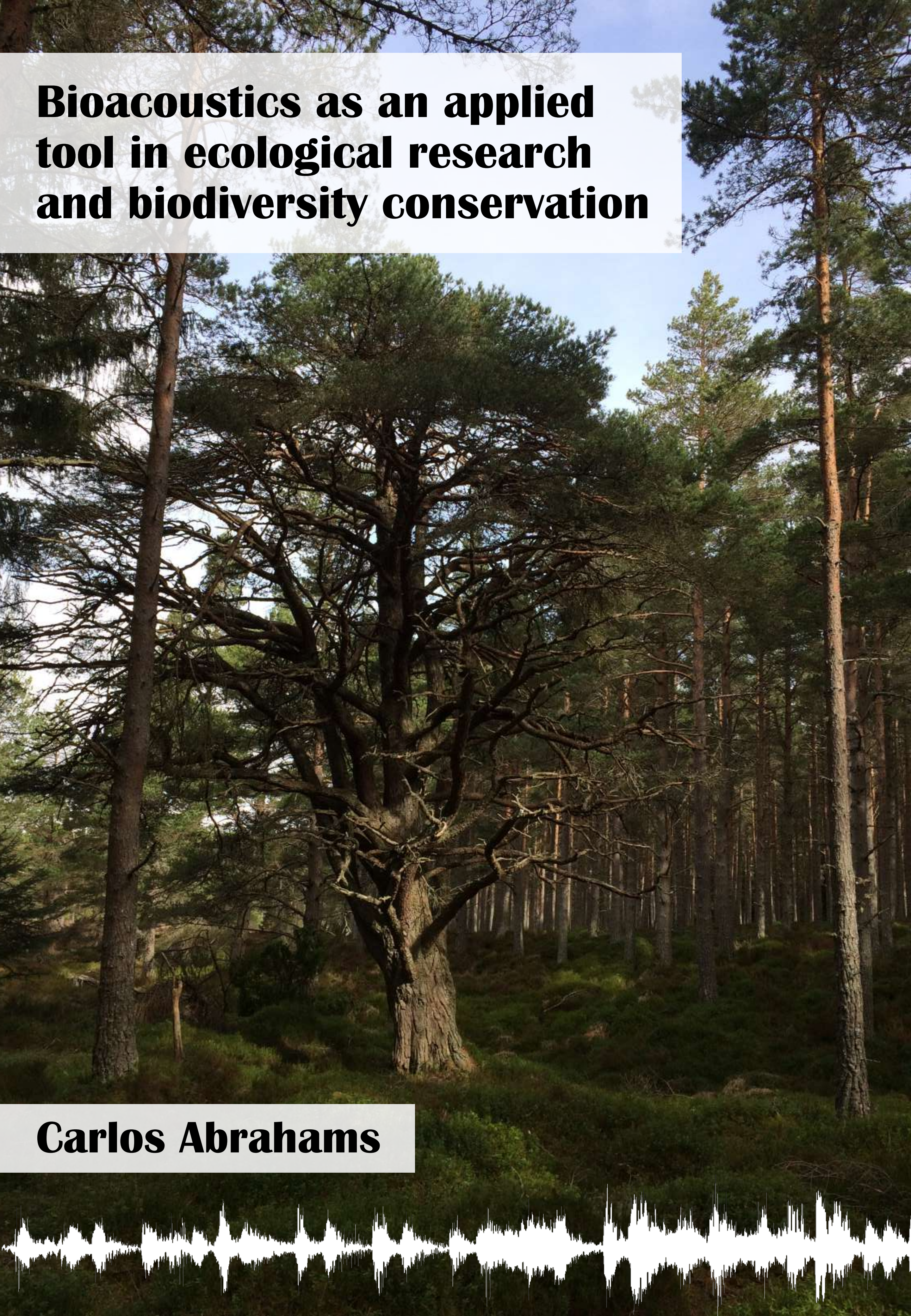
Bioacoustics as an applied tool in ecological research and biodiversity conservation



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BIOACOUSTICS AS AN APPLIED TOOL IN ECOLOGICAL RESEARCH AND BIODIVERSITY CONSERVATION

A thesis submitted in partial fulfilment of the requirements of Nottingham Trent University for the degree of Doctor of Philosophy

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ABSTRACT

1. Ecological data from effective survey and monitoring methods are vitally important for evidence-based nature conservation. This need is increasingly being met by technological developments that enable new approaches for collecting biodiversity data. Among these, acoustic techniques can potentially improve the detection and census of vocal taxa such as birds, and can inform habitat quality assessments.

2. Although improvements in hardware and software for acoustic data capture and analysis are providing new tools for scientific researchers and conservation managers, the advancing technology needs to be matched by methodological understanding, good practice, and accepted protocols. These norms and standards do not yet exist for effective application by users.

3. The published work presented here sets out novel research on bird bioacoustics and freshwater ecoacoustics, applying this to species and habitats of high conservation concern. The publications aim to show how the acoustic approach may be used to determine occupancy, assess population size, understand behaviour and determine community characteristics. Vocal activity rates in bird species are studied and occupancy models created, to interpret acoustic data captured in the field. Different song types, potentially related to breeding status, are identified for a priority species. The ecoacoustic approach is used to assess freshwater ecosystem quality, based on the overall soundscape.

4. The results of the published works have been used to better target acoustic monitoring studies and improve the quality of existing survey methods. This knowledge transfer has been enabled by the development and publication of acoustic protocols for bird survey and freshwater habitat assessment. Further testing is still required to establish optimal standard practices for survey and monitoring, but bioacoustics and ecoacoustics offer significant new approaches for more effective monitoring of species and habitats of conservation concern.

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Chapter 1

INTRODUCTION

1.1 Evidence-based survey methods

Increasing demands on the natural environment have led to escalating biodiversity loss, population declines and species extinctions (Butchart et al., 2010; Williams et al., 2020). These impacts can be reduced through the implementation of evidence-based conservation management actions and policies (Sutherland et al., 2004; Svancara et al., 2005). However, the effectiveness of many aspects of habitat and species management and policy development in the conservation sector remain untested (Pullin et al., 2004; Sutherland et al., 2004). High quality survey and monitoring data are required to develop the evidence base for sound decision-making, and can only be provided by the use of robust field methods (Gibb et al., 2018; Richardson et al., 2019; Kühl et al., 2020). Research effort has helped refine such data-gathering techniques, but recommended methods for species and habitat survey still frequently lack a scientific base. Frequently used methods often do not take into account issues such as observer abilities and biases, site access during survey (Keller & Scallan, 1999), species disturbance (Giese, 1996), detectability and spatio-temporal factors in survey design (Cherrill, 2016; Hutto, 2016; Richardson et al., 2019), and limitations such as classification errors (Bortolus, 2008; Cherrill, 2016). Also, ongoing technological, methodological and statistical developments mean that ecological survey guidelines must be regularly evaluated and updated to ensure they remain current and valid, with effective integration of new research evidence (Elphick, 2008; Marvin et al., 2016; Allan et al., 2018).

One of the key questions for the development of effective survey and monitoring methods is determining the relative costs (in time, resources and money) of new and different approaches, and how these balance against the benefits of improved data (Elphick, 2008). For example, the sampling effort needed to effectively survey a particular taxon is often unclear (Skalak et al., 2012; Balestrieri et al., 2017), but this is a critical design consideration, dictating the number of survey locations, as well as sampling duration, frequency and intensity (Watson, 2017). There is often a mismatch between published guidance or established survey practice, compared to the most effective survey methods determined by targeted studies (Calladine et al., 2009; Darras et al., 2019). Research findings often indicate that commonly used methods fail to accurately reflect species richness, population size or habitat condition (Watson, 2017; Richardson et al., 2019). Despite the central and critical role of monitoring in conservation management, these issues mean that many monitoring programmes are poorly designed in terms of their spatial coverage, sampling effort and statistical approach, and require improvements in their scientific underpinning (Bart, 2005; Schmeller et al., 2012).

1.2 Technological developments in ecological survey

Many established methods used to gather data on habitats and wildlife populations are subject to recognised limitations and biases, and are also often resource-intensive and invasive. Recent technological developments have enabled new methods to address some of these problems, making data capture and analysis easier, faster and more accessible. These technologies include acoustic monitoring, Global Navigation Satellite Systems (GNSS), satellite remote sensing, molecular techniques, Light Detection and Ranging (LIDAR), digital photography, and unmanned aerial vehicles (Berger-Tal & Lahoz-Monfort, 2018; Gibb et al., 2018). Supported by the automation of sensors and new analytical approaches including artificial intelligence (Christin et al., 2019), such technologies offer scalable, cost-effective monitoring methods that have greatly expanded the possibilities for biodiversity assessment and ecological research (August et al., 2015; Merchant et al., 2015). Ecological research is, therefore, increasingly moving toward automated data collection and big data (Hampton et al., 2013; Kitzes & Schricker, 2019). Such trends are increasing the spatio-temporal scope of ecological data, improving our ability to predict species distributions and population dynamics (Maldonado et al., 2015; Bischof et al., 2020; Laubmeier et al., 2020; Xia et al., 2020). These technological developments have also enabled our ability to tackle the drivers of biodiversity decline (Schmeller et al., 2015; Kitzes & Schricker, 2019), through improved evaluation of conservation efforts (Borker et al., 2014; Sugai et al., 2019), and the implementation of adaptive management (Lindenmayer et al., 2011; West et al., 2019).

1.3 An introduction to bioacoustics

Animals produce sounds for a range of functions, including intraspecific communication, navigation, establishing and defending territories, deterring predators and foraging for food (Obrist et al., 2010; Blumstein et al., 2011). The recording and analysis of such sounds can characterise individual behaviour, and can allow investigation of the ecology of species, populations and assemblages. This area of study, termed bioacoustics, has expanded considerably in recent years, reflecting its potential to generate high-quality data within research and practice contexts (Blumstein et al., 2011; Marques et al., 2013; Browning et al., 2017; Gibb et al., 2018). Parallel development in the study of wider environmental sounds, and their relationship to communities and ecosystems, has also allowed the development of the closely related field of ecoacoustics (Pijanowski et al., 2011). The expansion of these twin areas of research has been enabled by the increasing availability of digital acoustic sensors suitable for ecological fieldwork, which provide efficient, non-invasive, and taxonomically agnostic (i.e. non-selective) recording of wildlife populations and communities (Gibb et al., 2018; Sugai et al., 2019).

In bioacoustics practice, recording equipment is used to capture sound in the field or laboratory from a range of taxa such as bats, marine mammals, insects and birds (Obrist et al., 2010; August et al., 2015; Gibb et al., 2018; Sugai et al., 2019). Recording equipment includes both handheld mobile devices and automated audio recorders that can be left in the field to remotely survey fauna without human intervention (Haselmayer & Quinn, 2000; Blumstein et al., 2011; Merchant et al., 2015; Sugai et al., 2019). In the past 10–20 years, digital recording devices have enabled valuable new audio data collection methods for ecological research and conservation management. Data can now be collected over long periods (e.g. months/years) (Smith et al., 2020), in difficult to access environments (Bardeli et al., 2010; Buxton & Jones, 2012) and for species with low detectability (Zwart et al., 2014), extending the capabilities of previous survey methods that have relied on human surveyors, or analogue recording systems.

Once sounds have been captured, acoustic data can be pictorially depicted as spectrograms, which display sound frequency and amplitude against time. Analysts can then inspect the data visually, as well as aurally by playback, to detect sounds made by target species. Such methods may be labour-intensive, and automated (or semi-automated) analysis methods have thus been developed, in which software detects and classifies sounds of interest. Such methods require fewer resources, are repeatable and objective, and the performance of the software algorithm can be quantified to assess error rates (Marques et al., 2013). Beyond the recognition of individual species, recorded sound data can also be analysed to derive environmental sound metrics, which quantitatively summarise audio recordings to produce outputs comparable to species diversity indices (Digby et al., 2013; Sueur et al., 2014; Gibb et al., 2018).

1.4 Thesis aims and structure

The core of this thesis comprises a series of seven peer-reviewed publications, presented according to the Nottingham Trent University regulations for PhD by Published Work. Distinct but interrelated research topics are investigated, addressing current knowledge gaps within the scientific discipline and presenting a significant and original coherent body of work. Each publication stands on its own as an individual work and, when combined, the publications form a cohesive narrative that advances the development of acoustic methods for the study of avian and freshwater ecology, and for use in applied monitoring for biodiversity conservation (Figure 1.1).

A literature review (Chapter 2) presents a broad summary and analysis of the existing research context related to acoustic methods and their application to the study of ecology and conservation management. It covers the development of acoustic methods, the benefits for ecological data collection, and use to characterise species assemblages, enumerate populations, identify breeding status, and assess habitats.

The published works (Chapter 3) first set out the need for the development of improved evidence-based survey methods. They then develop differing acoustic methods to analyse vocal activity rates, investigate differences in song structure, generate occupancy models, and assess habitat quality. These all demonstrate how the application of acoustic methods and relevant practical guidance can advance our understanding of animal populations and their habitats, enabling assessment of the conservation status of species, including those that are rare and declining, and supporting practical conservation efforts. The seven publications upon which this thesis is based are listed below:

1. **Abrahams, C. & Nash, D. J. (2018). Do we need more evidence-based survey guidance? In Practice, 100, 53–56.**

   This publication (Section 3.2) set out the need for improving established survey methods, which have often been developed without a suitable evidence base. It highlighted that methods should be updated in line with existing evidence, new scientific findings and technological developments.

2. **Abrahams, C. & Denny, M. J. H. (2018). A first test of unattended, acoustic recorders for monitoring Capercaillie *Tetrao urogallus* lekking**

activity. Bird Study, 65, 197–207.

This preliminary study (Section 3.3) determined that capercaillie vocalisations can be recognised in lek recordings, that this process can be automated, and how the number of calls varies with location, weather conditions, and over time. It found that vocalizations can be readily recognised to species level using a combination of unsupervised software and manual analysis and that their number varies according to environmental parameters.

3. **Abrahams, C. (2019). Comparison between lek counts and bioacoustic recording for monitoring Western Capercaillie (*Tetrao urogallus* L.). Journal of Ornithology, 160, 685–697.**

   This detailed study on capercaillie (Section 3.4) captured vocal activity for a month at ten lek sites, during which traditional lek count surveys were also undertaken. Vocal activity was found to correlate with the number of birds recorded by human surveyors, and was also related to temporal and environmental variables. The data also suggested that traditional surveys may cause disturbance at lek sites.

4. **Abrahams, C. & Geary, M. (2020). Combining bioacoustics and occupancy modelling for improved monitoring of rare breeding bird populations. Ecological Indicators, 112, 106–131**

   This study (Section 3.5) assessed a novel combination of automated clustering and manual verification to detect and identify heathland bird vocalisations, covering a period of six days at 44 sampling locations. Data was analysed using occupancy modelling methods to provide estimates of occupancy and detectability for each species, incorporating environmental covariates from satellite imagery and land-cover mapping. This approach allowed the distribution and density of bird populations to be assessed.

5. **Docker, S., Lowe, A. & Abrahams, C. (2020). Identification of different song types in the European nightjar *Caprimulgus europaeus*. Bird Study, 67, 119–127**

   This study (Section 3.6) identified, for the first time, that male European nightjars use two distinct song types. The relative frequency of use of each song type changed through the breeding season, indicating a possible link to paired status.

6. **Abrahams, C. (2018). Bird bioacoustic surveys — developing a stan-**

dard protocol. In Practice, 102, 20–23.

This article (Section 3.7) set out a draft protocol for bird bioacoustic surveys, drawing on literature review and stakeholder consultation. It included practical guidance on survey design and recording methods, to provide a robust basis for gathering bioacoustics data for ecological assessments and conservation site management.

7. **Abrahams, C., Desjonquères, C., Greenhalgh, J. (2021) Pond Acoustic Sampling Scheme: A draft protocol for rapid acoustic data collection in small waterbodies. Ecology & Evolution, 11, 7532–7543.**

   This literature review, pilot study and protocol (Section 3.8) proposed the Pond Acoustic Sampling Scheme (PASS), to allow a standardised minimal audio sample to be collected rapidly from small waterbodies, alongside environmental and methodological metadata. The sampling scheme is intended to be incorporated into a variety of survey designs and allow access to a wide range of participants, enabling landscape-scale surveys, data sharing, and collaboration within the expanding freshwater ecoacoustic community.

Following the published works, further sections highlight their overall scientific contribution and impact (Chapter 4), discuss the research questions posed (Chapter 5) and provide a conclusion to the thesis (Chapter 6).

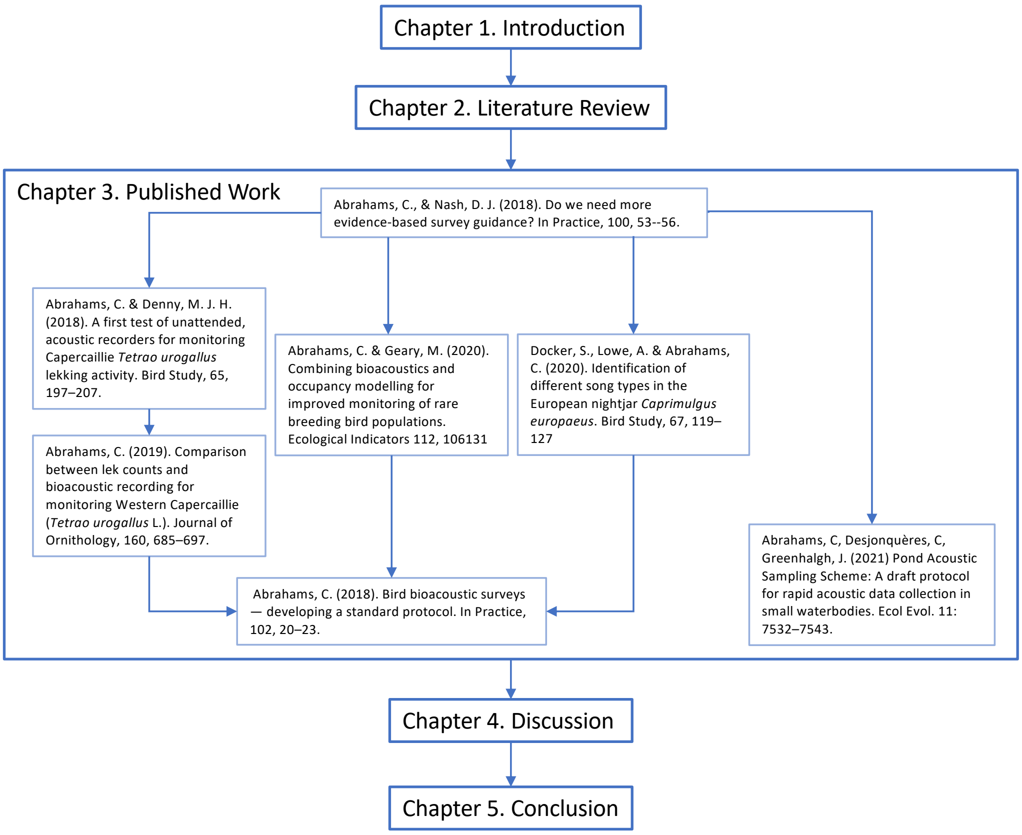

Figure 1.1: The thesis structure, demonstrating that the published work: (i) describes the need for evidence-based survey methods, (ii) provides information to address that need, and (iii) develops such guidance for birds and ponds.

Chapter 2

LITERATURE REVIEW

2.1 The bioacoustic approach

Over the last 100 years, methods for recording animal sounds have developed considerably, especially regarding the study of birdsong. Original attempts to transcribe the vocalisations of birds created onomatopoeic translations of their songs and calls, which often provided the common names for the species, for example, curlew and cuckoo. This verbal transcription developed into the use of standard musical notation (Mathews, 1904; Bruyninckx, 2018), and then hand-drawn graphical recording methods (Saunders, 1915; Rowan, 1924; Wheeler & Nichols, 1924). The invention of the spectrograph machine in the 1940s allowed a sound spectrum to be visually plotted, by etching shaded bands of frequency along a time axis (Potter, 1945). This innovation revolutionised sound recording, display and interpretation, paving the way for computer-based recording and processing (Brandes, 2008; Bruyninckx, 2018) (Figure 2.1). Due to the costs of technology and practical constraints, early bioacoustic research was largely confined to small-scale and laboratory-based studies of individual animals or species, and commonly investigated intraspecific variation, vocalisation behaviour, and evolution of communication systems (Bruyninckx, 2018; Gibb et al., 2018). However, the digital revolution of recent years, and the arrival of higher quality, more reliable and lower cost sensors, has empowered a rapid rate of development in bioacoustics and ecoacoustics, expanding access for researchers and practitioners.

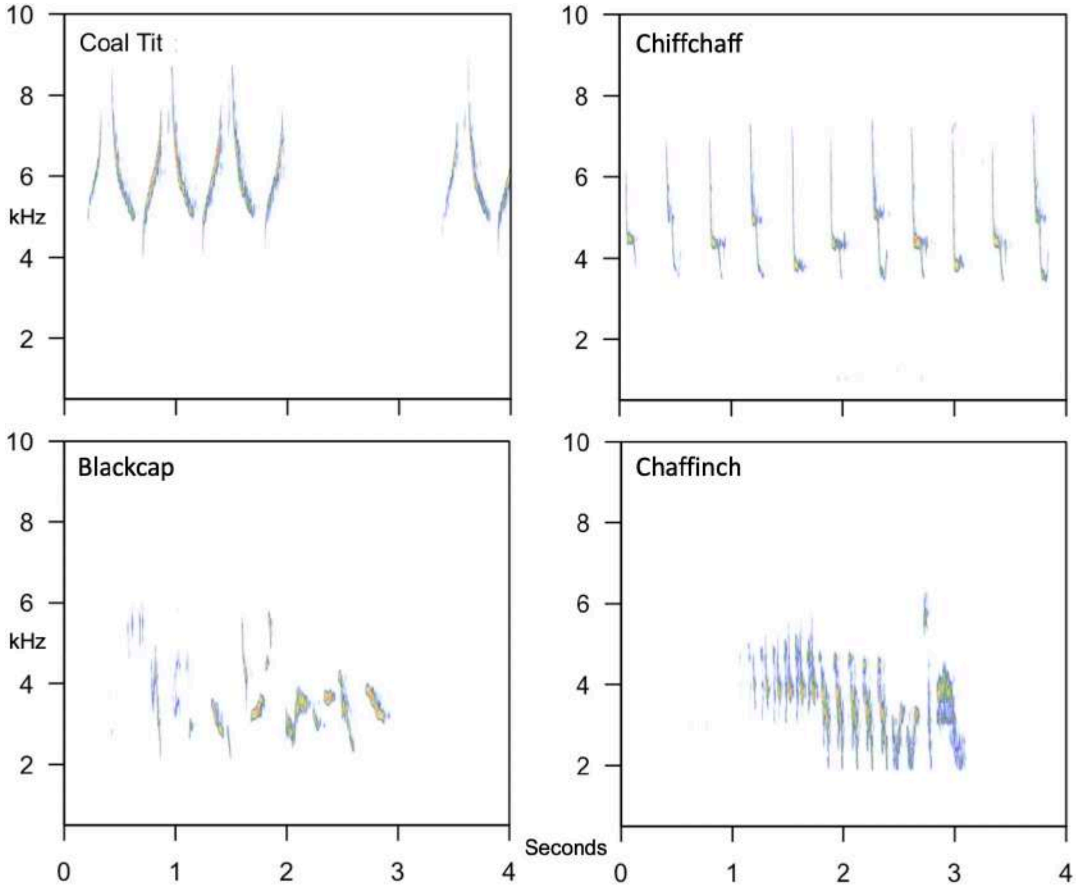

Figure 2.1: Spectrograms of four common bird species, showing their typical time, frequency and amplitude characteristics.

The potential of the acoustic approach in ecology is still being explored and established. This is evidenced by the recent publication of general reviews of the discipline (Browning et al., 2017; Gibb et al., 2018; Sugai et al., 2019) together with more targeted reviews on animal communication (Teixeira et al., 2019), bird bioacoustics (Shonfield & Bayne, 2017; Darras et al., 2018), freshwater habitats (Greenhalgh et al., 2020), acoustic data processing (Merchant et al., 2015), localisation of individuals (Rhinehart et al., 2020), and the estimation of population densities (Marques et al., 2013). Between 1992 and 2018, publication of original bioacoustics studies increased markedly, as the scientific potential of the approach was realised (Sugai et al., 2019). However, research subjects and working methods have been restricted, focussing primarily on recording bats with hand-held devices, mainly in Europe and North America, and with acoustic analysis undertaken using non-automated methods (Sugai et al., 2019). This research landscape is now changing, with affordable programmable recorders and more sophisticated and accessible data analysis tools widening the taxa, geographical regions and research questions investigated (Chambert et al., 2018; Sugai et al., 2019) (Figure 2.2).

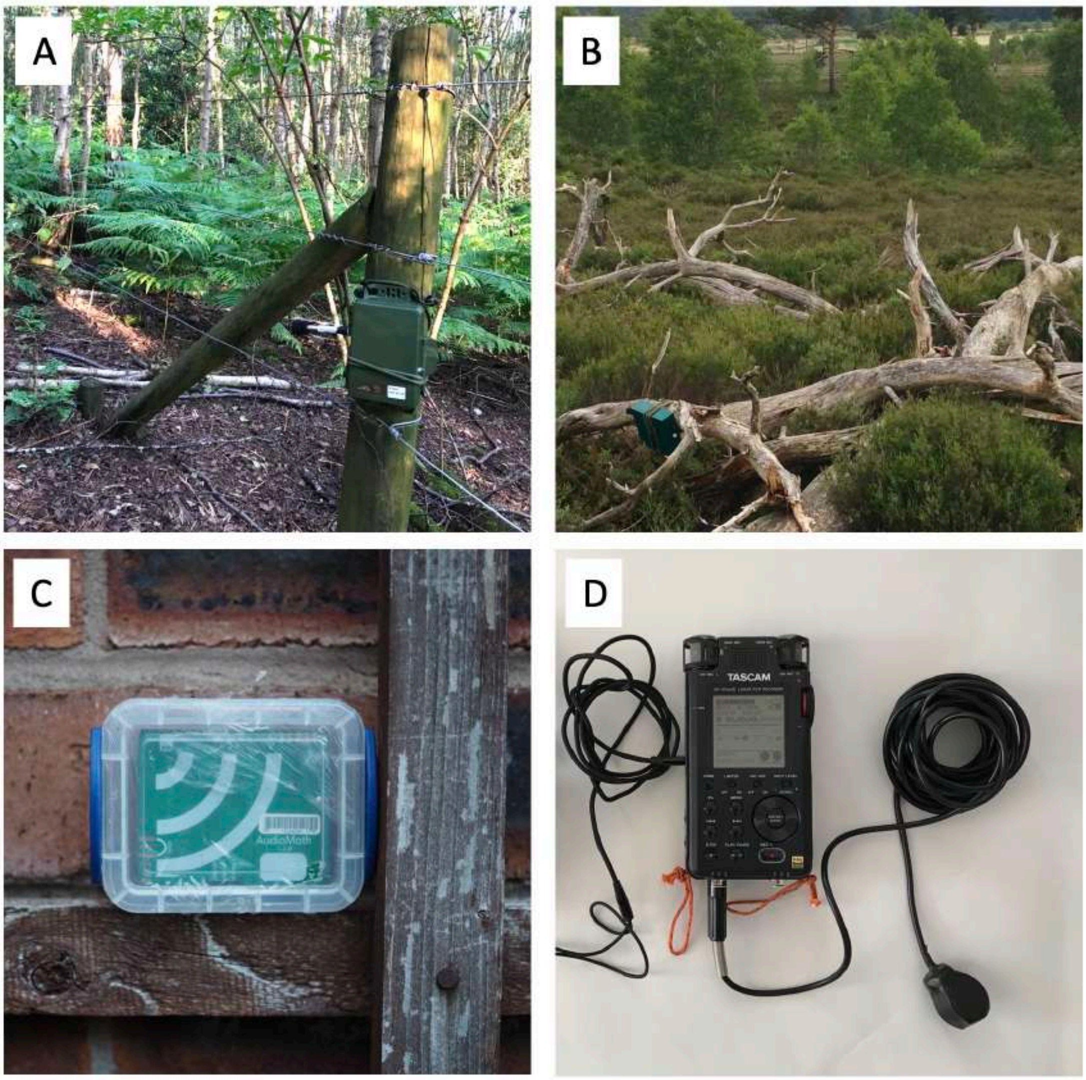

Figure 2.2: Acoustic research can be conducted in a wide range of locations and with a variety of equipment: (a) Wildlife Acoustics Song Meter 4 deployed in woodland to record activity at a badger sett; (b) Wildlife Acoustics Song Meter 2 deployed in heathland habitat to record breeding bird activity; (c) Audiomoth in a homemade casing, used to record the suburban soundscape as part of the Silent Cities project (DOI: 10.17605/OSF.IO/H285U); (d) Tascam DR-100 with cabled hydrophone for handheld recording of underwater sounds.

The application of acoustic methods has the potential to transform data collection and analysis in ecology, behaviour and conservation science, allowing standardised and non-invasive fieldwork at spatial and temporal scales not previously possible (Blumstein et al., 2011). The analysis of sound recordings can provide a wide range of ecological information (Stowell & Sueur, 2020). At the simplest conceptual level this may be detection of the presence of a particular species. Building upon this, acoustic methods can be used relatively easily to assess species richness or community composition at a site (Grava et al., 2008; Furnas & Callas, 2015; Chambert et al., 2018; Furnas & McGrann, 2018; Campos-Cerqueira et al., 2019). Deeper analysis can then provide evidence of phenology (Oliver et al., 2018), temporal dynamics (Gottesman et al., 2018), activity levels (Pérez-Granados et al., 2019), population numbers (Bradfer-Lawrence et al., 2020), or even individual identity (Chang et al., 2018). However, acoustic recordings are also rich in broader environmental information (Ross et al., 2020; Nguyen Hong Duc et al., 2021), characterising landscape or habitat structure (Fuller et al., 2015; Burivalova et al., 2019), weather conditions (Metcalf et al., 2020; Sánchez-Giraldo et al., 2020), anthropogenic noise levels (Gill et al., 2017; Alvares-Sanches et al., 2021), and atypical sounds such as illegal logging activity and gunshots (Hill et al., 2018; Sethi et al., 2020).

The ability to gather sound and interpret it for a wide range of applications has allowed researchers to move beyond the recording of individual animals and species, to understand the encompassing 'soundscape' of an ecosystem. This soundscape approach has driven the development of a new conceptual framework of ecoacoustics, bringing together the three sound fields from biological (biophony), geophysical (geophony), and human technological (anthrophony) domains (Schafer, 1977; Krause, 1987; Pijanowski et al., 2011) (Figure 2.3). The sonic character of the environment is now viewed as an essential component of landscape ecology, providing an integrated view of ecosystem dynamics and functioning (Villanueva-Rivera et al., 2011). It can track transformations in ecological communities, identify acoustically complex locations, or those suffering from noise pollution, detect environmental degradation from pressures such as climate change and habitat fragmentation, and inform protection or restoration actions (Blumstein et al., 2011; Farina, 2014).

