UNIVERSIDADE DE LISBOA
FACULDADE DE CIÊNCIAS
DEPARTAMENTO DE BIOLOGIA ANIMAL

Passive acoustic monitoring and audio subsampling: optimizing autonomous methods for avian biodiversity assessments

Thomas Wojciech Burfin

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Dissertação orientada por:
Ana Leal
Jorge Palmeirim

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Summary

The global decline of bird populations has prompted the search for innovative tools to inventory and monitor their communities. While standard surveys require an observer in the field, autonomous sound recorders are an alternative that demands less expertise and is more scalable in time and space. The literature is not consensual on the efficiency of this method and the factors that influence it, particularly in multispecies studies, although recent attempts have yielded encouraging results towards its applicability in practical monitoring situations. In this study, we conducted a set of observer and recorder-based bird point counts in cork oak woodlands in Portugal, in winter season. We compared both methods in terms of richness values and species-by-species, and assessed the role of the observer and sampling time in recorder performance. Additionally, we compared species richness values obtained through three types of intermittent audio file subsampling, and by intermittent and continuous approaches. We found the observer detected significantly more species, but its presence did not influence the recorder's results and the pool of species detected by both was similar. We found time of sampling to be relevant in autonomous recorders. The degree of intermittence generated different cost/benefit scenarios for audio processing. Lastly, intermittent subsampling surpassed the number of species detected through continuous subsampling by a factor of two. The results of this study showed that recorders tended to perform well in biodiversity surveys in winter, while being more flexible in scaling, especially when small portions of audio are analysed. However, they also suggest the observer should not be dismissed *a priori*, and highlight the complexity of factors that may influence the recorder's performance. We encourage future studies to test this performance over a variety of different time, spatial, and species-related constraints, to maximize the universality of a future all-year autonomous method monitoring protocol.

Key words: Bird surveys · Recorders · Efficient sampling

Sumário

O declínio global das populações de aves promoveu a procura de ferramentas inovadoras para inventariar e monitorizar as suas comunidades. Enquanto as amostragens tradicionais necessitam de um observador no terreno, os gravadores automáticos são uma alternativa que requer menos conhecimento especializado e permite aumentar a escala espacial e temporal da amostragem. A literatura é ambígua sobre a eficiência deste método, particularmente em estudos multiespecíficos, apesar de trabalhos recentes terem mostrado resultados encorajadores acerca da sua aplicabilidade em situações de monitorização. Neste estudo, realizámos um conjunto de pontos de contagem de aves baseados em observadores e em gravadores em zonas de montado, em Portugal, durante o inverno. Comparámos ambas as abordagens em termos de riqueza específica e espécie a espécie, tendo analisado o papel do observador e da janela temporal de amostragem no desempenho dos gravadores. Adicionalmente, comparámos os valores de riqueza específica obtidos através de três tipos de subamostragem de ficheiros áudio. Por fim, comparámos abordagens contínuas e intermitentes. Os resultados mostraram que o observador detetou mais espécies e que a sua presença não influenciou os resultados dos gravadores, que detetaram uma amostra de espécies semelhante. A janela temporal de amostragem foi considerada relevante e teve impacto nas estimativas dos gravadores. O nível de intermitência de subamostragem gerou diferentes cenários de custo/benefício para o processamento de áudio. Por fim, a abordagem intermitente permitiu a deteção de duas vezes mais espécies do que a contínua. Estes resultados sugerem que os gravadores têm um bom desempenho em contextos multiespecíficos no inverno, sendo mais flexíveis a grande escala, particularmente quando são analisadas pequenas porções de áudio. Por oposição, sugerem também que o observador é relevante e evidenciam a complexidade de fatores inerentes ao desempenho dos gravadores. Reiteramos a necessidade de estudos futuros testarem este desempenho em variadas condições espaciais, temporais e de espécies para maximizar a universalidade de um futuro protocolo para monitorização automática aplicável durante todo o ano.

Palavras-chave: Amostragem de aves · Gravadores · Amostragem eficiente

Resumo alargado

As aves são um constituinte essencial de uma grande variedade de ecossistemas. Para além de serem razoavelmente fáceis de observar, são sensíveis a alterações de habitat e ocupam diversas posições tróficas, elementos que fazem delas um importante indicador ambiental. Num período em que quase metade das espécies de aves a nível global apresenta tendências populacionais de declínio, torna-se prioritário desenvolver e agilizar técnicas de inventariação e monitorização que respondam às necessidades cada vez mais exigentes colocadas pela situação atual. Tradicionalmente, o estudo das populações de aves envolve uma componente de campo em que um ou mais observadores efetuam pontos de contagem ou transetos, com vista a inventariar as espécies e/ou contar o número de indivíduos detetados, visual e auditivamente, numa determinada área. Este método é de utilização transversal na ornitologia e serve de base para muitos propósitos relevantes, tais como monitorização de espécies e populações, estudos de impacto ambiental, delimitação de áreas prioritárias de conservação e monitorização da eficácia de medidas de conservação previamente implementadas. No entanto, o mesmo possui algumas desvantagens, nomeadamente o tempo necessário e a fraca capacidade de expansão temporal e espacial da amostragem. Estas duas características são um obstáculo de crescente relevância no contexto atual, uma vez que para se poder obter uma imagem mais precisa do problema é necessário tornar a amostragem mais rápida e versátil.

Os gravadores automáticos, utilizados para a monitorização acústica passiva, são uma ferramenta emergente que visa obter os mesmos tipos de dados, utilizando apenas técnicas acústicas e sem a necessidade da presença de um observador durante a amostragem. Vários estudos apontam para potenciais benefícios destas técnicas, particularmente ao nível do tempo despendido e da possibilidade de flexibilizar a área e o período de amostragem sem grandes custos adicionais. Além disso, mostram sinais encorajadores ao nível dos resultados obtidos, tanto a nível de riqueza específica como de estimativa de densidades. Todavia, a literatura não é consensual em relação à verdadeira eficácia dos gravadores automáticos na maioria das situações, particularmente em estudos multiespecíficos. Apesar de este método apresentar resultados globalmente positivos, o desempenho dos gravadores automáticos não é homogéneo e a sua variável qualidade de desempenho aparenta dever-se ao conjunto específico de fatores bióticos e abióticos presentes no estudo, tais como as espécies alvo, o habitat e o desenho amostral. Além disso, a componente de processamento coloca alguns entraves, na medida em que a identificação automática de espécies em ficheiros áudio ainda se encontra em aperfeiçoamento e a identificação manual continua pouco otimizada. Em particular, Cook et al. (2018) apresenta e valida o benefício da utilização de subamostragem (i.e. analisar apenas um fragmento da porção gravada) para estimar a riqueza específica. Desta forma, a multiplicidade de fatores potencialmente influenciadores nas estimativas finais, juntamente com uma fase de processamento

ainda pouco estabelecida, são as principais razões para a ausência de protocolos detalhados e universais para a utilização de gravadores automáticos em estudos com aves.

Neste trabalho, pretendemos abordar estas duas questões: analisar a influência de alguns fatores nas estimativas de riqueza específica dos gravadores automáticos e aperfeiçoar as técnicas de processamento manual de gravações de aves. Efetuámos pontos de contagem tradicionais (com observador) e pontos de contagem de acústica passiva (com gravadores) na Companhia das Lezírias, S.A. (Samora Correia, Portugal), em habitat de montado, durante o inverno de 2020. A escolha do período não-nidificante derivou da ausência de trabalhos focados nesta faixa temporal, nomeadamente considerando as implicações que a meteorologia e a redução da atividade vocal das aves neste período poderiam ter no desempenho dos gravadores. Na primeira secção, comparámos o desempenho do observador com o dos gravadores, utilizando a riqueza específica como medida comparativa. Explorámos também o potencial papel da presença do observador e do período de amostragem dos gravadores nos resultados da comparação anterior. Finalizámos com uma análise espécie a espécie, de forma aumentar a resolução das diferenças observadas. Na segunda secção, aprofundámos o conceito de subamostragem em ficheiros áudio. Começámos por comparar três tipos de subamostragem intermitente (i.e., subamostragem em que se analisam apenas alguns segundos de gravação para análise, seguidos de intervalos longos), nomeadamente pouco (10 s de gravação a cada 1 min), medianamente (10 s de gravação a cada 2 min) e muito espaçados (10 s de gravação a cada 4 min). De seguida, comparámos um tipo de subamostragem intermitente com um contínuo (i.e., subamostragem em que se analisa uma porção contínua significativa da gravação original). Ambas as comparações tiveram, da mesma forma, o número de espécies detetadas como termo comparativo.

Observámos um número significativamente superior de espécies detetadas pelo observador face ao gravador. A presença do observador no terreno aquando da amostragem com gravadores, que poderia perturbar o comportamento acústico de algumas aves, não teve influência na diferença observada, enquanto que a concentração do período de amostragem do gravador na hora de maior atividade das aves mitigou consideravelmente esta diferença. A análise espécie a espécie revelou que a quase totalidade das espécies foi detetada por ambos os métodos. Ainda assim, algumas espécies de vocalizações erráticas e/ou com frequências altas foram mais detetadas no gravador, enquanto outras espécies cuja identificação depende fortemente de pistas visuais foram mais detetadas pelo observador. Verificámos também que os tipos de subamostragem intermitente muito e medianamente espaçados ofereceram um bom compromisso de tempo de audição/número de espécies identificadas. Por fim, o número de espécies detetado em subamostragem intermitente foi cerca de duas vezes superior ao detetado em subamostragem contínua, sendo que o tempo necessário para o método intermitente igualar o número de espécies do método contínuo foi cerca de cinco vezes inferior.

Os resultados do nosso estudo sugerem que, de forma geral, os gravadores automáticos tiveram um bom desempenho neste contexto multiespecífico e no período de inverno, mostrando que a reduzida atividade vocal das espécies mais comuns neste período não constitui, à partida, um impedimento relevante. No entanto, reforçam que o observador não deve ser considerado dispensável, uma vez que a sua capacidade de seguir o som tridimensionalmente e os elementos visuais facilitam a identificação de certas espécies. A presença do observador e o afugentamento que poderá provocar nas aves não pareceu ter influência no nosso caso, embora apenas a adição de estudos futuros poderá confirmar se esta é a situação mais comum noutros habitats. Também se pode concluir que a escolha da hora de amostragem é importante no caso dos gravadores, sendo que uma concentração nas horas de maior atividade permite melhorar o número de espécies detetadas. Em relação à subamostragem, os resultados indicam que optar por este método, particularmente por um esquema de subamostragem intermitente, traz vantagens claras no número de espécies identificadas por unidade de tempo, sendo que o padrão de intermitência ideal deverá depender do objetivo do estudo; isto é, se compensa optar

por intervalos mais longos e, por isso, utilizar um maior número de gravadores ou se, por outro lado, o reduzido número de gravadores a utilizar permite subamostragens com intervalos mais curtos.

Em suma, este estudo vem reforçar a ideia, corroborada em outros estudos semelhantes, de que a acústica passiva utilizando gravadores automáticos é uma técnica que, quando ajustada à devida finalidade, produz resultados interessantes e comparáveis aos obtidos por métodos tradicionais, quer em estudos multiespecíficos, quer durante o inverno. Mostra também que, por um lado, há uma variedade considerável de fatores que podem influenciar o desempenho do mesmo e que devem ser avaliados e que, por outro, a subamostragem intermitente é uma solução eficaz para otimizar o processamento de gravações. Ao tomar em consideração os principais fatores que poderão afetar o sucesso das estimativas de riqueza específica utilizando acústica passiva, bem como ao agilizar a fase de processamento de áudio, estaremos a contribuir para uma aplicação mais universal desta técnica. A deteção e correção dos principais enviesamentos ligados aos gravadores, assim como a possibilidade de cobrir uma maior área de amostragem em menos tempo, representam um avanço no quadro da monitorização das comunidades e populações de aves. Algumas questões, tal como o cálculo de densidades a partir de dados acústicos, continuam a carecer de ferramentas acessíveis e universais; outras, como a sensibilidade do microfone, a época do ano e a estrutura de vegetação, são fatores que devem ser analisados a fim de averiguar o seu impacto no desempenho da acústica passiva. Apesar do que ainda falta escrutinar, este estudo é um complemento e um contributo relevante ao caminho experimental que já vem sendo percorrido, com o objetivo de definir as capacidades e as limitações desta técnica e de, num futuro próximo, poder conciliar a elaboração de protocolos com a aplicação dos mesmos em projetos a grande escala e durante todo o ano.

Palavras-chave: Amostragem de aves · Gravadores · Amostragem eficiente

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Chapter 1 - Introduction

1.1 Bird songs and bioacoustics

1.1.1 Anatomy, ontogeny, and development of sound production in birds

One of the most flagrant manifestations of nature's ecological dynamics can be obtained with a short walk around the local park. In most cases, "chirps", "chaffs", and other small or more complex sounds will eventually arise. Most birds sing and do so, not only with purpose, but also with efficiency. Their sounds range in pitch from high and inaudible to humans, to deep infrasound. Changes in pitch and energy delivered within bird songs are unique among animals, generating complex and intrinsically structured patterns (Gill 2007). These and other features have long caused fascination amongst naturalists and ornithologists, who have aimed to address a wide variety of questions over the years: How does a bird sing? Why does it sing? How does it learn to produce specific sounds? How do these sounds vary in time and space? While all of these questions remain relevant, here we focus on the anatomy, ontogeny, and development of the sound production itself.

Albeit several other taxa like primates, anurans, insects (Alexander 1957), crocodilians (Vergne et al. 2009), geckos (Brillet and Paillette 1991), and fish (Fay et al. 2008) are known to produce sound, only birds and a few other mammals (such as humans, whales, and some bats) can learn and integrate songs or some form of vocal language (Gill 2007). However, the uniqueness of a bird's sound comes from its vocal organ. In the human species, for example, the larynx is responsible for producing sound. In birds, this organ has no vocal functions. Instead, the syrinx, a unique organ to the class Aves (Greenewalt 1968), plays this pivotal role. The syrinx is located within the thoracic cavity and contains small parts of tissue known as labia. When these labia extend into the bronchial cavity, the passing air from the interclavicle air sacs causes them to vibrate, generating sound (Paruk 2018). Variations in pitch occur in consequence of muscle activity, which in turn control syrinx action during the airflow, enabling the production of numerous sound types (Nottebohm 1970). Furthermore, muscles on each side of the syrinx are controlled independently, which allows the two sides to produce different sounds simultaneously (Miller 1977). Besides syringe regulation, sound can also be modulated through alternate patterns of exhaling and inhaling, trachea length, and beak movement (Gill 2007).

As one would expect, avian sound production is not exclusively assured by the respiratory tract. It also depends on a complex set of complementary motor and neural systems (Podos et al. 2004). Two main neural pathways control bird songs. The first one, called the main descending motor pathway, regulates song production. The second one, the anterior forebrain pathway, is crucial for song recognition and learning in oscine passerines (Gill 2007). Moreover, bird song is lateralized (Nottebohm 1970), meaning it is fully controlled by the left hemisphere of the brain (unless damaged) in the adult life stages.

