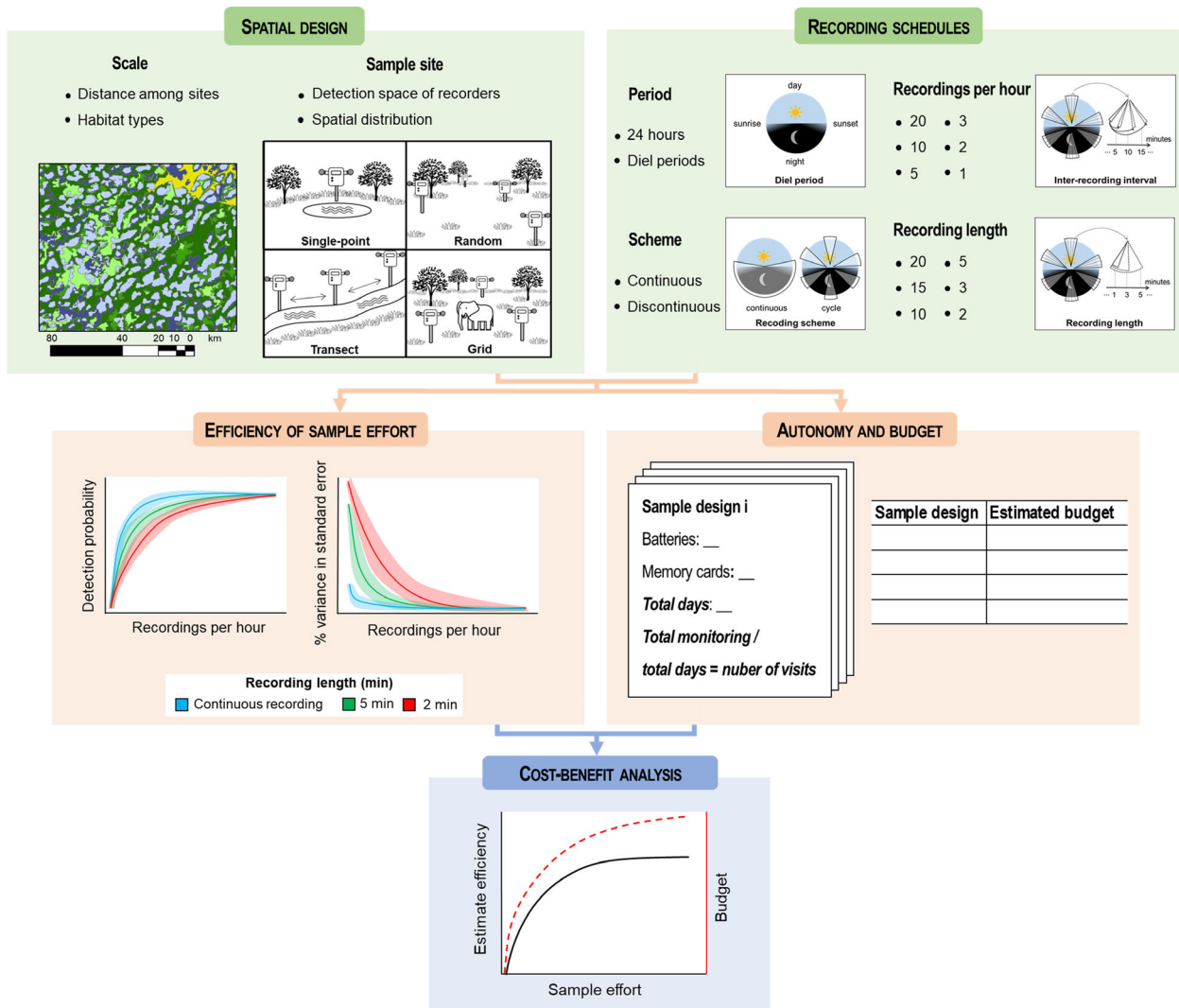


Figure 7. Workflow for planning and optimizing spatial and temporal sampling design in passive acoustic monitoring. Spatial design should consider aspects of spatial scale of inference and species detectability. Distinct recording schedules can be set according to specific monitoring period, continuous or discontinuous recordings, number of recordings per hours and the length of recordings. Whenever possible, 24-h recordings can be employed prior or during monitoring to address whether distinct recording schedules can retrieve the biological information obtained in 24-h continuous monitoring. Estimate the autonomy of distinct survey designs and their respective costs, and evaluate their suitability according to sampling effort, estimate efficiency and budget.

PAM. Additionally, for studies already on course, once the initial data are collected and analyzed, such estimates can assist in the interpretation of the results and provide a measure of data reliability. In cases when this procedure cannot be applied, such as in remote areas or on a limited budget, more intense schedules may be selected according to literature (Table 1).

- 4 Estimate sensor autonomy and associated costs for the distinct recording schedules. For each recording schedule, generate trade-off scenarios between autonomy and bias in biological estimates previously calculated. From

the scenarios generated, define which design is suitable considering budget, sampling effort and autonomy (Wintle et al. 2011).

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