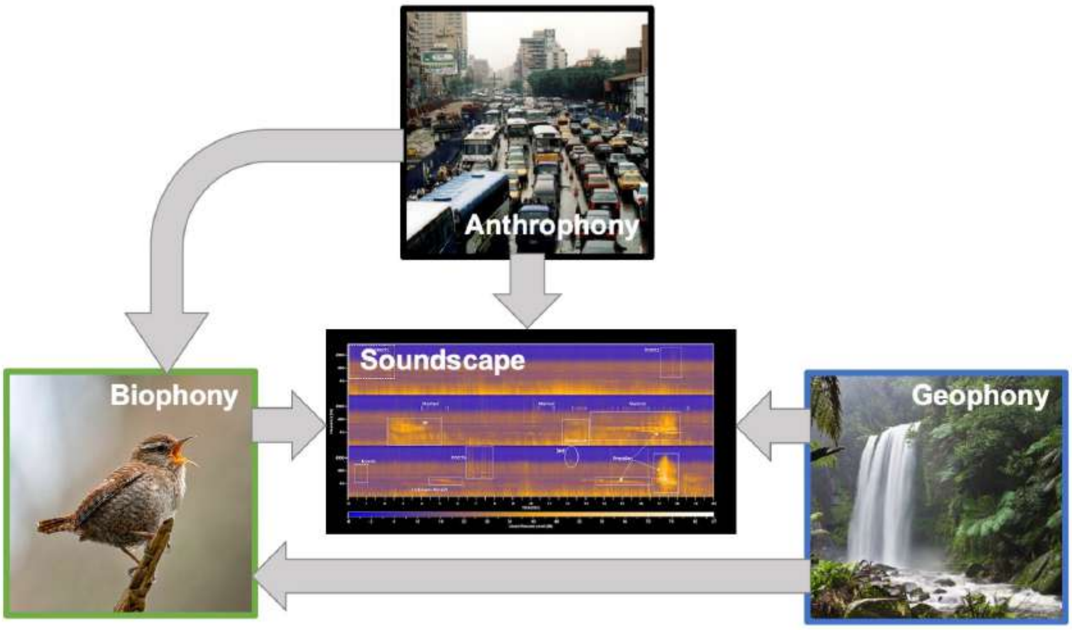

Figure 2.3: The soundscape ecology framework, comprising man-made sounds (anthrophony), abiotic environmental sounds (geophony), and biological sounds (biophony). These three sound fields inter-relate, and collectively produce the soundscape within a particular location.

Despite recent developments and recognised applications, bioacoustics and ecoacoustics are nascent scientific disciplines, and underpinning theoretical principles are not yet well developed (Farina et al., 2021). However, three key hypotheses governing the field have been formulated, covering physiological, ecological and evolutionary processes. These are the Morphological Adaptation Hypothesis (MAH) (Farina, 2014; Farina et al., 2021), the Acoustic Adaptation Hypothesis (AAH) (Forrest, 1994; Boncoraglio & Saino, 2007; Hardt & Benedict, 2021), and the Acoustic Niche Hypothesis (ANH) (Krause, 1987; Pijanowski et al., 2011; Eldridge & Kiefer, 2018). These hypotheses respectively describe how body size, the surrounding environment, and niche partitioning affect the sounds produced by vocalising animals, and the consequent character of the overall soundscape.

The MAH focuses on the anatomical differences between animals that produce acoustic signals. It refers to the features that determine the characteristics of the sound produced, including body size, trachea length and the structure of mouthparts or stridulation features. For example, an organism's body size is often inversely related to the acoustic frequencies produced, such that large animals produce low-frequency sounds and vice versa (Pijanowski et al., 2011; Farina, 2014).

Shifting attention from the animal sound source to the surrounding environment, the AAH states that the medium through which biological sounds are transmitted determines their character, and that species have evolved to cope with the resulting effects on the propagation of their signals (Morton, 1975). For example, in densely vegetated habitats, bird songs have adapted, or can be adjusted when needed, to use low frequencies within a narrow range. These particular sound parameters compensate for interference effects and maximise transmission efficiency in dense vegetation, while reducing the energetic costs of vocalisations (Boncoraglio & Saino, 2007; Farina, 2014).

The ANH provides a context for both the MAH and AAH, addressing how each species has its own acoustic niche. The sounds produced within a location by the full assemblage of species present combine into a complex and layered arrangement of non-overlapping signals. This arrangement has evolved to minimise costly interspecific competition, with species evolving, or adjusting their signals, to take advantage of specific niches in the frequency and time domains. A critical extrapolation of this hypothesis is that intact habitats and communities exhibit higher levels of coordination between species than anthropogenically impacted habitats, and display a more complete niche apportionment (Krause & Farina, 2016; Eldridge & Kiefer, 2018). As a result, a varied and complex natural soundscape arises from, and is an indicator of, a biodiverse ecosystem.

2.2 Avian bioacoustics

Birds are subject to considerable interest from scientists and the general public alike due to their ubiquity, visibility and attractive nature, and they are often used as indicators of ecosystem health (Bibby, 1999; Gregory et al., 2003; Burns et al., 2020). Their use as indicators is enabled by the extent and quality of information made available by decades of scientific and volunteer recording across the globe (Dickinson et al., 2010; Burns et al., 2020), and this interest has made them a particular target for bioacoustics research (Obrist et al., 2010).

Birds are highly vocal and sing in the same frequency range as human hearing. This makes them easily recorded with readily available equipment and highly suitable for bioacoustics studies (August et al., 2015). Despite visual cues being important for data collection in many bird surveys (Bibby et al., 2000; Gregory et al., 2004), sound is often the primary and most efficient cue for the detection of birds, especially in densely vegetated habitats, during surveys at night, or with cryptic species (Parker, 1991; Riede, 1993; Alldredge et al., 2007; Marques et al., 2013). Point counts and transect surveys are widely used techniques that depend upon both visual and auditory cues (Parker, 1991; Gilbert et al., 1998; Angehr et al., 2002). These methods rely on highly trained field personnel to identify species, and are inherently subjective due to differing skill levels (Brandes, 2008). This bias can make comparisons between data from different personnel unreliable (Angehr et al., 2002). The use of bioacoustic methods can significantly reduce this observer variability, since recordings are more consistent and can be subject to quality assurance processes (Haselmayer & Quinn, 2000; Hobson et al., 2002; Rempel et al., 2005; Darras et al., 2019). Studies comparing automated acoustic recording to point-count data have found similar results from the two methods, in terms of species richness and community composition, across a range of grassland and forest habitat types (Tegeler et al., 2012; Holmes et al., 2014; Alquezar & Machado, 2015; Furnas & Callas, 2015; Leach et al., 2016). Although acoustic recording will miss silent individuals, it will commonly detect some vocalising species that observers fail to record. Automated recording can also be deployed for long periods in the field, efficiently providing much larger volumes of data than human surveyors, with significantly less survey effort (Tegeler et al., 2012; Holmes et al., 2014; Zwart et al., 2014). The use of the acoustic approach, therefore, offers an effective alternative to traditional field surveys (Table 1) for assessing occupancy, species richness and population size (Obrist et al., 2010; Darras et al., 2018; Pérez-Granados & Traba, 2021), enabling significant advances in avian ecological research (Shonfield & Bayne, 2017).

Table 1. Benefits of the acoustic approach in comparison to traditional manual survey methods

Benefit	Reason	References
Flexibility	Programmable recorders can be deployed and retrieved at any time, making fieldwork more flexible.	Brandes (2008)
Non-invasive	The ability to gather data without surveyors present avoids disturbances to animal activity.	Venier et al. (2012)
Scale	Large spatial and temporal scales can be covered simultaneously, eliminating differences between samples.	Alquezar & Machado (2015); Furnas & Callas (2015); Stiffler et al. (2018)
Range	Some species are acoustically detectable at longer ranges than with other survey methods, increasing survey area coverage.	Marques et al. (2013); Crunchant et al. (2020)
Access/ conditions	Recorders can operate for long periods unattended in remote locations and regardless of weather conditions.	Gibb et al (2018); Pérez-Granados et al. (2018)
Detectability	Recorders can sample habitats with limited visibility (underground, underwater, or in thick foliage), and can also be used to monitor cryptic species (e.g. small, camouflaged, nocturnal species), increasing the likelihood of detecting rarer species.	Gibb et al (2018); Klingbeil & willig (2015); Marques et al. (2013); Shonfield & Bayne (2017); Teixeira et al. (2019); Williams et al. (2018); Wrege et al. (2017); Zwart et al. (2014)
Data quantity	Passive acoustic methods enable the automated collection and processing of large amounts of consistent digital data.	Holmes et al. (2014); Marques et al. (2013); Obrist et al. (2010); Tegeler et al. (2012)
Data processing	Audio recordings can be automatically scanned with standardised methods, avoiding observer bias.	Gibb et al (2018); Venier et al. (2012)
Permanent archive	Audio recorders create a permanent data archive, which can be revisited for future studies, comparisons and quality assurance.	Alquezar & Machado (2015); Gibb et al (2018); Newson (2017); Pérez-Granados & Traba (2021)
Information	Spectrogram analysis can reveal information not discernible by any other method, e.g. sound features or frequency components outside the human hearing range. This has, for example, led to the discovery of new species.	Obrist et al. (2010)

2.3 Population assessment using vocal activity rate

A core application of ecological survey is the assessment of population abundance, which is a critical measure for effective wildlife management, conservation and ecological research (Marques et al., 2013). Abundance data are often gathered by sighting animals from transects or points, or by using a form of capture-recapture on marked or identifiable individuals. In acoustic surveys, the number of animals cannot normally be counted in this way, because signals from different individuals may be confused. However, one potential approach for rapid and cost-effective assessment of population abundance is to count the density of sounds emitted from a species at a sampling location. This metric, the Vocal Activity Rate (VAR), is defined as the number of songs per time unit for the target species (Pérez-Granados & Traba, 2021). VAR is expected to increase with population density – and studies have confirmed such a positive relationship in different taxa, despite different singing behaviours, diurnal activity patterns and habitat preferences (Borker et al., 2014; Oppel et al., 2014; Pérez-Granados & Traba, 2021).

For birds, significant positive relationships have been found between VAR and the number of individuals of European bee-eater *Merops apiaster* and Dupont's lark *Chersophilus duponti* (Pérez-Granados et al., 2019), and with nest density and abundance in tern and shearwater colonies (Borker et al., 2014; Oppel et al., 2014). Vocal activity of petrels on islands can also be positively related to time since predator eradication, a proxy for population size (Buxton & Jones, 2012). These findings demonstrate that abundance assessment based on VAR is especially well suited for species that regularly vocalise in groups, such as seabird colonies (Buxton et al., 2013; Oppel et al., 2014).

Another potentially valuable area for developing links between population densities and vocal activity is for species with lek breeding systems (Pizo & Aleixo, 1998; Raynor et al., 2017). Lekking birds include grouse species, bustards, sandpipers and some passerines, such as *Mionectes* flycatchers. For these taxa, the males display against each other within a specific location to attract mates, and a typical lek consists of several male display territories in visual and/or auditory range of each other. An 'exploded lek', as seen in the houbara bustard *Chlamydotis undulata undulata* (Cornec et al., 2017) and capercaillie *Tetrao urogallus* (Wegge et al., 2013), has more widely separated male birds that are only within audible (not visual) range of each other. Both typical and exploded leks have vocal activity concentrated within a relatively small area, and can therefore be effectively surveyed using acoustic techniques. For individual lekking males, song characteristics such as the call rate and the length of time dedicated to singing are positively correlated to mating success (Westcott, 1992; Fiske et al., 1998;

Pizo & Aleixo, 1998). In addition, displaying males call more loudly when more females are present, such that the overall amplitude at leks will increase with greater female attendance (Raynor et al., 2017).

As a measure of singing activity in one location, VAR, therefore, allows the assessment of the conservation status of acoustically active wildlife (Borker et al., 2014). However, there is often not a simple relationship between call counts and animal density (Gibb et al., 2018), as sound-production rates vary over space and time due to factors such as behavioural state or sex-ratio differences. Further study is needed to determine how VAR varies between species, habitat conditions and types of vocalisations, and what survey and data analysis protocols (e.g. recorder layout, recording times, software performance) most effectively evidence these relationships (Marques et al., 2013; Pérez-Granados et al., 2019).

2.4 Occupancy modelling

Occupancy modelling is a different approach to VAR for population assessment with acoustic data. This method does not require vocal activity levels to be quantified, but instead uses simpler presence/absence data from multiple sampling locations to assess the proportion of locations in which the species of interest is detected (Royle & Nichols, 2003; Marques et al., 2013; Chambert et al., 2018) (Figure 2.4). This provides the measure of 'naive' occupancy for the species, which can be refined by including an assessment of detectability within the occupancy figures. Detectability is assessed by repeatedly surveying at each sampling location, to produce an 'encounter history' representing whether a species was detected or not detected on each survey event (MacKenzie et al., 2002; Campos-Cerqueira et al., 2019; Wood et al., 2019). Analysing this encounter history over a series of survey events enables detection probability parameters to be assessed for the target species (MacKenzie & Royle, 2005; Kalan et al., 2015; Gibb et al., 2018; Balantic & Donovan, 2019; Campos-Cerqueira et al., 2019). This assessment of imperfect detectability takes false-negative detections into account in the calculated occupancy levels, assigning a probability that a species occurs in the sample, even though it may be undetected (MacKenzie et al., 2006). This calculation can thus improve assessment of occupancy estimates and the accuracy of the inferred population status (MacKenzie et al., 2006).

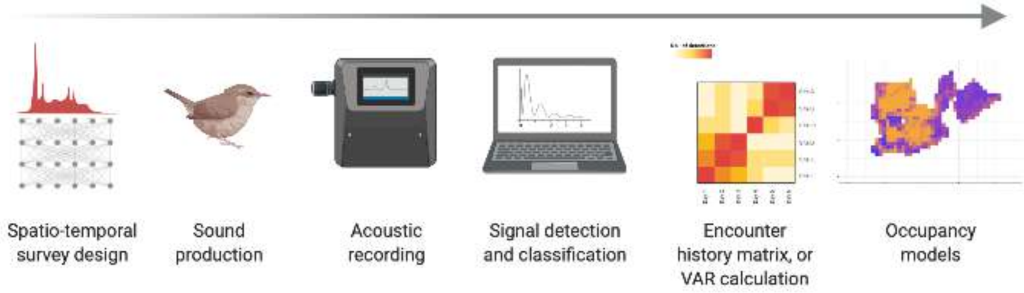

Figure 2.4: Workflow of bioacoustics data capture, processing and analysis for VAR and occupancy modelling. Created in BioRender.com.

There are substantial benefits to using acoustic data within an occupancy modelling framework to assess populations. Firstly, the binary presence/absence information required for occupancy modelling is more easily collected and analysed than abundance data (MacKenzie & Nichols, 2004; Furnas & Callas, 2015; Wood et al., 2019). It is therefore an efficient way to translate the large data volumes collected with acoustic monitoring into meaningful ecological outputs for understanding and mapping species distributions, especially across large spatial extents (Furnas & Callas, 2015; Campos-Cerqueira et al., 2019) (Figure 2.4). Effective methods for aggregating large quantities of automated detections (e.g. individual call phrases) into survey-level encounter histories have been developed, either based on the species-match probabilities provided by software algorithms (Balantic & Donovan, 2019) or by manual verification of detected events (Kalan et al., 2015; Campos-Cerqueira et al., 2019; Metcalf et al., 2019).

A second benefit of using acoustic data is that automated recorders can be easily programmed for the multiple repeat surveys needed for occupancy modelling. They can also be scheduled to repeat at the same times each day, reducing diurnal variability in modelled detection probability (Brandes, 2008; Furnas & Callas, 2015). Automated recorders can also capture sound for long periods (e.g. weeks) to produce the required detection information for encounter histories. This fieldwork efficiency reduces resourcing needs and minimises disturbance when compared to traditional survey approaches (MacKenzie et al., 2003; Shonfield et al., 2018; Balantic & Donovan, 2019; Campos-Cerqueira et al., 2019; Metcalf et al., 2019). Finally, unlike other field methods such as point counts, the permanent and verifiable acoustic data record mitigates against species identification errors that can severely affect occupancy modelling estimates (Royle & Link, 2006; Furnas & Callas, 2015).

Due to the stated benefits, occupancy modelling is becoming an increasingly widespread approach for assessing the distribution, habitat use and size of species populations

(Bailey et al., 2014), and is beginning to be used alongside acoustic methods for implementing monitoring programmes at local to national scales (Furnas & Callas, 2015; Chambert et al., 2018; Campos-Cerqueira et al., 2019; Wood et al., 2019). It has been employed for studies on koalas in Australia (Hagens et al., 2018), primates in the Ivory Coast (Kalan et al., 2015), and bats in the USA (Banner et al., 2018). However, there is minimal guidance on how wildlife researchers and land managers should translate large audio datasets into applicable occurrence models (Newson, 2017; Chambert et al., 2018). A key consideration for such guidance is the determination of a suitable sampling effort to yield robust inferences from an occupancy-based monitoring programme. It is clear, however, that passive acoustic approaches allow the number of sampling locations, the study duration, and the number of visits to be increased, enhancing overall detection probability and statistical power, and improving the accuracy and precision of occupancy models (MacKenzie & Royle, 2005; Campos-Cerqueira et al., 2019; Wood et al., 2019).

2.5 Identification of song types in relation to breeding status

Animal vocalisations allow individuals to communicate with conspecifics and other taxa, to transfer information or advertise their presence. The sounds used vary widely between species, often change between seasons according to life history, and can be differentiated at the intraspecific level, allowing identification of individual animals (Gilbert et al., 1994; Grava et al., 2008; Chang et al., 2018).

Passerine birds commonly have a small repertoire of typical song types, which are often used interchangeably, and hence do not appear to serve specific purposes. When differences in the use of song types are found, they are usually limited to a single function, such as territorial defence or mate attraction (Catchpole, 1983). For example, two song types, sometimes with or without a distinctive ending – respectively referred to as accented and unaccented – have been noted for some species, and are considered to be linked to breeding status (Catchpole & Slater, 2008). The accented songs used for courtship and pair-bonding are often longer, more complex, and more variable, while the unaccented songs used for territorial defence by paired males are shorter, slower, simpler and more stereotyped (Catchpole, 1983; Nemeth, 1996; Staicer et al., 2006; McKillip & Islam, 2009; Bessert-Nettelbeck et al., 2014). Singing behaviour can thus be used to assess the pairing status of a singing bird, based upon song type and rate (Morse, 1966; Catchpole, 1983; Kroodsma et al., 1989; Byers, 1996; Catchpole & Slater, 2008; Xia et al., 2019).

Individually distinctive vocalisations have been described in many bird species (Dhondt & Lambrechts, 1992; Terry et al., 2005; Policht et al., 2009; Průchová et al., 2017). This intraspecific variation is functionally important for birds, in familial (Mathevon et al., 2008) and courtship interactions (Laiolo et al., 2008). It may also enable ecological study, as call individuality can be used as a non-invasive ‘marking’ technique, for enumerating individuals within populations while minimising bias from disturbance (Adi et al., 2010; Průchová et al., 2017; Marin-Cudraz et al., 2019). For such use, the long-range advertising vocalisations of displaying birds are the most easily recordable and provide the highest potential for vocal individuality (Terry et al., 2005). However, one limitation with call individuality is plasticity, as some species have vocalisations that are stable between years (Gilbert et al., 1994), while others have call characteristics that alter significantly over time (Průchová et al., 2017; Deng et al., 2019; Raymond et al., 2020).

2.6 Environmental influences on acoustic recordings

Sound amplitude declines and frequency characteristics alter as signals travel through the environment (Priyadarshani et al., 2018). In addition, a wide variety of environmental factors affect animal behaviour and the production of the songs and calls recorded in acoustic studies (Angelstam, 2004; Laiolo et al., 2011). Hence, distance and habitat characteristics affect both the detectability and the assessment of occupancy of birds and other taxa (Walsh et al., 2004; Raynor et al., 2017; Fremgen et al., 2018). Understanding the effect of these environmental factors is therefore critical to improving data interpretation, such as when estimating population sizes of monitored species (Drummer et al., 2011; Sadoti et al., 2016; Priyadarshani et al., 2018).

The greatest environmental influence on acoustic detection is normally the distance between the source animal and the receiving microphone, with sound waves attenuating through air. After this, the most significant factor is likely to be the intervening topography between the animal and the acoustic recorder, with sound travelling best when there is line-of-sight between the two (MacLaren et al., 2018; Piña-Covarrubias et al., 2018). The vegetation structure in that space is also influential, but there is some contradiction in the research on how this affects detectability. A reduction in sound propagation in closed habitats, such as forests, would be expected due to the density of vegetation impeding sound (Yip et al., 2017; MacLaren et al., 2018). However, birdsong transmission, especially of lower frequency calls, can be significantly better in forest than in open grassland sites, due to the lack of interference by wind noise in this more enclosed habitat (Priyadarshani et al., 2018). Other aspects of weather/climate also affect acoustic recording, with increases in rainfall and atmospheric pressure significantly decreasing detection (Digby et al., 2013; MacLaren et al., 2018; Metcalf et al., 2020), whereas humidity increases detectability (Raynor et al., 2017; Yip et al., 2017). Air temperature may decrease (MacLaren et al., 2018) or increase (Raynor et al., 2017) detection rates, depending upon the interactions between physical sound propagation, humidity levels, and vocalization behaviour of the recorded species.

Seasonal and diel cycles, such as breeding activity and dawn chorus episodes, affect the levels of bioacoustic activity (Furnas & McGrann, 2018; Campos-Cerqueira et al., 2019). In addition, background anthrophony and geophony 'noise' levels vary over time, often being lower at night (Priyadarshani et al., 2018; Fairbrass et al., 2019). Understanding the effects of geophony, anthrophony, recorder location and the landscape setting on any field study can therefore enable the interpretation of acoustic data and allow results to be placed in context.

2.7 Freshwater soundscape ecology

Freshwater taxa, including amphibians, fish and macroinvertebrates, produce sounds by activities such as vocalisation, air movement or stridulation (Linke et al., 2018; Desjonquères et al., 2020). In addition, sounds are created in freshwater habitats by hydrological action and gaseous exchange in macrophytes and substrates (Linke et al., 2018), and from anthropogenic sources such as fishing activity or boat engines (Rountree et al., 2020). Therefore, recordings of underwater soundscapes can be analysed to assess a range of processes in freshwater ecosystems (Kuehne et al., 2013; Linke et al., 2018; van der Lee et al., 2020). However, most freshwater acoustic research to date has concentrated on single-species studies of fish in laboratory settings, and field surveys of waterbody soundscapes have scarcely been undertaken (Desjonquères et al., 2015; Greenhalgh et al., 2020). As a result, knowledge of both overall soundscapes, and the sounds produced by freshwater organisms such as macroinvertebrates, is lacking (Rountree et al., 2020). Despite these large gaps in understanding, the few studies that have employed ecoacoustic methods, without the need for species identification, have revealed differences between sites, reflecting variability in both biological communities and environmental factors (Kuehne et al., 2013; Bolgan et al., 2018; Putland & Mensinger, 2020; van der Lee et al., 2020).

Most field-based freshwater studies to date have installed automated recorders at single or few sites to investigate temporal acoustic variability (Desjonquères et al., 2015; Gottesman et al., 2018; Karaconstantis et al., 2020). Few studies have undertaken a wider spatial approach (Kuehne et al., 2013; Decker et al., 2020) and, as a result, the diversity of sounds present across varying freshwater systems at any spatial scale is poorly understood. The largest-scale study to date recorded the soundscapes of 19 lakes, 17 ponds, 20 rivers, and 20 streams (Rountree et al., 2020), with the vast majority of field studies being much smaller in scope. Further work at the landscape scale is therefore needed and is most likely to be enabled by active handheld recording covering multiple sites, or by collaborative approaches where standardised data can be pooled from surveyors across regions.

2.8 Research questions

Acoustic methods have undergone rapid development in recent years, as the digital revolution has enabled new and improved hardware and software tools.

This literature review has identified that considerable knowledge gaps exist in the use of acoustic methods for ecological research and conservation practice. Further research is needed to effectively develop more consistent data collection, improve classification of sound types, enable data interpretation in light of animal activity and behaviour, and advance understanding of the relationships with natural and anthropogenic environmental factors. In particular, research programmes will be strengthened by establishing methodological standards, and integrating acoustic data with other ecological information sources. To help address these needs, the overarching aim addressed in this thesis is:

> To investigate acoustic methods as a means of enhancing ecological research and monitoring, enabling improved characterisation of animal populations, habitat quality and conservation status.

The questions raised and addressed within the published works are:

1. How do vocal activity rates relate to bird abundance?
2. How can acoustic recordings enable the development of effective species occupancy models?
3. Can the breeding status of bird pairs be assessed by the identification of different song/call types?
4. How do environmental conditions, such as habitat structure and weather, affect

acoustic data?

5. How does the research inform the development of evidence-based acoustic survey and monitoring guidance?

Chapter 3

PUBLICATIONS

3.1 Introduction

Seven papers are included within this thesis and are collated in the following pages. The papers are not ordered chronologically, but by theme, to promote cohesion and progress more logically (Mason & Merga, 2018). The papers, in this order, address the overarching aim of the thesis by setting out the need for the research, providing evidence for the research questions, and concluding with methodological guidance.

Each article is presented in its published version, and figure and table numbering remains the same as the original, rather than being consecutive through the thesis. The published articles include their own references, and so the references listed at the end of the thesis are only those cited in unpublished sections.

3.2 Evidence-based survey guidance

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Big Ideas: Do We Need More Evidence-Based Survey Guidance?

Do We Need More Evidence-Based Survey Guidance?

Keywords: evidence-based, good practice, guidance, monitoring, survey

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As ecologists and environmental managers, we rely on good quality baseline information. However, the survey methods we currently employ are often unsupported by scientific testing and are not proven to provide high quality outputs. As a community of practitioners, we should seek to change this, taking on board new research and technological developments – and building more evidence explicitly into our survey guidance.

Figure 1. GPS-enabled tablets allow accurate field recording, with forms that can be customised to different types of survey or sites, to allow standardised data collection. Photo credit Carlos Abrahams.

Introduction

As ecologists and environmental managers, the data we gather through survey and monitoring programmes is vitally important in all aspects of our work. It allows us to predict impacts with some level of confidence, track and anticipate trends in biodiversity, and assess whether our management interventions are working – or not. To generate good quality data though, we need good quality survey methods, which are developed, reviewed and updated in line with existing evidence, new scientific findings and technological developments (Figure 1).

To an extent, we already have reasonable survey methods, which have provided much useful information in national monitoring programmes or in site-based assessments. We are lucky in the UK to have a well-developed history of voluntary and professional work in the conservation sector, and long established standards for surveying flora and fauna. However, if we consider the age of some extant survey guidance (such as the *Great Crested Newt Mitigation Guidelines,* English Nature 2001), against the pace of research and technological change, the need for ongoing updates becomes clear.

We all have a responsibility to ensure that our survey methods are fit for purpose. Both BS:42020 (BSI 2013) and the CIEEM *Code of Professional Conduct* require that methods used to undertake surveys should follow published good practice guidelines where they exist. However, if published guidance is out of date and/or better techniques have been developed, then we should take new innovative approaches where these could provide a better outcome. To make this type of judgment call we should be basing our decisions on *evidence* of what actually works best for our particular needs. However, in the first instance, how much of our established

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Big Ideas: Do We Need More Evidence-Based Survey Guidance? (contd)

and published good practice guidance is based on evidence? How frequently has testing of methods been undertaken, allowing comparisons between different survey approaches? And how many of our methods have been developed for site-based assessments by professionals, rather than for national monitoring by citizen scientists? For example, why do we still apply the *Great Crested Newt Mitigation Guidelines* recommendation of four visits for presence/absence surveys and six for population size class assessment (English Nature 2001) when recent publications (Kropfli *et al*. 2010, Sewell *et al*. 2013) state that up to six visits may be required to accurately record presence/absence at some ponds, and seven to eight surveys are needed to consistently gauge population numbers (although the population size class can probably be determined at the majority of sites from only four visits, Wynn 2013)?

CIEEM and its contributing members have done a very useful job in recent years of compiling the *Sources of Survey Methods*, and following this up with *A Guide to Good Practice Guidance*, as highlighted by Sally Hayns in the December 2017 issue of *In Practice* (Hayns 2017). Both resources list a wide range of references, which form the canon of our professional practice as ecologists. In January 2016, CIEEM also produced the excellent *Principles of Preparing Good Guidance for Ecologists and Environmental Managers*. This states at PRINCIPLE IV that good guidance should be explicitly based on good evidence:

> *'All guidance should be evidence-based and should reference original sources, where available, that illustrate that the techniques recommended are appropriate...... Where guidance is based on existing good practice, but the scientific evidence supporting it is limited, this should be stated and there should be sufficient flexibility in the guidance to allow for individuals to innovate. Scientific testing, e.g. comparative studies of different techniques, is strongly recommended where new approaches are suggested and the results should be published widely.'*

This principle sets out an aspiration for our survey guidance that is not being regularly met in our current documentation. Any review of guidance drawn from a range of sources will show that the reasons being put forward for specific recommendations are often not clear or appropriately justified even though the actual methods may be set out in great detail. This omission is well demonstrated in some of our most commonly used publications.

Survey Methods

Bats: The Bat Conservation Trust's (BCT) *Bat Surveys for Professional Ecologists* (Collins 2016) is one of the best pieces of guidance that we have available, and has been repeatedly updated to its current third edition. However, some areas remain that could benefit from increased explanation and by reference to the scientific literature.

When conducting bat surveys, a critical first step in determining the level of survey effort to be employed at a site is a habitat quality assessment into low, medium or high categories. This translates into the number of surveys that should be undertaken, with 1-3 emergence surveys, or 3-12 transects being recommended. Although the guidance for this habitat assessment process has been improved in the third edition, it is still limited and qualitative, with no obvious basis in evidence. Furthermore, why does the guidance recommend one visit to low-potential roost features and three visits to high-potential features – and why this way round? Has this approach been tested to determine whether it will provide accurate information about roost presence or absence? If so, it would be very useful to see the underlying evidence. The inclusion of background research would serve to increase confidence in the method and would reassure bat surveyors that the recommendations will provide sound and valid data. However, the broad rules of thumb put forward as 'good practice' in the BCT guidance don't appear to be based on scientific studies that determine how much survey is appropriate, or how survey effort should be programmed through the season. Research that has carried out method testing should be incorporated into guidance, and could help to improve the protocols for assessing building roosts (Underhill-Day 2017), inform the levels of survey effort needed to detect common or rare species at sampling locations (Skalak *et al*. 2012), and identify which type of bat detector we should be using to capture call data (Figure 2) (Adams *et al*. 2012).

Birds: There are a number of recognised survey methods for birds, depending on the habitats and taxa being targeted (Gilbert *et al*. 1998). However, many of these are designed for national survey programmes by volunteers, rather than being optimised for the needs of smaller-scale site assessments, such as EcIA studies. A notable exception is the windfarm survey guidance produced by the statutory authorities, e.g. Scottish Natural Heritage (2014). For breeding bird studies, the majority of consultants will probably use a territory mapping approach, based on Common Birds Census (Marchant

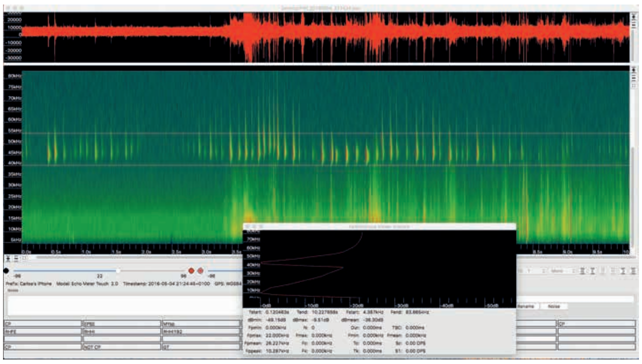

Figure 2. Full-spectrum audio recording allows high quality acoustic data to be collected from vocal species groups, such as bats and birds. Photo credit Carlos Abrahams.