Additionally, birds need to learn specific and well-reproduced songs to enhance their fitness in the wild. How birds learn to sing varies greatly among different groups. While some birds, like the European Chaffinch (*Fringilla coelebs*), have a restricted time frame in which they are most prone to learn new elements (Nottebohm 1970), others such as the Common

Nightingale (*Luscinia megarhynchos*) are open-ended learners who can acquire new song patterns throughout their lives. In most cases, however, song learning in birds is a two-step process. The sensory acquisition phase, in which birds are exposed to song models, consists of acquiring a viable auditory template, and the sensorimotor phase, in which practice is essential, aims to match the learned song to the template (Gill 2007). Further studies revealed birds with fixed repertoires learn songs in four stages: a critical learning period (when vocal information is absorbed for later use), a silent period (when learned elements are stored without rehearsal), a subsong period (when young birds practice without communicating) and song crystallization (when plastic song is transformed into real, improved and structured songs) (Paruk 2018). It is also worth mentioning that songs can be obtained through mimicry, learning and individuality itself. Thus, one must also not forget the role of habitat and social interactions in birds' complex patterns of imitation and improvisation (Gill 2007; Paruk 2018).

Bird song has long been issued in phylogenetic studies and is currently considered to be a consequence of the evolutionary process of different song traits within lineages, each with independent trajectories. A range of traits and corresponding selecting pressures may have contributed to the diversity of bird songs we observe today. Songs of birds can be shaped in time and limited, among others, by their performance ability and neuromuscular capacity, geographical separation of populations, imitation inaccuracies (Podos et al. 2004), unit rearrangement and invention of new elements, differential genetic heritability of song characteristics (Lanyon 1962) and sexual selection (Price 2015). Nonetheless, sexual selection and mechanical constraints are thought to be the main drivers of bird song evolution over larger time scales (Podos et al. 2004).

In summary, song production in birds is a complex and multivariate process (which arose through a variety of evolutionary selective pressures) and it represents a singular example of how a combination of genetics and behavioural learning is essential for the development of a key communicational tool.

1.1.2 Diversity, functions, and temporal variation of avian acoustic signals

Due to their refined anatomical and neuromuscular systems, birds are naturally designed to produce a wide range of vocal signals, that is, vocalizations that influence the behaviour of other conspecifics (Paruk 2018). Vocal signals vary greatly in amplitude and frequency, which is commonly related to the source's body mass (Wallschlager 1980). While Carrion crows (*Corvus corone*) may sing at very low frequencies (Siriwardena 1995), small-sized Goldcrests' (*Regulus regulus*) vocalizations are substantially high pitched and sometimes difficult to detect (Tucker et al. 2014). Because a signal is meant to be heard, it will only reach the listener if it successfully travels across the environment. Low-frequency sounds are favoured for long-distance communication due to the low attenuation of sound waves, while reverberation in forests causes birds to prefer simple songs. In the same way, broadband songs are better suited for open habitats as they are less prone to temperature or wind-related distortion (Gill 2007), whereas birds in urban areas sing with an adjusted pitch and increased song rate (Seger-Fullam et al. 2011). Hence, the diversity of physical structures in bird sounds is often an adaptive response to improve transmission efficiency (Gill 2007; Paruk 2018).

Two main types of vocal signals can be identified in birds. Songs, on one hand, represent tendentially loud, recognizable, and sometimes complex vocalizations used in mate attraction or territory defence. Calls, on the other hand, are generally shorter and simpler. The variety and degree of complexity of songs and calls are, to some extent dictated by their functions, which are varied (Paruk 2018). Common nightingales (*Luscinia megarhynchos*) sing constantly during the breeding season to defend territories (Kunc et al. 2005). Female Song sparrows emit aggressive calls when competing for resources (Arcese et al. 1988). In Common grackles (*Quiscalus quiscula*), male songs are vital for female choice in mating opportunities (Searcy 1992). Some calls are used to effectively distinguish neighbours from strangers (Osiejuk 2014), while others allow kin and non-kin discrimination (Sharp et al. 2005). In cooperative birds, vocal signals can be the key to effective sentinel behaviour (Bell et al. 2010). Vocalizations also inform about a potential predator, signalling alarm and causing an urgent fleeing response (Leavesley and Magrath 2005). Begging calls play a fundamental role in the American robin (*Turdus migratorius*) nestling's food provisioning (Smith and Montgomerie 1991) and some signals in adults inform mates about newly discovered food sources, even in colonially nesting species (Stoddard 1988). Other song and call functions include flight preparation, injury signalling, active courtship, seeking companions, and informing about the female's reproductive state or the male's overall condition (Marler 1956; Paruk 2018)

As stated before, bird songs and calls differ in both structure and function. Thus, it might not be efficient for an individual to maintain the same song/call choice and intensity throughout the year (Gill 2007). Indeed, different vocalization behaviours may reflect distinct seasonal needs (Rotella and Ratti 1988). In most species, songs are more frequent during the breeding season, sometimes with greater complexity (Hill et al. 2015), enhancing territoriality and mate attraction. Signals related to food sources, predators, and social contact are more prominent during the non-breeding season when birds typically do not defend territories as actively (Tremain et al. 2008). For instance, in Black-capped chickadees (*Poecile atricapillus*), mate attraction and territorial calls occur more intensely during spring, whilst vocalizations related to flock movements, food signalling, and aggression are more scattered across the remaining seasons (Avey et al. 2008).

Lastly, this pattern of temporal distribution of acoustic signals is sometimes related to weather changes. Wind and precipitation attenuate and distort sound waves, compressing the effective travelling distance of sound and limiting the amount of information a listener receives (Lanyon 1962). To compensate, species that experience varied pluvial regimes across their ranges tend to produce more complex songs (Medina and Francis 2012). Accordingly, variance in male song quality in bad weather is higher as individuals try to highlight themselves from the competition (Gil and Gahr 2002).

In short, birds provide a wide array of songs and calls which serve an adaptive purpose not only for the mean of transmission, but for the social function itself. These signals generate complex interactions whose purpose varies throughout a birds' life cycle. As a result, we observe different vocalizations across seasons and shifting vocal strategies related to weather conditions.

1.1.3 Study of bird sound as a tool in research

Similar to other vocal animals, birds use acoustic signals as a cue to communicate with conspecifics, survey the environment (Pillay et al. 2019), for orientation, territory defence, group interactions, and mate attraction (Obrist et al. 2010). Hence, knowing to what extent a bird is acoustically responsive and how the produced signals affect other individuals is fundamental for our understanding of their ecology (Sevgili et al. 2006). Years of development have led to the establishment of a research field that includes communication, sound production, and reception applied to population monitoring, acoustic ecology, and noise effects on animals. This field is known as bioacoustics (Ramsier 2016). In recent years, bioacoustics has proven to be helpful in a variety of bird-related studies.

Over the years, the study of bird acoustic signalling has allowed us to better understand the impacts of biophysical habitat characteristics and invasions (Boelman et al. 2007), evolutionary lineages (Päckert et al. 2004), analysing shifts in songbird communities (Sebastián-González et al. 2015) and proposing taxonomical reclassifications (Gwee et al. 2019). Acoustic signals captured by autonomous recorders have served as cues for many anthropogenic-based threats towards wildlife, such as pollution and hunting (Laiolo 2010). Additionally, they are being progressively tested as a tool for population control (Conklin et al. 2009) and human food source health assessment by monitoring the health condition of poultry (Mahdavian et al. 2020), both of economical relevance. Nonetheless, it is amid biodiversity inventories and population monitoring that we find most attempts at involving recorder-based autonomous acoustic in monitoring. The reasons behind this are, among others, lower cost and more accessible data collection of cryptic, migrant, or nocturnal birds using this method, especially in remote areas (Bardeli et al. 2010; Obrist et al. 2010; Steer 2010; Frommolt and Tauchert 2014). An extensive description of the advantages and disadvantages of acoustics in monitoring is provided in section 1.2.

Bioacoustics has thus moulded our perspective on how bird songs and calls represent an emerging tool in research. Not only do they deepen our understanding of already detected ecological features, but also grant access to previously unknown information regarding most of the current threats biodiversity has been facing in recent times.

1.2 Acoustic monitoring in birds

1.2.1 Observer-based acoustic monitoring

Birds are often used as bio-indicators to assess the ecological health of ecosystems (Cook and Hartley 2018) and because they regularly communicate using audible species-specific signals, sound detection is of utter importance for their study. Sound allows researchers to collect data on the presence/absence of species, the number of individuals, behaviour, and seasonal activity. Moreover, it can be used for most of the established field techniques, such as point counts, transects, and territory mapping (Sutherland et al. 2004). One of the most important study methods consists of a series of repeated surveys across the same study area, known as monitoring. Monitoring allows the measurement of population fluctuations, identification of some of its underlying causes, and evaluation of the degree of success of conservation actions, thus playing an essential role (Heywood 1995; Sutherland et al. 2004).

Most avian monitoring programs use point count surveys, where the aim is to record all birds identified by sight or sound, often including an estimate of distance when first detected, normally from a fixed position and following a certain duration (Rosenstock et al. 2002; Darras et al. 2019). Although their relevance fluctuates in accordance with variables such as targeted species or habitat of sampling, aural detections typically represent a significant proportion of the total number of detections. Consequently, local expertise and observer training is often crucial to gather valuable data, especially in environments that hinder visual observations (Sutherland et al. 2004; Kułaga and Budka 2019). Monitoring can also be performed with autonomous acoustic recorders and several arguments have been presented to support or undermine the importance of each approach (Digby et al. 2013; Truskinger et al. 2014).

When monitoring, human observers are undeniably benefited from subtle cues the habitat provides apart from the sound itself (Hutto and Stutzman 2009; Kułaga and Budka 2019). Besides the visual detection bonus and better spatial orientation, an observer is more likely to detect more distant birds (Yip et al. 2017), count individuals more accurately, collect behaviour-related information, and sample during harsh weather conditions (Darras et al. 2019). From a practical point of view, point counts have been used for decades and this accumulated information should be comparable with further approaches (Darras et al. 2018). However, observer-based point-counts eventually suffer in other criteria. Domains that rely on extended sampling periods and areas, such as phenology, detection of rare species, replicates collection and scaling, greatly reduce the value of human-based observations. “Live” observations do not also allow proofreading verification and may cause birds to flee due to human presence, a phenomenon known as the avoidance effect (Darras et al. 2018, 2019). Finally, other aspects may be more or less advantageous depending on the context. Material and labour costs vary in function of the sampled area, budget, and study purpose while misidentifications may be more or less pronounced following habitat type or amount of experience (Hutto and Stutzman 2009; Darras et al. 2018; Kułaga and Budka 2019).

Applying a human-based strategy in monitoring programs is thoroughly used nowadays. Much of it derives from sensory, historical, and practical advantages in doing so. However, some aspects may not be favoured under this method. Hence, it is worth considering them before deciding, as different field contexts or study purposes may affect the overall cost, data quality or even render it obsolete.

1.2.2 Recorder-based autonomous acoustic monitoring

Acoustic monitoring using autonomous recorder units (ARU) has long been proposed as an alternative to human observations (Ralph et al. 1995). In this method, a previously placed recorder autonomously gathers acoustic data, which is then brought to the laboratory to be processed either by listening or by automated species recognition systems (Browning et al. 2017).

Since then, a considerable number of studies have addressed the conveniences and drawbacks of this approach. A few straightforward obstacles include the lack of essential visual cues for certain types of data, material and labour costs, and difficulties in sampling on rainy or windy days (Darras et al. 2019). Habitat and vegetation at the local scale seem to affect the recorder’s performance (Yip et al. 2017). Some studies state that at best and for the same sampling period and area, autonomous recorders detect from fewer to the same number of species as a human observer (Shonfield and Bayne 2017; Kułaga and Budka 2019). Other authors go even further, affirming this approach is not suited to replace human observations, especially being less cost-effective (Hutto and Stutzman 2009).

However, human-based point counts are costly in time, financial, and human resources when applied to larger areas (Abrahams 2018; Cardinale et al. 2012). Recent technological advances have lowered the costs of recorders and have brought in new customizable features (Hill et al. 2018). When scaled, ARUs provide data that is comparable with traditional point counts while having well-documented advantages over them (Celis-Murillo et al. 2009; Borker et al. 2015; Klingbeil and Willig 2015; Shonfield and Bayne 2017; Abrahams 2018; Castro et al. 2019). Further, they assure less invasive, permanent, and constant data collection (Truskinger et al. 2014). Recorders are more suitable for low-accessibility areas and to detect rare or elusive species. They also do not require highly experienced ornithologists (Kułaga and Budka 2019) and reduce temporal and observer bias (Celis-Murillo et al. 2009; Digby et al. 2013). Lastly, ARUs relevance increases when high temporal or spatial coverage is needed (Darras et al. 2019).

Like the human-based method, autonomous recordings generate valuable information. This includes species richness, species composition, and acoustic proxies for metrics of biodiversity (Hobson et al. 2002; Celis-Murillo et al. 2009; Truskinger et al. 2014; Browning et al. 2017). Other useful and emerging measurements include indicators for abundance inference and density estimation (Pérez-Granados et al. 2019; Pérez-Granados and Traba 2021). However, and as previously indicated, it is difficult to confidently affirm one approach is better or comparable to the other in all contexts. This is why some authors encourage using autonomous recorders as an extension to standard point counts, stating their advantages do not fully replace a person in the field, but complement a considerable number of the latter's' flaws (Hutto and Stutzman 2009; Celis-Murillo et al. 2012; Shonfield and Bayne 2017).

Furthermore, and to originate comparable data, sampling must be standardized. Generalizing aspects of the acoustic sampling process, as the volume of data required, can be a daunting task and is dependent on the project objectives, species targeted (Shonfield and Bayne 2017) and bird density in the field (Pérez-Granados et al. 2018). Together with data processing, these could be the reasons why there are so few standardized protocols for autonomous acoustic sensor deployment designed to date (Abrahams 2018; Darras et al. 2018; Pérez-Granados et al. 2018). Although still insufficient, the number of published articles with guidance for ARU deployment and audio file analysis is gradually expanding (O'Donnell and Williams 2015; Abrahams 2018; Pérez-Granados et al. 2018), and attempts to generalize its guidelines to different ecological contexts and weather conditions are becoming more frequent. Nonetheless, further research and testing are needed (Shonfield and Bayne 2017).

Succinctly, an increasing volume of literature is focusing on the possibility of generalized autonomous bird monitoring with recorders. Overall comparisons between methods reveal conflicting results. However, recorder-based point counts complement human observations in many contexts, while being the only solution available in others. Further research may confirm if the former is suitable to be generalized for most monitoring scenarios.

1.3 Recordings in the laboratory: processing of avian acoustic data

1.3.1 Manual and automated data processing

Autonomous recorders do not suffer from the same time-related constraints as traditional point counts. As a result, it is frequently advised to analyse longer recording periods in order to explore ARU's full potential (Rempel et al. 2005; Klingbeil and Willig 2015; Cook and Hartley 2018). High temporal coverage enables more species to be detected and reduces confidence intervals in estimations of population parameters (Digby et al. 2013). Nonetheless, this carries additional problems (Towsey et al. 2014). Longer recordings result in larger amounts of acoustic data that must be processed. Fast and accurate identification of avian species in these files remains a challenge and researchers frequently aim to achieve the best balance between the two. Nevertheless, a couple of these identification methodologies abide.

On one side, detection and classification of signals can be done manually (e.g. La and Nudds 2016). With specialized software, sounds are visualized and labelled using a spectrogram. Different frequencies and amplitude modulations generate distinct wave shapes, enabling species classification (Obrist et al. 2010). This method is generally very time-consuming, especially for longer files. Expert presence is sometimes mandatory for accurate species identification and the listener's skill level may introduce an important bias (Browning et al. 2017; Cook and Hartley 2018). However, it currently remains the most reliable solution in terms of accuracy, particularly when a diverse bird community may generate confusion in automated identification approaches (Shonfield and Bayne 2017).

On the other side, semi and fully-automated species identification tools have been progressively used in research (i.e. O'Donnell and Williams 2015). In this case, gathered signals are matched to a sound template, called "recognizer", in order to evaluate if the species is present or absent. Most of these techniques use supervised machine learning (Shonfield and Bayne 2017). Although automatic detection software is suited for species with low-variability calls (Digby et al. 2013), they remain excessively species-specific (i.e. Sebastián-González et al. 2018), struggle with complex acoustic scenarios (Truskinger et al. 2014), and tend to underperform when multiple species are evaluated (Bardeli et al. 2010; Obrist et al. 2010).

Dealing with large acoustic datasets is still an obstacle. Automatic species recognition is possible and yields good results if it focuses on a few species with rather simple and distinct vocalizations. For bird biodiversity assessments, this method is often unmanageable. Despite being time-consuming and sometimes biased due to personal skill level, manual analysis currently remains the most viable choice for multispecies approaches.

1.3.2 Subsampling in acoustic data processing: intermittent and continuous approaches

As depicted above, manual detection and classification of songs is probably the most sensitive method available. Nonetheless, a clear dilemma emerges. Autonomous recorders become increasingly useful the more we extend our temporal and spatial coverage in the field, which increments the amount of data. We have also acknowledged earlier that the amount of time required in manual processing is a major weakness. Thus, it seems impossible to aim for scaling and fast manual processing simultaneously. This means we need to abdicate from one of them. Whereas reducing coverage would be neutralizing the positive effects of autonomous monitoring, accelerating manual processing can only be done by analysing portion of the collected recording time. This approach, known as subsampling, is based on the premise that by retrieving fragments of the original data, we will get an approximate result that answers our ecological question while greatly reducing the processing effort. In this context, Digby et al. (2013) raised an important question: how much acoustic information are we willing to sacrifice to reduce time and effort in processing while preventing excessive bias and maintaining reasonable ecological inferences?

The majority of studies that used acoustic subsampling picked continuous fragments from the original recordings (i.e. (O'Donnell and Williams 2015; La and Nudds 2016). These fragments typically range from 5 to 15 min each, to mimic the duration of a standard point count, and are chosen randomly. This reduces processing time and originates data that is comparable to human point counts. However, it still denies the possibility of substantial scaling in time and space, which is particularly problematic when cryptic or rare species are present (Hutto and Stutzman 2009).

A different attempt consists of a stratified "on-off" time sampling in which one analyses only a fraction of the extracted fragment (for example, one minute every ten) (Cook and Hartley 2018), compiling a large number of small intercalated "snapshots" of the avian community. With this intermittent approach, longer periods can be covered for the same effort whilst the temporal correlation of species is reduced (Kułaga and Budka 2019). Intermittent subsampling also facilitates data storage and extends battery life (La and Nudds 2016; Shonfield and Bayne 2017). To our knowledge, Cook & Hartley (2018) published the only study that directly compares composite samples of intermittent fragments to regular continuous point count samples. The authors found a significantly greater number of species was detected and fewer samples were needed to detect the same number of species using intermittent sampling. Still, this comparison is restricted to a fraction of the morning period, when bird activity is at its peak. Although most species are expected to be detected during this timeframe, rare and elusive ones may not (Pérez-Granados et al. 2018). Thus, longer temporal coverage may indicate whether the practical application of this method is effective.

1.4 Thesis relevance and objectives

Some concerns related to acoustic monitoring and data processing persist. Despite a considerable amount of literature dedicated to the comparison between autonomous and observer-based point counts, overall results appear to be indecisive. Indeed, a few questions remain unanswered. Are the autonomous and observer-based methods always comparable? Which factors determine certain biases in each method? Furthermore, and as Digby et al. (2013) affirmed, "*It is mostly unknown whether certain subsets of species are systematically over-or underrepresented by different survey techniques [autonomous and human-based]".* Additional studies in different habitats could give answers about to which extent one method exceeds the other.

Standardization of autonomous acoustic monitoring is also not established currently. Protocols for their application in the field are scarce and limited to a particular group of species. Additionally, most studies apply or suggest protocols for autonomous monitoring in the breeding season. The wintering season is, as far as we know, almost disregarded. Similarly, the subsampling of acoustic data in processing raises other issues. Which type and pattern of subsampling give the best cost-efficient option when analysing multi-species environments? Are these methods suitable for real and scaled surveys, where species richness is the main target? Answering these questions would help to improve current knowledge and application of autonomous acoustics in both field deployment and data processing.

This thesis aims to increase the understanding of the assets and detriments of autonomous acoustic monitoring. It also intends to improve the efficiency of manual processing of acoustic data and explore its challenges in the wintering season. Lastly, it tries to facilitate future protocol designs of autonomous acoustic methods in ecological and conservation studies.

1.5 Thesis outline

Following the introduction, this thesis is structured in three parts. In Chapter 2, we compare avian diversity data obtained through autonomous recorders and observers and analyse the impact of two factors (presence of the observer and timing of sampling) in recorder-based results. In Chapter 3, we evaluate which intermittent pattern is more cost-efficient for avian biodiversity assessments. We then compare two different acoustic file subsampling methods (continuous and intermediate intermittent). Both chapters 2 and 3 contain its objectives, hypothesis, methods, results, and discussion. Lastly, a general conclusion is provided in Chapter 4, including the relevance of our findings, suggestions on good passive acoustic practices and some final remarks.

Chapter 2 – Comparing species richness estimates between observer and recorder-based point-counts

2.1 Objectives

In this section, our objectives were to: (1) estimate and compare species richness from presence data obtained using two different methods: observer- and recorder-based point counts; (2) test the influence of the observer's presence in species richness estimates obtained from both recorder- and observer-based point counts; (3) identify changes in species richness estimates obtained from recorder data when the most acoustically active timeframe in the morning is considered; (4) analyse and compare the prevalence of each species in both methods using an acoustic prevalence index.

We expected: (1) observer-based point counts to detect more species overall because of the aid of visual cues; (2) the observer's presence to decrease the number of species detected in both methods as a result of an avoidance effect; (3) species richness estimates to improve when the most vocally active period is considered in recordings due to a higher detection probability; (4) the recorder method to detect a greater proportion of species whose identification does not heavily rely on visual cues.

2.2 Materials and methods

2.2.1 Study area

This study was carried out in Portugal, on a large farm managed by the state-owned "Companhia das Lezírias" (38º48'N-8º49'W) (***Figure 2.1***). It extends for 11,071 ha, 6100 of which are occupied by cork oak (*Quercus suber)* woodlands. These managed cork oak woodlands are agro-silvopastoral systems present in several Mediterranean countries (Pinto-Correia et al. 2011). The study area is used for cork production, extensive livestock rearing and includes pine and eucalyptus plantations, cereal fields, and rice paddies, although all sampled points were located in cork oak woodland. Sampling points were chosen following four criteria: a) cork oak density; b) cork oak age and size; c) distance to nearest sampling point; d) distance to the nearest road. Medium tree density was chosen as ideal. Adult medium-sized trees were preferred to avoid placing recorders around trunks with excessive diameter, as it would muffle the sound coming from behind them. The minimum distance between points was set as 300 m to ensure independent detections (Yip et al. 2017) and they were deployed at least 100 m from the nearest paved road to reduce exposure to sounds originating from the road. Vehicle circulation and human presence are strictly limited in "Companhia das Lezírias", so anthropogenic noise was not a concern in this study.

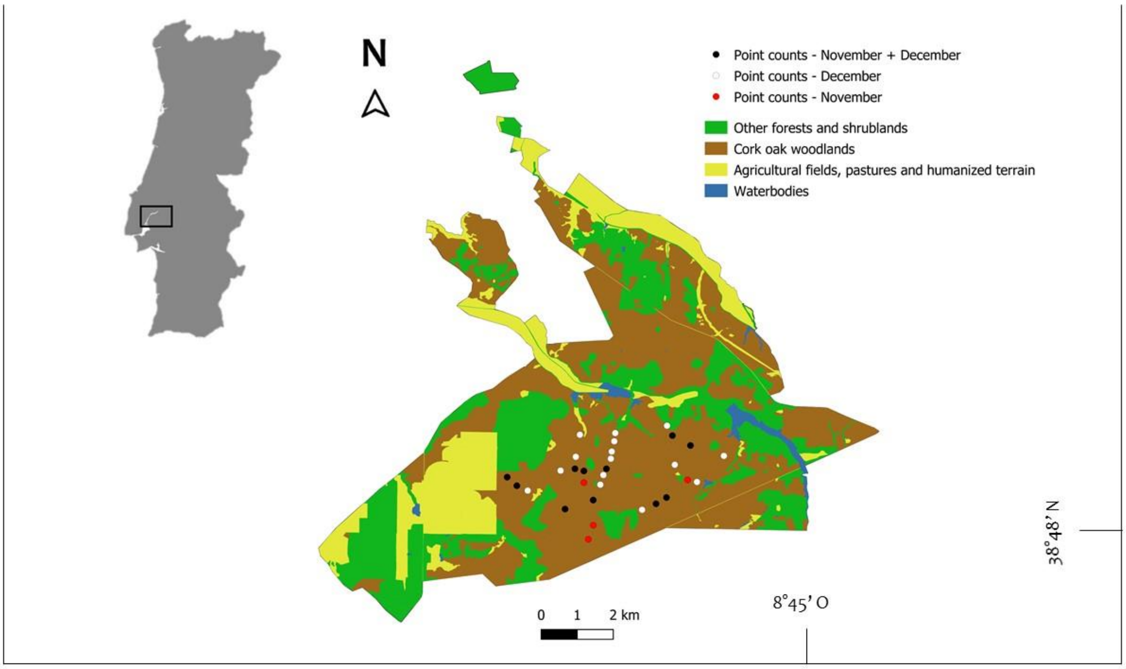


Figure 2.1 - Location and map of the study area. Black dots represent point counts that were performed two times (November and December).

2.2.2 Recorder waterproofing and battery testing

For this study, we used AudioMoth® recorders, which are small, low-cost, smart, and customizable acoustic devices (Hill et al. 2018). Battery duration was previously tested in the laboratory. Using a 48 kHz sample rate with medium gain and 5 s sleep duration every hour, we concluded that devices would be able to record a minimum of 82 consecutive hours before filling a 32 GB SD card. We waterproofed the recorders by sealing them in electrical boxes. A small hole was drilled in front of the microphone. This hole was covered with an acoustically tested 500 μ steel mesh, which proved to concede the best balance between reasonable sound amplitude and low microphone signal-to-noise ratio.

2.2.3 Sampling in the field

2.2.3.1 Recorder configuration and deployment

A total of 24 recorders were deployed from the 11 to 14 February 2020 and set to record for 4 full consecutive days. These were chosen according to their favourable weather forecast. Recorders, each representing a sampling point, were attached exclusively to cork oak trees at a height varying from 1.5 m to 2.5 m, to effectively capture birdsongs whilst keeping them secure from ground-based intrusion. They were programmed to continuously capture sounds with a 5 s sleep duration per hour, and with a sampling rate of 48 kHz and medium gain, which was considered adequate for multispecies bird sampling. The extended schedule was intended to gather as much data as possible and to store it as a permanent record for future comparisons. After the scheduled recordings, devices were retrieved, checked, and brought to the laboratory, where the audio files were analysed.

2.2.3.2 Observer-based point counts (OBS)

While recorders were actively recording, 33 ten-minute observer-based point counts (OBS) were consecutively performed at the locations where they were placed. The same observer performed all OBS. Since only 24 recorders were put in the field, the remaining nine point counts were completed in repeated locations, following a chronological criterion. All points were visited between 7h30 and 10h40, as the observer moved between points. In each point count, the observer vocally signalled the beginning of the count to the active recorder and registered all avian species seen or heard. We performed an average of 12 OBS per day, alternating the visiting order to avoid visiting locations that were too close to each other, both in time and space.

2.2.4 Data processing in the laboratory

2.2.4.1 Simulating recorder-based point counts with observer presence (WOP)

After retrieving, verifying, and storing the recorders' content, we simulated point counts in the laboratory using version 2.4.1 of Audacity® recording and editing software (Audacity Team 2021). A set of 33 recorder-based point counts with 10 min each was created. These point counts were defined as recorder-based with observer presence (WOP), as an observer performing OBS was present next to the recorder thorough their duration. The starting moment of a WOP was defined by the observer's vocal signal in the recording (visible through a spectrogram) so that both WOP and OBS represented data recorded at the exact same time.

2.2.4.2 Species identification in WOPs

Species identification was performed manually with the aid of a spectrogram by a single person, different from the one who performed the OBS. In order to minimize discrepancies in identification experience between both individuals, a set of two hour recordings from previous years and in similar habitats was used as practice. This allowed a period of trial identifications and cross corrections and aimed to reduce misidentification errors. Regarding our study's recordings, all songs and calls attributed to a species were registered. For practical reasons, signals that we were unable to identify either visually or acoustically were ignored. For a more fruitful comparison between methods and to mimic a practical time-restrictive situation, the listener was only allowed to play the audio track once. However, no time limit was determined for the processing of each point count, thus enabling careful visual interpretation of the spectrogram. The main preference settings used for species identification are presented in ***Table 2.1***.

Table 2.1 - Spectrogram visualization settings for species identification in recorder-based point counts. These refer to the software Audacity and were kept constant throughout the listening period.

Preference Type	Setting	Value/Option
Effect's preview	Length of preview	15 s
Sampling	Sample rate	44100 Hz
	Sample format	24-bit
Algorithm	Window size	2048
	Window type	Gaussian (a = 4.5)
Colours	Display gain	15 dB
	Display range	80 dB
	Grayscale	Enabled

2.2.4.3 Influence of the observer's presence in recorder-based species richness estimates

A third set of 33 additional 10 min point counts was created from recordings. These were called point counts with no observer presence (NOP). They were set as the control group and retrieved from the same sampling sites, 15 min before the other two surveys occurred, leaving a 5 min pause interval between the two groups (NOP and WOP/OBS) (see ***Figure 2.2***). This was to ensure that during NOPs no disturbance was present, while securing independence between samples. All detected species were registered.