Figure 3. The use of bioacoustics is common practice for bat surveyors, but could be used effectively by ecologists studying other groups of species. Here an acoustic recorder is deployed to record capercaillie *Tetrao urogallus* in north-east Scotland. Photo credit Carlos Abrahams.

Figure 4. The use of artificial cover objects (ACO) has long been the mainstay of reptile surveys. In the absence of rigorous scientific testing, there are still disagreements over the number, material and colour of ACOs that should be used. Photo credit Carlos Abrahams.

1983). This method is useful for providing detailed information on the distribution of bird territories, but is time-consuming, and difficult to apply and interpret. As there is no set number of site visits for this method when used by consultants, the number of surveys carried out within EcIA studies is often determined by the consultant's qualitative assessment of the site or their own established practice. The appropriate level of survey effort required to accurately assess the composition and species-richness of a bird assemblage in a particular location has not been determined in many cases (Calladine *et al*. 2009). In addition, territory mapping may not even be the best option for EcIA purposes: point counts, line transects or bioacoustic recording might provide equal or better quality data, and probably with less survey effort (Figure 3) (Abrahams and Denny 2018; Gregory *et al*. 2004).

Reptiles: Our current reptile survey guidance consists principally of Froglife's (1999) *'Advice Sheet 10: Reptile Surveys'*. There was an attempt to update this with Natural England's (2011) *Mitigation Guidelines (TIN102)*, which were rapidly withdrawn, and the more recent survey protocols from Sewell *et al*. (2013), which incorporated seasonal variations in detectability by species. This latter document was perhaps the first major advance in our approach to reptile survey in the past two decades, but remains unknown to many practising ecologists. The lack of scientific support for established methods and the need for improved approaches was recently highlighted in a review of reptile monitoring programmes (Nash 2018), which showed that new evidence is available to support the revision of survey protocols (Figure 4).

Using Evidence

We need to use science more to tell us the answers to two important questions: (i) which survey methods are best – or at least 'good', and (ii) how much survey effort is needed to generate a sound understanding of a study area? If we want to develop robust and accurate ecological baselines for Environmental Impact Assessments (and other purposes), then we should make sure that our methods are up to the job. It may be that the methods we currently employ are just fine, and incorporating referenced research into our existing guidance would allow us to demonstrate this. If so, we have no need for concern. However, if the methods we use have no demonstrable scientific basis then we need to recognise this as an industry and develop new protocols over time to promote the best practicable methods for data collection, clearly based on evidence. After all, this is the absolute bedrock of our day-to-day work, on which we base assessments, make recommendations and stake our reputations. How can we not take a more evidence-based approach to survey?

Creating survey guidance is a hard and thankless task. Building the content, gaining agreement from a range of professionals with their own views and experiences, and then getting organisations to approve the finished article will never be easy. Griffiths *et al*. (2015) note that *'The uptake of new methods by professional practice will..... be strongly influenced by cost, practicality and the explicit requirements of regulatory authorities'*. However, there is always room for developments in practice where these are supported by good argument and good evidence, so each of us as individuals – and as a community of practitioners – are free to pave new ways where they are needed. One could (correctly) argue that professional judgment should be applied by all ecologists when designing their surveys, and we should all be prepared and able to go beyond standard survey guidance. However, we don't always have time to keep up to date with technical developments in all the fields in which we might work. Accessing information on methodological advances can be difficult in itself, especially for those who aren't fortunate enough to have access to the scientific literature.

To help develop a better scientific context for our published guidance, there are a number of ways forward. Firstly, any new guidance that is produced should explicitly state the evidence on which it is based, 100

Big Ideas: Do We Need More Evidence-Based Survey Guidance? (contd)

and provide appropriate references. Or, if it is only based on best-guess rules-of-thumb, this should be stated clearly. Secondly, consultants, consultees and regulators should all take a more flexible approach to survey methods, and concentrate more on the quality (and meaning) of outputs rather than whether standard protocol has been slavishly followed. Most importantly though, we would make a call for a 'Survey Evidence' initiative for ecologists, along similar lines to Conservation Evidence (www.conservationevidence.com). This would gather, assess and disseminate research findings to allow optimal survey and monitoring recommendations to be developed. This could be done within an organisational setting, or perhaps better, in a crowd-sourced, Wikipedia-style, online forum to which anyone interested could contribute. Such an approach would allow new research findings to be added regularly, allowing constant ongoing development of scientifically supported survey methods and technological innovations – and rapid communication of these across the sector, instead of waiting for irregular approval by a formal authority. It would be independent, authoritative and available to all, demonstrating good practice for our work and enabling us to make better, informed decisions on how we gather data. It would require us to examine our established, and often outdated, methods. In the end, it would raise the questions we should all be asking ourselves. Is our good practice guidance actually proven to be good enough? And if not, how can we all make it better?

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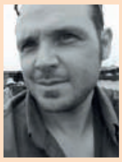

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3.3 Acoustic recorders for monitoring capercaillie

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A first test of unattended, acoustic recorders for monitoring Capercaillie *Tetrao urogallus* lekking activity

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ABSTRACT
Capsule: Automated acoustic recording can be used as a valuable survey technique for Capercaillie *Tetrao urogallus* leks, improving the quality and quantity of field data for this endangered bird species. However, more development work and testing against traditional methods are needed to establish optimal working practices.
Aims: This study aims to determine whether Capercaillie vocalizations can be recognized in lek recordings, whether this can be automated using readily available software, and whether the number of calls resulting varies with location, weather conditions, date and time of day.
Methods: Unattended recording devices and semi-automated call classification software were used to record and analyse the display calls of Capercaillie at three known lek sites in Scotland over a two-week period.
Results: Capercaillie calls were successfully and rapidly identified within a data set that included the vocalizations of other bird species and environmental noise. Calls could be readily recognized to species level using a combination of unsupervised software and manual analysis. The number of calls varied by time and date, by recorder/microphone location at the lek site, and with weather conditions. This information can be used to better target future acoustic monitoring and improve the quality of existing traditional lek surveys.
Conclusion: Bioacoustic methods provide a practical and cost-effective way to determine habitat occupancy and activity levels by a vocally distinctive bird species. Following further testing alongside traditional counting methods, it could offer a significant new approach towards more effective monitoring of local population levels for Capercaillie and other species of conservation concern.

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The Western Capercaillie *Tetrao urogallus* (hereafter Capercaillie) is a bird of high conservation concern in the UK, and elsewhere in Europe, on account of its low population size and historical decline (Storch 2000, Eaton *et al.* 2015). Thought to have become extinct in Scotland in the mid to late eighteenth century, it was successfully reintroduced, but has declined again in the twentieth century. Whilst the reasons for this decline are complex and not fully understood, research has shown that low breeding success associated with climate change, and mortality resulting from adult birds flying into forest fences, have contributed to the decline (Moss 2001, Ewing *et al.* 2012). The Scottish Capercaillie population has been subject to concerted conservation management efforts over the past few decades, which appear to have stabilized the population at a critically low level but not increased it (Wilkinson *et al.* 2018), rendering it susceptible to extinction again in Britain (Moss 2001).

A range of methods have been used for Capercaillie monitoring, including counts of displaying males at leks (Picozzi *et al.* 1992, Summers *et al.* 2010) and genetic capture–recapture techniques (Jacob *et al.* 2010) to assess population status. For national status surveys in Scotland, line transects are conducted in winter (Ewing *et al.* 2012, Wilkinson *et al.* 2018). However, the species currently has a low population density and variable detectability relating to habitat type, sex and temperature (Ewing *et al.* 2012). As a result, the 2015/16 national transect survey only recorded an average of one Capercaillie encounter per 12.3 km of transect. Whilst there are good reasons for applying a winter transect count method for the national survey (Ewing *et al.* 2012, Wilkinson *et al.* 2018), the low encounter rates hinder the ability of this survey method to sensitively track changes in the population at smaller temporal and spatial scales.

Capercaillies have a polygonous mating system with an 'exploded' lek breeding system, where males display over a dispersed area to indicate their breeding condition and quality (Wegge *et al.* 2013). The leks

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occur in forest habitat, centre on a display ground covering an area of approximately 0.30 ha, and have mean numbers of male birds of between 0.5 and 20+ per lek, dependent on the quality and quantity of the surrounding old forest habitat (Hjorth 1970, Picozzi *et al.* 1992, Storch 1995, Angelstam 2004, Summers *et al.* 2004, Laiolo *et al.* 2011). Since 2002, Capercaillies in Scotland have been counted at lek sites each April, with a subset of 69 leks subject to consistent monitoring effort. Between 2004 and 2010, the number of male birds at regularly counted leks declined from 215 to 152 birds, a fall of 29.3% (Ewing *et al.* 2012). This may have been due to an overall population decline, abandonment of traditional lek sites in favour of new sites or a combination of these processes. One of the advantages of acoustic monitoring is the potential for wider spatial and temporal systematic sampling, facilitating the identification of newly occupied lek sites.

The quality of data from traditional lek counts may be affected by differences in detection probabilities between habitats or survey events (e.g. in ambient background noise), or measurement and identification errors. Biases may occur in traditional bird count data, with large inter- and intra-observer errors (Celis-Murillo *et al.* 2009, Simons *et al.* 2009) – sometimes due to existing knowledge about the survey area (Hancock *et al.* 1999). For Capercaillie, the surveyed lek sites are often remote, experienced surveyors are few in number, and the necessary timing and seasonal constraints on field survey methods raise difficulties. As a result, the spatial and temporal coverage of Capercaillie sites is currently limited, leading to low confidence in the results from point counts. In addition, Capercaillies are known to be susceptible to human disturbance (Summers *et al.* 2004, Ewing *et al.* 2012), and regular disturbance due to traditional counts has the potential to negatively affect populations. There is a clear need for improved monitoring techniques, especially at important sites, or locations where management actions have been implemented, to determine site occupancy and finer scale temporal and spatial trends. In this way, significant short-term population changes could be identified more readily to alert conservationists to both acute problems and management intervention success. The use of automated acoustic detection, alongside existing survey methods, could reduce the recognized biases and act as a complementary method to enable more accurate population estimates, but there are always going to be logistical and cost implications undertaking both methods in parallel.

As an alternative or complement to existing techniques, we test here the use of unattended sound recorders (often called 'passive' or 'autonomous' recorders) for monitoring Capercaillie leks. Recording of vocalizations has previously been used to monitor other bird species, such as Great Bitterns *Botaurus stellaris* (Gilbert *et al.* 2002), Corncrakes *Crex crex* (Peake & McGregor 2001) and European Nightjars *Caprimulgus europaeus* (Zwart *et al.* 2014). Unattended sound recording is especially applicable in situations where populations are remote, sensitive to disturbance, or the species is cryptic, as recorders can be deployed in the field for long periods of time with minimal surveyor influence at the monitoring site. Hence, this method is potentially highly applicable for Capercaillie.

The displays of Capercaillie males at lek sites commonly entail a sequence starting with vocalizations from a tree perch, before moving to the ground to commute to the lek centre and later adding visual signals to their continuing display songs (Wegge *et al.* 2013). The typical full Capercaillie display song (Figure 1) consists of a low frequency broadband rattle between 1 and 5 kHz, then a deep pop, followed by a repeated scratchy sound between 2.5 and 6.5 kHz. This sequence is described as 'drum roll – cork pop – whetting' by Liaolo *et al.* (2011).

As part of a monitoring programme, effective recording and recognition of Capercaillie vocalizations within large audio data sets could allow the occupancy of a site to be determined, and an index of relative use to be developed (Briggs *et al.* 2012, Cornec *et al.* 2014). It may also be possible to assess the number of male birds at a lek from sound recordings. Laiolo *et al.* (2011) found that Capercaillie song rate (the number of songs per minute from an individual bird) is significantly associated with the number of displaying males. This is likely to be as a signal of intimidation, as the birds attending the lek stimulate each other by increasing their vocal display. Therefore, song rate, recorded using automated bioacoustic techniques, could be used as a proxy for lek counts undertaken by traditional methods.

This study sets out to determine whether Capercaillie vocalizations can be recognized to species level in recordings, and whether this recognition can be automated and calls counted using readily available software. The results are then used to determine how the number of calls varied according to location, weather conditions, date and time of day.

Methods

Four Wildlife Acoustics (www.wildlifeacoustics.com), SM2 acoustic recorders were placed at known Capercaillie lek sites near Aviemore, Scotland (57.19°N 3.82°W) in April 2016. Each recorder was programmed to record in stereo, with one Wildlife Acoustics SMX-II

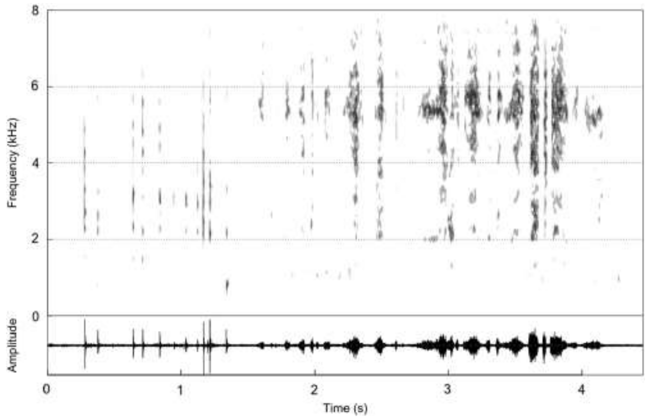

Figure 1. Typical spectrogram of an example Capercaillie call showing frequency spectrum in upper window and amplitude in lower window.

omnidirectional microphone (left channel, 0) mounted on the recording unit and another (right channel, 1) at the end of a 50 m extension cable. The recorder and cabled microphones were both attached to trees at approximately 1.5 m off the ground, and oriented horizontally in opposite directions N–S or E–W. The microphone and recorder were both placed in the vicinity of the lek centre as indicated by a surveyor familiar with the sites and the normal lek count hide locations. A global positioning system device was used to record coordinates of all recorder and microphone locations. The four recording devices were placed at three lek sites, each separated by a distance of kilometres. At one lek site, two recorders (9333 and 9898) were placed together, with the four microphones mounted on the recorders and associated cables forming the corners of an approximate $50 \times 50\ m^2$. The reason for doing this was the fact that previous count surveys and checks for field signs had been unable to accurately define the location of the lek at the site.

The recorders were programmed to record between 04:00 and 10:00 hours every day, starting at 04:00 on 23 April 2016 and ending at 10:00 on 6 May 2016. Recording was limited to these times based on standard lek count practice and surveyor advice (Haysom 2013, S. West, pers. comm.), whilst saving the limited battery life and data storage capacity. Sunrise time at the start of the survey period was at 05:46 hours, getting earlier to 05:14 hours at the end of the survey. During each survey day, the recorders created a series of 10-minute duration full-spectrum data files in Waveform Audio File (.wav) format, recording at a sampling rate of 24 000 Hz and 16 bits per sample. Recording was constant during the set times, without triggers being set. No high or low pass filters were used, and a gain setting of +48 dB was applied. The SMX-II microphones used have a typical sensitivity of −40 to −43 dBV/pa and frequency response of 20–20 000 Hz (Ehnes & Foote 2015, Turgeon *et al.* 2017).

The survey provided a data set covering 14 days (84 hours) at each of the four recorders, with the data from each recorder comprising 505 stereo files (total 2020). The final day of recording (04:00–10:00, 6 May) was used to produce a set of training data for developing an automated call recognizer in the software. The remaining 13 days were retained for analysis purposes.

Data were analysed using Kaleidoscope Pro 4.0.0 software (Wildlife Acoustics 2016), using its 'cluster analysis' method. This process searches for repeated phrases in the recordings (e.g. the song of a particular bird species) and groups these into a number of clusters based on their similarity. It provides a numerical score to quantify the 'distance' of each individual vocalization phrase from the centre of the cluster (low scores being better matches with this average). According to the software protocol, a preliminary analysis was conducted on the training data to scan and cluster recordings. The clustering process identified individual 'phrase segments' within the training data, each of these being a mono recording (from either the right or left channel), >2 and <7 seconds in duration (the typical song length of Capercaillie), comprising a sequence of 'syllables' occurring close enough together in time such that the defined 'maximum inter-syllable gap' of 1 second is not exceeded. All the phrase segments from the training data were individually reviewed and manually identified as either Capercaillie calls or other sounds, by viewing the sonogram and listening to playback. In addition, the performance of the clustering process was assessed by comparing clustered data to a stratified sample of the original recordings. Each phrase segment selected by clustering could include vocalizations by more than one bird species, if these were singing simultaneously within the frequency band, but they were assigned as Capercaillie if calls from this species were included. From this manual review, the cluster with the highest proportion of Capercaillie phrases from the training data was identified, and this cluster was then used as a recognizer to identify matching Capercaillie phrases within the 13-day sequence of analysis data, using the same analysis parameters as used for the training data.

To assess the effectiveness of the classification process, all the phrase segments identified in the analysis data as 'Capercaillie' matches were manually checked by viewing the sonogram and listening to playback. This allowed the proportion of false positive matches to be assessed. To identify the proportion of false negatives, a random selection of 500 (4%) 'non-Capercaillie' phrase segments from the analysis data was also manually checked.

For call analysis with Kaleidoscope Pro, the following analysis parameters were used: Daily subdirectories created; Files split to 60 seconds max duration; Split channels; Signal of interest 1500–4000 Hz; Duration 2–6 seconds; Maximum inter-syllable gap 1 seconds; Max distance from cluster centre to include outputs in cluster.csv = 1.0; Fast Fourier Transforms window = 5.33 ms; Max states = 12; Max distance to cluster centre for building clusters = 0.5; Max clusters = 500.

As environmental context for the acoustic data, weather data for the Met Office MIDAS station at Aviemore was accessed through BADC (badc.nerc.ac.uk/cgi-bin/midas_stations/station_details.cgi.py?id=113&db=midas_stations) and DATA.GOV.UK (using the Aviemore weather station codes DCNN 0585 and RAIN 817692). Daily rain data for Northern Scotland was also accessed from Hadley UKP (www.metoffice.gov.uk/hadobs/ hadukp/data/download.html). Statistical tests were carried out using R and R Studio software (R Core Team 2013, R Studio Team 2015).

Results

The first stage of analysis used clustering to identify and group similar vocalizations within the single day of training data. This identified 5401 individual phrase segments, produced by a variety of bird species, grouped into ten clusters. The total duration of these phrase segments amounted to 4.88 hours, out of a total recording time of 48 hours (4 recorders × 6 hours × 2 channels). All 5401 training data phrase segments were manually reviewed (taking less than eight hours), with 258 segments (5%) identified as having Capercaillie calls, and 5143 segments without Capercaillie (Table 1). Of the 5401 phrase segments, 80 were assigned to Cluster 09, in which 52 (65%) were manually confirmed to contain Capercaillie calls (the highest proportion of Capercaillie calls of any cluster). The remaining 206 phrase segments that included Capercaillie vocalizations (often overlapping calls from other species) were spread through the remaining clusters. Most of these were in Cluster 08, which had Capercaillie vocalizations in 20.1% of its phrase segments, whilst all remaining clusters had less than 5% of phrase segments being positive for Capercaillie. Hence, clustering of the training data at this initial stage provided a single main Capercaillie cluster which picked out 52 (20%) of 258 Capercaillie phrase segments manually identified from the data set. The check back of clustered data against the original recordings showed that the clustering performed well according to the set parameters. The clustering correctly identified the presence or absence of Capercaillie in the 10-minute .wav files 75% of the time, with false positives (calls incorrectly assigned to Cluster 9) in 8% of cases and false negatives (calls missed or assigned to another cluster) in 17% of cases. This manual review also indicated that there were a number of short Capercaillie sequences or individual spaced calls present that were outside the parameters of the clustering process due to their limited duration (often being less than 1 second).

Using Cluster 09 to identify similar Capercaillie recordings, the remaining 13-day sequence of analysis data was processed to determine whether Capercaillie phrases could be effectively identified within the recorded data set. A total of 13 626 phrase segments were produced from the analysis data (Table 1), of which 907 (6.7%) were assigned as a match to the Cluster 09 Capercaillie data. These were all manually checked and 758 of the 907 (83.6%) were confirmed as Capercaillie, with 149 (16.4%) false positive matches. To identify the proportion of false negatives, a random selection of 500 phrase segments (4%) out of the

Table 1. The error matrix produced from: (a) the clustering process which produced the classifier from the single-day training data set and (b) applying this classifier to the 13-day analysis data set. False negatives are where the species was present but not detected by the software (read along the rows less the diagonal cell). False positives are where the software identified the species to be present when it was not (read down the columns less the diagonal cell).

		Software classifier			
		Capercaillie	Other	Total	False negative (%)
(a) Training data set					
Manual identification	Capercaillie	52	206	258	79.8
	Other	28	5115	5143	0.58
	Total	80	5321	5401	
	False positive (%)	35.0	3.87		
(b) Analysis data set					
Manual identification	Capercaillie	758	1399 (estimate)	2157	64.9
	Other	149	11,320 (estimate)	11,469	1.3
	Total	907	12,719	13,626	
	False positive (%)	16.4	11.0		

remaining 12 719 were manually checked. Of these, 55 phrases (11%) were confirmed as including Capercaillie vocalizations and hence being false negatives. The greatest proportion of these was in Cluster 08, which had 29% false negatives, and Cluster 01, which had 13%. The remaining clusters 02–07 all had a false negative proportion of <10%. Hence, overall there were estimated to be 1399 ($0.11 \times 12\ 719$) phrase segments containing Capercaillie calls in the analysis data set which were not discovered. This equates to the supervised clustering successfully identifying 83.6% of Capercaillie vocalizations in Cluster 09, and correctly extracting 35% of all Capercaillie phrase segments. These findings mean that the limited number of false positives in Cluster 09 could be manually screened quickly, with a low rate of false negatives scattered through the other clusters – these often being low 'quality' phrase segments with single calls or poorly recorded, and therefore difficult and time-consuming to identify manually.

The data set of 758 Capercaillie phrase segments identified by the cluster process and manual confirmation was used for further analysis. The spectrograms were first analysed to ascertain the characteristics of the recorded calls. Within the data set, the vocalizations had a mean frequency of 3083 Hz, within a general range of 2000–4000 Hz (Figure 2). Some variation was found between the data from different locations, with means between 2874 Hz at recorder 9558 and 3234 Hz at 9333. A median duration of 4.512 seconds was found for the identified phrase segments, with a minimum of 2 seconds and a maximum of 6.94 seconds (as constrained by the software settings).

The differences in the total number of recorded phrase segments (from all species), and those of Capercaillie, were investigated across different recorder locations and between left and right stereo channels. The numbers of all of these varied widely between recorder locations, with almost no vocal activity recorded at 9333, moderate levels at 9558 and highest activity at 9898 and 9573 (Table 2). As context, the number of males recorded during lek counts at these sites in the same season (but not concurrently with recording) were three birds at 9333/9898, five at 9573 and seven at 9558 (S. West, pers. comm.). A great deal of variation was found between the two stereo channels on each recorder, with all locations recording many more calls on one channel than the other. Review of the Capercaillie call data revealed very few instances ($n = 8$, approximately 1%) where near-simultaneous calls were recorded on both left and right channels, that is from the same bird being recorded simultaneously on both channels. Hence large differences were found between data from microphones located 50 m apart. In addition, recorders 9333 and 9898 were both placed in the vicinity of a single lek site and recorded widely differing numbers of vocalizations. A possible reason for this is discussed below.

The number of calls recorded per day was investigated to determine whether there was any trend across the survey (and lekking) period. The overall levels of Capercaillie vocal activity, pooled across all recorder locations, varied day-to-day between 1 and 191 phrase segments, but were highest at the start (23 April) of the survey and declined (with daily variations) throughout the rest of the period (Figure 3). This is likely to reflect a true decline in lekking activity, as the survey was undertaken at the tail end of the main lekking season. The highest daily total of phrase segments at a single recorder was a maximum of 146 at recorder 9898 – this being more than half of all segments recorded at that location, recorded in a single day.

Prior to the study, an early morning peak in vocal activity was expected, with units set to record between 04:00 and 10:00 hours. This assumption was found to be correct, with our data clearly indicating that the highest levels of call activity were recorded in the 2-

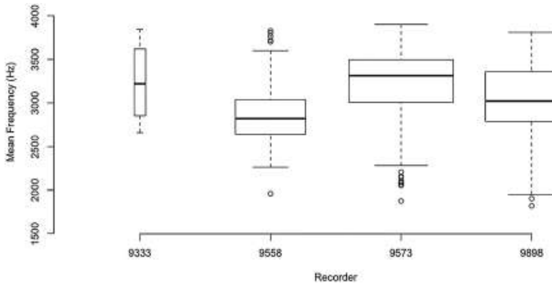

Figure 2. Box plot of mean frequency of Capercaillie phrase segments at each recorder location. The centreline of each box indicates the median value for all phrase segments at each recorder location. Boxes represent the data between lower and upper quartiles, and the whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range. Outliers in each population are represented by dots.

hour period around sunrise (Figure 4), with a median time for all calls of 36 minutes before sunrise. There are significant differences between the recorder locations though (Kruskal–Wallis chi-squared = 289.13, df = 3, $P < 0.01$), with unit 9573 being significantly earlier than the other three locations.

If the morning peak in activity is related to sunrise time (i.e. light levels), then we would expect this to get earlier through the survey period as day length changes. This relationship between peak vocalization time and sunrise appears to be demonstrated in Figure 5, where in addition, the high level of calls around 04:00 hours, the start of the recording session, are indicated.

Relationships between the total number of vocalizations per day with three weather parameters were tested using Spearman's rank correlation (Table 3). A significant negative correlation ($P < 0.05$) was found with windspeed (Figure 6), but there was no significant relationship with temperature or rainfall.

Discussion

Our results confirm that automated passive acoustic recorders can effectively be used to detect and record Capercaillie vocalization activity in the field. This study has also shown that semi-automated call analysis can rapidly identify individual vocalization phrases for a target species, with call classification having an accuracy of over 80% accuracy and correctly extracting 35% of all Capercaillie calls (most of those not extracted being of poor quality) – and only producing 16% false positives. The clustering process applied here is a different approach to the use of pre-constructed species-specific recognizers used in many other studies (Brandes 2008, Bardeli *et al.* 2010, Oppel *et al.* 2014). It is primarily intended to be a human-supervised process which organizes sound data into call-type groups to allow rapid manual review and labelling. With the appropriate manual checks, including identification of false negative and positive classifications, it was very successful in correctly identifying Capercaillie vocalizations in the analysis data set, even when based on a small single set of training data – albeit with a relatively high omission error (64.9%). Although the clustering process used here, based on a limited number of individuals, was suitable for identifying birds at the study sites, it is expected that improved rates of detection, with fewer false positives and negatives, could be achieved in future studies with a larger training data set (Digby *et al.* 2013). In addition, it is worth noting that our method

Table 2. Total numbers of phrase segments at each recorder location.

Recorder		9333	9898	9558	9573
Lek site		A	A	B	C
Lek count (males)		3	3	7	5
All phrase segments	Microphone 1/2 Left/Right	449/75	1445/743	186/1750	5599/3379
	Total	524	2188	1936	8978
Capercaillie phrase segments	Microphone 1/2 Left/Right	4/0	206/59	0/152	272/65
	Total (% of all phrases)	4 (0.76%)	265 (12.11%)	152 (7.85%)	337 (3.75%)
	Mean(range)/day	0.31(0–2)	20.38 (0–146)	11.69 (0–40)	25.92 (0–101)

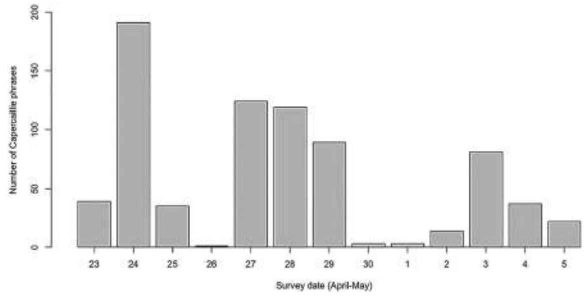

Figure 3. Total number of Capercaillie phrase segments recorded per day, across all detectors.

did not attempt to exhaustively identify every Capercaillie vocalization in the recorded data set. The clustering approach allowed a user-determined set of search parameters to be applied to the data, with vocalizations that matched the settings being selected as phrase segments. As a result, it is accepted that vocalizations not matching these criteria (e.g. short individual calls) would not have been identified, and the Capercaillie phrase segments used in our analysis are a reduced subset of the overall recorded activity. However, the defined criteria used in the clustering ensure that vocalizations of the same type and quality are being compared between different days and detector locations, allowing a coherent analysis of the call data. This rapid analysis method, with low levels of false positives, is particularly suited to ascertaining the presence of Capercaillies at a site, which could be a very useful tool for a species with low densities and fluctuating lek site occupancy.

The numbers of calls recorded varied widely between recorder locations and also between left and right channels on the same recorder. The former could indicate differences in the levels of vocal activity between different lek sites, whilst the latter indicates that Capercaillie calls do not travel well over distance, that is detectability is limited at distances over 50 m. This is similar to detection ranges found in other bioacoustic studies of forest birds (Venier *et al.* 2012, Sedláček et al. 2015). Using the same type of recorders and microphones, Turgeon *et al.* (2017) found bird call detection radii of between 13 and 203 m, dependent on the species, background noise levels and microphone condition. For comparison, the spacing between individual Capercaillies at leks has been recorded as 64–212 m (with interactions between males sometimes occurring at less than 10 m), and calls from this species can generally be heard at a distance up to approximately 200 m by the human ear (Hjorth 1970, Moss & Lockie 1979, Wegge *et al.* 2013). This relationship between detection distances and bird density clearly raises the issue of detectability during surveys, for both human

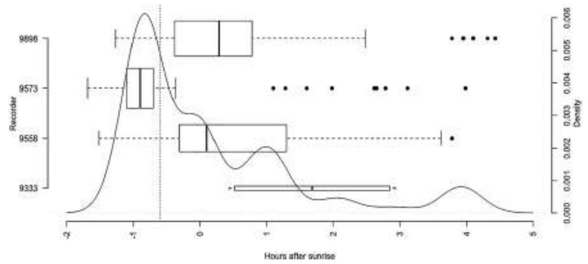

Figure 4. Capercaillie vocalizations in relation to sunrise time. Box plots indicate median times, quartiles and ranges for Capercaillie phrase segments at each recorder location, in relation to sunrise. Box plot width indicates relative sample size. The median time for all Capercaillie phrase segments recorded is indicated by the dotted vertical line at 36 minutes before sunrise. The kernel density of Capercaillie phrase segments over time is shown by the solid line.

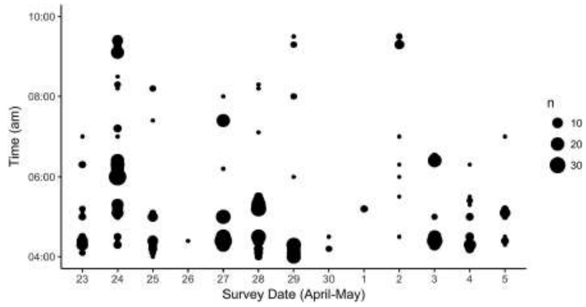

Figure 5. Timing of Capercaillie vocalizations in relation to date, for all recorder locations combined. The size of circles indicates the number of phrase segments recorded within each 10-minute recording period.

Table 3. Spearman''s rank correlation of weather conditions with total number of Capercaillie calls per day.

Variable	S	*P*	rho
Wind	576.64	0.036	−0.584
Temperature	523.22	0.135	−0.437
Rain	532.46	0.111	−0.463

counters and automated recording equipment (Yip *et al.* 2017). This indicates that, for bioacoustics methods, careful thought needs to be given to the number, layout and response of recorders and microphones, as well as the characteristics of the recording environment. In addition, when recording and analysing sound files, the appropriate audio settings, such as gain, sample rate and the use of high and low pass filters should be considered. The development of good practice guidance for this should be prioritized to ensure repeatable results from any future monitoring programme (Eyre *et al.* 2014, Pocock *et al.* 2015), and further research should focus on elucidating the optimum number of microphones, and distance between them, at a lek site.

In this study, the pair of recorders 9333 and 9898 were located either side of a wide electricity pylon way leave through the forest, with the lek site thought possibly to be present within the open way leave habitat between. However, the recorder on the northern side of the way leave (9898) recorded 265 Capercaillie phrases, compared to only four on the south side (9333). This is likely to indicate that the lek site was actually present within the forest to the north of both recorders, and audible sounds were only picked up by the closest set of equipment.

Differences were found in median call timings between locations, with recorder location 9573 recording calls significantly earlier in the day compared to other locations. This could perhaps be due to habitat differences, such as forest structure, aspect or altitude. For example, 9573 was the lowest of all four sites at

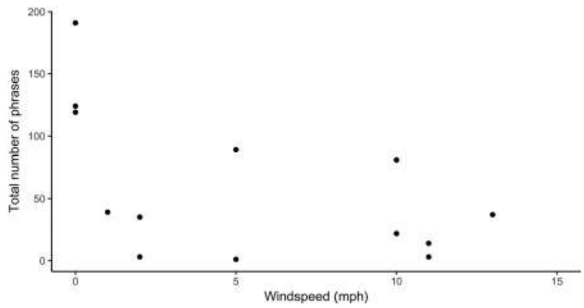

Figure 6. Inverse relationship between number of phrase segments recorded per day and wind speed. Spearman's rank correlation coefficient ($S = 576.64$, $P = 0.036$, rho $= -0.584$).

255 m above sea level (asl) and in relatively open forest habitat, whilst the rest were at 325–375 m asl, and in denser plantations. Further exploration of how the environment might affect Capercaillie lekking behaviour would be worthwhile (Angelstam 2004, Laiolo *et al.* 2011).

Lek monitoring at the local scale rather than winter transect counts, which are subject to low encounter rates (Ewing *et al.* 2012), should be seen as an important method of monitoring the effects of management and alert practitioners to local population changes. As discussed above, there are significant limitations to traditional manual lek counts, and the automated acoustic approach provides a promising alternative or complement. Within our study, large differences were found between the number of Capercaillie vocalizations recorded at each of the three locations. This may partly be due to the precise location of the recorders in relation to the lekking birds, given the range detectability issue discussed above (which is also likely to affect human observers), but could also be a true reflection of bird numbers and activity levels at each site. We anticipate that the level of call data recorded using our methods should be indicative of population size and lekking activity, but comparison with human observer counts has not been attempted in this study, due to the limited number of leks covered and the lack of synchronous count data. Further work is clearly required in this area, but studies have shown that recorded calling rates are positively relate to lek size in White-bearded Manakin *Manacus manacus* (Cestari *et al.* 2016) and White-bellied Emerald *Amaziliu candida* (Atwood *et al.* 1991), and to nest density at Cory's Shearwater *Calonectris borealis* breeding sites (Oppel *et al.* 2014). These findings indicate that acoustic monitoring may be useful to document relative changes in local bird populations over time. In particular, the day-to-day variation we recorded in call activity at each site over the survey period (Figure 3) must sound a note of caution to reliance on Capercaillie population data from single visit lek counts.

Haysom (2013) recommends that Capercaillie lek surveys in Scotland should take place during the peak period of mid-April to early May, with variation according to spring temperatures. The call activity we recorded was highest at the start of the survey period (23 April) and declined through the survey period. Hence, this indicates that earlier activity might have been missed in this study. Further unattended acoustic research of Capercaillie leks should aim to test whether there is activity prior to mid-April, to understand whether the recommended seasonal parameters of traditional lek surveys need to be adjusted.

The peak of highest levels of call activity, across all recorders, occurred at 36 minutes before sunrise. The standard guidance by Haysom (2013) recommends that leks should ideally be counted from 04:00 to 06:00 hours. However, relatively high levels of call activity were recorded at the start of our daily survey period (04:00–10:00 hours), so for future studies, an earlier survey start is recommended, for example, 2–3 hours before sunrise (02:30–03:30 hours).

The number of recorded vocalizations decreased with increasing wind speed. This could be due to: (i) reduced calling (and possibly lekking) activity in adverse weather conditions, (ii) reduced detectability of calls in high winds or (iii) increased masking by background noise in high winds (Digby *et al.* 2013). There is anecdotal recognition of the effects of environmental parameters – weather and altitude – on call activity from human observers at lek counts. The impacts of this on results could benefit from further investigation to allow the quality of count data to be assessed against weather conditions, with weather factors being modelled into data analysis. It would be more practicable to achieve this with the long data sets possible from automated recording, than those provided by the limited resource of human surveyors (Oppel *et al.* 2014).

In conclusion, this study has shown that Capercaillie can be effectively recorded in the field using automated passive acoustic methods. The equipment necessary to do this is simple and readily available, and enormous progress in signal processing and pattern recognition in recent years has made it possible to incorporate automated methods into the detection of vocalizations (Bardeli *et al.* 2010). As a result, there is a clear opportunity for acoustic monitoring of this species over extended periods, with rapid analysis of the recorded vocalizations. The time and cost savings of this approach over manually reviewing all of the sound data are significant. In this study, a total equivalent of 56 days of recording was completed with only two days of fieldwork and one–two days of call analysis. This is not uncommon; Digby *et al.* (2013) assessed that autonomous recorder methods required less than 3% of the time needed for a comparable traditional field survey.

The continuing vulnerability of the Scottish population of Capercaillie makes regular and consistent monitoring a priority. The use of acoustic techniques could eliminate or minimize observer biases, reduce disturbance caused by surveyors and provide standardized field data that can be permanently archived. It could also help resolve problems associated with surveying in pre-dawn darkness, hard to access survey sites and with the limited availability of expert field observers (Hobson *et al.* 2002, Celis-Murillo *et al.*

2009, Zwart *et al.* 2014). Acoustic recording methods could allow for cost-effective lek occupancy checks of suitable, but previously unmonitored or unoccupied, areas, which would be unfeasible using manual lek surveys. Acoustic data may also be useful in testing when (in terms of weather conditions, season and time of day) manual monitoring would be most effective and could help gauge the accuracy of point counts. As a result, it is a developing tool that could potentially have great application and significance, offering to fill a methodological gap especially for the census of cryptic taxa such as Capercaillie (Dawson & Efford 2009, Bardeli *et al.* 2010, Laiolo 2010, Zwart *et al.* 2014).

The next step in the development of bioacoustics for birds should be in the establishment of recognized survey protocols and statistical approaches to be employed by practitioners such as conservation professionals and ecological consultants (Marques *et al.* 2013), to set out good practice and allow greater comparability between studies of different species and at different locations. This will require testing and work to compare traditional versus acoustic methods – probably developing an improved approach which combines the two into an integrated system. For Capercaillie, the obvious first step is to correlate lek count numbers against the numbers of calls recorded during the same survey event, or better, over a longer survey period surrounding a number of repeated counts at each lek.

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3.4 Lek counts and bioacoustic recording

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ORIGINAL ARTICLE

Comparison between lek counts and bioacoustic recording for monitoring Western Capercaillie (*Tetrao urogallus* L.)

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Abstract

Bioacoustics is the study of animal sounds. The importance of bioacoustics for biological research and the survey and monitoring of bird populations is becoming increasingly recognized. This is particularly the case for the capture of long-term data on rare species that are prone to disturbance or are otherwise difficult to survey. The global population of the Western Capercaillie (*Tetrao urogallus* L.; hereafter 'Capercaillie') is declining, and its status in the UK is highly precarious. Current methods for monitoring this species are subject to a number of constraints that affect the quality of collected data. Bioacoustics could provide a useful complement to these existing methods, in particular for the assessment of activity at leks. This study used acoustic recorders to survey Capercaillie vocal activity for a month at ten lek sites, and quantified the numbers of calls produced. Traditional lek count surveys were undertaken at all sites during this time. The recorded vocal activity data (1) correlated with the number of birds recorded by human surveyors, (2) indicated that traditional surveys may be causing some disturbance at the lek sites, and (3) showed that call numbers are related to temporal and environmental variables. The bioacoustic approach can provide high-quality, long-term data, that can be effectively combined with the traditional lek survey technique. It should be utilized more frequently as a survey and monitoring tool to provide structured, coherent results that can be used to aid conservation efforts.

Keywords Rare species · Point count · Survey · Conservation

Zusammenfassung

Vergleich zwischen Balzplatzzählungen und bioakustischen Aufnahmen beim Monitoring des Auerhuhns (*Tetrao urogallus* L.)

Die Bioakustik befasst sich mit der Untersuchung von Tierstimmen und deren Nutzen für die biologische Forschung. Sie gewinnt zunehmend an Anerkennung bei der Erfassung und dem Monitoring von Vogelpopulationen. Dies ist vor allem der Fall bei der Erhebung von Langzeitdaten zu seltenen Arten, welche störungsanfällig oder auf andere Weise schwer zu erfassen sind. Die globale Population des Auerhuhns (*Tetrao urogallus* L.) nimmt ab und ist vor allem im Vereinigten Königreich in einer höchst prekären Lage. Aktuelle Methoden beim Monitoring von Arten unterliegen zahlreichen Einschränkungen, welche die Qualität der gesammelten Daten beeinflussen. Die Bioakustik könnte eine nutzvolle Ergänzung oder Alternative zu diesen existierenden Methoden bieten, vor allem bei der Beurteilung von Aktivitäten an den Balzplätzen. Diese Studie verwendete akustische Aufnahmegeräte, um die Rufaktivität des Auerhuhns für einen Monat an zehn Balzplätzen zu untersuchen und die abgegebene Anzahl an Rufen zu quantifizieren. An allen Plätzen wurden während dieser Zeit zusätzlich traditionelle Balzplatzzählungen durchgeführt. Die aufgenommenen Rufaktivitätsdaten (i) korrelierten mit der Anzahl an Vögeln, die von den Beobachtern selber erfasst wurden, (ii) deuteten darauf hin, dass traditionelle Zählungen mit großer Wahrscheinlichkeit Störungen an den Balzplätzen verursachen und (iii) zeigten, dass die Rufanzahl in Zusammenhang mit Umweltvariablen steht. Der bioakustische Untersuchungsansatz bietet (neben anderen Vorteilen) Daten mit besserer Qualität, über einen längeren Zeitraum und mit einem geringeren Ressourcenbedarf als die traditionellen Verfahren der Balzplatzzählung. Sie sollte daher häufiger zu Untersuchungs- und Monitoringzwecken verwendet werden, um strukturierte, kohärente Daten zur Verfügung zu stellen, welche für Naturschutzbestrebungen unterstützend hinzugezogen werden können.

Communicated by S. Kipper.

Extended author information available on the last page of the article

Introduction

Bioacoustic techniques, involving the recording of animal sounds, have a long history in ecological study. However, technological innovations in the last 10–20 years have greatly increased the potential of this approach for research in a wide range of habitats and for a variety of taxa (Sueur et al. 2008; Marques et al. 2013). One particularly valuable area for development is the survey of bird assemblages or populations, including rare, cryptic and disturbance-prone species such as the Corncrake (*Crex crex* L.), Bittern (*Botaurus stellaris* L.), Nightjar (*Caprimulgus europaeus* L.) and Western Capercaillie (*Tetrao urogallus* L.) (Abrahams and Denny 2018). Automated static recording units (often called 'passive' or 'autonomous' recorders) are especially well suited to point count-type surveys for highly territorial and lekking species, where systematic spatial and temporal sampling can help determine occupancy, species composition or population size (Brandes 2008; Gasc et al. 2017; Shonfield and Bayne 2017).

Western Capercaillie (hereafter 'Capercaillie') is a rare and declining bird species in the UK, with a small remnant population in forest habitats in northeast Scotland (Wilkinson et al. 2018). The species has an 'exploded' lek mating system, where males display over a dispersed area to indicate their breeding condition—the numbers of birds attending dependent on the quality and amount of the surrounding old forest habitat (Hjorth 1970; Picozzi et al. 1992; Laiolo et al. 2011; Wegge et al. 2013). Alongside other methods (e.g. Jacob et al. 2010), counts of displaying males at leks in spring are used to assess breeding population status and abundance for Capercaillie, for regional/national monitoring programmes (Picozzi et al. 1992; Pollo et al. 2005; Summers et al. 2010). In Scotland, these showed a decline in numbers of 29% between 2004 and 2010 (Ewing et al. 2012), although figures from 2010 to 2016 showed modest between-year fluctuations, with no significant overall trend (Wilkinson et al. 2018).

Although lek counting is one of the few ways to gain regular population data on this elusive species, there are a number of recognized problems with this method. Firstly, Capercaillies are known to be susceptible to human disturbance (Ewing et al. 2012; Mollet et al. 2015), and regular impacts due to traditional counts could potentially have a negative effect on local populations. Surveys normally attempt to limit this disturbance by using trained surveyors and employing hides while at the lek site (Haysom 2013). Secondly, the remoteness of many lek sites, combined with few suitably experienced surveyors, produces practical constraints on surveys, limiting their spatial and temporal coverage. With few monitoring visits taking place, the quality of data from lek counts may be affected by differences in detection probabilities between sites or survey events, or by measurement and identification errors (Simons et al. 2009; Celis-Murillo et al. 2009). Finally, Capercaillie behaviour may affect lek attendance, and make the interpretation of count data difficult. Lek attendance is age dependent, with males aged > 2 years defending territories close to the lek centre, while younger males establish peripheral territories or do not display territorial/lekking behaviour (Mollet et al. 2015). Time of day and date in the season can also impact lek-attendance patterns, and hence, lek counts. Such sources of variation need to be considered when assessing count data, and the detection probability of birds estimated, protocols standardized, and lek counts adjusted to properly estimate populations (Walsh et al. 2004).

The use of acoustic recording, alongside existing survey methods, could reduce the recognized biases outlined above, enabling the improved monitoring of Capercaillie lek sites and providing more accurate population estimates (Laiolo et al. 2011; Oppel et al. 2014). This study used automated recording units for monitoring leks and aimed to determine how data from bioacoustic recording compares to the traditional human lek count method. The objectives of the study were: (1) to compare methods of population assessment, by comparing counts of males from traditional surveys with levels of recorded call activity from the same leks; and (2) to determine whether the levels of call activity from different lek sites can be related to environmental variables, such as weather conditions.

Methods

Acoustic field recording

Ten Wildlife Acoustics (www.wildlifeacoustics.com) Song-Meter SM2 acoustic recorders were placed at known Capercaillie lek sites near Aviemore, Scotland (57.19°N, 3.82°W). A further two were also placed, but failed to record correctly, and were excluded from the analysis. The lek sites were commonly 3–5 km apart, with the furthest points at 27.5-km distance and encompassing an area of 209 km^2. The recorders were positioned on 4–5 April 2017, but programmed to start recording on 10 April 2017. Recorders were collected on completion of the 10 May 2017 recording session, after 31 days of operation.

Each recorder was programmed to record in mono, with one Wildlife Acoustics SMX-II omnidirectional microphone mounted on the recording unit. The recorders were placed in the vicinity of the normal lek count hide locations, with the microphones oriented horizontally towards the assumed lek site 'centre'. The recorders were attached to trees at approximately 1.5 m off the ground and Global Positioning System (GPS) coordinates taken.

The recorders were programmed to operate daily, from 1.5 h before sunrise until 1.5 h after sunrise. This resulted in a recording period from 0451–0751 hours on 10 April 2017 to 0326–0626 hours on 10 May 2017. Recording was limited to these times based on previous experience (Abrahams and Denny 2018), standard lek count practice (Haysom 2013) and surveyor advice (S. West, personal communication), whilst saving the limited battery life and data storage capacity.

Data was recorded in 10-min-duration full-spectrum data files in Waveform Audio File (.wav) format on SD cards at a sampling rate of 8000 Hz and 16 bits/sample. This resulted in recordings covering the frequency range up to 4000 Hz, sufficient to record Capercaillie vocalizations, but exclude higher frequency bird song and other sounds. All recordings had the date, time and recorder site reference appended as metadata.

Lek count

Lek counts took place between 16 April and 1 May 2017, during the period when recorders were placed on site. Hides were set up at the lek sites on the day before the count, and then surveyors entered the hides during the evening. The following morning, surveyors recorded Capercaillie activity and attempted to determine the number of male birds displaying (Haysom 2013). All sites were visited twice during the survey window, except for site 8528, which was only visited once. Survey visits were separated by 1–12 days (mean of 5 days). At two locations, two separate hides were used (giving separate counts), as the lek areas were too large to cover with one hide only. At these two locations, recorders were placed to match the hides (i.e. with recorders 8552 and 9306 at one location, and 8535 and 8607 at another). Hence these two locations are effectively treated as each representing two separate lek sites. This may not be the case ecologically, but it is the case practically, in terms of both the lek counts and using acoustic recorders. The recorders were sufficiently spaced to avoid any double counting in the acoustic data, with separation distances of 260 m between sites 8535 and 8607, and 85 m between sites 8552 and 9306 (Venier et al. 2012; Sedláček et al. 2015; Abrahams and Denny 2018). Site names and details are not given here due to landowner confidentiality.

Call analysis

Data sets

The audio recordings taken from the field consisted of 5580 .wav files (49.9 GB of data). This dataset was analysed using a semi-automated system to identify Capercaillie vocalizations in the recordings, with a three-stage process to produce a Capercaillie call 'recognizer' and final output. An additional dataset was used for recognizer training, consisting of recordings collected in the same area of Scotland in 2016 (Abrahams and Denny 2018). This 2016 dataset consisted of 1586 .wav files (28.2 GB data) collected over 14 days at three lek sites. It was originally recorded at 12-kHz sample rate, and so was downsampled to 8 kHz to match the 2017 recordings.

Data were analysed using Kaleidoscope Pro 4.3.2 software (Wildlife Acoustics 2017), using its cluster analysis method. This process uses hidden Markov models to search for repeated phrases in the recordings (e.g. the song of a particular bird species), and groups these into a number of clusters based on their similarity. This study represents one of the first published tests of this software, filling a recently identified gap in the literature (Knight et al. 2017; Priyadarshani et al. 2018).

Training data recognizer development

The Kaleidoscope software was used to process the 2016 training dataset with unsupervised clustering, default settings and a 1–3 kHz frequency signal of interest (see "Appendix" section). This preliminary analysis scanned the raw recordings to identify individual phrase segments within the training data, each of these being 1.0–6.9 s in duration (the typical song length of Capercaillie), and comprising a sequence of syllables with a maximum inter-syllable gap of 1 s. These segments were then grouped by the software into clusters of similar sound characteristics (e.g. different species or song types), and the results saved.

All of the phrase segments from the 2016 training data were manually reviewed by a visual check of spectrograms and by listening to playback, and then tagged as 'CP' if Capercaillie vocalizations were present, or 'NOTCP' if Capercaillie vocalizations were not present (when the segment was a record of sounds of other bird species or other noise). Each phrase segment could include vocalizations by more than one bird species, if these were singing simultaneously within the target frequency band, but they were assigned as CP if calls from Capercaillie were present. The clustering process enabled a rapid review of the segments, as similar vocalizations were grouped together.

After all phrases had been tagged, a second pass classification was carried out on the training data by re-scanning the manually tagged recordings. This second run used the identification tags to create a pairwise CP/NOTCP recognizer file with which to analyse the 2017 data. No further manual check was done at this second stage, as the sole intention of the second pass is to use the manual identification tags entered into the first pass results to produce the recognizer file for future analysis.

Audio data analysis using call recognizer

The pairwise recognizer, produced from the 2016 training data, was used to analyse the 2017 data. Using the automated process within the Kaleidoscope software, this identified phrase segments in the data, using the same parameters as above, and assigned these vocalizations as either CP or NOTCP. The analysis output was a spreadsheet of call data, with one row per phrase segment (hyperlinked to the associated .wav file), providing information on the vocalization (e.g. duration and frequency), the recorder site, date and time, and whether it was assigned to CP or NOTCP.

Metrics were calculated to report the quality of the recognizer process in detecting vocalizations of the target species. The proportions of false positives and false negatives within the output dataset were estimated by manual review of a random sub-sample of the clustered phrase segments, and precision, recall, and *F*-score calculated (Knight et al. 2017; Chambert et al. 2018). Precision is the proportion of classifications that are true detections of the target species, while recall is the proportion of target species vocalizations correctly recognized. The *F*-score is a combined score, summarising precision and recall together. The best recognizer models should have both high precision and recall, indicating low levels of false positive and false negative identifications.

Environmental data

The altitudes of recorder locations were derived from Ordnance Survey maps, based upon the logged GPS locations. Daily weather data for the Met Office MIDAS station at Aviemore was accessed through the Centre for Environmental Data Analysis (www.ceda.ac.uk). This included the following parameters: precipitation amount (millimetres), maximum air temperature (degrees Celsius), minimum air temperature (degrees Celsius), grass temperature (degrees Celsius), concrete temperature (degrees Celsius), sun duration (hours), wind speed (miles per hour) and maximum gust speed (miles per hour). The altitude and weather parameters were all tested separately for relationships with the daily levels of call activity, using Spearman's rank correlation. All data visualization and statistical tests were carried out using R and R Studio software (R Core Team 2013; RStudio Team 2015).

Results

Lek counts

The lek counts recorded between zero and seven males at each site (Table 1), with the maximum of seven males at two sites: 8621 and 9319. No males were recorded at sites 8535 and 8528, but only one count took place at the latter site. The number of males counted in repeat surveys stayed the same at only one site, and mostly varied by one or two individuals between visits.

Phrase segment classification

Analysis of the 2016 training data produced 20,493 phrase segments, grouped into 12 clusters. A total of 2114 segments

Table 2 Phrase segment identifications at each analysis stage

Identifier	Training: manual	Training: automated	Analysis: automated	Analysis: manual
CP	2114	3371	23,688	1146
NOTCP	18,379	14,666	62,936	2609

Number of phrase segments with Capercaillie vocalizations present (*CP*) and no Capercaillie vocalizations present (*NOTCP*) for both manual and automated identifications with the training and analysis data sets

Table 1 Lek count data at each recorder site (with date of lek count survey)

Recorder site	First lek count date	No. of males	Second lek count date	No. of males
9348	19 April 2017	3	24 April 2017	4
9319	19 April 2017	5	1 May 2017	7
8528	16 April 2017	0	–	–
8621	22 April 2017	7	26 April 2017	5
8535	23 April 2017	0	30 April 2017	0
8607	23 April 2017	3	30 April 2017	1
9306	26 April 2017	2	29 April 2017	2
8552	26 April 2017	6	29 April 2017	5
9345	19 April 2017	1	23 April 2017	2
9558	21 April 2017	5	22 April 2017	6

(10.3%) were manually assigned as CP, with the remaining 18,379 segments (89.7%) tagged as NOTCP (Table 2).

A total of 86,624 phrase segments were obtained from the 2017 analysis data. Of these, 23,688 (27%) were matched by the software recognizer to CP, and 62,936 (73%) to NOTCP (Table 2). A random sample of 3755 phrase segments was manually reviewed, and 1146 (31%) identified as CP, with 2609 (69%) identified as NOTCP (see Table 3). These manually identified segments were individually compared to the automated recognizer classifications, with 2952 segments (79%) correctly classified by the recognizer to either CP or NOTCP. There were 803 (21%) false identifications, comprising 583 (15%) false positives, and 220 (6%) false negatives. These values mean that the recognizer classification had a precision of 0.61, recall of 0.81 and F-score ($\beta = 1$) of 0.70.

Call rate at each site

The mean number of automated CP phrase segments recorded over the month was 2369 per site (76/day per site) (Table 4). The highest levels of vocalization were recorded at site 8552, with 4114 CP segments recorded over the month (mean 133/day). The smallest number of segments was at site 8607, with only 794 (mean 26/day). Sites 8528 and 8535 had no males recorded in lek counts, but respectively had 2580 and 881 CP phrase segments. However, manual review confirmed that these were likely to be nearly all false positives. The proportion of manually identified CP phrase segments at each recorder site, as identified in the sub-sample of 3755 segments, varied between 0 and 90% (Table 4). This confirmed occupancy at all sites, apart from site 8528. A secondary check of all phrase segments for this particular recorder site confirmed that all CP phrase segments were false positives, despite the relatively high number of CP segments identified by the automated recognizer.

To compensate for the incorrect classifications from the automated recognizer, the number of automated CP phrase segments for each recorder site was multiplied by its manually identified CP percentage to produce a simple CP call index. This is shown in the final column of Table 4. It is proposed that this index provides a more accurate assessment of Capercaillie vocal activity at each recorder site than the uncorrected number of CP phrase segments.

The primary aim of this study was to compare the results from lek counts and bioacoustics monitoring. A significant positive relationship was found between the numbers of males recorded by lek counts and the CP call index ($S = 223.52$, $\rho = 0.804$, $p < 0.01$) (Fig. 1). So, it appears that the greater the number of males, the larger the number of vocalizations over the course of a month. In a shorter time frame, there was no significant relationship between the number of males and the number of automated CP segments recorded on the day of the lek count survey ($S = 738$, $p = 0.14$).

One notable feature of the results is the differences between the 'paired' recorders at sites 8552/9306 and 8535/8607. The lek count results within these pairs differed, with 5–6/2 males and 0/1–3 males respectively. The

Table 3 Automated vs. manual identification error matrix, indicating the numbers of phrase segments manually reviewed and their match or mismatch with the automated recognizer identifications; for abbreviations, see Table 2

	Manual CP	Manual NOTCP	Not checked
Automated CP	926	583	22,179
Automated NOTCP	220	2026	60,690

Table 4 Number of CP phrase segments identified by automated recognizer and manually confirmed phrase segments at each recorder site from a sub-sample of 3755 segments

Recorder site	Automated CP phrase segments (A)	Manually confirmed CP	Manually confirmed NOTCP	Manually confirmed CP % (B)	Manually confirmed NOTCP %	CP call index (=A×B)
8528	2580	0	117	0.0	100.0	0.0
8535	881	2	35	5.4	94.6	47.6
8552	4114	190	33	85.2	14.8	3505.2
8607	794	4	35	10.3	89.7	81.4
8621	3237	123	112	52.3	47.7	1694.3
9306	1901	59	62	48.8	51.2	926.9
9319	2274	85	47	64.4	35.6	1464.3
9345	1290	14	69	16.9	83.1	217.6
9348	3032	236	25	90.4	9.6	2741.6
9558	3585	213	48	81.6	18.4	2925.7

CP call index calculated from the automated CP phrase segments (A) and the manually confirmed CP percentage (B) is also shown; for other abbreviations, see Table 2

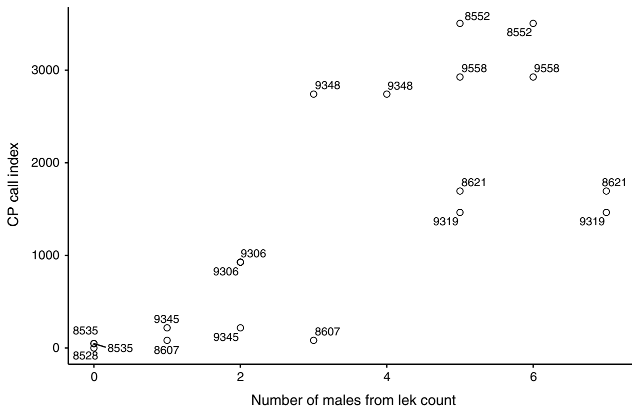

Fig. 1 Capercaillie vocalizations present (*CP*) call index is positively correlated to the number of males recorded in lek counts. Spearman's rank correlation test results: $S = 223.52$, $\rho = 0.804$, $p < 0.01$

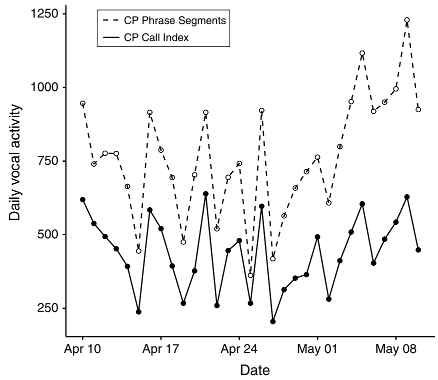

Fig. 2 CP call index and number of automated CP phrase segments totalled across all sites showed substantial daily variation, but no obvious trend through the survey period

CP call index and number of CP phrase segments differed substantially between the first pair of sites (where recorders were only 85 m apart), but matched closely at the second pair (Table 4, Fig. 1).

Call rate in relation to date/time

The CP call index and number of automatically identified CP phrase segments recorded per day varied in total across all locations (Fig. 2), and at each recorder site (Fig. 3). The total number of CP segments recorded ranged from 362 on 25 April, to 1229 on 9 May, with CP call index tracking this closely, except towards the end of the survey period. The highest numbers of CP segments, recorded during May, were presumably due to increasing dawn chorus activity from bird species other than Capercaillie.

There were relatively continuous, but dynamic levels of daily activity at each recorder site where Capercaillie were present. The CP index varied daily (especially at site 9348), but with no overall trend through the survey period. The median date of CP segments varied between recorder sites. Sites 9306 and 9348 were 'early season' sites, with median dates of 22 April, while 8535 and 8607 (one of the sets of paired sites), which were the 'latest' in the season with median dates in May, were the least vocally active and showed high levels of false positives in their data.

A broad daily peak in call activity was recorded in the hour before sunrise. However, there was variation between recorder sites, with sites 9319 and 9558 showing a peak earlier in the morning, and 8621 and 9306 showing a peak closer to sunrise (Fig. 4).

Call rates in relation to environmental factors

The weather variables were tested for correlation with both the number of CP phrase segments and the CP call index, but no significant relationships were found.

The altitude of the lek sites varied between 200 and 390 m above ordnance datum. A significant negative relationship was found between altitude and the CP call index using Spearman's rank correlation ($S = 1845.5$, $\rho = -0.619$, $p < 0.01$). Although this is mainly due to the levels of vocal

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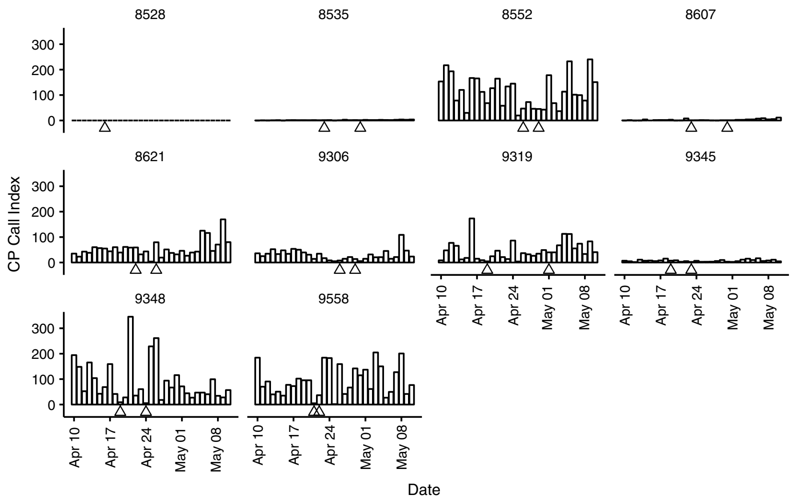


Fig. 3 CP call index varied widely between dates and locations. Plots show the CP call index each day at each recorder site. Lek count survey dates are shown by triangles along the baseline

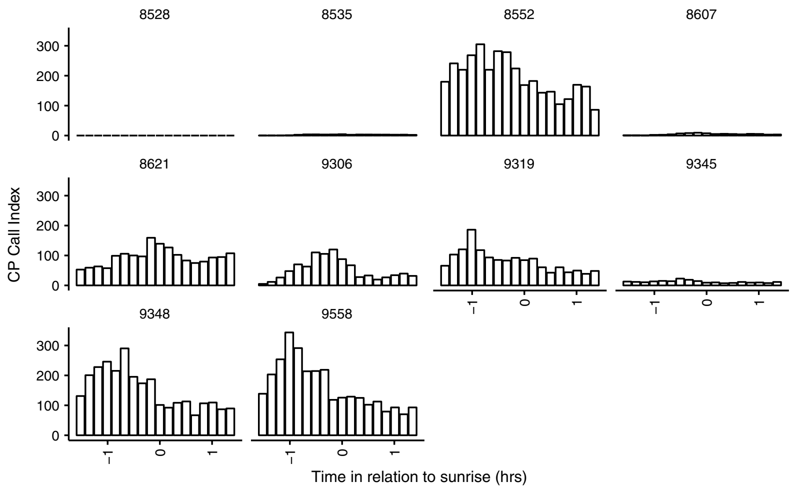


Fig. 4 Timing of Capercaillie call activity varied between recorder sites. Plots show the CP call index in 10-min periods related to sunrise at each recorder site

activity of the birds present, it also appears to be partly attributable to the number of males in attendance at the lek, which is also negatively related to altitude ($S = 1662.8$, $\rho = -0.458$, $p = 0.048$).