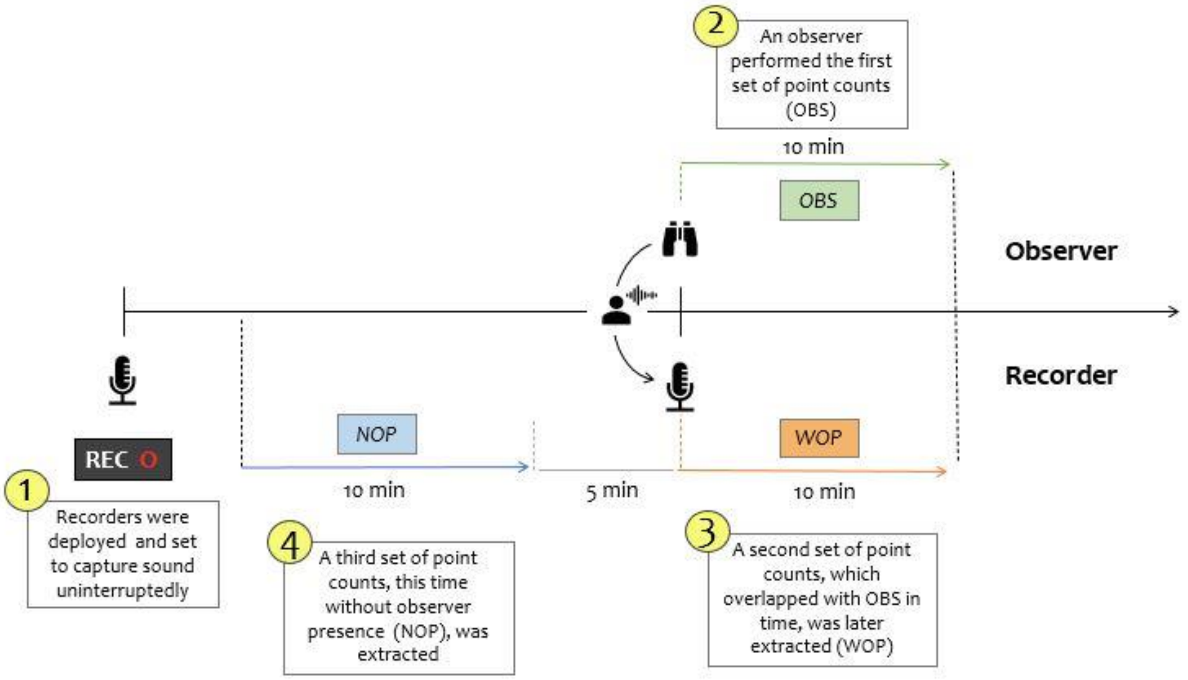


Figure 1.2 - Sampling design of recorder- and observer-based point counts of this study. The highlighted numbers display the order in which each procedure was performed. Both recorder-based point counts (WOP and NOP) were created based on the timing of the observer-based ones (OBS). The simultaneity of OBS and WOP was possible through a vocal signal emitted by the observer, which is represented by the soundwave icon in the figure.

2.2.4.4 Comparison of the observer and recorder species richness estimates using the most active avian timeframe

While an observer suffers from time-related constraints when sampling different point counts, the use of multiple recorders assists in bypassing these issues. As such, a fourth set of 33 point counts was generated from recordings. This time, all point counts started at 8h00. This timeframe was found to be the peak of avian activity in the mornings, in our study area, during the selected sampling period in winter (see ***Figure 6.1*** - Annex Section). They also lasted 10 min and followed the methodology of the points as described above. To simplify, we called them vocally active point counts (VOC). Once again, all species detected and identified were registered.

2.2.5 Statistical analysis

All statistical analysis of this chapter was performed using statistical software R version 3.6.0 (R Core Team, 2019) and Microsoft Excel (2013). To compare observer-based data with standard recorder-based point counts, and with recorder points at peak activity, we used a Wilcoxon rank-sum test. To test the influence of the observer's presence in the estimates of the recorder points, we used a paired t-test.

Regarding species-by-species analysis, we used an acoustic prevalence index (API) based on Cook et al. (2018), calculated as follows: API = number of points where the species is present/total number of points. We then performed individual Z-tests to compare API scores from recorders and observer. Only species present in at least three point counts in both methods were considered.

2.3 Results

2.3.1 Observer and recorder species richness comparison

We found a significant difference between species richness estimates from observer (OBS) and recorder-based (WOP) point counts ($W = 811$, $p < 0.05$). The observer detected on average 2.39 more species than the recorder in the same survey period, thus corresponding to a 21.64 % increase (***Figure 2.3***).

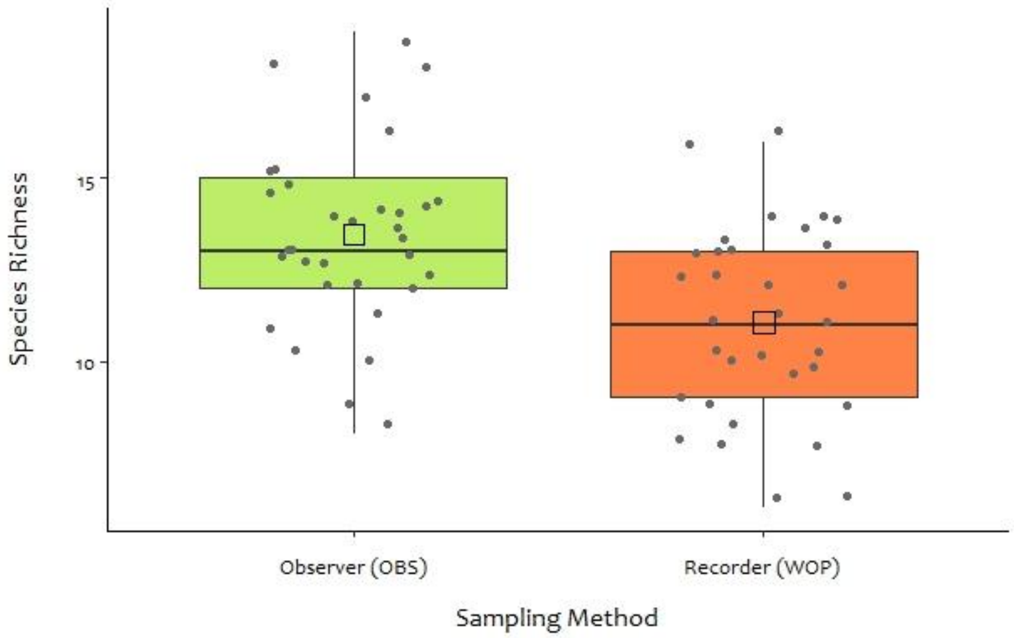


Figure 2.3 - Comparison between detected species richness in observer-based (OBS) and recorder-based (WOP) point counts. Each grey dot represents a single point count, whereas squares portray the mean values (n = 66).

2.3.2 Influence of the observer's presence in the species richness estimates of WOP and NOP

We found no significant difference between species richness estimates of recorder-based estimates with (WOP) and without (NOP) observer presence ($t = 0.223$, $df = 32$, $p = 0.825$).

2.3.3 Recorder's estimates in the most active avian timeframe

Our results showed that when only the peak timeframe of avian activity is considered (VOC), species richness estimates increase relatively to those of WOP (***Figure 2.4***). Despite this gain, differences between VOC and OBS estimates remain significant ($W = 775$, $p < 0.05$).

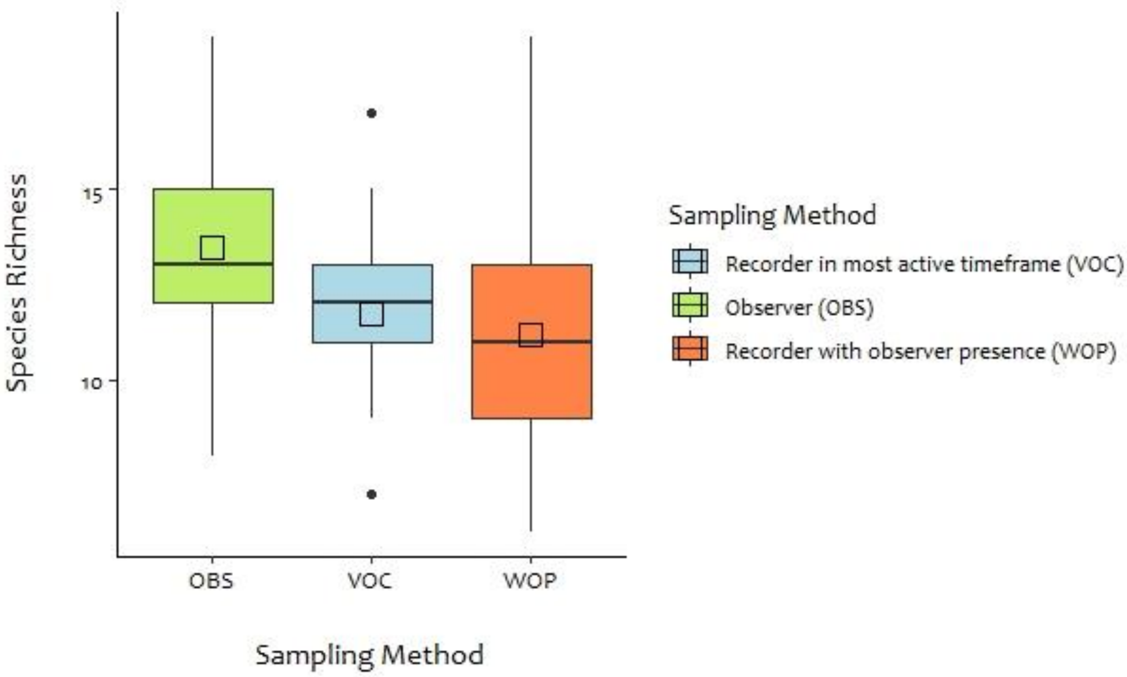


Figure 2.4 - Comparison between detected species richness of three sets of point counts (OBS, WOP and VOC). Grey dots refer to outliers and squares represent the mean values for each set (n = 99).

2.3.4 Acoustic prevalence of species in recorder and observer point counts

Our results show that most species were detected by both recorders and the observer (***Figure 2.5***). Only 3 species were detected more frequently in recorders (Long-tailed tit *Aegithalos caudatus*, Eurasian blackcap *Sylvia atricapilla*, and Cirl bunting *Emberiza cirlus*). In contrast, Common buzzard *Buteo buteo* and Meadow pipit *Anthus pratensis* showed a significant difference in detection in favour of the observer, and House sparrow *Passer domesticus*, Crested tit *Lophophanes cristatus*, and Goldfinch *Carduelis carduelis* were exclusively detected by the latter. Chaffinch *Fringilla coelebs* was the only species detected in all of the recorder and observer point counts of the study.

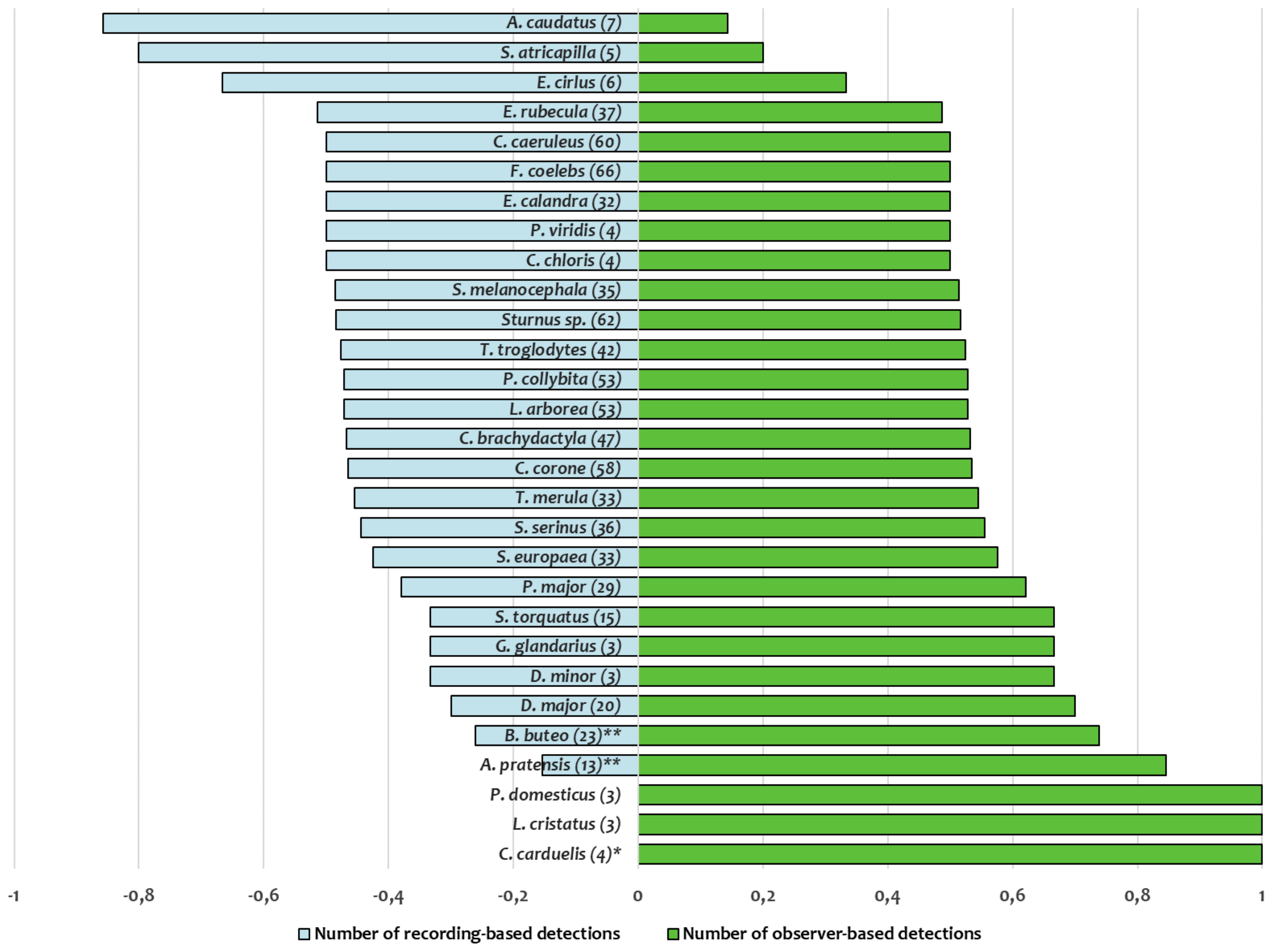


Figure 2.5 - Acoustic prevalence index (API) values of species detected in recordings and by the observer in the field. Number of detections for each species are shown in brackets. Asterisks represent significant differences between z-scores of both methods for that species. The number of asterisks indicates the degree of significance of that same difference (*$p < 0.05$, **$p < 0.01$). Species with less than three detections were excluded from this analysis.

2.4 Discussion

2.4.1 The observer's higher performance over the recorder is context dependent

Our results indicate that the observer detected substantially more species than the recorders over a ten-minute sampling period. A considerable number of studies have been focusing on comparisons of species richness estimates between observers and autonomous recorders under different conditions and constraints (see Castro et al. 2019). However, the results have not pointed to a single conclusion, thus leading to polarizing suggestions on how to apply autonomous recordings in today's standard avian acoustic sampling.

If one desires, it is possible to categorize these studies in three groups, based on their discussions and conclusions. On one hand, some studies show a higher number of species detected in observer-based sampling. This first group, the smallest of the three, collectively suggests that an observer has a few invaluable advantages over the recorder which are currently very difficult to overcome. These include visual cues, tri-dimensional sound spacing, and movement tracking, which are either impossible or difficult to obtain using recorders alone (Darras et al. 2018). Furthermore, they argue that audio file analysis in the laboratory may be too time consuming and complicated, thus not representing a viable alternative (Hutto and Stutzman 2009).

In other studies, the number of species detected by the recorder matched or even surpassed the ones detected by the observer. Here, a case is made for autonomous sampling: recorder-based files are less prone to observer bias (Celis-Murillo et al. 2009), overlooked birds, misidentification and avoidance effect (Darras et al. 2018, 2019), while reducing the expertise cost (Hobson et al. 2002). Furthermore, recorders can operate simultaneously and be scaled in space and time, thus reducing the relevance of other hindrances such as the lack of visual cues in accurate species richness estimation (Darras et al. 2019).

Finally, the middle ground between the two previous stands is represented by a third group. Here, results of recorder performance suggest this method should not be discarded in avian sampling, as it can scale monitoring in time with minimal cost. They also point out that both methods should be viewed as complementary techniques (Borker et al. 2015), and the decision of whether to use one or the other is dependent on the study's aim and specificities (Celis-Murillo et al. 2012; Klingbeil and Willig 2015; Kułaga and Budka 2019). Nonetheless, they highlight the need to adjust and improve the autonomous method and its protocols and conclude that both methods are comparable (Digby et al. 2013; Castro et al. 2019) .

Our results initially converge to the first group. The observer had visual cues and tri-dimensional sound spacing at their disposal, both of which may explain the difference in species richness values. There may have been some factors influencing our results, the first of which being the disparity of experience. At the start, the observer who performed the OBS had some more avian identification experience than the one in charge of WOP. Despite having implemented a practice stage beforehand, this might have not been enough to fully mitigate the difference, which in turn may have motivated more unidentified and misidentified sounds, particularly those of rare and elusive species. However, an additional factor may suggest a different explanation. Acoustic files retrieved from the recorders had weaker signals, with lower quality, compared to those obtained by the observer in the field. This empirical comparison illustrates a preliminary difficulty in species identification through this method and may also explain the persistence of lower species richness in recorder data. An additional aspect is the season. Our study was conducted in winter, where birds are less conspicuous, especially regarding sound activity (Robbins 1981b). As acoustic elements become less frequent, visual cues gain particular relevance for species identification. Here, the observer in is the better position. We also generally assume the detectability distance is the same for both methods (Venier et al. 2012), when it may not be true. In these situations, both distances should be calculated and potential correction factors applied for calibration (Yip et al. 2017). Lastly, a previous study suggests that fewer visits per site favour the observer (detection of silent species) (Kułaga and Budka 2019). In our study, we performed a reasonable number of point counts, albeit only two visits per site on average for each method, which could benefit the observer.

Hence, the results showed an advantage of the observer over the recorder, which signifies that some of the observer's advantages and other recorder-based hindrances limit the bonuses of using an exclusive autonomous approach. Nevertheless, this advantage may be dependent on variables ranging from sound quality and observer experience to the season in which sampling is performed. Therefore, stating that the observer has inherent advantages in all situations might not be appropriate, especially if some above mentioned variables are controllable or manageable. In the same way, recorder-based approaches should not be completely discarded, as their efficiency may increase in some contexts, e.g., if several visits are made to the same site. For this reason, further attempts should be made in other seasons with observers with a similar degree of experience and using different acoustic equipment, in order to evaluate and quantify the impact of these factors on species richness estimations. Additionally, detectability distances for both methods should be estimated to ensure they are comparable. Factors such as height, number and signal-to-noise ratio of recorders should be accounted as predictors for variability in these distances (Darras et al. 2018). Lastly, multiple visits to the same point counts must be guaranteed, as it generates better estimates and representation of avian diversity (Abrahams 2018).

2.4.2 Absence of an avoidance effect: truth or artefact?

Our comparisons between recorder-based point counts with and without observer presence revealed no significant difference in species richness estimations. This suggests that an avoidance effect is either absent or too small to be detected in our data.

The avoidance effect is thoroughly documented in the literature and happens when a bird flees in response to a predator (in this case, an observer) being too close to it. The distance at which a flight response is triggered is referred to as “flight distance” (Møller 2008a). Nonetheless, this phenomenon does not happen with the same intensity in every situation. Flight distance might vary depending on vegetation structure (Fernández-Juricic et al. 2004), degree of noise (Møller 2008b), season (Robbins 1981b), body mass (Hedenstrom and Alerstam 1992), intruder’s starting distance (Blumstein 2003) and species themselves (Møller 2008a). Birds often have a clear flight response when confronted with human presence. However, some individuals may present behavioural flexibility to fear in response to a changing environment (Carrete and Tella 2011). Accounting for this variability in flight response is important in avian sampling, as it may contribute to an underestimation of the species richness and abundance.

We believe the near absence of avoidance effect depicted in our results was closely related to the habitat type present in the sampling area. Studies have shown that the high number of obstacles to sound transmission present in forest-type habitats may cause birds to produce more efficient and longer-travelling vocalizations, extending their duration and using higher reverberation (Slabbekoorn et al. 2002; Nemeth et al. 2006). Additionally, birds adapted to these environments tend to produce songs with lower frequencies, lower frequency ranges and longer inter-element intervals than their counterparts in open habitats (Boncoraglio and Saino 2007). Consequently, these sounds suffer lower attenuation (Morton 1975) and are easier to perceive by human ears. If we further assume there is less wind acting as an obstacle in a forest, one may acknowledge it is possible to hear sounds coming from distant sources. This amplifies the pool of individuals heard in a single point count. From a species richness perspective, when no individuals are counted, one may miss a given species which is singing relatively close but compensate it by hearing another individual singing from a more distant point. Hence, even if the closer bird fled, a further one will result in the same outcome. Additionally, such vegetation structure causes visual obstruction, which can also reduce the intensity of the flight response (Fernández-Juricic et al. 2002). However, should the habitat be a decisive factor, this degree of disparity in results between observer and recorder would rather be expected if sampling occurred in extreme habitat types in terms of vegetation (e.g. open plain and dense forest) (Kułaga and Budka 2019), which is not the case. It is also worth mentioning it is not known whether such degree of avian sound adaptations exists in birds occupying temperate woodlands.

In light of these results alone, elaborating a definitive conclusion on the complete absence of an avoidance effect does not seem clear cut. A more extensive analysis would be necessary to determine whether this effect is truly not taking place or if the forest-type habitat counterbalances it by providing visual shelter for both the observer and the birds, while incorporating better sound efficiency. Nonetheless, and following the results of Darras et. al (2018), our data suggests avoidance was not an issue, which in itself may bring some enlightenment on why species richness in observer-based point counts remains higher than in recorder ones. It should also be noted that we interpreted the presence of this phenomenon through species richness values, which may not be representative of the phenomenon's complexity. We encourage further studies to explore avoidance effect intensity in different habitats, using abundance or density as measurement. We further suggest a species-by-species analysis in different forest-type habitats to determine the differential impact of sound transmission and flight responses in point count efficiency.

2.4.3 Autonomous sampling during the most active period is a better, albeit not an ideal, solution

Focusing autonomous sampling on the most active timeframe in the morning improved species richness estimates of the recorder. The higher number of vocally active species and individuals in this period (Robbins 1981a; Farina et al. 2015) may explain why more species were detected within the same 10 min of sampling than when sampling periods were scattered throughout most of the morning period. Additionally, this approach reduced the variance of these estimates. The fact that more species are present and vocalizing at the same time grants more vocal elements that serve as reference to differentiate species acoustically. Therefore, having a substantial proportion of conspicuous species present at the same time and reducing misidentifications may have resulted in an improved and more robust estimate of species richness.

Nonetheless, despite the increase in species richness estimations relatively to WOP, they remained significantly lower than those of the observer. In other words, the observer detected more species than the recorder, even when the latter retrieved acoustic data during the best period at the same locations. This result contradicts our initial predictions and in our eyes is somewhat surprising. If we assume the observer was exposed to a lower number of species than the recorder in VOC, with all the benefits that manual species identification in the laboratory include, one would expect a closer species richness value between the two. However, the results did not accompany these predictions. We thought of several explanations that could justify our results, all of which follow the same reasoning: if the observer keeps detecting more species than the recorder, it is due to either human or non-human advantages.

Firstly, recorder-based estimations may have suffered from the equipment itself. Although further tests are needed to assess its true relevancy, AudioMoth® recorders were invariably limited by their default microphone's quality and sensitivity, parameters which should be considered in this type of sampling (Turgeon et al. 2017; Yip et al. 2017). At the time of the study, AudioMoth® Dev recorders (https://www.openacousticdevices.info) were not available, thus precluding the integration of more sensitive microphones. It is possible that some species had "escaped" the recorder for this very reason.

Secondly, season may have affected recorder performance. In temperate regions of the northern hemisphere, where our study area is located, birds tend to be less active during winter (i.e. vocalize less), in that it's not breeding season and active territory protection is less acute (Paruk 2018). Additionally, steady rain and strong wind, which are common during this time of the year, have a profound negative effect on sound transmission and bird behaviour (Robbins 1981b). Therefore and comparing to a similar situation in spring, there is a lower number of aural clues for the person analysing the recorder files to identify all species. In this context, not only the recorder presents its drawbacks, but the observer also gains an edge. As avian vocal activity goes down, visual cues gain relevance for species identification (Yip et al. 2017), offering a clear advantage to the observer. Lastly, harsh weather conditions during winter often delay the dawn chorus, causing bird activity to reduce in intensity but extend in time (Robbins 1981b, a).

In the end, do our results demonstrate that the observer will always detect more species than the recorder and therefore is the better method? We do not believe this is the case. This comparison suggests that centring autonomous sampling in the best period in the morning is an effective tool to yield better and more robust species richness estimates. We think that the difference would be more noticeable if the total number of points sampled was higher. As to whether VOC estimates will match or surpass those of an observer, we believe it is dependent on the equipment and season in which sampling is performed. In this section, we aimed to explore the potential of synchronized recordings (i.e. recordings performed in different locations at the same time) which is one of many features that differentiate autonomous and traditional methods. We admit some of these other features may be more efficient at improving species richness estimates for recorders than the one we used. For further studies, we recommend testing microphones with varied degrees of sensitivity, while comparing species richness between autonomous and observer-based methods in migration and breeding season. We also advocate for the need to register the proportion of exclusively visual detections done by the observer, if their number is relevant, in order to monitor the impact that visual cues have on recorder estimations.

2.4.4 Recorders and observer: comparable for most, contrasting for some

Following our previous attempts at defining the factors that drive higher species richness in observer point counts, the species-by-species analysis revealed one dominant pattern: most species were detected by recorders and the observer in a similar number of points. This is relevant for it means that in our study area, most species could have been detected using autonomous recorders alone. The same conclusion prevails in other studies (e.g. Celis-Murillo et al. 2012), with estimations ranging from 56% of species in peatland meadows (Kułaga and Budka 2019) to 80% of species in riparian habitats (Celis-Murillo et al. 2009). Klingbeil and Willig (2015) found that both recorders and observers lead to similar results in terms of species composition and detected no differences in alpha or beta diversity between traditional surveys and automated recordings. Additionally, Celis-Murillo et al. (2012) identified a 92–100% level of similarity between both methods in determining species composition, across three types of vegetation structure. If we further account for the findings of a meta-analysis on overall recorder performance (Darras et al. 2018), we should be able to predict that recorders can in most cases detect a similar number of species as observers. This is especially relevant regarding our season of sampling: it was expected that due to lower vocal activity, recorders would not detect as many species as the observer in winter, which was not the case. In our case, the reasons behind this trend are difficult to retrieve and we would need a deeper analysis in correlating the biology of each species and equipment variables (such as microphone sensitivity and detection distance) with their overall detection. Nonetheless, this pattern may be due to a handful of reasons. Firstly, factors such as visual cues, overlooked birds or avoidance effect tend to have less influence on species richness estimates as detection distances of both methods become equivalent (Darras et al. 2019). Secondly, the difference in the number of species detected by both methods is habitat-dependent and less pronounced in forests. Lastly, most species that are targeted by point count surveys are easier to detect by both methods, as they have small to medium-sized territories and often defend them through vocalizations, thus being constantly present in the sampled area (Kułaga and Budka 2019). Since calculating detection distances for each species and defining an average detection distance for the equipment is difficult (Celis-Murillo et al. 2009), along with the absence of open-type habitat data in our study and our focus in the wintering season, it becomes clear that further investigation is needed to assess the validity of these possible explanations.

Moreover, some species appear to show differences in recorder and observer-based detection. On a more general note, these are normally due to discrepancies in species identification in the laboratory and in the field (Celis-Murillo et al. 2009), habitat-related variables (Kułaga and Budka 2019), difficulty in assessing true detection distances for each species when song amplitude data in not available (Shonfield and Bayne 2017), number of visits per site (Klingbeil and Willig 2015), bird behaviour, characteristics of vocalization, species richness, sample size, study design or recording system (Celis-Murillo et al. 2012). In our case, the disparity may result from two factors which were not specifically monitored: detection distances and equipment sensitivity. Autonomous recorders have typically smaller detection radiuses than observers (Yip et al. 2017), although they can improve with recorder height (Castro et al. 2019). This could have impacted the detection of birds vocalizing from a more distant position, such as buzzards and woodpeckers. The exact spot where recorders are placed also seems to influence detection, along with the sound filtering ability of humans, which allows us to move our heads in the direction of the acoustic signal (Castro et al. 2019). This could have been relevant since our microphones were not entirely omnidirectional. Finally, Yip et al. (2017) showed microphones can be more or less attuned to different frequencies, which in turn affects detection probability of a certain set of species.

Nevertheless, some species were almost exclusively detected by one of the methods. Regarding recorder-dominant detections, species such as the Cirl bunting do not typically sing during the main segment of the dawn chorus in our study area. Hence, they may have been more easily ignored by the observer (Darras et al. 2019) and benefited from spectrogram analysis, which reduces overlooked birds (Darras et al. 2018). The Cirl bunting in particular does not sing frequently, and species with scarce vocalizations are favoured by the recorder (Celis-Murillo et al. 2009). The Long-tailed tit is in our view an interesting example, for its call, similar in frequency to that of the Goldcrest *Regulus regulus*, may not be heard by a fraction of the human population (Tucker et al. 2014). It is possible that spectrogram visualization may once again have given an anticipation advantage to the recorder (Darras et al. 2019). Indeed, overlooked birds and misidentifications are two frequent explanations for this type of pattern (Hutto and Stutzman 2009).

In observer-dominant detections, species such as the Meadow pipit, both woodpeckers and the Common buzzard apparently pose the same type of challenges to the recorder. Their detection relies heavily on visual cues, and because they have larger territories and tend to vocalize from more distant positions, they may be too far for the recorder to capture a reliable signal (Hutto and Stutzman 2009). Other studies have reinforced this hypothesis, with woodpeckers being more difficult to detect when no additional visits are performed, and the detection of birds of prey, along with crows and ravens, also depending greatly on visual cues (Celis-Murillo et al. 2009, 2012; Klingbeil and Willig 2015; Kułaga and Budka 2019). Conversely, smaller birds with equally smaller-sized territories, such as chaffinches and flycatchers, tend to be more present in recorders (Celis-Murillo et al. 2009; Klingbeil and Willig 2015).

Overall, our results supported the concept that unless we are dealing with adverse or specific conditions in a study, recorders detect most of the species present in a given area, even in wintering season. Furthermore, the species composition between recorder and observer data is roughly the same. Some bigger species with larger territories tend to be omitted by the recorder, whereas smaller passerines with high frequency songs and calls can be overlooked by the observer. It is nonetheless difficult to support a reliable conclusion on these species, as the number of point counts in which some species were present is too low and can act as a confounding factor. Further studies should account for this problem by maximizing the number of performed point counts. Moreover, testing and adjusting microphone sensitivity along with calculating detection distances according to the species and equipment involved should provide more insight into which species are at risk of being ignored by each method.

Chapter 3 – Subsampling of acoustic data: intermittent versus continuous approaches

3.1 Objectives and hypothesis

In this section, we aimed to: (1) compare three types of intermittent subsampling (short, intermediate, and extended) of recordings to evaluate the cost-efficiency of species richness estimates; (2) compare the intermediate subsampling type with a continuous one, also using species richness as an indicator.

We predicted that the intermediate sampling type will be the most efficient, meaning it would yield good species richness estimates with a substantial decrease in processing time. We also expected this same intermittent sampling type to yield better species richness estimates than the continuous approach in accordance with Cook et al. (2018).