Call rates during lek counts

The data in Fig. 3 suggested that the CP call index and number of CP phrase segments may be lower on lek count days than on average, which possibly shows disturbance by surveyors on these occasions. This hypothesis was tested using Mann–Whitney *U*-test and a significant difference was found between the number of CP phrase segments on lek count days in comparison to the days when no surveyor count was conducted ($U = 1482.5$, $p < 0.001$). Lower vocal activity was recorded on lek count days (Fig. 5), with the median number of phrase segments decreasing from 62 to 23 per day.

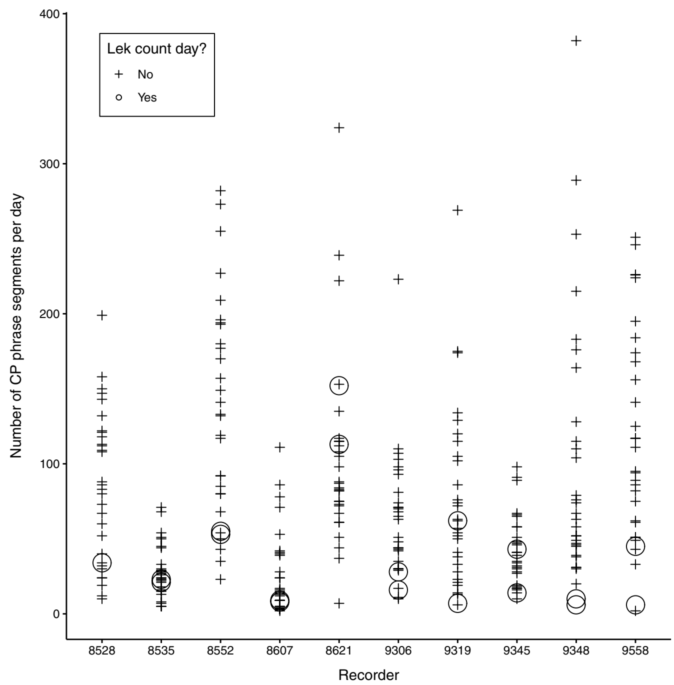
Discussion

Acoustic data analysis

Autonomous recorders are being increasingly used to determine the presence/absence and abundance of bird species (Shonfield and Bayne 2017). Recorders can be left in the field for long periods to acquire significant quantities of data, but manual processing by human observers can then be labour intensive. To counteract this, automated methods are being developed, either to recognize species vocalizations outright or to classify and group recordings, to make manual checks more efficient (Priyadarshani et al. 2018). Due to the recent release of the Kaleidoscope Pro software employed in this study, tests of its use and validity are rare in the literature.

Similar analytical methods to those used here have been undertaken in previous studies on avian acoustics (e.g. Machado et al. 2017). A semi-automated process can substantially reduce the time required for analysis, but

Fig. 5 Number of CP phrase segments was significantly lower than average on the days when lek counts took place. Mann–Whitney *U*-test of survey against non-survey days $U = 1482.5$, $p < 0.001$



introduces the potential for machine errors in call recognition, with both false negative and false positive classifications likely to result. Due to this, a range of studies have compared the efficiency of manual identification with a variety of automated or semi-automated methods. These have found that automated methods require less time for data processing, but sometimes identify fewer target sounds than manual analysis, and can make more false positive identifications (Swiston and Mennill 2009; Knight et al. 2017). The best approach is therefore likely to be an integrated approach with automated and manual methods combined, as used in the current study.

Recognizer metrics were calculated using manual identification of a subset of the automated data to assess the quality of the analysis (Knight et al. 2017; Chambert et al. 2018). Only 4% of the overall dataset was used for this assessment, but Chambert et al. (2018) state that quality assurance of automated recognizers can be achieved with a manual review of as little as 1% of the total data. The metrics indicated that the Kaleidoscope recognizer classification, as implemented here, had a precision of 0.61 and recall of 0.81. A number of previous studies reviewed by Knight et al. (2017) had a mean precision of 0.71 and mean recall of 0.60. The current study, therefore, had a precision lower than these reported cases, with a relatively high number of false positives. However, recall was high due to the low number of false negatives. In practical terms there is a benefit, in single-species studies like this one, from weighting analysis towards false positives, as the smaller dataset of 'positive' identifications is easier to manually review, instead of finding missed calls in the larger 'negative' dataset.

The moderate level of precision in this study means that the number of CP phrase segments is likely to be an overestimation of the actual Capercaillie calls in the data set (as presented in Table 4). This is especially clear in the data from site 8528, where all segments identified as CP were false positives. This potential inaccuracy was compensated for in this study by using the results from the manual review as a correction factor for the number of CP segments, to produce a CP call index that more accurately reflected actual Capercaillie vocal activity. As a consequence, taking into consideration the time and costs of analysis, an appropriate approach is believed to have been taken in this study to find a balance in terms of the accuracy required to generate useful data. Clearly the levels of false positive and false negative classifications could be reduced, if needed, with more detailed manual checking of the data.

Capercaillie call activity is related to lek count numbers

The primary objective of this study was to determine whether bioacoustics could be used to assess lek activity levels, and could be related to the numbers of displaying males present. It is established for some species that call rate can be used as a proxy for population abundance (Laiolo et al. 2011; Oppel et al. 2014; Knight et al. 2017), and that vocal display effort can increase in line with lek size or visitation rates to the lek (Westcott 1992; Pizo and Aleixo 1998; Cestari et al. 2016).

For Capercaillie, vocal characteristics often correlate with male quality, health condition, and competition levels—'fitter' males using lower frequencies, higher song rates and longer display durations. Displaying Capercaillie males from neighbouring grounds are also known to stimulate each other by increasing song rates, and song rate has been found to be significantly correlated to the number of displaying males in an area (Laiolo et al. 2011).

A significant positive relationship between Capercaillie lek count numbers and call activity was identified in this study, indicating that the CP call index and total number of CP phrase segments over an extended survey period (such as the month-long duration used here) may serve as an indicator of lek size. However, this does not appear to be true over shorter time frames, due to the considerable daily variation in call activity. This variation is likely the result of factors such as the date within the lekking season, and weather conditions affecting bird behaviour—factors that could also affect lek counts, and which are perhaps not considered fully within that method at the current time (Raynor et al. 2017; Fremgen et al. 2018). In addition, the mobility of Capercaillie around the lek site, with birds potentially displaying from different places on different mornings, may affect their detectability on a day-to-day basis, and adverse weather conditions (i.e. high winds and rain) could potentially mask calls in the recordings on some days.

The correlation found between lek numbers and call activity in this study indicates the potential for bioacoustics to be used alongside existing population monitoring methods for Capercaillie. Bioacoustics could be used effectively to calibrate the results gained from lek counts, especially when monitoring a large number of sites, conducting surveys at night, and covering a broad timescale, which are all difficult to achieve with many traditional survey methods (Furnas and Callas 2015; Gasc et al. 2017). This would add a new dimension to the vital understanding and flexibility of approach gained from human surveyors undertaking lek counts, with both methods being employed together to provide complementary information on lek activity (Venier et al. 2012; Shonfield and Bayne 2017).

Effects of lek count surveys on vocal activity

In this study, recorded vocal activity dropped to approximately 1/3 of average levels on days when surveyors visited the lek sites. As the most extreme examples of this, the lek counts at sites 9348 and 9558 both occurred on the 2 days when the lowest levels of call activity were recorded at these sites. This raises two potential issues. Firstly, it could indicate that surveyors caused sufficient disturbance to affect and reduce the vocal activity at the lek. This would be of concern, if true, as there could potentially be ecological effects of this on Capercaillie. The species is known to be susceptible to human disturbance, particularly at lek and brood-rearing times (Summers et al. 2009; Moss et al. 2014), and recreational impact studies have shown that disturbance of lekking birds may lead to local population effects, either by preventing display, avoidance of disturbed sites by hens, or preventing recruitment of young males (Marshall 2005). Studies have rarely been conducted on any bird species to determine whether the presence of surveyors has any significant impact on birds. One previous study, by Campbell and Francis (2012), used acoustic recording to assess point counts of passerines in old field habitat and found no difference in the results when an observer was present or absent. How this finding relates to other habitats or species assemblages is not known. Despite the lack of investigation into surveyor impacts on lek activity, the potential for this to occur in Capercaillie has been fully recognized, with precautions to avoid disturbance recommended as part of published survey methods (e.g. Haysom 2013). In this study, the overall correlation between Capercaillie vocal activity and lek counts suggests that there are likely no longer-term effects over the lek period. In addition, the observations of normal behaviour in the field during lek count visits gave no indication of other apparent adverse impacts.

A second potential explanation for the reduced call activity on count days is that it is just a chance effect, and that no disturbance is caused by lek counting. However, this raises the question that if call activity (and hence lekking) happens to be lower on the necessarily limited number of survey visits due to other factors such as weather, then the results from the survey might not accurately reflect the size of the lek, and could underestimate the number of males present. This would have an effect on the quality of the population assessment achieved from the count surveys. Further work on this issue is clearly needed.

Capercaillie call activity is related to temporal and environmental variables

The age and sex biases of lek counts are well recognized (Storch 1997; Mollet et al. 2015). In addition, there are a number of temporal and environmental conditions that can affect detectability and occupancy at leks (Walsh et al. 2004; Raynor et al. 2017; Fremgen et al. 2018). An understanding of these factors is critical to improving population estimates for the species being monitored (Drummer et al. 2011; Sadoti et al. 2016; Priyadarshani et al. 2018). Within this study, the levels of vocal activity were affected by date, time and altitude, but (perhaps surprisingly) no relationship with weather variables was found.

The number of CP phrase segments recorded on a daily basis, totalled across all sites, varied by a factor of nearly 4, but with much greater variation within sites. There were differences between the CP call index and number of CP segments, with the latter showing the highest levels of call activity at the end of the survey period, during May. The median dates for CP call index ranged between 22 April and 5 May, and a daily peak was recorded at 0.5–1 h before sunrise, at approximately 0500 hours (similar to Abrahams and Denny 2018). These key periods of activity confirm the recommendations of Haysom (2013) that Capercaillie lek surveys in Scotland should take place from mid-April to early May, and between 0400 and 0600 hours. As the numbers of birds present at the lek will vary depending on time of day and season, the programming of surveys is of high importance. For Black Grouse, Cayford and Walker (1991) found that the highest counts were obtained in April and early May, 1 h either side of sunrise, and also that counts varied by as much as 80% depending on the time and month they were taken. Bioacoustic monitoring therefore has great potential to confirm when best to conduct lek counts, or to allow inter-calibration of counts conducted at different dates across a season.

Lek attendance is likely to vary by latitude and elevation for a range of species (Sadoti et al. 2016). The negative relationship with altitude found in this study appears to be driven both by the number of male birds present and their levels of vocal activity, with more birds calling more frequently at lower altitudes. This finding appears to contrast with research from other parts of Europe, which has found that Capercaillie prefer elevated sites, such as ridgelines (Rolstad and Wegge 1987; Saniga 2002), although Haysom (2013) notes that, in Scotland, leks usually occur on raised areas but not on the tops of hills. It is possible that the more populated leks here tend to occur in lower lying areas where environmental conditions are more benign. It is known that egg-laying becomes later with increasing altitude, so this variable does have an impact on life history. However, the leks studied here were in a relatively narrow altitude band, and it is possible that the relationship identified would not hold across a wider range of altitude.

Abrahams and Denny (2018), Drummer et al. (2011) and Sadoti et al. (2016) have all found an inverse relationship between lekking activity and wind speed. This may be related to noise sensitivity, as noted in the Greater Prairie Chicken *Tympanuchus cupido* (Walsh et al. 2015), so the use of detailed weather information from lekking areas is an important avenue for future study to better understand effects on lek attendance and vocal activity patterns. In addition, masking by wind noise will also affect the quantity and quality of bird vocalizations recorded by bioacoustic methods, so this should be taken into account when analysing and interpreting audio data. Despite the daily variation identified here in vocal activity, many studies often use single survey counts to assess lek attendance and population numbers. However, this cannot be recommended, as lek attendance and activity levels may be suppressed even when weather conditions are within the recommended ranges for surveys. As a result, multiple visits may be required to gain accurate lek count numbers, to counteract variations in detectability and occupancy; this should be incorporated into survey guidance (Cayford and Walker 1991; Sadoti et al. 2016).

Conclusion

The continued precarious state of the Capercaillie in Scotland means that effective monitoring at both national and local levels is required. Large-scale surveys can track overall population trends and changes in distribution, but can not effectively inform assessments of localized populations or conservation management actions. Recent developments in national survey methods (Wilkinson et al. 2018) have improved the accuracy of winter transect data. The same effort is now required to refine lek monitoring techniques. The recommendation by Wilkinson et al. (2018) that greater consistency should be developed in lek count methods is echoed here, to allow a better understanding of how lek counts relate to actual numbers of birds and how numbers vary across the season.

The deployment of the acoustic recorders in this study successfully recorded Capercaillie vocal activity at a number of lek sites, providing comparable, simultaneous and long-term data from each location. This has provided new understanding of lekking activity levels over time, has indicated a potential weakness in human lek count methods, and has raised the possibility of using bioacoustics for efficient and effective population monitoring. There are limitations to the bioacoustics approach in recording only audio data, with issues over quiet individuals/species, range of detection, the spacing of recorders, etc. However, the collection of valuable biological data, over long time periods and across large, difficult to access, areas, is a recognized benefit of the bioacoustics approach, enabling reliable estimates of species occurrence and, potentially, abundance (Swiston and Mennill 2009; Blumstein et al. 2011; Furnas and Callas 2015; Gasc et al. 2017; Shonfield and Bayne 2017). Longer-term surveys using acoustic methods could provide an alternative data source where lek counts are not possible, or potentially allow calibration between lek counts undertaken at different sites on different days (Sadoti et al. 2016). This would help to address variation in lek attendance through the season (Sadoti et al. 2016; Fremgen et al. 2018). In addition, bioacoustics offers a non-intrusive survey method in comparison to other techniques such as lek counts, GPS/radio tagging and use of dogs. The benefits of this when dealing with small, declining and disturbance-sensitive populations at a critical stage of their life history should not be underestimated.

In the future, the use of multiple microphone arrays could allow the location of individual male birds to be plotted across a site, to develop a map of distribution and activity areas across a lek (Mennill et al. 2012). This could potentially be combined with individual call recognition and genetic capture-recapture techniques to allow highly detailed assessments of Capercaillie ecology and conservation status (Jacob et al. 2010). There is an increasing body of scientific studies on avian bioacoustics (Gasc et al. 2017; Shonfield and Bayne 2017), but standard and consistently applied guidance is still lacking for conservation managers (Browning et al. 2017; Abrahams 2018). However, as a first step, the relatively simple techniques demonstrated here should be developed and implemented to gather valuable new types of data that will help inform the conservation efforts for this iconic species.

Acknowledgements Many thanks to The Royal Society for the Protection of Birds staff for providing access to lek locations and assisting with deployment of recording equipment, and to the landowners who allowed use of their sites. Thanks also to Adam Bates, Edward Raynor and other reviewers for their comments on a previous version of this article. This study complied with the current laws of the country in which it was performed.

Appendix: Kaleidoscope 4.3.2 software settings

File parameters:

- No subdirectories
- No split to max duration
- Split channels—yes.

Signal parameters:

- Signal of interest 1000–3000 Hz
- 1–6 s
- Max inter syllable gap 1 s

Scan and cluster recordings:

- Max distance 1.0
- FFT window 5.33 ms
- Max states 12
- Max distance for building clusters 0.5
- Max clusters 500

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3.5 Bioacoustics and occupancy modelling

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Combining bioacoustics and occupancy modelling for improved monitoring of rare breeding bird populations

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ABSTRACT

Effective monitoring of rare and declining species is critical to enable their conservation, but can often be difficult due to detectability or survey constraints. However, developments in acoustic recorders are enabling an important new approach for improved monitoring that is especially applicable for long-term studies, and for use in difficult environments or with cryptic species.

Bioacoustic data may be effectively analysed within an occupancy modelling framework, as presence/absence can be determined, and repeated survey events can be accommodated. Hence, both occupancy and detectability estimates can be produced from large, coherent datasets. However, the most effective methods for the practical detection and identification of call data are still far from established. We assessed a novel combination of automated clustering and manual verification to detect and identify heathland bird vocalizations, covering a period of six days at 44 sampling locations.

Occupancy (Ψ) and detectability (p) were modelled for each species, and the best fit models provided values of: nightjar $\Psi = 0.684$, $p = 0.740$, Dartford warbler $\Psi = 0.449$, $p = 0.196$ and woodlark $\Psi = 0.13$, $p = 0.996$. Including environmental covariates within the occupancy models indicated that tree, wetland and heather cover were important variables, particularly influencing detectability.

The protocol used here allowed robust and consistent survey data to be gathered, with limited fieldwork resourcing, allowing population estimates to be generated for the target bird species. The combination of bioacoustics and occupancy modelling can provide a valuable new monitoring approach, allowing population trends to be identified, and the effects of environmental change and site management to be assessed.

1. Introduction

1.1. Bioacoustics for Biodiversity monitoring

Biodiversity monitoring is central to nature conservation, allowing species status to be evaluated or assessments to be made of biological responses to environmental changes (Pereira and Cooper, 2006). Long-term monitoring of designated nature conservation sites is particularly needed to identify population trends and inform management planning efforts, especially in the context of factors such as climate change and habitat loss/severance (Noss, 1990; Furnas and Callas, 2015). However, existing monitoring practices and protocols are often sub-optimal, especially in terms of unbiased spatial coverage, sampling effort optimization, the statistical use of the data, and the lack of repeated sampling (Schmeller et al., 2012).

We assessed the potential to improve the existing monitoring methods currently used on sites that are internationally important for their breeding bird populations. The most common methods for monitoring of bird numbers and distributions are transect or point count surveys by human observers. These have recognised disadvantages, such as observer bias, the availability of skilled/experienced surveyors (Brandes, 2008; Celis-Murillo et al., 2009; Rempel et al., 2005; Sedláček et al., 2015), and the infrequent and short-term nature of survey visits (Shonfield and Bayne, 2017; Zwart et al., 2014). In response to these issues, passive acoustic monitoring is increasingly being used as an alternative monitoring technique. This method uses automated recording units, which can be deployed in the field for days or weeks at a time to capture animal sounds. The advantages of this approach include the production of a standardised, long-duration, permanent dataset and record of species identification, which can be repeatedly analysed and

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subject to validation by independent reviewers (Abrahams and Denny, 2018; Celis-Murillo et al., 2009; Rempel et al., 2005). Automated recorders can be synchronized to occur simultaneously across large spatial extents, reducing temporal variability in studies (Brandes, 2008; Furnas and Callas, 2015; MacKenzie and Nichols, 2004), and offering large data volumes at low cost and with little resourcing requirement (Acevedo and Villanueva-Rivera, 2006; Hill et al., 2018; Holmes et al., 2014; Zwart et al., 2014). Due to potential benefits such as these, the use of automated recorders has increased significantly over the last ten years (Shonfield and Bayne, 2017), and some researchers have advocated the use of automated recorders instead of expert personnel for conducting surveys (Darras et al., 2018; Rempel et al., 2005; Brandes, 2008; Zwart et al., 2014).

There are potential barriers to the widespread uptake of passive acoustic monitoring for bird surveys. These include the need for specific expertise and the increased time required for post-processing compared to some traditional surveys (Banner et al., 2018; Knight et al., 2017), together with the costs of equipment (Beason et al., 2018; Farina et al., 2014; Hill et al., 2018). However, open source or low-cost recording devices are being produced and post-processing methods are constantly improving – although automated species identification, including machine-learning approaches, is still in development (Acevedo et al., 2009; Salamon et al., 2016). For fieldwork, a practical disadvantage is the fact that acoustic monitoring does not allow the collection of visual clues which can sometimes be vital for the identification of cryptic/quiet species, or for assessing abundance (Klingbeil and Willig, 2015; Sedláček et al., 2015). In some cases, the use of audio recording units has resulted in detection of fewer species and detection at shorter distances than human observers (Holmes et al., 2014; Yip et al., 2017), but the potential for longer term data capture with recording units means that this constraint can normally be addressed by longer deployment times (Darras et al., 2018; Sedláček et al., 2015; Shonfield and Bayne, 2017; Zwart et al., 2014). However, microphone performance and maintenance needs to be considered as part of the planning of fieldwork campaigns (Turgeon et al., 2017; Yip et al., 2017).

1.2. Occupancy models

Alongside the technological advances in bioacoustics, there has been a dramatic recent increase in the development and application of occupancy models that explicitly incorporate species detectability (Furnas and McGrann, 2018; MacKenzie and Nichols, 2004; MacKenzie et al., 2002; MacKenzie et al., 2006). The presence/absence of a species in a sample can be used to calculate occupancy (Ψ) – the proportion of an area, or number of sites, occupied by a species. The frequency with which a species is repeatedly recorded at each sampling site can also be used to assess detectability (p), to allow for the estimation of, and correction for, imperfect detection (Banner et al., 2018; MacKenzie et al., 2002; MacKenzie et al., 2006). The ability to factor these two parameters into assessments allows improved estimates of populations and greater understanding of ecological patterns such as species/habitat relationships (MacKenzie et al., 2006).

Despite the clear potential and utility of combining bioacoustic techniques and occupancy models, only a few studies have united these methodological developments to model the population status of a range of vocal species (Yates and Muzika, 2006; Furnas and Callas 2015; Kalan et al., 2015; Campos-Cerqueira and Aide 2016; Stiffler et al. 2018; Wood et al., 2019). This study, therefore, provides an important additional case-study in new geographical, habitat and spatiotemporal contexts. Furthermore, it also addresses one of the most critical questions in this area of study – how to most effectively extract useful information from acoustic recorders to feed into the occupancy models and allow population estimates to be generated.

Although fine-grained data can be gained from acoustic recorders, a significant benefit of the occupancy modelling approach in field studies is that it relies only on presence/absence data, rather than metrics of abundance such as counts of individuals (MacKenzie et al., 2006). This is normally much easier to determine, requiring less interpretation in the field/lab, and counteracting the potential for inter-observer or inter-survey error (MacKenzie et al., 2006). Although some information is perhaps lost by this approach, data accuracy may be gained as, for rare species, it can be very difficult to correctly estimate abundance during surveys, whereas estimation of occupancy may still be possible with a high level of confidence (Campos-Cerqueira and Aide, 2016; Mackenzie and Royle, 2005). Finally, occupancy and abundance will be linked in most populations, and at small spatial scales and with territorial species, occupancy may be regarded as equivalent to population size and can be used for investigating population dynamics or spatial variation (MacKenzie et al., 2006; Royle and Nichols, 2003; Furnas and Callas, 2015; Campos-Cerqueira and Aide, 2016; Wood et al., 2019).

1.3. Heathland bird monitoring

Our study was conducted on European nightjar *Caprimulgus europaeus*, woodlark *Lullula arborea* and Dartford warbler *Sylvia undata*. These three birds are specialists of lowland heathland habitats, and are rare and declining species considered to be of international conservation importance (Clark and Eyre, 2012). Despite significant legal and policy protection, however, their breeding site habitats are threatened by air pollution, urban development, inappropriate management and recreational disturbance (Fagúndez, 2013; Mallord et al., 2007).

Monitoring a variety of bird species, with differing behaviours, over extensive heathland sites, presents significant challenges for conservation managers. In particular, a number of different surveyors are inevitably involved in the surveys used for monitoring the target species. Inter-observer differences are therefore likely to produce variations in data, particularly with nocturnal nightjar surveys, where it is hard to differentiate individuals and accurately map territories (Liley and Fearnley, 2014). Automated recorders, used by themselves or in conjunction with existing methods, have great potential to reduce bias and variability in survey results and account for the effects of detectability between sites and surveys, to produce more reliable and consistent population estimates.

Our goal in this study is to establish effective methods for combining bioacoustic techniques and occupancy models in the monitoring of rare breeding bird populations. We capture an acoustic dataset and demonstrate how to efficiently process recordings to detect and identify species vocalizations within this, using a novel clustering technique. We then analyse the acoustic data to estimate occupancy and detectability for the three target species, using single-species, single-season occupancy models, and combine this with environmental covariates, to determine the effects of habitat on model outputs. This provides useful occupancy and detectability estimates for the target species, highlighting the potential for bioacoustic methods to be used as an alternative or complement to current monitoring practices, with benefits in terms of consistent, verifiable and permanent field data.

2. Materials and methods

2.1. Study area

We conducted the study on parts of the Thames Basin Heaths SPA and the Wealden Heaths SPA. These are two large, internationally important, nature conservation sites in southern England, made up of 18 heathland sites of varying size and character. These sites comprise a mix of dry and wet heath vegetation, with mire, bog, waterbodies, permanent grassland, scrub and blocks of woodland (Fig. 1). Together, they cover a total of 12,199 ha, of which 5702 ha is classified as lowland heath (Clark and Eyre, 2012). Within this overall context, we gathered data at three heathland sites to which access could be readily gained: Chobham Common, Horsell Common and Thursley Common, which together cover an area of 992 ha.

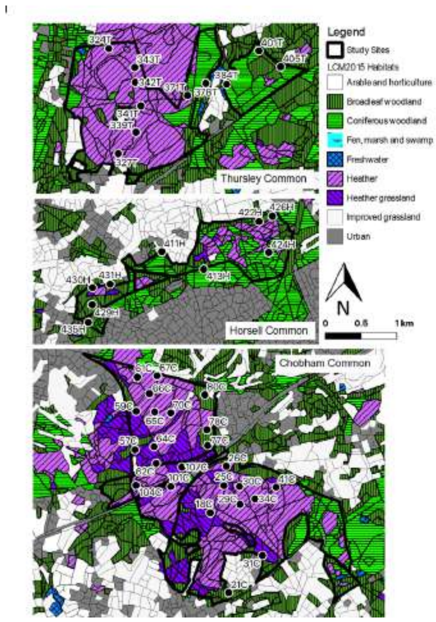

Fig. 1. Land Cover Map 2015 habitat data and acoustic sampling site locations.

2.2. Acoustic monitoring

We used Wildlife Acoustics SongMeter SM2 recorders, equipped with a single mono omnidirectional microphone to record audio data (see Supplementary Information: Appendix 1). These automated recording units were programmed to record a 1 minute audio sample every ten minutes (i.e. one minute on, nine minutes off), from two hours before sunrise, until three hours after, and then from one hour before sunset until two hours after. Daily sampling therefore took place within a 5 h period at dawn, and 3 h at dusk. The units were deployed at a single sample site for a period of six days during May-June 2018, so that each site had 288 min of recording. The audio samples were all recorded as .wav files onto an SD card, at 48 kHz sampling rate and 16-bit depth (Abrahams, 2018). All microphones were calibrated to ensure comparable sensitivity and performance before deployment (Turgeon et al., 2017; Yip et al., 2017).

Sample locations were defined across the study area by using GIS to place a regular 250 m point grid across the three heathland sites. It was considered that this would be a sufficient distance for recordings to be independent of each other, and relevant to the territory sizes of the species being studied. From the 166 possible grid points, 48 were randomly selected, stratified to the relative area of each heathland site, to provide 9 sampling sites at Horsell Common, 15 at Thursley Common, and 24 at Chobham Common. As 16 recorders were available for the study, the 48 sampling sites were divided into three sessions of field recording: 26–31 May, 5–10 June, 16–21 June. The sites were randomly assigned to one of the three survey sessions, so that 3 sites at Horsell Common, 5 at Thursley Common, and 8 at Chobham Common would be sampled at each session. Despite differences in date, all site samples were treated equally as individual samples within a single season. A closure assumption was therefore made that bird distribution, population size and density did not change over the course of the three survey sessions.

All sites were given an identification code consisting of a number and site suffix of H, T or C (Fig. 1). Field placements matched the GIS locations as closely as features on the ground would allow. During the deployments, one recorder failed to record evening sessions repeatedly (at three sampling sites), and another suffered battery failure on one occasion. These failures were all at Thursley Common (sites 315T, 319T, 332T, 391T) and the sites were removed from the dataset, leaving 44 sampling locations.

2.3. Audio data

The audio recordings taken from the field were analysed using a semi-automated system to identify target species vocalizations (termed 'phrases') in the recordings. Kaleidoscope Pro 4.3.2 software (Wildlife Acoustics, 2017) was first employed, using its cluster analysis method with default settings (https://www.wildlifeacoustics.com/images/documentation/Kaleidoscope-Pro-5-User-Guide.pdf). This process analysed the time and frequency characteristics of the recorded audio files, using Hidden Markov Models, to search for sounds within a 1500–7000 Hz frequency band and of 2–20 s duration, with a maximum inter-syllable gap of 1 s – creating each as an individual new .wav file. The analysis process grouped similar phrases in the recordings (e.g. the song of a particular bird species) into clusters based on their sound characteristics. After the automated clustering was complete, the phrases detected by the software were manually reviewed by listening to playback and by the visual inspection of spectrograms to classify the presence/absence of the target species in each phrase.

2.4. Environmental data

In order to investigate the influence of habitat on occupancy and detectability at each of the study sites, we obtained data from a combination of satellite and terrestrial mapping sources. The proportion of Broadleaf trees, Coniferous trees, Heather and Heather grassland within 100 m of each sample site was calculated from Land Cover Map 2015 (LCM2015) vector data, accessed from the Centre for Ecology and Hydrology (Rowland et al., 2017). Distance to the nearest road was calculated based on Ordnance Survey OpenMap-Local vector data (OS data © Crown copyright and database right 2018). We also used pre-processed satellite data from Copernicus Pan-European High Resolution Layers (HRL; https://land.copernicus.eu/pan-european/high-resolution-layers) representing Tree Cover Density (TCD), Water and Wetness (WAW) and Imperviousness (IMD) at a 20 m resolution. The Tree Cover Density (forest) HRL provides the level of tree cover in a range from 0 to 100% for each pixel. The Water and Wetness HRL shows the occurrence of water and wet surfaces over the period from 2009 to 2015, on a scale from (1) permanent water, to (4) temporary wetness. The Imperviousness degree HRL HR captures the spatial distribution of artificially sealed (i.e. urbanized/road) areas. We used Zonal Statistics to summarise these measures for each sampling site, to produce the sum of all pixel values within a 100 m radius of the site. All spatial analyses were performed in QGIS (QGIS Development Team, 2018). Weather was represented in our environmental variables by 'derived 24hr sun duration' from the weather station at Wisley, Surrey (Ref. src_id 719/DCNN 5237, WGS84 51.3108, −0.47634), accessed from BADC (badc.nerc.ac.uk). Other weather variables were unavailable from this source as records for the survey period were sparse.