3.2 Materials and methods

The sampling for this chapter was performed in the same study area (see section 2.2.1) and using the same materials and methods (see section 2.2.2) as the ones described in Chapter 2. For this set of experiments, 26 recorders were deployed from the 6 to 11 November 2019, set to record for four full consecutive days with the settings described in Chapter 2, and retrieved for further analysis in the laboratory. Because of time-related constraints, only six recorders were selected from the original 26 for later analysis. This selection process was based on ensuring an even spatial coverage of the study area. Thus, the subsequent processing analyses in this section are exclusively related to acoustic data from the six selected recorders.

3.2.1 Data processing in the laboratory

3.2.1.1 Intermittent subsampling

We generated three types of intermittent subsampling using the software Audacity (https://audacityteam.org). Firstly, we isolated the most active avian period in the morning (7h30–9h30) (see ***Figure 6.1*** – Annex Section) in the data collected from all six recorders. Then, we segmented these 2 h into 10 s fragments. Lastly, we established the intermittent subsampling types:

- In the first type (A), we considered the first 10 s of every minute of recording;

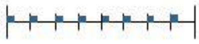
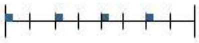
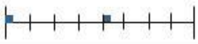
- In the second one (B), we considered the first 10 s of every two minutes of recording;

- In the third one (C), we considered the first 10 s of every four minutes of recording.

This means that for types A, B, and C we examined a total of 120, 60, and 30 fragments of 10 s recordings, respectively (***Table 3.1***). Accordingly, types A, B, and C accounted for a total accumulated listening period of 20, 10, and 5 min, respectively. In each of them, all species detected and identified in each fragment (by either listening or spectrogram visualization) were registered.

Species identification procedures and visualization settings were equal as those described in the previous chapter (see section 2.2.4.2).

Table 3.1 - Description and schematization of the three intermittent subsampling types created in the study. Sets of two hour-long continuous recordings (7:30-9:30) were used as base, from which all types of subsampling were cropped. Total fragment and listening period values presented below are relative to a single two-hour period.

Type of Intermittent Subsampling	*Subsampling pattern*	*Total fragments*	*Total listening period*
A - Short	10 s of every 1 min 	120	20 min
B - Intermediate	10 s of every 2 min 	60	10 min
C - Extended	10 s of every 4 min 	30	5 min

3.2.1.2 Continuous subsampling

As mentioned before, a comparison between the intermediately spaced subsampling type and a continuous subsampling approach was also performed. For this, we extracted and isolated 10 min of continuous recording from the most active timeframe (8h00 to 8h10) from the same six recorders. All species detected were registered following identical procedures (see section 2.2.4.2).

3.2.2 Statistical analysis

To compare the species richness estimates obtained through each intermittent subsampling type, we used sample-based rarefaction curves, first obtained in Past 3.26® (Hammer et al. 2001) and then graphically improved in Microsoft Excel (2013). To compare intermittent and continuous approaches, we graphically compared the sample-based rarefaction curve of the continuous method with the maximum average species richness estimate of the intermittent type

3.3 Results

3.3.1 Comparison between intermittent subsampling types

The rarefied species richness curves revealed a higher number of detected species with method A, followed by B and C. These differences became more evident as the covered period extended, as exemplified in the data of one of the recorders (***Figure 3.1***). Both of these patterns were detected across all six recorders (***Figure 6.2*** – Annex Section).

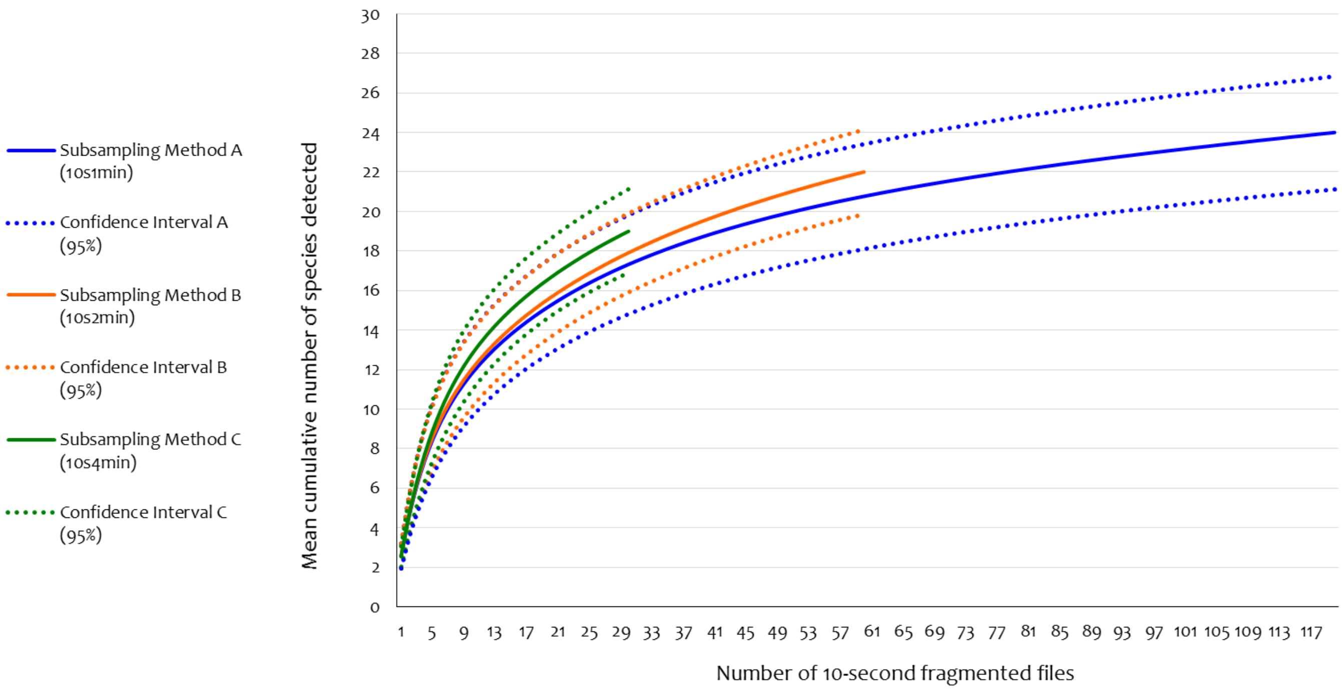


Figure 3.1 - Rarefied species richness curve for three types of intermittent subsampling methods. These curves are relative to one of the six recorders, and is shown as an example of the most common pattern found across all analysed recorders (for the remaining ones see Figure 6.2 in Annex Section). Despite the fragments being evenly distributed along the two hour period, the visual representation of the rarefaction curves was condensed in order to allow better understanding of the ratio between gained species and number of analysed files for each method.

When the average maximum number of species is compared between methods, the gain in species is higher (about 4.5) from types C to B (26.73%), than from B to A (about 2.5, with an 11.72% increase) (***Figure 3.1***).

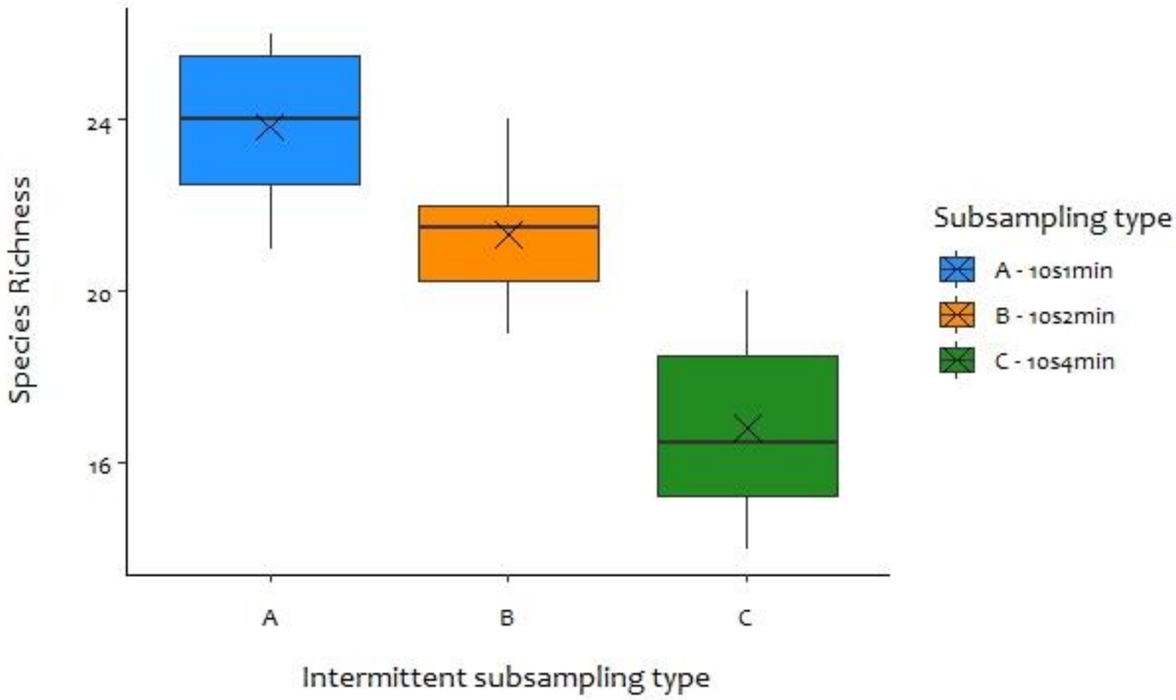


Figure 3.2 - Comparison between the average maximum values of species richness detected in three intermittent subsampling types. The X symbol represents the mean values for each type.

3.3.2 Intermittent versus Continuous approach

We found that the number of species detected by the intermittent and the continuous approach was different and higher for the intermittent. Our result showed that approximately 5.5 more point counts of 10 continuous minutes are needed to detect the average maximum number of species detected by a single 10 min intermittent point count (***Figure 3.3***)

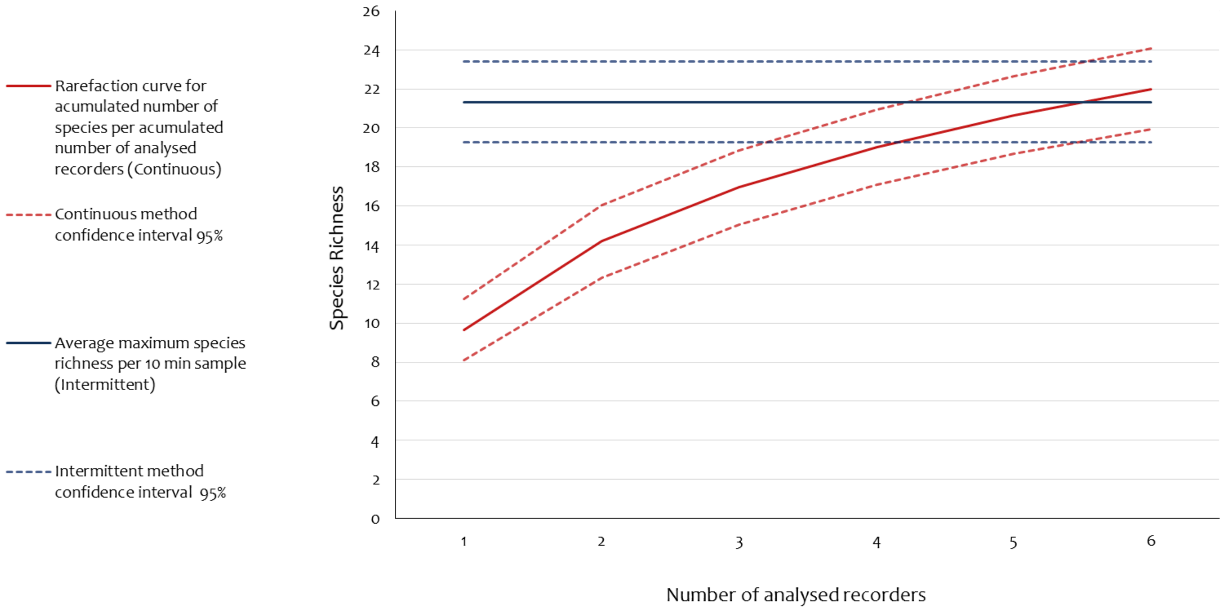


Figure 3.3 – Comparison of species richness between continuous and intermittent approaches. The red lines represent the accumulated number of species detected in 10 min sets of continuous recording, from 1 to 6 recorders. The blue lines mark the average number of species detected in one recorder, using an intermittent approach.

3.4 Discussion

3.4.1 Degree of intermittence in subsampling revolves around study design

In this section, we attempted to explore in more detail the intermittent form of subsampling, applied by Cook et al. (2018), in which only a fraction of each continuous segment of recording is analysed. Although the above mentioned study presented encouraging results, the authors only addressed one type of intermittent subsampling (10 s every 1 min) from a 30 min base sample. Here we compared three types of intermittent subsampling (short, medium, and extended) over a 120 min base sample.

After drawing the extended rarefaction curves for each type, we noticed two parallel patterns across all recorders. Firstly, as intermittent spacing becomes more extended, the rate at which new species are detected per 10 s of processed audio file increases. In other words, we registered more species per aural unit of time in the 10 s per 4 min (extended - C) type than in the 10 s per 1 min format (short - A). This would suggest that the more we space our segments thorough a two-hour period in the morning, the greater our benefit/cost rate in obtaining species richness data. This was expected and is consistent with species diversity and vocal turnover rate in the dawn chorus (Robbins 1981a, b; Kunc et al. 2005; Avey et al. 2008; Farina et al. 2015). It can be primarily beneficial in studies where field sampling time is the main constraint and only the most common or vocally active species are the target. For the remaining ones, identifying all species in a given area may be of greater importance, making time-related gains secondary.

Secondly and most importantly, the average gain of species in the two-hour period is not homogenous across all methods. Switching from short to medium intermittent format decreases species richness by 11.7%, whereas opting from medium to extended further decreases it by 26.7%. A first glimpse at these results would alert about a greater number of ignored species when audio segments are too widespread, meaning an intermediate format would allow a solid species richness estimation at a reasonable time cost (which was our initial prediction). However, we believe both methods B and C, intermediate and extended respectively, can be adequate for species richness sampling, depending on the study's goals and design.

If we assume the two-hour period after sunrise to be ideal for multispecies sampling (Robbins 1981a; Ralph et al. 1995; Farina et al. 2015), then the primary question should be: how to best allocate the audio file hearing time during this period, in order to maximize species detection and reduce time consumption? On one hand, in studies that focus on larger areas, opting for an extended version of intermittence would magnify the species detected/time spent ratio, and allow more acoustic stations to be deployed and analysed. On the other hand, choosing and intermediate type of intermittence would be more beneficial if one aims to sample small areas and/or species with reduced distributions and erratic vocal behaviours. Not needing to scale acoustic points in vast areas means more time can be spent at each recorder, resulting in greater species richness values.

In summary, we have demonstrated how breaking long continuous audio files into smaller fragments is beneficial for the rate at which new species are detected. While these results promote the usage of intermittence, the optimal time interval between fragments may be dependent on the study design and sampled species. It is also important to note that in order to compare these types of intermittence we used a "fixed sampling time" rule, which means two hours of continuous sampling were the foundation to create all types. It is possible that evaluating their efficiency would be favoured if a "fixed hearing time" rule was added, to appraise how species richness curves behave when all three have been granted the same total hearing time. We thus encourage further studies to model the efficiency of different types of intermittence, using vocal activity rate (Pérez-Granados et al. 2019) and sampled area as potential predictors. We also suggest a comparison with fixed hearing time to improve the quality of the comparison between them.

3.4.2 Intermittence surpasses continuous files: "snapshots" give a better representation than a continuous recording

The attempt we made at comparing species richness estimates obtained through 10 min of continuous and intermittent subsampling was driven from two factors, both mentioned in Cook et al. (2018): 1) the decreasing independence of two calls when these are recorded closer to each other in time; 2) the idea that sampling from a more extended period, for the same total intensity, might produce better results. The results confirmed our predictions: we would need an average of 5.5 continuous blocks of 10 min to match the species richness value of a single 10 min intermittent one. We highlight two comparison values in particular. Firstly, the average number of species detected in one continuous block (n=10) is more than two times lower that of an intermittent block (n=21). Secondly, the above mentioned 5.5 fold increase in listening time (in continuous subsampling) is necessary to match the values of one intermittent block. The patterns we found not only converge to the results of Cook et al. (2018), but also surpass them in intensity. These authors detected a 25% increase from continuous to intermittent subsampling in one sample/block (compared to our near 200%) and a 2.5 fold increase in continuous subsampling listening time to reach the intermittent subsampling (compared to our 5.5 fold).

We believe the reason behind this general pattern, also found in studies applying subsampling to time of day (La and Nudds 2016) and efficiency of shorter recordings (Thompson et al. 2017), is the same as depicted in Cook et al. (2018): hearing smaller and spaced segments of audio instead of a continuous recording reduces false-positives in identification, ensures calls are more independent and generates a higher species detection rate. However, the expanded intensity of this pattern in our case may be due to differences in temporal resolution. As mentioned by Cook et al. (2018), the pattern demonstrated in their study was a finer temporal version of the one that La and Nudds (2016) found. Our results exhibit the increasing benefit of intermittence when longer temporal scales are considered. Cook et al. (2018) used 5 min blocks from a 30 min recording retrieved from 8h00-8h30, whereas we used 10 min blocks from a 120 min recording retrieved from 7h30-9h30. Addressing longer timeframes often means dealing with species with differential vocal rates, but finding them requires more spread out sampling designs in terms of time, which is significantly more difficult when using continuous recordings. Nonetheless some level of intermittence always seems to be valuable when species richness is needed, whether it is in full day, morning or 1 h after sunrise sampling sessions.

All results of studies comparing these two subsampling strategies, including ours, point to a single direction: for the same amount of hearing time, intermittent subsampling is a much better alternative to continuous ones. Indeed, for a fast and reliable inventory, processing small “snapshots” of the species present at different times gives a much more representative image of the community than analysing big portions of audio. Yet, one of the main questions that persist is if this pattern changes when non-standard inventories are performed. Aiming at nocturnal birds or birds with restricted distributions and/or specific behaviours that make their detection difficult may require this method to be adapted, and thus we suggest further investigation on this matter.

Chapter 4 – Conclusions

4.1 Relevance of our findings and main key points

Avian sampling and birds in general have always been a structural part of biodiversity assessments and long term monitoring programs. In recent years, bioacoustics has emerged as a promising new tool for a number of bird-related topics and data collection, such as species richness, abundance, territory size, occupancy modelling, acoustic behaviour and even phenology (Darras et al. 2018). However, the use of autonomous recorders poses a number of difficulties and factors such as the equipment, weather conditions, human skillset, bird behaviour, sampling design and study objectives that seem to influence their efficiency. Despite a number of previous studies evaluating the performance of recorders under numerous conditions, the literature does not show unanimous conclusions on this matter, which in itself is an obstacle for the creation of standardized protocols.

In this study, we aimed to clarify the impact of a variety of elements related to bird sampling on the efficiency of autonomous recorders, using species richness as an indicator. We began by exploring how species richness values varied between traditional and autonomous methods. We then engaged in a finer scrutiny on factors that could explain the results of this comparison, such as time of sampling and avoidance effect. We subsequently performed a species-by-species analysis to improve the resolution of the comparison, while looking for different patterns of under and overrepresentation of species in each method. In the second part, we addressed subsampling of audio files and how they could improve manual listening and species richness estimations. First, we evaluated different types of intermittent patterns and then we compared intermittent to continuous subsampling methods.

The entirety of these experiments, along with their results and comparison with current literature, allowed us to highlight some key points that stand out from our study that we list below:

1. Recorders perform well overall, even in winter. Most of the species present at the study area were detected by both methods, which was also the case in similar studies. However, we present the first evidence that records perform well in wintering season in this region. Furthermore, multispecies surveys with morning sampling strategies seem to be a good fit for autonomous recorders in this type of habitat.
2. Observer is still relevant. Recorders can match the observer species richness values, but human filtering ability combined with visual cues may be crucial to detect certain species in habitats with little or no visual shelter.
3. Avoidance effect should not be a huge problem. However… this may be dependent on the habitat. Despite several examples of studies comparing observers and recorders, only a small proportion of them measured their performance simultaneously. Behavioural habituation to humans and vegetation structure may influence avian flight distance. Hence, absence of an avoidance effect should not be always assumed *a priori*.
4. Time of sampling matters. Depending on the target species, allocating hearing time in the most profitable time period in terms of vocal activity is beneficial. Allowing simultaneous recorders to gather data from several locations at the best hour may save time and improve species richness estimations.
5. Intermittence is the answer. Following the combination of results on this matter, we firmly believe that opting for an intermittent subsampling strategy for long acoustic files is nothing but favourable for species richness estimations. Intermittence reduces listening time and gives a more complete picture of the avian community.

4.2 Suggestions on good practices using autonomous recorders

After the set of "take-home messages" listed in the point above, we believe we have learned enough through this process to leave some suggestions regarding autonomous recordings. Whether those derive from our clear results, our extensive literature review, slight trends or things we could have improved, we consider that all of the following ideas could help future studies, researchers and environmental technicians to improve the efficiency of their autonomous bird sampling:

1. Define and understand your target species. Knowing the general activity pattern and vocal timing in particular of your target species is an advantage in autonomous recordings. If your aim is species richness, being able to isolate a timeframe where most of your species of interest are active allows you to better concentrate your sampling effort.
2. Account for erratic vocal behaviours. If you are aware of the presence of species with erratic vocal behaviours in your study area, make sure you adjust your sampling strategy. Rare, silent, marginally distributed or overall hidden species may be detected faster if the methodology acknowledges their unusual patterns.
3. Trust the recorders but take season into account. Despite the encouraging results we have found, breeding and wintering season are not the same, both ecologically and acoustically. Maximize efficiency by balancing dawn chorus duration, intensity and diversity with your survey's goals. Short dawn choruses, rich in species, demand a different approach than long ones with slow species turnover.
4. Set up a practice stage beforehand. The degree of difficulty in species identification by sound is generally hard to evaluate prior to a sampling session. Since the autonomous method calls for a different set of abilities by the researcher, one must ensure the level of experience between all people engaged in a given survey is roughly similar. Contrary to traditional methods, recorders do not require high level of experience, thus a practice stage should be sufficient to mitigate most biases.
5. Measure microphone sensitivity. Different microphones react differently to high and low frequency ranges of sound transmission. This means some species may be consistently over or under looked by a given recorder. Be sure to check the quality and settings of your microphone, and make any adjustments you see fit.
6. Calculate detection probabilities for each species… if you can. This can be both a daunting and an essential task: daunting if you are reaching for species richness in a diverse environment, but essential if you are dealing with abundances. Counting individuals using sound alone and without any visual cues is very challenging. A few indexes have been proposed to infer or even calculate densities through sound, yet most of them require calculated detection distances in order to assess how far a recorder can register a given individual of that species. If it is possible, we greatly encourage to combine sound amplitude at the source (bird) and microphone capabilities to establish an effective radius of detection for each species.
7. Use intermittent subsampling. As mentioned above, intermittence has yielded surprisingly positive results in time saving and species richness estimates. Space your listening segments along the sampling period to obtain a more complete picture of the species present at a given site. You may want to increase listening time at few locations, or scale into more locations. The way you space it is up to you and your needs. Either way, intermittent subsampling has shown to generate an interesting outcome and will certainly help through the sampling process.

4.3 Final remarks

There has been an alarming decline of biodiversity around the world in recent years (Butchart et al. 2010; Cardinale et al. 2012). Birds in Europe are a good example of this pattern, as the abundance of native breeding birds has declined 17-19% since 1980 (Burns et al. 2021). A significant proportion of these losses represent agricultural birds, which suffer greatly from fallow land reduction in Mediterranean countries (Traba and Morales 2019). Thus, there is an increasing need to improve rapid and effective tools for biodiversity assessment, especially regarding temporal and spatial scaling. Our study was focused on one of these tools, autonomous recorders, and in cork oak woodlands, which are a sensitive habitat that require balanced human management to retain its biodiversity (Pinto-Correia et al. 2011). By combining these two factors, we hope to have contributed for a better understanding of how to better apply this innovative technique in semi-agricultural ecosystems all year long. We also feel confident that this study represents more than just a step forward towards the refinement of a promising method, since its standardized application through adjusted protocols could revolutionize the way we hear, perceive and study bird communities in all their complexity.