2.5. Occupancy models

The occupancy of each of the three target species was modelled separately using a single-species, single-season modeling approach with observation and habitat covariates (Furnas and Callas, 2015; MacKenzie et al., 2002; MacKenzie et al., 2006; Stiffler et al., 2018), using established protocols with the 'Unmarked' package in R (Fiske and Chandler, 2011; R Core Team, 2013; RStudio Team, 2015). The acoustic data was summarised to day-level temporal resolution of presence/absence, to produce a detection history at each sampling site comprising 6 replicate surveys. The naive occupancy for each species was checked and confirmed to be > 0.1, so that detection histories were not too sparse to fit single-species models. We first created null models, without covariates, to represent equal probability of detection and/or occupancy across all survey sites and days. We then developed models including covariates representing the areas of different habitat types within 100 m of the sampling location (from LCM2015 and Copernicus data), and distance to the nearest road (as shown in Table 2). We anticipated that detection probability might change over the course of the survey period (Campos-Cerqueira and Aide, 2016; Furnas and McGrann, 2018) due to seasonal and weather reasons, and used Julian day of survey and 24-hour sun duration to represent this information. All variables were scaled and centered around zero prior to analysis. The broadleaf and coniferous covariates were excluded as these duplicated the TCDsum habitat type, and the LCM2015 data were more zero-inflated than the Copernicus data. IMDsum was also rejected as the data were very sparse. Covariates were applied first to the detection parameter, before the occupancy parameter. Each model was inspected to check estimates, standard errors and convergence. All models tested are listed in Table 2.

We assessed model fit using Akaike's Information Criterion (AIC), ranking and comparing models based on AIC relative differences between the top ranked model and each other model (ΔAIC) and AIC weights. We considered models with $\Delta AIC < 2$ to be equally supported (Burnham and Anderson, 2002) and combined these by applying model averaging using the MuMIn package in R (Barton, 2018), to estimate occupancy and detection for each species. Initially, models without occupancy covariates were fitted to select the most appropriate covariates for detection. These covariates were then retained for all candidate models when occupancy covariates were added. The models generated for each species were used to assess occupancy levels at the study sites, define potential habitat areas and calculate provisional population estimates.

3. Results

3.1. Clustered audio segments

Kaleidoscope clustering of the complete audio dataset detected 28,775 phrases as individual .wav files, an average of 109 phrases per site/day. Each phrase included bird vocalizations and other sounds. With a mean duration of 6 s (range 2–20.9 sec), the clustered phrases comprised 48 h of audio – 23% of the total recorded dataset. The phrases were grouped into 55 clusters by the software.

Manual review of all the clustered phrases identified the three target species in the dataset, with 757 phrases across 30 sites having vocalizations of nightjar, 327 of woodlark at 7 sites, and 115 of Dartford warbler at 14 sites. This gave a total of 1,199 phrases recorded for the three target species. Nightjar and Dartford warbler were recorded at all three SPA sites, but woodlark was only recorded at Chobham and Thursley Commons.

3.2. Patterns in activity

The total number of phrases recorded per day across all sampling sites varied from 1974 on 30 May to 1145 on 17 June. The daily number of phrases was relatively even between recording sessions 1 and 2, but declined for session 3 in mid-June. This pattern was matched somewhat by the daily numbers of target species vocalizations (Fig. 2). Nightjar and Dartford warbler vocalizations were recorded throughout all three recording sessions, but woodlark was mostly confined to the early June session only – although this is likely to be related to presence at the sites being sampled at that time, rather than any reason to do with seasonal timing.

The most vocally active sites were 61C and 70C (north Chobham) for nightjar, 29C and 25C (south Chobham) for woodlark, and 339T and 343T (central Thursley) for Dartford warbler – see locations at Fig. 1. Significant numbers of calls were not recorded for any species at the Horsell Common sites.

3.3. Environmental parameters

The recorders were placed in habitats that varied from open heath to mature forest (Fig. 1). Thursley Common can be divided into a western part, dominated by Heather, with the eastern part being Coniferous and Broadleaved woodland. Chobham Common is a mosaic of Heather and Heather grassland, with Coniferous and Broadleaved woodland around its fringes. This site has a much larger cover of WAW than the two other sites. Horsell Common is mostly Coniferous and Broadleaved woodland, with patches of Heather at its eastern end. The means and ranges of the GIS-measured environmental parameters are listed in Table 1.

3.4. Occupancy modelling

Naive occupancy was calculated for each species, based on the presence of the species across all 44 sample sites in the study. The naive occupancy values, equal to the proportion of sites with positive detections, were 0.68 for nightjar, 0.32 for Dartford warbler and 0.16 for woodlark.

Models incorporating covariates on the detection and occupancy parameters were generated for each species (Table 2). Two models for nightjar had equal support ($\Delta AIC < 2$) and so were averaged to produce covariate estimates. The averaged model included Julian date (JULIAN), Tree Cover Density (TCDsum) and Water and Wetness (WAWsum) as detectability covariates with no covariates acting on occupancy. The best fit model for nightjar (NJmdet3), with an AICwt of 53%, indicates an occupancy of 0.684 (SE 0.071) with a detectability of 0.740 (SE 0.035), varying only slightly from the null model ($\Psi = 0.682$, $p = 0.733$).

There were four favoured models for Dartford warbler, including the null model, with TCDsum, WAWsum, and distance to road (HubDist) featuring on the detectability parameter. Heather grassland was the only indicator for occupancy. The averaged model for Dartford warbler used only distance to road as a detectability covariate, with no covariates acting on occupancy. The best-fit model for Dartford warbler (DWmdet5), with an AICwt of 36%, indicates an occupancy of 0.449 (SE 0.107), with a detectability of 0.196 (SE 0.053), an increase from the null model occupancy of 0.382 (SE 0.091), but decrease in detectability from 0.258 (SE 0.057).

Woodlark had two favoured models, sharing Julian date, WAWsum, distance to road, Heather and Heather grassland as detectability covariates, and WAWsum, Heather and Heather grassland for occupancy covariates. The averaged model for woodlark had five significant covariates, and again, these were all on the detection parameter. Julian date, WAWsum and Heather were all positively related to detectability, while distance to road and Heather grassland were negative indicators. For woodlark, the best-fit model (WLmocc2), with an AICwt of 59%, indicated an occupancy of 0.13 (SE 0.117), lower than the null model figure of 0.162 (SE 0.056), and a detectability of 0.996 (SE 0.012), which varied substantially from the null model detectability of 0.491 (SE 0.081).

Predicted occupancy varied little between sampling sites for nightjar and Dartford warbler (Fig. 3), as only single covariates were acting on these species - TCDsum and Heather grassland respectively. Woodlark occupancy predictions varied more widely due to the number of habitat covariates acting on the models for this species – including WAWsum, Heather and Heather grassland. Detectability predictions

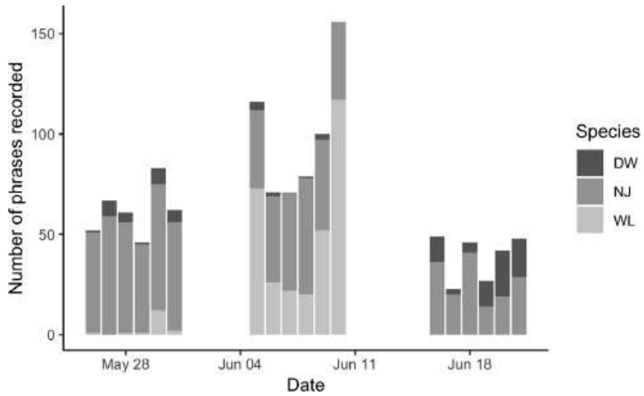

Fig. 2. Number of target species recorded per day across all sampling sites, for Dartford warbler (DW), nightjar (NJ), and woodlark (WL).

Table 1
Measured habitat parameters (n = 44 sampling sites).

Habitat variable	Mean value	Range	Units
TCDsum	2570	0–6209	Sum of % per pixel
WAWsum	36.8	0–252	Sum of 1–4 index per pixel
Distance to Road (HubDist)	351	29–961	Metres
Heather	14,459	0–31318	Sum of pixels
Heather grassland	4204	0–31060	Sum of pixels

were sensible for nightjar and Dartford warbler, but highly polarised to 0–1 in the models for woodlark, due to the small number of positive sampling sites (see Fig. 3).

Our results can be used to provide a baseline for assessing the population of the three heathland bird species studied. We assumed that occupancy is a good surrogate for abundance (MacKenzie and Nichols, 2004) and that we could quantify the relative abundances of the bird species, based on the proportion of sampling sites in which they were recorded to be present. Given the separation distances between recorder locations in this study, it is considered reasonable to assume that each occupied sampling site represented a separate territory/pair. Using the occupancy estimates from the null models for the three species we can calculate that the areas of occupied habitat for each species, from a total 992 ha, are: nightjar 676 ha, Dartford warbler 379 ha, woodlark 161 ha (Table 3). Combining these habitat areas with published breeding densities of 0.074–0.078 males/ha for nightjar (Berry, 1979; Conway et al., 2007), 0.32–0.42 pairs/ha for Dartford warbler (Bibby and Tubbs, 1975), and 0.05 pairs/ha for woodlark (Langston et al., 2007; Sitters et al., 1996), gives estimated population levels of: nightjar 51 males, Dartford warbler 140 pairs, and woodlark 8 pairs (Table 3).

4. Discussion

4.1. Bioacoustic approach

To our knowledge, this is the first study in Europe to combine bioacoustic survey with occupancy modelling. It is also the first in the UK to undertake a large scale survey for multiple bird species using automated recorders. It therefore expands the geographic scope of case

Table 2
Model selection list for all species – with detectability and occupancy covariates.

Model	Formula	AIC	ΔAIC	AICwt
Nightjar				
NJmdet3	~JULIAN + TCDsum + WAWsum ~ 1	259.62	0.00	0.528
NJmocc3	~JULIAN + TCDsum + WAWsum ~ TCDsum	260.64	1.02	0.317
NJmocc2	~JULIAN + TCDsum + WAWsum ~ TCDsum + HubDist	262.33	2.70	0.136
NJmocc1	~JULIAN + TCDsum + WAWsum ~ TCDsum + WAWsum + HubDist + Heather + HeatherGrass	267.64	8.02	0.010
NJm0	~1 ~ 1	267.79	8.17	0.009
Dartford Warbler				
DWmdet5	~TCDsum + HubDist ~ 1	157.11	0.00	0.364
DWmocc3	~HubDist + TCDsum ~ HeatherGrass	158.19	1.08	0.212
DWmdet4	~TCDsum + WAWsum + HubDist ~ 1	158.40	1.29	0.191
DWm0	~1 ~ 1	159.00	1.89	0.142
DWmocc2	~HubDist + TCDsum ~ WAWsum + HeatherGrass	160.06	2.95	0.083
DWmocc1	~HubDist + TCDsum ~ TCDsum + WAWsum + HubDist + Heather + HeatherGrass	164.89	7.79	0.007
Woodlark				
WLmocc2	~JULIAN + WAWsum + HubDist + Heather + HeatherGrass ~ WAWsum + Heather + HeatherGrass	69.31	0.00	0.593
WLmocc3	~JULIAN + WAWsum + HubDist + Heather + HeatherGrass ~ WAWsum + HeatherGrass	70.75	1.44	0.288
WLmocc1	~JULIAN + WAWsum + HubDist + Heather + HeatherGrass ~ TCDsum + WAWsum + HubDist + Heather + HeatherGrass	73.10	3.79	0.089
WLmdet3	~JULIAN + WAWsum + HubDist + Heather + HeatherGrass ~ 1	75.29	5.98	0.030
WLm0	~1 ~ 1	100.55	31.24	0.000

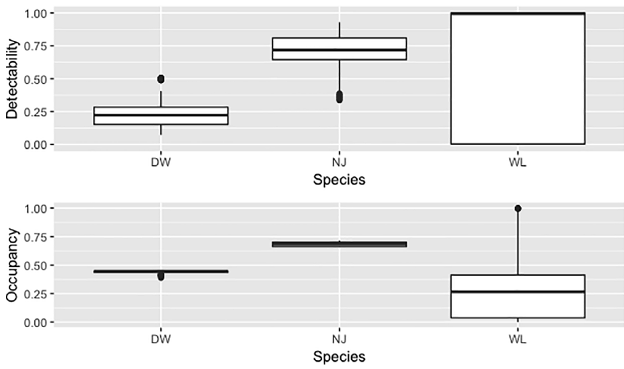

Fig. 3. Model-averaged predicted occupancy and detectability across all sampling sites, for Dartford warbler (DW), nightjar (NJ), and woodlark (WL).

studies for these methods, and applies them in a new habitat, beyond the American forested ecosystems in which most previous studies have been located (Furnas and Callas, 2015; Campos-Cerqueira and Aide, 2016; Furnas and McGrann, 2018; Wood et al., 2019).

We used species detection data from six repeated days of recording at 44 sampling sites (Fig. 4), combining this with environmental covariates to estimate occupancy and detectability for three bird species. Our results show that the bioacoustic approach can be used effectively for the survey and monitoring of heathland bird populations. Although we included models where habitat covariates could influence occupancy in our candidate sets, the 'best' models for each species suggested that the habitat variables were not important indicators of occupancy at the scale studied. This is possibly due to the fact that the study areas were all lowland heathland sites, generally suitable for the study species, and so the distribution of individuals was likely to relate to micro-habitat features that were not detectable at the scale of the field survey, satellite and map data applied. The satellite data used was at 20 m pixel size, but the average size of the LCM polygons was 2.4 ha, equivalent to 87 m radius. Although the covariate data was sampled at a similar scale (100 m radius) to previous studies (Furnas and Callas, 2015; Campos-Cerqueira and Aide, 2016), these were landscape-scale surveys less dependent on small habitat features to differentiate plots. Thus, we would agree with the finding of Niedballa et al. (2015), that both the spatial scale of habitat covariate data, and the radius sampled around survey sites, can affect the fit of occupancy models. Higher resolution data is needed for a site-based scale of assessment, if habitat covariates are to be included in analyses. For future studies, this should be gained from either field survey or high-resolution aerial/satellite imagery, such as the 5 m resolution RapidEye imagery used by Niedballa et al. (2015).

Identification of species vocalizations is commonly done either by complete manual analysis or, increasingly, by the use of automated recognizers, which require the *a priori* compilation and analysis of a large library of known species vocalizations (Knight et al., 2017; Shonfield and Bayne, 2017). Our analysis workflow included automated clustering of the acoustic data set, followed by manual validation of candidate vocalizations of the target species (Abrahams and Denny, 2018). This process has two benefits. Firstly, the automated clustering identified signals, that may be target bird species, but filtered out noise. In the current study, this allowed 77% of the total acoustic dataset to be filtered out, before identifications were attempted, significantly reducing the later workload in manually reviewing data for target species vocalizations. The second benefit of the analysis approach taken here, was that the manual validation step helped to minimize false-positive detections (Campos-Cerqueira and Aide, 2016), which are often a significant issue with automated species identification systems (Zwart et al., 2014; Salamon et al., 2016). Misclassification errors such as this violate a major assumption of most occupancy models, and can lead to substantial errors in occupancy estimates (MacKenzie et al., 2006; Banner et al., 2018). The issue can potentially be addressed by complete manual identification of all recordings, but this is highly time-consuming, while the hybrid automated/manual approach taken here reduced the workload in the manual review stage to less than a quarter of what it would have been. The corollary is that the data rejected by the automated clustering may contain target species vocalizations, and hence false-negatives may result. However, with the summation of the detailed call data down to daily presence/absence at each site, the potential loss of some target species phrases is considered unlikely to significantly affect the occupancy and detectability estimates derived from the modelling (Shonfield et al., 2018). The combined use of automated clustering and manual verification is therefore recommended as a valid approach for identification in bioacoustic studies.

4.2. Spatial sampling design

In bioacoustic studies with static sampling locations, the layout of recorder placements is of high importance. For occupancy modelling especially, the distance between sampling sites should be relevant to the territory size of the taxa being recorded (Niedballa et al., 2015), while also ensuring that the detection process is independent at each site by preventing overlap between the recording radius around each recorder. While this distance is variable, for many bird species the effective recording radius of most detectors is in the region of 50 m –

Table 3
Calculated areas of occupied habitat, based on intercept-only occupancy estimates.

Species	Occupancy (SE)	Occupied habitat (90% CI)	Density ha^{-1}	Pairs (90% CI)
Nightjar	0.682 (0.0702)	676 ha (562–791)	0.075	51 (42–59)
Dartford warbler	0.382 (0.0914)	379 ha (230–528)	0.37	140 (85–195)
Woodlark	0.162 (0.0562)	161 ha (69–252)	0.05	8 (3–13)

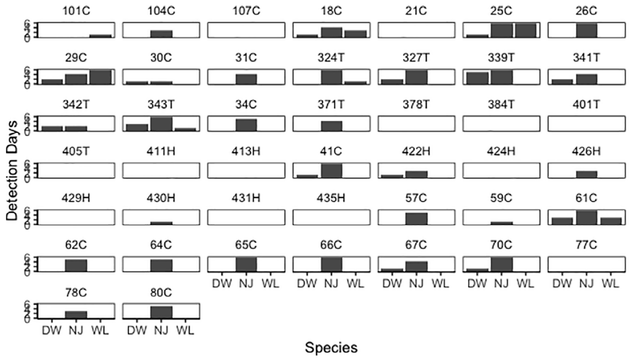

Fig. 4. Number of detection days for each species at each site.

although this is dependent on microphone model, variability and condition (Furnas and Callas, 2015; Turgeon et al., 2017; Yip et al., 2017). Within our study, the closest spacing between sampling sites was set by the ~250 m sampling grid. The mean nearest neighbour distances of the recorder sites were 316 m for Chobham, 346 m for Horsell, and 329 m for Thursley (range 202–703). Due to the sampling sites being spread across three survey sessions, the mean nearest neighbour distances between recorders in each session were 608 m, 466 m and 508 m.

For nightjar, a threshold of 350 m distance between registrations has been proposed to differentiate between male territories (Conway et al., 2007), while Stiffler et al (2018) applied a minimum spacing of 400 m for recording wetland birds. The spacing of the recorders within the current study related well to these studies, and as a result, there can be a reasonable confidence that there was no double-counting for the bird species being studied. A 250 m sampling grid, as set out in the draft protocol of Abrahams (2018) is therefore considered to be appropriate for future studies, although additional refinement of detector placement may be warranted to maximise coverage of sites, dependent on the vocal and territorial characteristics of the species being studied. For example, recent research has indicated that, for a desired threshold of detection efficiency, careful selection of optimised placements based on topography, vegetation and weather patterns, may be most efficient (Piña-Covarrubias et al., 2018).

4.3. Temporal sampling design

In any occupancy study, the balance between the number of sites and number of sampling events differentially affects the accuracy and precision of the occupancy and detectability estimates. We recorded for six days at 44 sites, which we considered likely to balance fieldwork resourcing with sufficient sample site density. This was a longer deployment time than the two–three days used by Furnas and Callas (2015) and Stiffler et al. (2018), and equivalent to that employed by Campos-Cerqueira and Aide (2016) and Wood et al. (2019). For rare species with a high probability of detection (i.e. woodlark for this study) the required survey effort should maximize the number of sites covered, while for common species with low detection (i.e. Dartford warbler) the most efficient sampling approach is to increase the number of survey occasions (Mackenzie and Royle, 2005). With the low occupancy for woodlark found here, it is likely that an increased number of sampling sites (and lower number of survey days if necessary) would be likely to improve the modelling results (Mackenzie and Royle, 2005; Banner et al., 2018). This modified sampling approach would, however, have to be considered in terms of its costs/benefits, taking into account the potential effects on Dartford warbler modelling and increased fieldwork time or equipment requirements.

4.4. Detectability

Using the null models, without covariates, we estimated detectability as 0.73 for nightjar, 0.49 for woodlark and 0.26 for Dartford warbler. The national Breeding Bird Survey (BBS) (Johnston et al., 2014) found a much lower detectability of 0.30 for nightjar, which is perhaps unsurprising, due to the difficulties with surveying this species within a standard (mostly daytime) survey method. However, the BBS detectability estimates of 0.47 for woodlark and 0.37 for Dartford warbler are similar to those found in this bioacoustic study. In this comparison, nightjar is much better detected by acoustic recorders (as found by Zwart et al., 2014), but Dartford warbler less so, while detectability for woodlark is matched.

Taking detectability into account during traditional bird surveys requires repeated visits across the season. The time often occurring between site visits may then invalidate the assumption that detection probability remains constant across the survey events. The protocol used in this study enabled six days of back-to-back recording, simultaneously at 16 sites (Fig. 4), minimising the risk that detection probability would change between sampling events. This would have been difficult to achieve without the use of automated recorders. The greater number of survey replicates achievable with the bioacoustics approach is therefore able to improve occupancy and detection estimates (MacKenzie et al., 2006; Stiffler et al., 2018).

We found that survey date, combined with habitat characteristics, explained detectability and improved the performance for some of the species models generated here, similar to the finding of Furnas and Callas (2015). Wetland (WAWsum) was a positive parameter on detectability for all three species, and woodland (TCDsum) was also positive for nightjar, as was Heather for woodlark. The probability of detecting a species during a bioacoustic survey is a function of both the probability of it vocalizing and the recorder detecting the call. The vocalization rates of many birds vary due to age, sex, breeding status, time of day, and seasonal variation (Campos-Cerqueira and Aide, 2016; Furnas and McGrann, 2018). As a consequence, both survey timing and the number of visits need to accommodate species vocalizing behavior to ensure accurate detection, particularly for species with sporadic vocalization patterns (La and Nudds, 2016). Age and sex-specific variation in vocalization rates cannot be accounted for easily when using automated recorders, but our methods allowed for the other variation factors, as we sampled over a relatively short period of time during the breeding season, and sampled over a wide timeframe every day, thereby minimising the potential for seasonal and diurnal variation in call rates. Our results, together with those of Johnston et al. (2014), showing how detection probability varies by species, should be considered in decisions about study design when planning to survey birds using automated recorders or traditional methods.

4.5. Occupancy

We calculated occupancy as 0.682 for nightjar, 0.382 for Dartford warbler and 0.162 for woodlark, showing that nightjar is widespread across the study sites, while woodlark has a much more restricted distribution. This is in line with other survey data for the sites, collected by traditional survey methods (J.Eyre and J.Clark; D. Boyd pers. comms.), and previous occupancy studies (Furnas and Callas, 2015; Campos-Cerqueira and Aide, 2016; Wood et al., 2019). Although the occupancy figures provide a population estimate in themselves, they could potentially be used to generate an estimate of the number of pairs, as the common measure for population size. We did this provisionally, using a combination of habitat area and previously recorded breeding densities to give the following numbers: Dartford warbler 140, nightjar 51 and woodlark 8.

The occupancy modelling indicated a positive relationship between nightjar and TCDsum. This corresponds to associations with woodland found in previous studies (Bright et al., 2007; Conway et al., 2007). The negative relationship between Dartford warbler and Heather Grassland was surprising, as this species is generally associated with dry-humid heath, and gorse, sometimes with a grassy component (Bibby and Tubbs, 1975). Woodlark occupancy was positively related to Heather Grassland, and negatively to WAWsum and Heather. These results are more expected, as nest sites for this species are generally found in tall/dense heather or grass (Mallord et al., 2007), while foraging sites have short grass and bare ground (Conway et al., 2009).

5. Conclusion

Our study demonstrates the suitability of the bioacoustics approach to identify the distributions and assess the populations of target bird species on heathland study areas. Occupancy and detectability estimates were produced, taking into account imperfect detection. If carried out on a regular basis, this method could provide a valuable new approach for monitoring of population levels and favourable conservation status. For future studies in this setting, and with these species, methods might be improved by increasing the number of sample sites at which recording takes place. This approach would be likely to improve the modelling for woodlark, but would need to be balanced against potential effects on models for the other two species studied.

The field of conservation biology is continuously adopting improved, cheaper and more readily available technologies. In the near future, automated interpretation of recordings using machine learning methods will become increasingly viable, allowing effective identification of a range of bird species (Brandes, 2008; Acevedo and Villanueva-Rivera, 2009; Knight et al., 2017; Shonfield and Bayne, 2017, Stowell et al., 2019). The permanent nature of bioacoustic recordings will allow these ongoing developments in call analysis and automated identification to be used to re-analyse previously collected data, perhaps alongside new recordings (Shonfield and Bayne, 2017; Stiffler et al., 2018). The use of bioacoustics will, therefore, be indispensable for conducting long-term and potentially continuous monitoring over large spatial scales, aiding understanding of the ongoing effects of threats and management practices on bird populations on heathland and in other environments.

Author contributions

CA conceived the ideas, designed methodology; collected and analysed the data. CA led the writing of the manuscript, with MG contributing to establishment of occupancy modelling methods and development of the text. Both authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data accessibility

Data, metadata and R script has been archived at Mendeley Data.

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3.6 Song types in the European nightjar

BIRD STUDY
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Identification of different song types in the European Nightjar *Caprimulgus europaeus*

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ABSTRACT
Capsule: Two distinct song types were identified for male European Nightjars *Caprimulgus europaeus* with their relative frequency of use changing through the breeding season, indicating a possible link to paired status.
Aims: To test whether two song types could be defined in audio recordings and whether use differed in relation to the paired status of males.
Methods: Unattended acoustic recording devices were placed at a Nightjar study site in Nottinghamshire, United Kingdom, and recordings of churring vocalizations were made during two periods of the breeding season. These recordings were then analyzed to identify the presence/absence of the song terminal phrase and associated audible features.
Results: Two distinct song types were identified in the recorded audio data that differed in their terminal phrasing and overall song duration. The number of Nightjar songs with a terminal phrase increased significantly between the two sampling periods, from lower levels during the site arrival period, to higher levels during the first clutch initiation period.
Conclusion: This study showed that the use of Nightjar song types appears to vary through the breeding season, with males being more likely to produce song with a terminal phrase during the first clutch initiation period, when they are more likely to be paired or in the presence of a female. The unattended acoustic recording method may provide a minimally intrusive means of assessing the number of Nightjar breeding pairs and not just singing males.

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Introduction

Bird vocalizations vary widely between and within species. They allow birds to communicate with conspecifics and other individuals, transferring information or advertising their presence. The songs and calls emitted also provide one of the main cues enabling ornithologists to survey avifauna. A change in song type during the breeding season has, in particular, been linked to male pairing status for a number of bird species (Catchpole & Slater 2008). Paired males often appear to put less effort into their vocalizations once a mate has been attracted, with species such as Great Reed Warbler *Acrocephalus arundinaceus* singing shorter, simpler songs (Catchpole 1983), American Redstart *Setophaga ruticilla* singing less often (Staicer *et al.* 2006), Reed Bunting *Emberiza schoeniclus* producing slower songs (Bessert-Nettelbeck *et al.* 2014, Nemeth 1996), and Cerulean Warbler *Setophaga cerulea* having both a slower song rate and lower minimum frequency (McKillip & Islam 2009). In addition, a number of bird species have been found to have songs of two different types, with or without a distinctive ending – referred to as accented and unaccented respectively. The unaccented song type in these species appears to function primarily between males in the context of territorial defence, whereas the accented song type is produced more when a female is present and is associated with courtship and pair bonding (Byers 1996, Catchpole & Slater 2008, Kroodsma *et al.* 1989, Morse 1966).

The European Nightjar *Caprimulgus europaeus* (hereafter Nightjar) is a species of conservation concern in Britain, having suffered a decline in breeding numbers and contraction in its range (Eaton *et al.* 2015). The male has a distinctive 'churring' song, comprising an extended repetitive trill occupying a frequency band of 1–2.5 kHz, normally delivered around dusk and dawn from a perched location on a horizontal branch (Bibby *et al.* 2000, Cadbury 1981, Conway *et al.* 2007, Evans *et al.* 1998, Mustoe *et al.* 2005, Wilson 1985). The song has a well-defined structure consisting of a short initial phrase, followed by alternating major and minor phrases, sometimes divided with silent intervals. The major

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phrases have a higher maximum frequency and are delivered at a lower repetition rate than those comprising the minor phrase (Hunter 1980, Rebbeck *et al.* 2001). Experienced Nightjar fieldworkers have reported that the song may end in one of two ways, either with the churring ending abruptly, or with a distinctive terminal phrase. This terminal phrase sounds like a 'machine slowing down' and is sometimes accompanied by non-vocal wing-claps and 'dweep' calls (Coward 1928, Lowe 2011, Mullarney *et al.* 1999, Sample 1996, Wilson 1985). It has been suggested that this behaviour might be used by males that are in a pair or that are in the vicinity of a female (Ferguson-Lees *et al.* 2011, Lowe 2011, Selous 1899, Wilson 1985).

Although there is a rich legacy of field observation and study of the Nightjar in the United Kingdom (e.g. White 1769), the species is difficult to observe due to its crepuscular activity patterns (Cresswell & Alexander 1992, Wilson 1985), and it suffers from low detectability in surveys (Johnston *et al.* 2014, Zwart *et al.* 2014). This reduces the ability to accurately assess population sizes and trends. The latest national census, undertaken in 2004, estimated the UK population to be 4606 singing males (95% confidence limits +/− 913; Conway *et al.* 2007). During such assessments, the locations of churring males are used to determine territories, based on the presence of simultaneously churring males, registrations over 350 m apart or clusters of registrations (Conway *et al.* 2007, Evans *et al.* 1998). While this method does provide a useful indicator of population size, the assumption is normally made that the number of singing males/territories is equal to the number of breeding pairs. However, this is not necessarily the case, as singing males are only indicative of possible breeding (BTO 2014) and do not, by themselves, provide evidence of breeding pairs. Moreover, male Nightjars, especially unpaired individuals, can be very mobile and may vocalize repeatedly from different locations within an area of habitat (Feather 2015, Sharps *et al.* 2015, Spray 2006). Therefore, if assessments are based upon the number of churring males, there is the potential to over-estimate the number of breeding pairs at a site.

Audio recording of Nightjar songs could potentially be used to improve population estimates in monitoring schemes. If the two song endings described above can be shown to be detectable in recorded songs, and linked to paired status, then this could potentially be used to refine survey data, and more accurately assess the number of pairs, instead of the number of singing males. This would lead to more accurate population assessments for the species and improved conservation action. In addition, the data for such an assessment can potentially be gathered by unattended acoustic recording devices (ARDs), which automatically capture the vocalizations of birds, offering a survey approach that is minimally intrusive and a comprehensive means of recording avian subjects (Brandes 2008, Celis-Murillo *et al.* 2012, Farina *et al.* 2011, Frommolt & Tauchert 2014, Trifa *et al.* 2008, Zwart *et al.* 2014). The song of a male Nightjar may be readily captured by such devices, allowing the detailed analysis of song components such as time and frequency characteristics, and the presence and structure of distinctive phrases. Although the terminal phrases heard by fieldworkers have been anecdotally described, they have not previously been assessed and used within a bioacoustics framework. If the terminal phrase difference between the two song types can be detected using ARDs, then this may allow pairing status to be determined and offer a valuable new census tool to determine the spatial distribution and population size of Nightjar breeding pairs.