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Chapter 6 - Annex Section

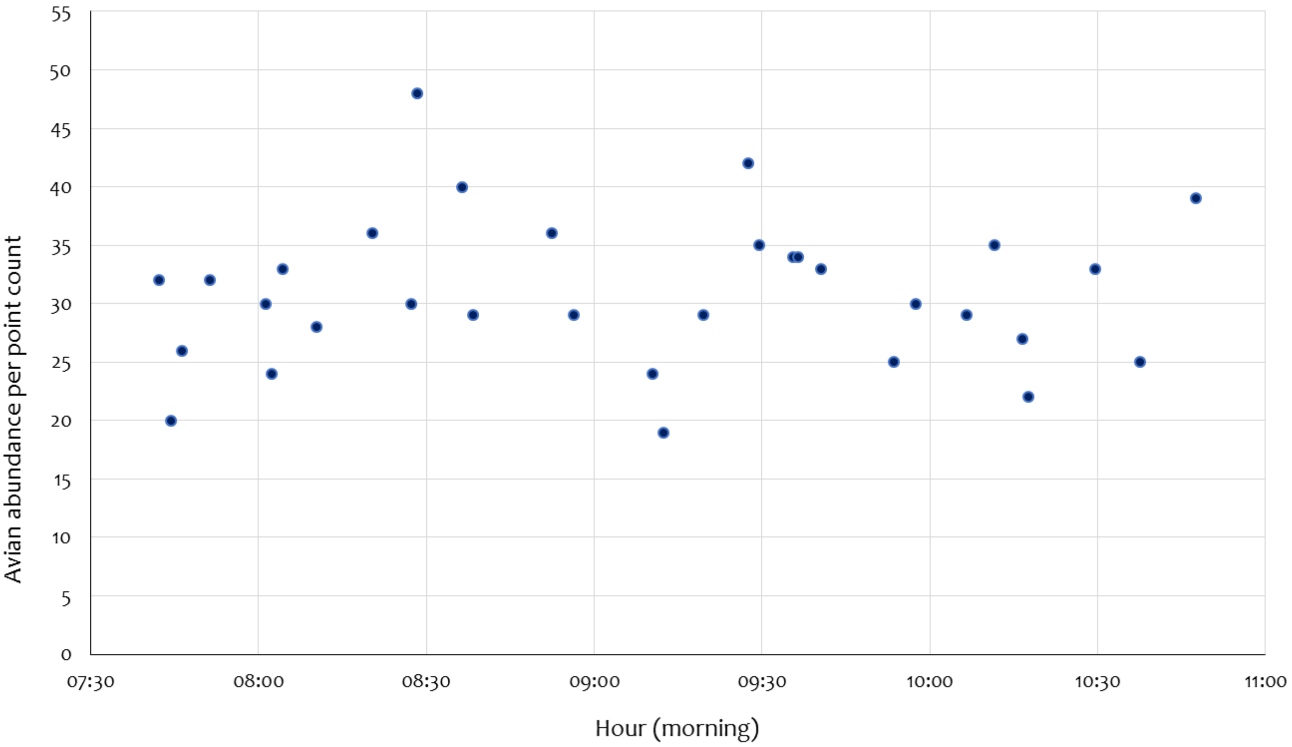
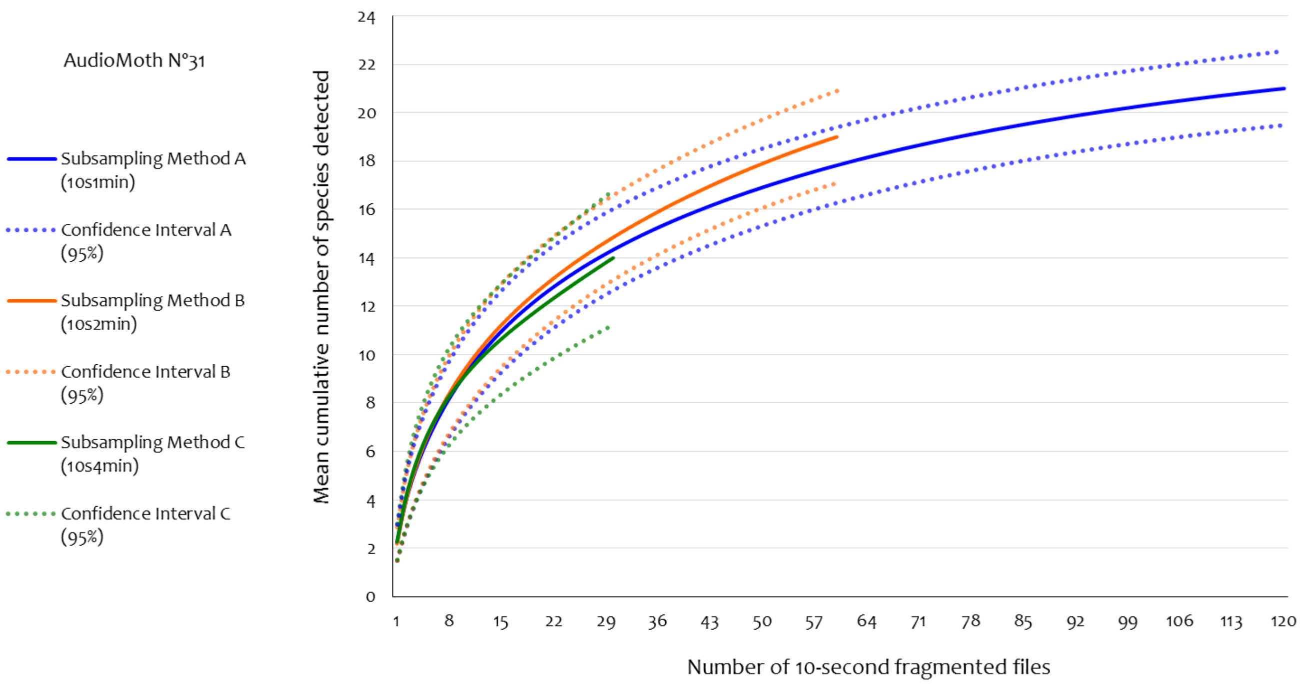
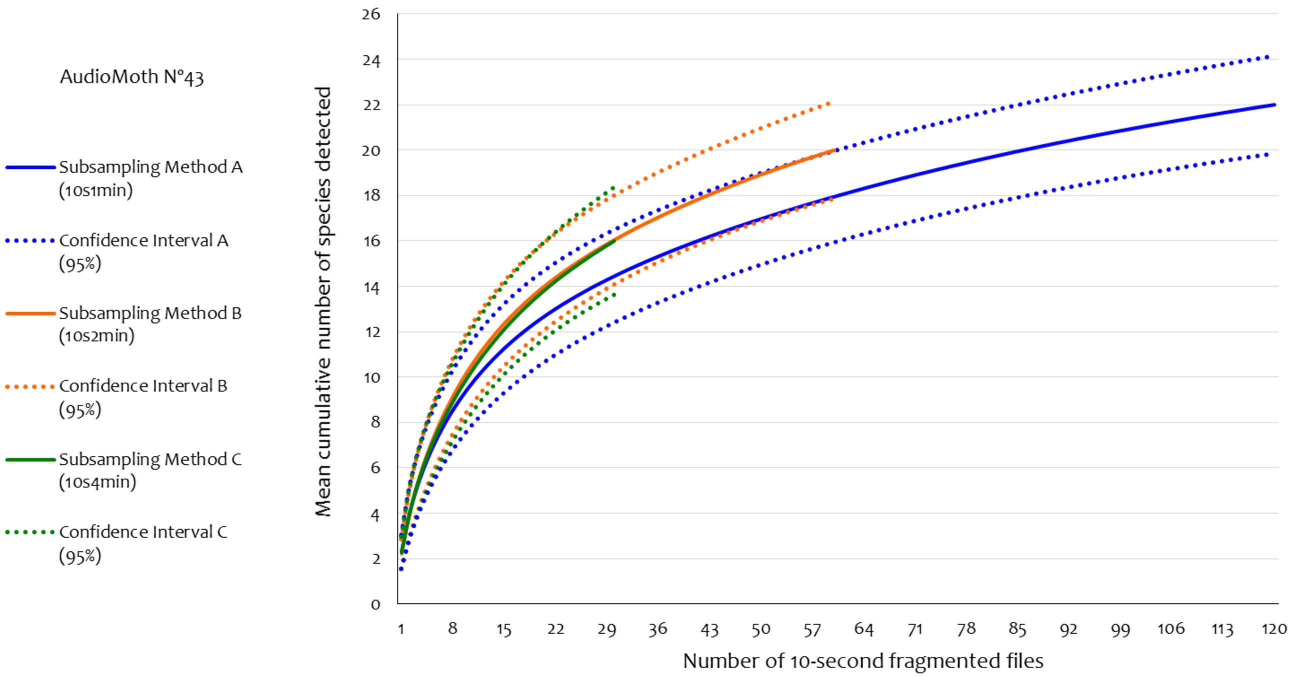
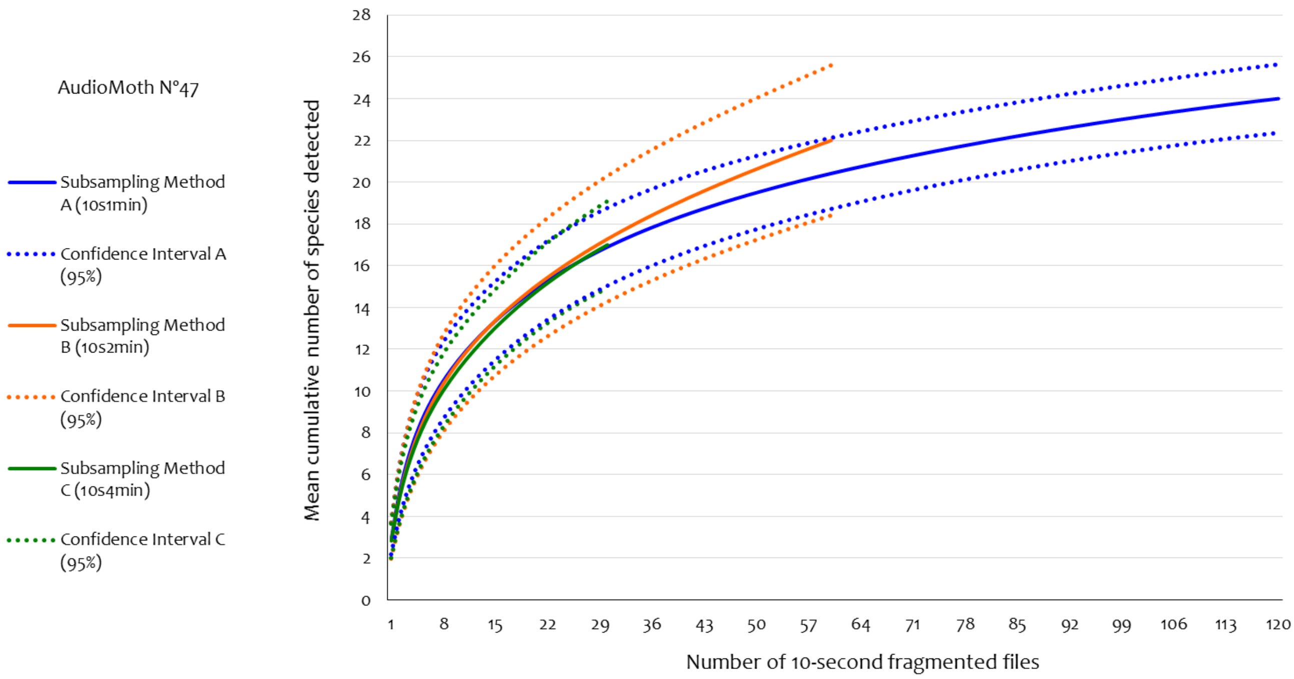
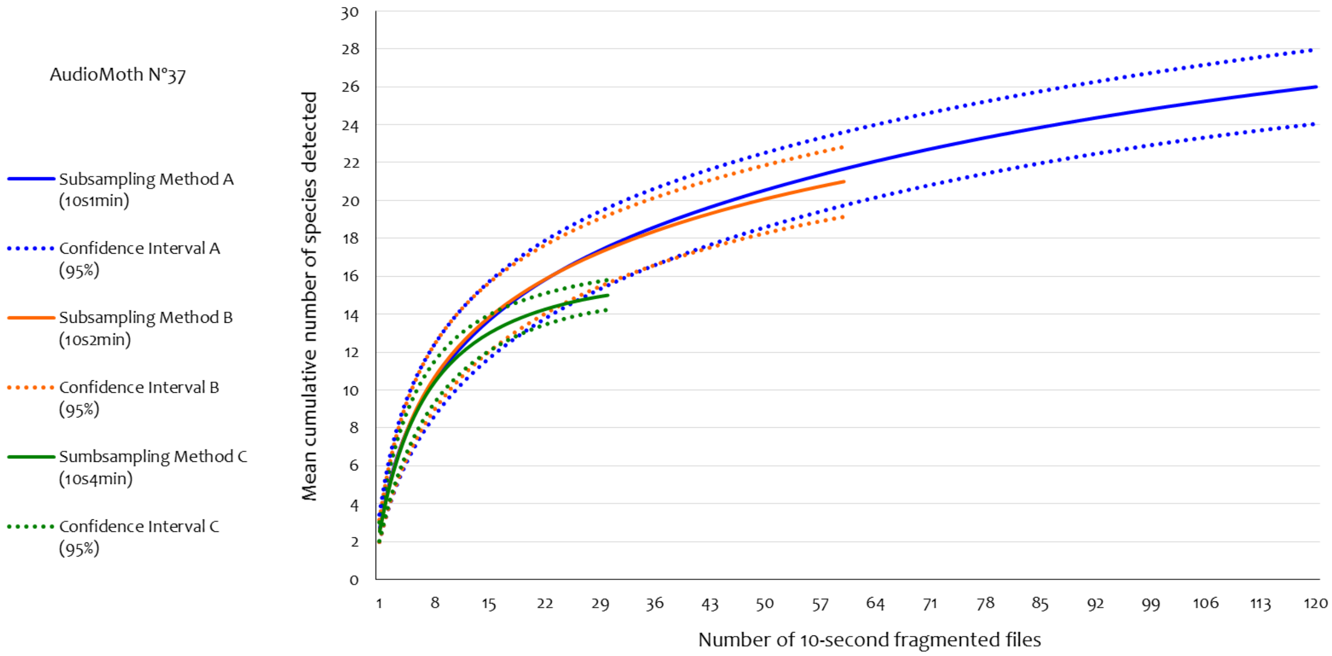


Figure 6.1 – Abundance of detected birds per point count in the morning period. Sunrise occurred at 7:45. Each blue dot represents a performed point count. All birds seen and heard by the observer were counted. Duplicate counts of same individuals were avoided to the best of the observer's ability.

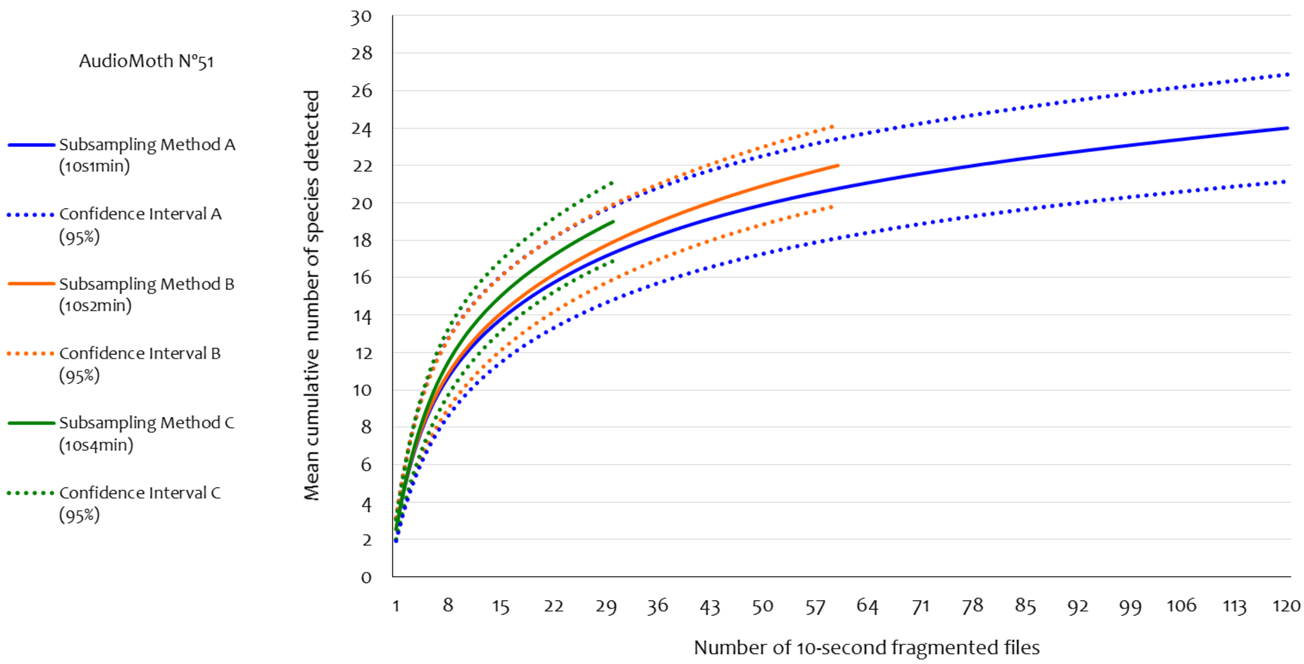



AudioMoth N°43
Subsampling Method A (10s1min)
Confidence Interval A (95%)
Subsampling Method B (10s2min)
Confidence Interval B (95%)
Subsampling Method C (10s4min)
Confidence Interval C (95%)
Mean cumulative number of species detected
Number of 10-second fragmented files


AudioMoth N°47
Subsampling Method A (10s1min)
Confidence Interval A (95%)
Subsampling Method B (10s2min)
Confidence Interval B (95%)
Subsampling Method C (10s4min)
Confidence Interval C (95%)
Mean cumulative number of species detected
Number of 10-second fragmented files



AudioMoth N°37
Subsampling Method A (10s1min)
Confidence Interval A (95%)
Subsampling Method B (10s2min)
Confidence Interval B (95%)
Sumbsampling Method C (10s4min)
Confidence Interval C (95%)
Mean cumulative number of species detected
Number of 10-second fragmented files



AudioMoth N°51
Subsampling Method A (10s1min)
Confidence Interval A (95%)
Subsampling Method B (10s2min)
Confidence Interval B (95%)
Subsampling Method C (10s4min)
Confidence Interval C (95%)
Mean cumulative number of species detected
Number of 10-second fragmented files

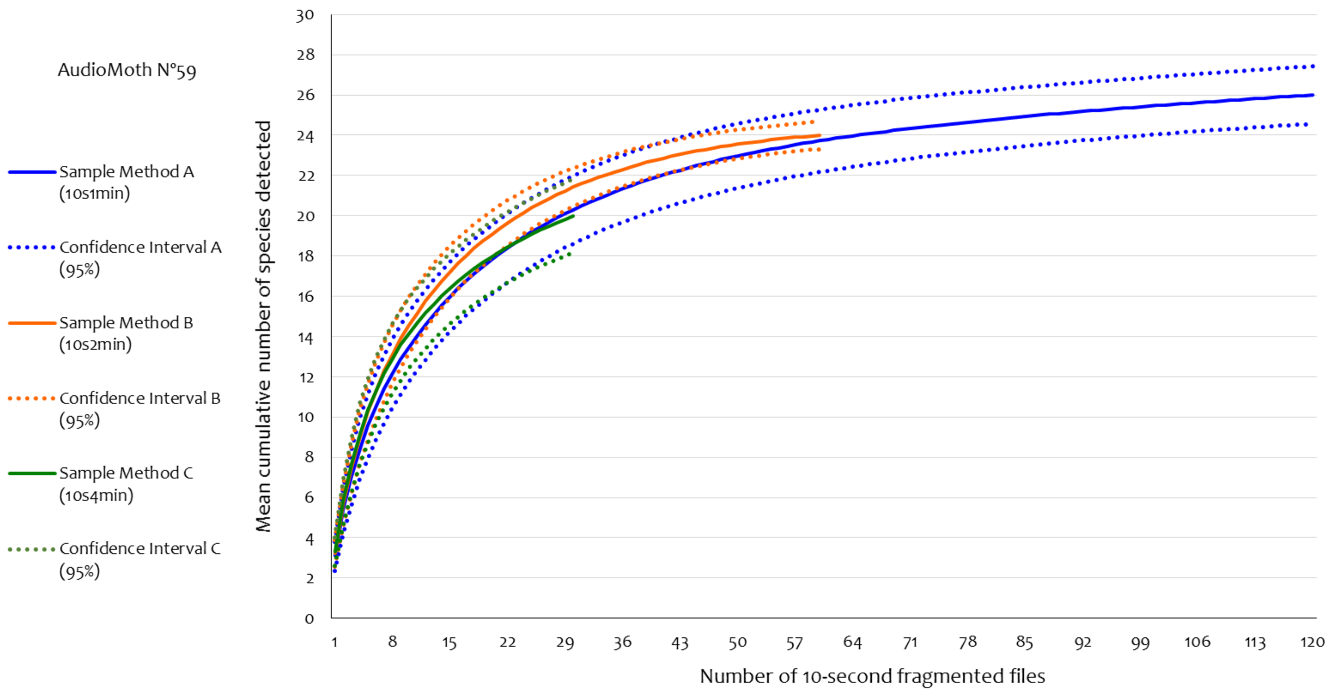


Figure 6.2 - Rarefied species richness curves for three types of intermittent subsampling method – data from all six recorders. Detailed description of the image identical to Figure 3.1. The subsampling method types used were the same across the recorders.