We aimed to determine whether the two song types, with and without the terminal phrase, could be recognized and quantified by reviewing audio recordings taken from the field. We then related this finding to additional information on the Nightjar populations at the study site, to determine whether the use of the two song types varied through the breeding season and was therefore potentially linked to the paired status of the males present.

Methods

Study site selection

The Nightjar is a summer migrant to the UK, where it is known to breed throughout much of the country where suitable habitat is present, but particularly in the south and east (Conway *et al.* 2007). The species is ground-nesting, with a clutch size of two, is sometimes double-brooded, and birds are often faithful to nest sites between years (Berry 1979). Mate-switching between broods has been recorded by Cresswell & Alexander (1990). The species is insectivorous, foraging over a range of habitat types, and may travel some distance from the nest-sites, depending on the availability of feeding habitat nearby (Langston *et al.* 2007). Song territory sizes have been recorded as being in the region of 10 ha, but home ranges, including such foraging habitats, may be an order of magnitude greater than this (Bright *et al.* 2007, Sharps *et al.* 2015).

The study was conducted at Sherwood Pines Forest Park in Nottinghamshire, UK (53°9′N 1°5′W). The site, which has a long-documented history of Nightjar occupancy, is managed by the Forestry Commission and consists of coniferous plantation woodland and heathland clearings over a total area of 13.4 km^2 (Lowe *et al.* 2014). This part of Nottinghamshire has been regarded as a stronghold for the species in the past, but the 2004 national census indicated a 10% population decline in the region (Conway *et al.* 2007). An annual survey of the study area, conducted for ten years between 2001 and 2010, estimated the annual breeding population at the site to be 13–20 nesting pairs (Lowe *et al.* 2014).

Audio data collection

To record Nightjar vocalizations, Wildlife Acoustics Song Meter® 2+ ARDs with Firmware R.3.3.7 (Wildlife Acoustics, 2014) were located throughout the study site during the Nightjar breeding season, with five devices deployed between 23 May and 22 August 2014 and ten between 24 April and 29 July 2015. More devices were employed than strictly necessary to allow for redundancy in the data collection process, and some device locations were repeated between years.

The ARDs were fitted with an SMX-II omni-directional microphone and programmed to record nightly, from 30 min before sunset, until 30 min after sunrise. They were set with a gain of +48 dB and a sampling rate of 44,100 samples per second, covering a frequency range up to 22 kHz. The recordings were saved as 30 min duration Waveform Audio (WAV) files on to SD memory cards within the ARDs.

As the ARDs were deployed at the start of the season, prior to territories and nest sites being established, the devices were positioned under the guidance of the Birklands Ringing Group (BRG), based upon past survey data and their knowledge of the site. To avoid overlap between the ARDs in terms of the males recorded, the minimum distance between devices was 452 m, i.e. much greater than the 350 m distance recommended by Conway *et al.* (2007) to separate territories, and thus minimizing the chance of double counting. The use of ARDs was minimally intrusive to the population of Nightjars, as it was only necessary to make a brief daytime visit to each device every two weeks in order to change the batteries and memory cards.

Nightjar breeding data collection

During both study seasons, the BRG used a co-ordinated count technique to estimate the number of male Nightjars within the study site (Conway *et al.* 2007, Evans *et al.* 1998). This consisted of a number of surveyors simultaneously counting the number of 'churring' males present at dusk. This survey was repeated six times during June and July.

Nightjar nests were also located in both 2014 and 2015 using the method described by Lowe (2011), and the distance of each Nightjar nest from the nearest ARD was measured after the Nightjars had finished nesting and the young had fledged. This method allowed the number of breeding pairs to be determined, together with the estimated egg laying dates for each nest.

Audio data analysis

Two sets of audio data were sampled from the recordings made by the ARDs, each covering a period of five nights of recordings with six ARDs. An early breeding season Sample A was taken from recordings captured during the site arrival period in May, when it was assumed that males would be likely to be unpaired. These data was taken from the period after the date of the first recorded male Nightjar song at the ARD location. However, five consecutive nights could not be used in all cases because some nights included an unacceptable level of background noise. When this occurred, the five nights closest to the date of the first recorded male Nightjar song were selected.

A later breeding season Sample B was then taken from recordings made in June, when males were assumed to be paired. These data was selected based upon the first clutch initiation period. The date the first egg was laid at the closest nest to each ARD was designated as Night 3, with two nights before and two nights after this date being selected.

The selection of ARDs used for provision of audio data was based upon the presence of Nightjar vocalizations within recordings, the spread of ARD locations within the site, available date parameters and the proximity of an active nest. The ARDs and nights utilized also excluded sites where licenced Nightjar ringing or song-lure activities had taken place in close proximity to an unattended ARD. With these selection criteria, Sample A was taken from May 2015, while Sample B was taken from both June 2014 (ARDs B1–B3) and June 2015 (ARDs B4–B6).

Kaleidoscope® v2.1.0 software (Wildlife Acoustics, 2014) was used to manually analyse the audio recordings, by listening to playback and visual inspection of spectrograms. This allowed the Nightjar songs to be located within the dataset – an individual male Nightjar song being defined as having one or more major or minor phrases of the same signal strength and no silent intervals exceeding one minute in duration. Time and frequency variables were then measured for each song, including the duration of the song, identification of the presence/absence of a terminal phrase and its duration, and the presence of silent intervals, wing claps and terminal 'dweep' calls. Songs without a terminal phrase were termed song Type I and songs with a terminal phrase (and associated wing-claps

Table 1. Summary of measured variables for Nightjar Song Types I and II.

Song type	N	Duration of song in minutes, excluding terminal phrase (median and range)	% songs with one or more silent interval	% songs ending with a major phrase	% songs ending with a minor phrase	% songs with associated wing claps	% songs with associated 'dweep' calls	Duration of terminal phrase in seconds (median and range)
Type I – without Terminal Phrase	440	2.19 (0.03-32.02)	53	66	34	2	4	n/a
Type II – with Terminal Phrase	219	0.98 (0.03-16.48)	27	7	93	87	23	6 (1-54)

and 'dweep' calls) were termed Song Type II. For each recorded song, the sample (A/B), date, time and ARD location was noted.

Following analysis of the audio recordings, data exploration was carried out following the protocol described in Zuur *et al.* (2010). Generalized linear models (GLM) were used to assess the influence of variables on the production of the two song types. Each song was treated as a separate observation ($n = 659$), and binomial models with a logit link were fitted using function GLM in R (R Core Team, 2018). The logit link function ensures positive fitted values, and a binomial distribution was used for the binary outcome of Song Type I (coded as 0) or II (coded as 1). Categorical variables included Plot (the ARD location on the ground – a factor with $n = 7$ levels), Sample (A or B, $n = 2$), Year ($n = 2$). Numerical variables were NightHour (number of hours after 19:00 h), and its quadratic term.

Full models were checked for overdispersion and adequacy (Zuur *et al.* 2010). Model selection followed an informatic-theoretic approach (Burnham & Anderson 2002), with models fitted for all possible combinations of explanatory variables without interactions. These were ranked by corrected Akaike Information Criteria (AICc), and the best fit model was selected. Statistical tests were conducted using MuMin, ARM and base packages in R (Bartoń 2018, Gelman & Su 2018, R Core Team 2018, RStudio Team 2015).

Results

Nightjar breeding data

Using the combination of co-ordinated counts of churring males (Conway *et al.* 2007, Evans *et al.* 1998) and nest searches (Lowe 2011), the BRG estimated the study site to support 18 male Nightjars during the 2014 breeding season (6 unpaired and 12 paired), and 17 male Nightjars (5 unpaired and 12 paired), during the 2015 breeding season. Therefore, approximately 33% of male Nightjars were unpaired during the period of the study. The distances between the Sample B ARD locations used and their nearest nest sites varied between 29 and 190 m.

Audio data

A total of 659 male Nightjar songs were identified in the Sample A/B dataset. Review of the recorded 'churring' vocalizations could effectively identify the terminal phrase, when present, and differentiate the two distinct song types expected. Whilst both song types included major and minor phrases and sometimes silent intervals, the endings and durations were different (Table 1). Song Type I (Figure 1) ended abruptly and was rarely accompanied by non-vocal wing claps (only 2% of occasions). Song Type II concluded with a distinctive terminal phrase – a gradual descent in

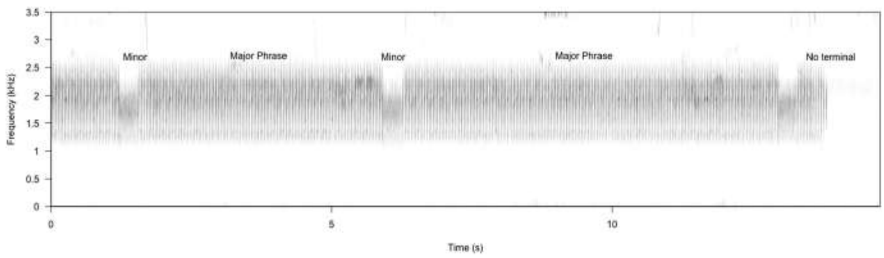

Figure 1. Spectrogram (acoustic frequency plotted against time) showing the major and minor phrases, the principal constituents of male Nightjar song. This is Song Type I, without a terminal phrase, ending abruptly on either a minor phrase or a major phrase.

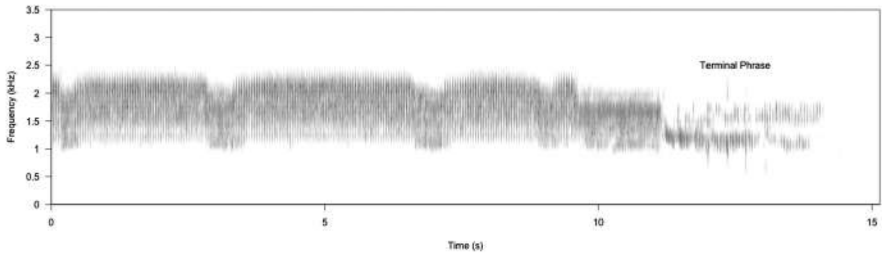

Figure 2. Spectrogram showing male Nightjar Song Type II, with a terminal phrase. The terminal phrase may be preceded by either a minor phrase or a major phrase.

frequency with a median duration of 6 s (Figure 2). This was frequently accompanied by non-vocal wing claps (87% of occasions). In addition, the duration of Song Type II was, on average, shorter than that of Song Type I (medians of 57 s and 132 s respectively).

Both song types had similar peaks in occurrence at dusk and dawn, concentrated in the 50 min after sunset (to 23:00 h) and the 80 min before sunrise (from 02:00 h) (Figure 3). However, Song Type II appeared to be particularly common around dawn.

More Nightjar songs were recorded during the later sampling period, with 32% of songs in the dataset recorded during the site arrival period (Sample A), and 68% during the first clutch initiation period (Sample B). Of the 659 songs, 67% were Song Type I and 33% Song Type II (Table 2). The proportion of Song Type II was higher in Sample B, with each ARD deployment having 27–47% (38% overall) Song Type II, while the proportions in Sample A were 13–39% (24% overall) (Table 3).

The data exploration found no constraints in terms of outliers, collinearity or zero-inflation. Model validation was also suitable, with no evidence of over-dispersion from review of a binned residual plot. The best-fit model used Sample and the quadratic term for NightHour as covariates, with Sample B (the first clutch initiation period) and later night hours resulting in higher probabilities for Song Type II (Table 4, online Table S1). This indicates that males appeared to use Song Type II more readily during the first clutch initiation period (Figure 4), compared to site arrival, and that it was used more at dawn than dusk (Figure 5).

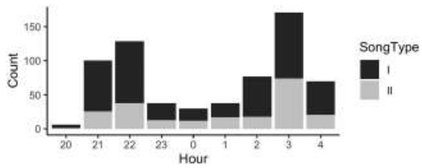

Figure 3. Timing of Type I and Type II Nightjar song recordings, showing peaks in vocal activity at dusk and especially at dawn.

Discussion

Use of different song types

Our bioacoustic approach, analysing recordings taken from ARDs, allowed two Nightjar song types to be differentiated, based upon the presence or absence of a distinctive terminal phrase, and differences in the song duration (Song Type II including the terminal phrase and being of shorter duration). To our knowledge, this is the first time this has been confirmed for Nightjars using spectrogram analysis. Although the use of these two song types by Nightjars remains unclear, previous work on a range of other species shows that song character changes and vocal effort declines in paired males (Bessert-Nettelbeck *et al.* 2014, Byers 1996, Catchpole & Slater 2008, Catchpole 1983, Kroodsma *et al.* 1989, McKillip & Islam 2009, Morse 1966, Nemeth 1996, Staicer *et al.* 2006).

The two song types were confirmed to differ in their prevalence between the two recording periods – Type II, with the terminal phrase, being significantly more common during the first clutch initiation period in

Table 2. Numbers of Nightjar Song Type I (without Terminal Phrase) and Song Type II (with Terminal Phrase) produced during the site arrival period and during the first clutch initiation period.

Song Output	Sample A Site Arrival Period	Sample B First Clutch Initiation Period	Total
Song Type I	163 (76%)	277 (62%)	440 (67%)
Song Type II	51 (24%)	168 (38%)	219 (33%)
Total Nightjar Songs	214 (32%)	445 (68%)	659

Table 3. Audio sampling periods and number of Nightjar songs recorded at each ARD location used.

ARD	Location (OS GR)	Start Date (Night 1)	End Date (Night 5)	Datum*	Number of Songs	Song Type II (%)
A.1	SK60616169	12 May 2015	16 May 2015	7 May 2015	44	39
A.2	SK60176224	13 May 2015	20 May 2015	10 May 2015	24	25
A.3	SK61916040	14 May 2015	18 May 2015	10 May 2015	41	24
A.4	SK61166183	12 May 2015	16 May 2015	11 May 2015	55	13
A.5	SK61216106	15 May 2015	22 May 2015	12 May 2015	17	18
A.6	SK61876085	19 May 2015	23 May 2015	16 May 2015	33	24
B.1	SK60596103	1 Jun 2014	5 Jun 2014	3 Jun 2014	55	47
B.2	SK62036066	5 Jun 2014	9 Jun 2014	7 Jun 2014	74	38
B.3	SK61146180	6 Jun 2014	10 Jun 2014	8 Jun 2014	152	39
B.4	SK60536097	7 Jun 2015	11 Jun 2015	9 Jun 2015	64	42
B.5	SK60176224	8 Jun 2015	14 Jun 2015	12 Jun 2015	36	31
B.6	SK61166183	20 Jun 2015	24 Jun 2015	22 Jun 2015	64	27

*Datum Events: A.1 to A.6 – Date of the first recorded male Nightjar song, B.1 to B.6 – Date first egg laid at first nest.
Notes: ARD A.2 positioned at the same location as ARD B.5, ARD A.4 at the same location as ARD B.6.
OS GR = Ordnance Survey Grid Reference.

June, compared to the site arrival period in May. Although we have identified this temporal difference in song type use, the relationship with paired status is still not entirely clear. Despite the terminal phrase being long-reported as a part of the song repertoire for Nightjar males, its function is not understood. Anecdotal reports have linked it to the presence of nearby females, which may be mates, but whether it is a communication towards the female or other males is unknown. Song Type II was more common in Sample B, the June first clutch initiation period. These recordings were taken from territories where a breeding pair and nest was present within 200 m, and were captured during a period when male birds would

Table 4. Results of best-fit generalized linear model, indicating significant positive relationships with NightHour and Sample variables.

		95% confidence interval for odds ratio		
	B (SE)	Lower	Odds Ratio	Upper
Constant	−1.54*** (0.22)			
Night Hour (quadratic)	0.008** (0.003)	1.002	1.008	1.015
Sample B	0.75*** (0.19)	1.45	2.11	3.10

Note: R^2 = .023 (Hosmer-Lemeshow), .029 (Cox-Snell), .04 (Nagelkerke).
Model $\chi^2(2) = 19.39$, $^{**}P < 0.01$, $^{***}P < 0.001$.
Night Hour = number of hours after 19:00.
Sample = A (site arrival) or B (first clutch initiation).

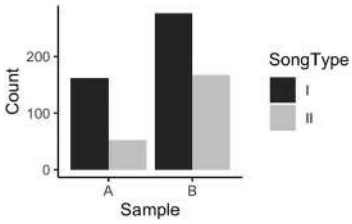

Figure 4. Numbers of Song Type I and Song Type II recorded in Sample A (site arrival) and Sample B (first clutch initiation), showing higher proportion of Type II songs in Sample B.

be expected to be actively displaying. It is known that paired males tend to stay close to their breeding territory when churring, whilst unpaired males roam over a larger area in search of a female (Feather 2015, Spray 2006, Wilson 1985). However, in this study, we have not definitively linked the Type II song to known paired males. Our results therefore only give limited support to the hypothesis previously raised by field workers that the Type II song is related to paired status and the presence of a female.

One confounding factor to this hypothesis is that Song Type II was recorded during the site arrival period, when males would not be expected to be paired. This use may be due to Song Type II not being exclusive to paired males, but being used more generally in the presence of females. In this case, the occurrence of Song Type II in the early season could arise if some females arrived early from migration to the breeding grounds (Mullarney *et al.* 1999) – despite females average arrival time often being several days after the males (Berry & Bibby 1981 found an average of 10.9 days whilst Lowe *et al.* 2014 noted a range of 1–10 days). Although it was not known when the

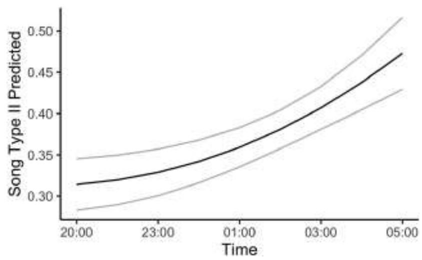

Figure 5. The predicted song rate from the best-fit generalized linear model indicates that the proportion of Song Type II increases through the night.

females arrived at the site, it is possible that unpaired males may initially react to the presence of a female at the breeding grounds but then increase their output of Song Type II once paired with a female.

One issue with the analysis of the audio data is dependency of the song type at a recorder location, as songs are highly likely to be the same individuals sampled on multiple occasions. Without the identification of individual males, this pseudoreplication is hard to deal with. Further studies to identify the use of the terminal phrase by individual known birds, with defined paired status, would clearly be beneficial. This could potentially be done by combining vocal individuality data (Rebbeck *et al.* 2001) with that obtained from radio-tracking or gobal positioning system-based studies (Spray 2006).

Vocal activity levels

We recorded Nightjar vocal activity throughout the night, but found that it was concentrated around dusk and dawn, confirming previous findings by Cadbury (1981) and Zwart *et al.* (2014).

Alongside differences in the proportion of song types, varying levels of vocal activity were found between the two Sample A/B periods. Matched amounts of acoustic recording time were undertaken for each period and twice as many Nightjar songs were recorded during the first clutch initiation period in June compared to site arrival in May. This could potentially be due to: (i) fewer males initially being present, as the full cohort arrives over a period of time, and/or (ii) males only singing sporadically on arrival, as they recover from migration. More frequent singing around egg-laying time would then be expected, as all males are now present, paired males are maintaining territories, and males that remain unpaired are displaying actively to challenge for females, perhaps aiming to mate for second broods (Cresswell & Alexander 1990, Lack 1930, Wilson 1985). In our dataset, a small number of spectrograms contained simultaneous 'churring' i.e. at least two males singing at the same time and place.

Implications for survey, surveillance and monitoring

The breeding status of birds is sub-divided by the British Trust for Ornithology (BTO) into four classifications: non-breeding, possible, probable and confirmed breeding; according to the evidence available (BTO 2014). For Nightjar, current survey methods assume that any churring male holds an active territory and is part of a breeding pair, however, this is unlikely to be true. The findings of this study point the way to a possible refinement of this assessment, based upon the prevalence of Song Type II at a sampling location. Now that this song type has been positively identified using acoustic analysis, it may be possible to link its use more definitively to paired status, and then use this information to help define the breeding status of recorded males. For example, it could be possible to establish a threshold value for Song Type II, above which probable breeding status may be ascribed. Based upon this study, a threshold value in the region of 30% or more Song Type II would define a sample indicating a probable paired male (with limited misclassification in either direction).

The potential to more accurately define paired status in Nightjars is an important goal for advancing survey and evaluation methods for this species, enabling the assessment of favourable conservation status. The findings of this study are a useful step forward in bioacoustic monitoring for this purpose, highlighting the potential of song type analysis to provide individual behavioural information. Further developments should allow improved counts of the numbers of breeding pairs of Nightjars, adding to the already proven use of bioacoustics to determine presence/absence (Zwart *et al.* 2014).

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Declaration of authorship: This was a joint project between SD and AL following a one year trial undertaken by AL and Baker Consultants to test the effectiveness of unattended acoustic recording devices at suitable sites, to ascertain Nightjar presence and breeding. Following AL original concept for the identification of Nightjar breeding status via male song type, SD and AL designed the methodology and conducted the fieldwork. SD analysed the audio data. SD and CA wrote the manuscript, with CA conducting the statistical analysis. The work also formed the basis of SD dissertation as part of the Manchester Metropolitan University MSc in Biological Recording. All authors contributed critically to the drafts and gave final approval for publication.

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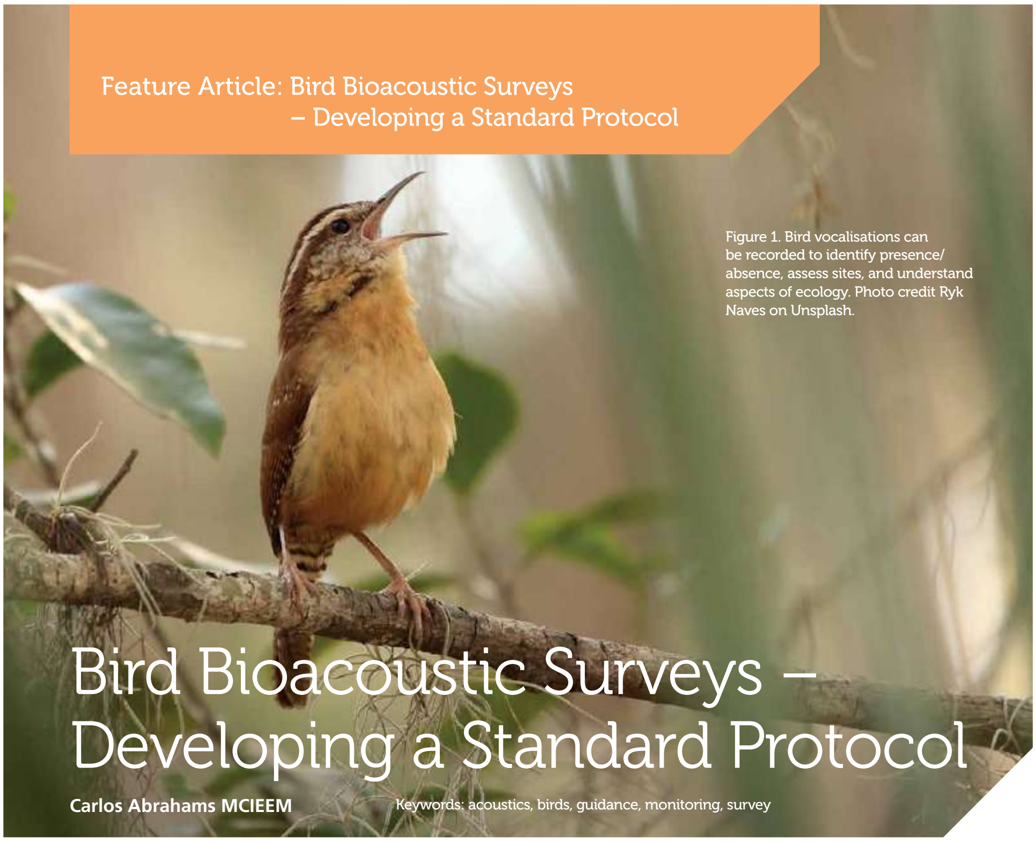
3.7 Bird bioacoustic surveys



Feature Article: Bird Bioacoustic Surveys – Developing a Standard Protocol

Figure 1. Bird vocalisations can be recorded to identify presence/absence, assess sites, and understand aspects of ecology. Photo credit Ryk Naves on Unsplash.

Bird Bioacoustic Surveys – Developing a Standard Protocol

Carlos Abrahams MCIEEM

Keywords: acoustics, birds, guidance, monitoring, survey

Bioacoustic surveys can be used to capture useful and robust data on bird vocalisations to inform studies on avian distribution and ecology. However, currently there are no recognised standard methods for their use in the UK. This article sets out a draft protocol for testing and adoption, and invites feedback from CIEEM members to further develop good practice.

Introduction

Animals produce sound. Birds, amphibians, fish, invertebrates and mammals sing, squeak, click, snap, crackle, pop, rattle and hum. As ecologists, we can use these signals to detect animals in the dark or at remote locations, identify what species are present, and work out what they are doing (Figure 1). Ornithologists have always used this capacity to tell the difference between species yet, unlike bat workers, do not routinely make recordings of birds in the field as part of standard survey practice. We're missing a trick.

Birds create species-specific sounds that can be readily recorded using automated or manually-controlled recording systems. Such devices allow acoustic surveys to be undertaken for extended periods of time, with data being saved for later analysis using machine techniques and/or human assessors. This bioacoustics approach is familiar to any bat surveyor, as detectors are absolutely vital to pick up ultrasound calls to which human ears aren't attuned. However, birds can normally be seen and heard in the field without the use of specialised equipment. So, why use a bioacoustics approach for bird survey and monitoring?

The benefits of using automated recording, especially alongside traditional surveys, are well documented in scientific research (see Box 1). In particular, the ability to produce a standardised, long-duration, permanent dataset, which can be repeatedly analysed, and subject to quality assurance checks, is a major advantage over standard field surveys (Darras *et al*. 2018). There are some disadvantages – principally the lack of visual cues that would be used by a human surveyor in the field, and the fact that the static bioacoustic approach does not lend itself to preparing the territory maps often used in bird assessments (see Box 2). However, depending on the aims of the survey, bioacoustics methods have many advantages. For example, Zwart *et al*. (2015) found that acoustic recorders offered a 217% increase in nightjar *Caprimulgus europaeus* detection over human surveyors, (with 19 detections in 22 survey periods compared to 6 detections by humans). With these recognised benefits, the use of automated recorders in scientific research has increased significantly over the last ten years (Figure 2).

Human vs. machine

The bioacoustics approach, using static recorders, is equivalent to point-count bird surveys. Several studies have compared point-count data to automated acoustic recording in a variety of habitats such as rainforest (Leach *et al*. 2016), tropical savanna (Alquezar and Machado 2015), temperate woodlands (Holmes *et al*. 2014, Furnas and Callas 2015), and temperate meadows (Tegeler *et al*. 2012). These have shown that the results are comparable in terms of species-richness and bird assemblage composition when used for equivalent lengths of time. However, automated recording can easily provide larger amounts of data than human surveyors, often with less survey effort (Holmes *et al*. 2014). For example, Tegeler *et al*. (2012) gained >1,100 additional hours of data using automated recorders, and recorded more species with a quarter of the personnel effort. Using both methods together often provides the best overall results as their respective strengths and weaknesses are complementary (Klingbeil and Willig 2015, Shonfield and Bayne 2017).

Developing a draft survey protocol

Although there are myriad survey methods for bird assemblages, taxon groups and single species (Gilbert *et al*. 1998), few organisations have yet developed guidance on the use of bioacoustics methods (Darras *et al*. 2018). The World Wide Fund for Nature has recently published an introductory guide (Browning *et al*. 2017), with more detailed methods produced for tropical bird assemblages (Lacher 2008), Canadian forest birds (Saskatchewan Ministry of Environment 2014) and Australasian bittern *Botaurus poiciloptilus* (O'Donnell and Williams 2015).

To start the development of UK guidance, the first national workshop on bird bioacoustics was held in June 2017, attended by more than 40 delegates from academia, consultancies and conservation bodies. Participants were asked to grade the relative pros and cons of the approach (see Boxes 1 and 2), and a draft survey protocol was developed from the contributions (Box 3). Further input on this prototype is sought from CIEEM members, but it is considered to be a sound basis for gathering bioacoustics data for ecological assessments and site management in the UK.

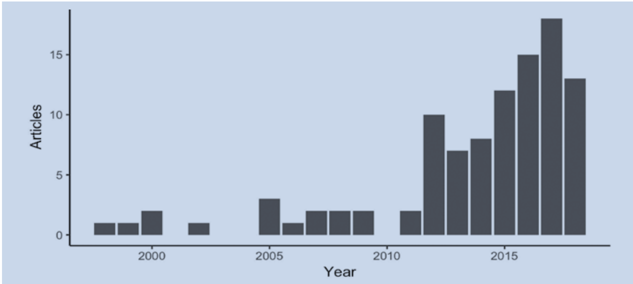


Figure 2. Number of original research articles that used recording units for avian bioacoustic studies. Search conducted on Web of Science database in September 2018 using the following search term: (bird* OR avian) (automated OR autonomous OR *acoustic) (recorder OR aru OR ard).

Box 1.

Advantages of bioacoustics	Grade 10=major; 1=minor
Long-duration data capture	7.3
Ability to **repeatedly listen** to and re-analyse data	7.1
Permanent raw data record	6.9
Greater **standardisation** in data collection	6.3
Quality assurance opportunities, with ID verification	6.0
Reduced **subjectivity** and observer **bias**	5.7
Less **disturbance** to surveyed birds	4.5
Opportunities to **share raw data**	4.3
Less reliance on **availability** of expert surveyors	3.5
H&S – avoids **night-time** work, reduces visits to **remote** areas	3.4

Box 2.

Disadvantages of bioacoustics	Grade 10=major; 1=minor
Capital **cost** of equipment	7.1
Need for improvements in **automated classification** systems	6.7
Lack of **expertise/skills** in bioacoustics	6.0
Reduced ability to cover a wide **spatial area** compared to transects	5.9
Data storage requirements	5.5
Potential for **loss of data** if units fail	5.1
Availability of **hardware/software**	4.8
Comparability with established methods	4.8
No **visual recording** of birds	4.8
The method is not yet widely **proven/accepted**	4.3

Survey considerations

1. Survey effort and timing

The recording and data volume requirements of any survey will vary depending on the project objectives and the species concerned (Bayne *et al*. 2017). The seasonal programme and daily timing of recording need to be considered, to maximise the long-term data capture benefits of automated recorders, whilst avoiding an overwhelming data mountain (Klingbeil and Willig 2015).

Bird detection probability normally varies with time of the day, so recording times distributed throughout the day will sample the entire community most effectively

Feature Article: Bird Bioacoustic Surveys – Developing a Standard Protocol (contd)

(La and Nudds 2016). Scientific studies have found that a stratified 'on-off' time sampling programme (e.g. recording 1 minute in every 10), can capture comparable data to continuous recording, with consequent benefits in terms of battery life, data storage and processing time (La and Nudds 2016, Bayne *et al.* 2017). This is especially the case when recording is focused on the main dawn and evening chorus times. With prices reducing and availability of data storage increasing, continuous recording, that can be sub-sampled later in the processing stage, is also a realistic option for fieldwork.

2. Recorder placement

For coverage of a site, the aim should be to sample across the range of the habitats and species of interest, with recorders placed to limit overlap of detection radii so that counts are independent (O'Donnell and Williams 2015). The effective radius of most recorders is in the region of 50 m, so a minimum separation distance of at least 100 m should be used (Yip *et al.* 2017). As a recommended standard, a larger 250 m spacing between recorder locations would provide 16 sampling locations/km^2. This is dense enough to provide a good level of survey data, and is also likely to be relevant to the territory sizes of bird species of interest within ecological assessments. However, alternative separation distances between 100-500 m could also be used, depending on survey requirements.

When placing recorders in the field, omnidirectional microphones should be used, located horizontally 1-2 m from the ground (or higher if security is an issue), and in a mounting position that does not block the field of sound or increase the levels of background noise from wind and water (Klingbeil and Willig 2015, La and Nudds, 2016)

3. Recording equipment

There are many options in terms of recording equipment, but the best current approach uses off-the-shelf, single recorder units, which incorporate a microphone, circuitry, power source and recording media in a single unit. Examples of this are the Wildlife Acoustics Song Meters, Cornell Labs Swift or AudioMoth. These are both scaleable and easily available to a range of users.

Recorder model, microphone type, and settings should be standardised across a study and carefully recorded in metadata. Microphone management, calibration and checking is very important before and after field deployments, as degradation in microphone quality over time can significantly affect results.

4. Audio settings

For good quality audio data, a non-compressed digital file format (i.e. .WAV rather than MP3) should be used. If possible, recordings should be in stereo using a sample rate of 48 kHz and 24-bit depth (although 44.1 kHz and 16-bit depth is acceptable). These settings will cover the entire audible range, producing detailed data on frequency and amplitude to produce clear spectrograms and analysis information. If, however, the study is focussed on particular target species, with lower frequency calls, then a lower sample rate can be used to save on storage and battery life.

5. Metadata recording

With each survey deployment, appropriate metadata including location, dates/times, weather, habitat and equipment identifiers should be recorded. This can be done using paper/tablet, or by speaking into microphones while they are recording, so the metadata becomes part of the recorded data itself. This background data is clearly needed to accurately organise and archive recordings, and can be used for any detailed analysis of how environmental characteristics determine the bird acoustic assemblage. It is also important to make acoustic data as comparable as possible across different surveys, allowing use in larger-scale monitoring projects and contributions to databases.

Box 3. Draft Bird Bioacoustics Survey Protocol

1. Survey effort and timing

Surveys should include a minimum of two deployments, in April to mid-May, and mid-May to end of June, with a four-week gap between deployments. Recording should cover a five-hour period from two hours before sunrise until three hours after, with a one minute sample taken every ten minutes. Each deployment should cover a minimum of three days recording. The same methods should be used for evening recording, e.g. for dusk chorus, owls and nightjars, but using a three-hour sampling period, from one hour before sunset, until two hours after.

2. Recorder placement

Use a regular grid-based or stratified random sampling system across the survey area, with a minimum distance between sampling locations of 250 m. Recorders should be located 1-2 m from the ground, on tripods, narrow poles or trees <0.2 m diameter, avoiding branches/leaves around the unit as far as possible.

3. Recording equipment

Commercially available, off-the-shelf, single recorder units should be used to provide consistency in data collected between different studies. The recorder should be a programmable, automated unit, using omnidirectional acoustic microphones, with a flat response across the range of audible frequencies. Recorder and microphones should be individually numbered, checked and calibrated on a regular basis (at least once per year).

4. Audio settings

Recordings should be made as non-compressed .WAV files, ideally with a sample rate of 48 kHz and 24-bit depth. Lower sample rates may be used when surveying for lower-frequency, bird species (e.g. bittern) to save on storage and battery life. Before deployment, ensure that hardware and software settings are recorded and standardised across all units.

5. Metadata recording

At the start of each deployment, record the date/time, surveyor name, sampling location and recorder/microphone identifiers. Photographs of location and set-up should be taken. Weather conditions during the survey period should also be recorded.

6. Data analysis methods

Identify the presence/absence of each species in one minute audio samples and calculate the proportion of samples in which each species is recorded. Provide a summary of species observations per day or sampling event. If using any automated recogniser or clustering process, then the error rates should be checked and reported so that the quality of the recogniser can be properly assessed.

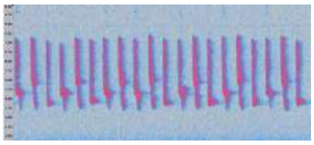


Figure 3. Bioacoustic software can be used to manage, view and analyse recordings, allowing identification of species present in the dataset, such as this chiffchaff *Phylloscopus collybita*. Image credit Carlos Abrahams

6. Data analysis methods

The analysis of data gained from acoustic recorders is perhaps the most difficult area in which to make standardised recommendations. A range of software is available to manipulate, view and analyse acoustic recordings (e.g. Kaleidoscope, Raven, Audacity, Luscinia and packages in R), some of which allow the clustering or automated recognition of bird calls (Figure 3). However, much scientific research has simply relied upon ornithologists listening to audio files and viewing spectrograms. At present, a human-supervised semi-automated process probably offers the best balance between accuracy of call classification and time required for analysis. Whichever method is used, the data analysis protocol should be fully described, and identification error rates calculated, providing metrics such as precision and recall if a recogniser has been used (Knight *et al*. 2017). The simple and robust metric of call activity, as set out in Box 3, will provide a species list for each sampling location, together with the relative vocal activity levels for each species. This presents a basic assessment of the data and will allow comparability between different studies. (Bayne *et al*. 2017).

Conclusion

Although there are still challenges to the widespread adoption of bird bioacoustics in the UK, the approach and technology is well proven around the globe in a wide variety of ecosystems and with a range of species and communities. Fully automated software to allow the recognition of all bird calls has not yet been developed, but this should not stop the use of the methods that are currently available. The draft protocol in Box 3 is targeted at the collection of species assemblage data for a particular site, such as for a breeding or wintering bird survey, but it could equally be used to focus on particular target species. Such single-species (or small group) approaches are extremely valuable, and acoustic surveys have already been conducted for conservation priorities like nightjar, corncrake *Crex crex*, bittern *Botaurus stellaris*, owls and capercaillie *Tetrao urogallus* (Abrahams and Denny 2018).

There is a good scientific basis to bird bioacoustics, great benefits to its use and a useful set of methods to follow. By sharing experience and building the practical evidence, the technique can be taken up effectively by the profession. Please help to test and refine the approach by using the draft protocol and offering feedback to Carlos Abrahams at c.abrahams@ bakerconsultants.co.uk

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3.8 Pond acoustic sampling scheme

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ORIGINAL RESEARCH

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Pond Acoustic Sampling Scheme: A draft protocol for rapid acoustic data collection in small waterbodies

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Abstract

1. Freshwater conservation is vital to the maintenance of global biodiversity. Ponds are a critical, yet often under-recognized, part of this, contributing to overall ecosystem functioning and diversity. They provide habitats for a range of aquatic, terrestrial, and amphibious life, often including rare and declining species.
2. Effective, rapid, and accessible survey methods are needed to enable evidence-based conservation action, but freshwater taxa are often viewed as "difficult"—and few specialist surveyors are available. Datasets on ponds are therefore limited in their spatiotemporal coverage.
3. With the advent of new recording technologies, acoustic survey methods are becoming increasingly available to researchers, citizen scientists, and conservation practitioners. They can be an effective and noninvasive approach for gathering data on target species, assemblages, and environmental variables. However, freshwater applications are lagging behind those in terrestrial and marine spheres, and as an emergent method, research studies have employed a multitude of different sampling protocols.
4. We propose the Pond Acoustic Sampling Scheme (PASS), a simple protocol to allow a standardized minimal sample to be collected rapidly from small waterbodies, alongside environmental and methodological metadata. This sampling scheme can be incorporated into a variety of survey designs and is intended to allow access to a wide range of participants, without requiring complicated or prohibitively expensive equipment.
5. Adoption of this sampling protocol would enable consistent sound recordings to be gathered by researchers and conservation organizations, and allow the development of landscape-scale surveys, data sharing, and collaboration within an expanding freshwater ecoacoustic community—rather than individual approaches that produce incompatible datasets. The compilation of standardized data would improve the prospects for effective research into the soundscapes of small waterbodies and aid freshwater conservation efforts.

KEYWORDS
acoustic monitoring, bioacoustics, ecoacoustics, pond, rapid assessment methods, soundscape, survey

1 | INTRODUCTION

1.1 | Pond conservation

Freshwater biodiversity is globally threatened by overexploitation, pollution, hydrological modification, habitat destruction, and invasive species (Cantonati et al., 2020; Dudgeon et al., 2006). These impacts, exacerbated by the interconnected nature of freshwater ecosystems, have resulted in population declines and species distribution changes, with consequences for a range of ecosystem services.

Even though ponds (small waterbodies <2 ha in area) can be relatively abundant in many landscapes and provide critical habitats for diverse floral and faunal communities, they have been under-recognized and neglected compared with larger freshwater habitats (Biggs et al., 2005; Bolpagni et al., 2019; Wood et al., 2003). Ponds are physically and biologically heterogeneous habitats, which offer migration stepping stones and breeding sites for aquatic, amphibious, and terrestrial species, and can support regional metapopulations and a high proportion of rare species (De Meester et al., 2005; Williams et al., 2004). Due to this diversity and function, pond ecosystems contribute significantly to freshwater (and terrestrial) biodiversity across the globe (Indermuehle et al., 2010; Williams et al., 2004). Despite their value, ponds are not covered by legal protection and policy in the same way that larger lakes and rivers are (Bolpagni et al., 2019; Hill et al., 2018), limiting options for their protection and enhancement.

In terms of scientific research, ponds also offer good model systems for surveys or hypothesis testing through experimental manipulation, providing potential for studies in ecology, evolutionary biology, and conservation biology (De Meester et al., 2005). The majority of recent publications on ponds have covered the interactions between environmental factors and species spatial patterns (focusing on zoobenthos), and have had a distinct applied research character, with increasing interest in methodological studies (Bolpagni et al., 2019).

1.2 | Pond survey

Effective and accessible survey methods are needed to enable evidence-based conservation action. However, established standard methods for the assessment of ponds are rare. The Predictive SYstem for Multimetrics (PSYM) was developed in the late 1990s, followed later by PLOCH and IBEM methods (Biggs et al., 2000; Indermuehle et al., 2010; Oertli et al., 2005), to allow assessment of the biological quality of ponds using aquatic plants and macroinvertebrates. However, these methods are all limited in their geographic applicability, the types of ponds to which they can be applied, the time and resource requirements for implementation, and the considerable amount of identification expertise needed to get reliable results (Biggs et al., 2000; Harper et al., 2019; Indermuehle et al., 2010; Labat, 2017; Oertli et al., 2005; Pond Conservation, 2010). As a result, ponds have often been neglected in limnological studies, and there is limited scientific knowledge of pond ecology (Mainstone et al., 2018; Oertli et al., 2005). The ecological basis for pond management is therefore poorly established, with practical conservation efforts often led by management "myths" rather than solid evidence (Biggs et al., 2005).

To enable accessible and efficient pond survey and monitoring, the need for a "Rapid Assessment Method" for ponds has been recognized (Labat, 2017; Menetrey et al., 2005; Pond Conservation, 2010; Sueur, Pavoine, et al., 2008). A Rapid Assessment Method is a standardized procedure that allows efficient generation of an index score, representing the ecological status or ecosystem function of a particular site, and summarizing key components of habitat integrity (hydrological, physical, chemical, and biological; Dorney et al., 2018; Mainstone et al., 2018). Developing such an approach for ponds would have value for researchers and citizen scientists, meeting a clear requirement for (i) improved collation and sharing of harmonized data, (ii) the integration of biological, physical, and chemical parameters, and (iii) increased geographical coverage of information on pond quality and biodiversity (Cantonati et al., 2020; Heino et al., 2020).

Although existing survey approaches, using invertebrate and macrophyte data, have significant value (Biggs et al., 2005; Bolpagni et al., 2019), there is an obvious need for expansion of widely applicable assessment tools that can develop coherent and transferable field data and metrics. Developments in technology are currently enabling such new approaches (August et al., 2015). For example, the use of environmental DNA and metabarcoding allows the identification of single species or assemblages from a simple water sample (Harper et al., 2019; Lim et al., 2016). The use of underwater sound recordings could offer the potential to assess pond habitats with minimally intrusive and easily employed field visits, allowing the identification of taxa present or calculation of overall metrics of environmental quality (Sueur, Pavoine, et al., 2008). Here, we propose the Pond Acoustic Sampling Scheme (PASS), a simple draft protocol to allow standardized minimal samples to be collected rapidly from small waterbodies.

1.3 | Freshwater ecoacoustics

Many freshwater taxa produce sound—notably fish, arthropods, and amphibians (Desjonquères et al., 2020; Linke et al., 2018). In addition, environmental sounds are also created by water flows, wave action, and gaseous exchange in macrophytes and pond substrates (Linke et al., 2018). These natural sounds, alongside anthropogenic noise, can all be captured using underwater microphones (hydrophones) to provide data on pond ecosystems (Greenhalgh et al., 2020; Kuehne et al., 2013; Linke et al., 2018; van der Lee et al., 2020). The benefits of using acoustic recording, especially alongside traditional surveys, are well documented from scientific research in other habitats. In particular, the ability to produce a standardized, long-duration, permanent dataset, which can be repeatedly analyzed, and subject to quality assurance checks, is a major advantage over standard field surveys (Desjonquères et al., 2020; Linke et al., 2018; Sugai, Silva, et al., 2019). The use of ecoacoustics in scientific research has therefore increased significantly over the last ten years—and studies in freshwaters are becoming more common (Greenhalgh et al., 2020). Acoustic surveys can clearly only capture sounds from soniferous taxa, and a further current disadvantage is that the knowledge of sounds produced by different freshwater species is highly limited (Rountree et al., 2020). In addition, the recent emergence of the field means that there are no agreed standards for sampling the soundscape of a given habitat, and guidance is also lacking on how recordings can best be used for effective biodiversity monitoring (Bradfer-Lawrence et al., 2019; Sugai, Silva, et al., 2019).

A recent review of the freshwater bioacoustics literature (Greenhalgh et al., 2020) identified a bias toward single-species studies of fish sounds (44% of studies), conducted in a laboratory setting (53%). Pond habitats were included in just 11% of studies, and aquatic arthropods were only represented in 26% of studies, despite their significant contributions to freshwater ecosystem function and soundscape composition. The soundscapes of temperate freshwater ponds were not investigated at all prior to the study by Desjonquères et al. (2015). Despite these current gaps in the research literature, ecoacoustic methods have revealed differences in the freshwater soundscapes over different types of sites and across environmental gradients (Desjonquères et al., 2018; Kuehne et al., 2013; van der Lee et al., 2020). In perhaps the largest-scale study to date, Rountree et al. (2020) recorded the soundscape of 19 lakes, 17 ponds, 20 rivers, and 20 streams in New England (USA), capturing 7,000 sounds at 173 sampling locations. They found that freshwater habitats contain a diverse array of unidentified biological sounds and that anthropogenic noises (transport, boats, fishing) dominated the recorded soundscapes, imposing significantly on natural sounds.

Recent developments in acoustic sensors and automated processing methods now allow researchers to collect and process large datasets of recordings (Sethi et al., 2020; Sueur, Pavoine, et al., 2008). This ability is rapidly expanding the field of acoustic research in freshwaters, but the majority of studies to date have focused on temporal rather than spatial variability, targeting a limited number of waterbodies over long periods, with autonomous acoustic recorders (Desjonquères et al., 2015; Karaconstantis et al., 2020). There is, however, considerable benefit in focal recording by surveyors, with active listening in the field, as opposed to later playback and analysis. This approach allows for a deeper understanding of the diversity of sounds present and can prevent the misidentification of some anthropogenic and environmental sounds coming from biological sources (Rountree et al., 2020). Despite this benefit, very few studies have undertaken this approach. Rountree et al. (2020) conclude that researchers should attempt to increase the number of studies using real-time sound monitoring in the field, with visual observations of the recorded soundscape, alongside other projects that focus on the collection of long-term soundscape recordings.

1.4 | Aims of the PASS

This paper does not set out to describe a survey method. Similar to a five-minute point count for birds (Bonthoux & Balent, 2012), or a three-minute net sample for aquatic invertebrates (Hill et al., 2016; Williams et al., 2004), we simply suggest an approach to standardize the collection of a single audio sample recording the soundscape of a pond. This individual data capture can be employed within a wide variety of survey designs, based on the needs of the study, enabled by the multipurpose nature of the raw audio data. Sugai, Desjonquères, et al. (2019) identified three main challenges for the expansion of ecological acoustic research: nonstandardized monitoring procedures, time-consuming acoustic analysis, and limitations on data curation and data sharing. This draft protocol is intended to address the first and last of these.

Despite the potential benefits of acoustic survey in freshwaters, there are currently no recognized standard field methods. We aim to support filling this gap at an early stage in practice development, by promoting coherent data gathering that will allow effective data sharing between surveyors and studies. While recognizing the potential disadvantages to defining set methods when the science is still developing, we believe that a standardized sampling protocol would have considerable benefits to the uptake of the ecoacoustics approach in freshwaters and the usability of the data collected.

We hence propose a simple protocol to allow standardized minimal samples to be collected from small waterbodies, producing a sound recording with associated environmental information and metadata. The protocol is intended to be accessible to a wide range of users, including researchers, consultants, conservation managers, and citizen scientists, without requiring complicated or expensive equipment. It is designed for use with a single handheld recorder and hydrophone, and for short site visits.

This sampling protocol should be built into a defined survey plan with additional guidance on spatial and temporal coverage, for example, to generate data across a range of sites for a regional survey, or to allow long-term monitoring of ponds through repeated visits. The proposed sampling method is expected to yield useful data on pond soundscapes and lead to an improved understanding of how these relate to wider ecological function and site condition. Uptake of this method would allow consistent data to be gathered by a range of interested parties, allowing much-needed data sharing and collaboration in this developing area (August et al., 2015; Linke, Gifford,

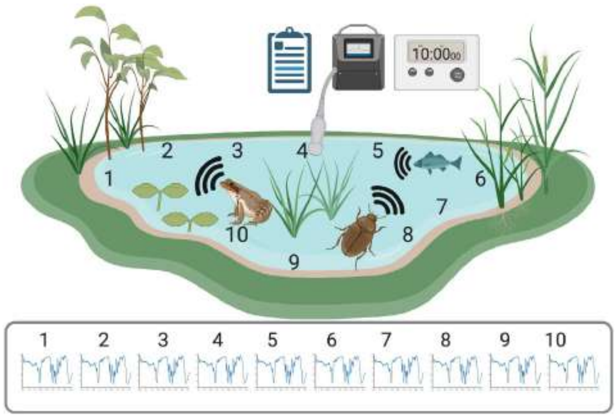

FIGURE 1 Pond Acoustic Sampling Scheme. Each sample consists of a 10-min underwater sound recording from the pond, comprising 10 recordings, each of 1-min duration, taken at different locations around the waterbody. Environmental parameters and survey metadata are systematically collected to accompany each sound sample

et al., 2020). The recordings can also be used to document freshwater soundscapes for educational, artistic, or historical purposes (Barclay et al., 2020; Sugai & Llusia, 2019). We invite feedback from contributors to further develop good practice and demonstrate how this sampling protocol can be applied in full studies.

2 | SAMPLING PROTOCOL

2.1 | Recording the sound sample

The sound recording collected for each sample is a 10-min recording, saved as an uncompressed .WAV file. To represent potential variation across the waterbody, each 10-min sample should be divided into ten 1-min subsamples recorded in different mesohabitats around the edge of the pond (Figure 1). The 1-min recording length has become common practice for ecoacoustic research, used in many studies (e.g., Bayne et al., 2017; Campos-Cerqueira et al., 2020; Eldridge et al., 2018; Farina et al., 2011; Farina & Gage, 2017; Fuller et al., 2015; Gottesman et al., 2018; Pieretti et al., 2015; Wimmer et al., 2013), and has benefits over longer recording periods in terms of acoustic index accuracy, and computational requirements (Cifuentes et al., 2021). The 10-min survey time is suggested as the minimal survey effort required for each sample and is partly pragmatic, based on keeping field visits to each pond of a reasonably short duration, and thereby enabling more sites to be visited in one field day. However, the review by Sugai, Silva, et al. (2019) of 460 published acoustics studies showed that 91% of those using discontinuous recording used sample lengths of 10 min or less. In addition, existing protocols of traditional surveys using auditory cues can offer guidance to determine recording lengths for acoustic monitoring. For long-term monitoring of amphibian population trends, call surveys with 3–5 min lengths per hour have been shown to be adequate for most species (Dorcas et al., 2009; Shirose et al., 1997), whereas for birds, studies have often used lengths of 5–20 min (Bonthoux & Balent, 2012). Similar recording lengths have also been used for insects, for example, 3-min recordings (Thompson et al., 2019). Critically, previous research has commonly found that acoustic diversity is better represented with a greater number of short-duration samples than with fewer, longer-duration samples (Bayne et al., 2017; Linke, Decker, et al., 2020; Sugai, Desjonquères, et al., 2019). This is particularly true if those visits are spread across times, days, and seasons (Browning et al., 2017). We therefore consider that 10 recordings of 1 min is a valid design choice, supported by a considerable body of research and established practice—and one that also allows efficient processing of the sound files by R software (Jorge et al., 2018).

When recording the sample, the hydrophone should be deployed at approximately 10 cm below the surface, and allowed to settle

FIGURE 2 Typical recording equipment for PASS, consisting of headphones, recording unit, and cabled hydrophone

TABLE 1 Hydrophones available for use in freshwater ecoacoustic surveys

Hydrophone model	Manufacturer	Cost (£)	Sensitivity (dB re: 1V/μPa)	Flat frequency response range	Compatible with
Standard/D series	Jez Riley French	50	N/A	N/A	Any device with a 3.5 mm or 1/4 microphone input
H2a	Aquarian Audio	148	−180	20 Hz to 4 kHz	Any device with a 3.5 mm microphone input
SQ26-H1B	Cetacean Research Technology	N/A	−169	20 Hz to 45 kHz	Any device with a 3.5 mm microphone input
Pro	Dolphin Ear	320	N/A	1 Hz to 24 kHz	Any device with XLR connection
HTI-96	High Tech, Inc.	N/A	−165 (with preamp)	2 Hz to 30 kHz	Any recorder

prior to starting the recording to allow any noise from air bubbles or vegetation movement to cease. The ten recording locations should be arrayed around the pond to sample the mesohabitats present, for example, marginal vegetation, submerged vegetation, and open water, in accordance with their relative area, and to capture the diversity of soniferous animals likely to be present (Aiken, 1991).

The sound file should be stored as a single 10-min .WAV file to ensure that the recordings from a single sample remain together. This can either be achieved by using the recorder pause button between subsamples while in the field, or by recording 10 separate files and combining these together into one file after the field visit. The first approach may be easier, but less accurate in timing. The latter would allow files in excess of 60 s to be recorded and then cut accurately to length, before stitching them together, and hence would allow potential overlaps or inaccuracies in the length of subsamples to be avoided. Once recorded, files should be archived using a file naming protocol that includes a prefix (e.g., location and surveyor name), followed by date and time: PREFIX_YYYYMMDD_HHMMSS.wav. This convention follows the Wildlife Acoustics Song Meter system and is machine-readable using seewave::songmeter in R (Sueur, Aubin, et al., 2008).

2.2 | Recording equipment

The 10-min sound sample is recorded using a hydrophone and connected sound recording device (Figure 2). A range of manufacturers and models are available, and any of these can be used for this protocol (see Box 1 and Tables 1 and 2 for examples). The critical issue is to make sure that the equipment used is recorded in survey metadata, together with audio settings such as the use of frequency filters. Recorders should have low self-noise, and the hydrophone should have a flat response across the range of audible frequencies.

Manufacturers such as Zoom, Tascam, and Olympus produce a range of handheld field recorders that differ in the number of available channels, maximum gain settings, battery life, and price. However, relatively inexpensive and effective setups can be purchased that are well suited for short-duration acoustic surveys.

A handheld Zoom recorder (e.g., models, H2, H4n, and H6) in combination with the H2a Aquarian Audio hydrophone is a popular equipment choice among some researchers (Decker et al., 2020; Karaconstantis et al., 2020; Linke, Gifford, et al., 2020). Rountree and Juanes (2020) used a Cetacean Research Technology SQ26-H1B hydrophone and Zoom H1n recorder to describe the sounds produced by six piranha species in the Pacaya-Samiria National Reserve, Peru. Other hydrophones used to record fish sounds in the field have included Cetacean Research Technology SQ26-08 and C54XR, and the High Tech Inc. 96-min (Rountree et al., 2018, 2020). Desjonquères et al. (2015) used Wildlife Acoustics SongMeters with RESON TC 4033 to record in ponds, while Gottesman et al. (2018) and Desjonquères et al. (2018) used a SongMeter with a HTI-96 hydrophone for deployment in a swamp and secondary river channels, respectively. Other autonomous recorders such as the new AudioMoth 1.2 version with potential for a 3.5 mm jack input (https://www.openacousticdevices.info/audiomoth), or the Frontier Labs Bioacoustic Audio Recorder (https://frontierlabs.com.au/bioacoustics.html) are potential alternatives.

2.3 | Audio settings

To ensure high-quality sound data, recordings should be made with a sample rate of 44.1 or 48 kHz, and 16 or 24 bit depth. These recording parameters will ensure that the sound amplitude is recorded at high resolution, and enable recording of sounds up to 24 kHz, hence covering the range from low frequency fish sounds (Popper & Hawkins, 2019) to higher frequency invertebrate stridulations (Aiken, 1985). Lossless .WAV files should be used, rather than .MP3, to ensure that sound quality is not lost through file compression.

Recording volume (amplitude) is controlled by the gain setting on the recorder. The appropriate level is dependent on the equipment used and the sound levels in the waterbody, so needs to be set by the surveyor. It is normal in acoustic recording to set the peak amplitude to reach −6dB to prevent "clipping" and distortion of the noise files. Manufacturer recommendations should be referred to here, and some trial and error will be involved.

TABLE 2 Commonly used field recorders in freshwater ecoacoustic research

Recorder	Manufacturer	Cost (£)	Maximum battery life (hr)	Number of SD card slots	Bit depth	Maximum sample rate (kHz)	Maximum gain (dB)	Weather-proof?	Programmable recording schedules?
H1n	Zoom	80	10	1	16, 24	96	39	No	No
H2n	Zoom	112	50	1	16, 24	96	39	No	No
DR-100 MKIII	Tascam	250	12	1	16, 24	192	24	No	No
SM4 BAT FS	Wildlife Acoustics	743	230	2	16	500	12	Yes	Yes
AudioMoth (version 1.2.0)	Open Acoustic Devices	60	192	1	16	384	N/A	Yes	Yes

2.4 | Metadata and environmental information

A standard data form is provided (PDF and CSV in Data S1) for recording environmental information about the waterbody, together with survey metadata. This has been designed for compatibility with the information collected for two existing survey methods in the UK: the Great Crested Newt Habitat Suitability Index (Oldham et al., 2000; https://www.arguk.org/info-advice/advice-notes/9-great-crested-newt-habitat-suitability-index-arg-advice-note-5/file), and the Freshwater Habitats Trust's Pond Habitat Survey (https://freshwaterhabitats.org.uk/wp-content/uploads/2015/03/HABITAT-MANUAL-FINAL.pdf). Further information on field assessment of the recorded environmental variables is outlined in the field data form provided. The field survey data form includes geographic coordinates, which allow important additional variables to be derived (e.g., altitude and local pond density).

For each site visit, the date/time, surveyor name, sampling location, and recorder/microphone identifiers should be recorded. A photograph of the pond can be useful (Rountree et al., 2020). Weather conditions during the survey period, especially the occurrence of rain, should also be recorded. Adverse weather should, however, generally be avoided, as this is likely to dominate the soundscape during recordings, and mask biological sounds.

3 | APPLICATIONS FOR THE PASS

3.1 | Survey design

Samples collected following PASS can be put to use as part of wide-scale surveys featuring the appropriate temporal and spatial replication levels. We recommend that its use should span a range of sites and sampling periods. The phenology of different taxa through the course of a year will affect the extant assemblage in a waterbody (Aiken, 1991), and Hill et al. (2016) showed that macroinvertebrate sampling across all seasons provides the best record of the community, with autumn samples the most diverse. Gottesman et al. (2018) recommend that recordings should cover a range of seasonal and diurnal periods to capture the temporal dynamics that are part of the acoustic diversity of a given site (Decker et al., 2020; Karaconstantis et al., 2020; Kuehne et al., 2013). In addition, wide spatial coverage across numerous sites is also encouraged, as further research is needed to understand spatial heterogeneity and its effect on the variability of acoustic assessments (Linke, Gifford, et al., 2020).

3.2 | Data storage and sharing

Several studies have highlighted the need for open science in freshwater assessments (Beck et al., 2020), and the development of open platforms to share and store freshwater recordings (Linke, Gifford, et al., 2020; Linke et al., 2018; Rountree et al., 2020). Well-known sound archives, such as the Macaulay sound library (www.

macaulaylibrary.org) and Xeno-Canto (www.xeno-canto.org), are mainly dedicated to bird sounds. Several other sound libraries are part of the collections of Natural History Museums such as the Sonothèque in Paris (https://sonotheque.mnhn.fr), BioAcoustica (Baker et al., 2015), or the Animal Sound Archive in Berlin (https://www.tierstimmenarchiv.de). However, most sound archives are centered on focal recordings of single species rather than location soundscapes. Moreover, in these libraries, recordings and metadata are not readily downloadable in batches for use in scientific studies.

Inspired by "Silent Cities," a participative project to record during the COVID-19 confinement in urban areas (https://framaforms.org/silentcities-1584526480), we propose an integrated solution for storing and sharing recordings collected using PASS. We have set up a Zenodo community (https://zenodo.org/communities/pass) to allow the upload and validation of acoustic data and associated metadata. This dataset is freely available to anyone for scientific, educational, or artistic purposes. It is expected to provide unprecedented opportunities to unravel the potential of rapid acoustic surveys for freshwater ecological assessments.

3.3 | Data analysis

Acoustic recordings can be analyzed in a variety of ways including manual annotation and measurements, automatic signal processing with the use of species recognizers, or integrative acoustic indices (Eldridge et al., 2018; Fuller et al., 2015; Sueur, Pavoine, et al., 2008; Wimmer et al., 2013). The PASS particularly lends itself to a rapid assessment approach using acoustic indices. The 1-min subsamples can be processed to produce individual acoustic index scores, and these averaged to create a mean value and maximum–minimum range for the 10-min sample. These values can then be assessed across several site visits, with metadata and environmental information being used as covariates with the analysis.

Acoustic indices are calculated by considering variations in amplitude and frequency over time in audio recordings. Their calculation can be automated and standardized, for example, using the R packages Seewave (Sueur, Aubin, et al., 2008) and Soundecology (Villanueva-Rivera & Pijanowski, 2018), to facilitate the analysis of large data sets in a repeatable way. Gottesman et al. (2018) calculated six acoustic indices to assess the soundscape of a swamp in Costa Rica for 23 days. The study discovered clear diurnal patterns in the soundscape with active night choruses and quieter day periods.

Spectrograms visualize sound in the frequency and time domains (Figure 3) and can be generated using a variety of software to help interpret sound recordings. Some notable examples include the free and open-source Audacity (https://www.audacityte

BOX 1 Potential equipment setups for Pond Acoustic Sampling Scheme (and general freshwater acoustics work) varying in sensitivity and price

Inexpensive handheld survey option: JRF standard hydrophone, with Zoom H2n recorder (total cost = £165)

Moderately priced survey option: Aquarian H2a hydrophone and Tascam DR-100 recorder (total cost = £400)

Expensive survey option: Dolphin Ear Pro hydrophone with Zoom F8 recorder (multitrack) (total cost = £850)

Automated survey option: Aquarian H2a hydrophone, with AudioMoth recorder (version 1.2.0) (total cost = £208)

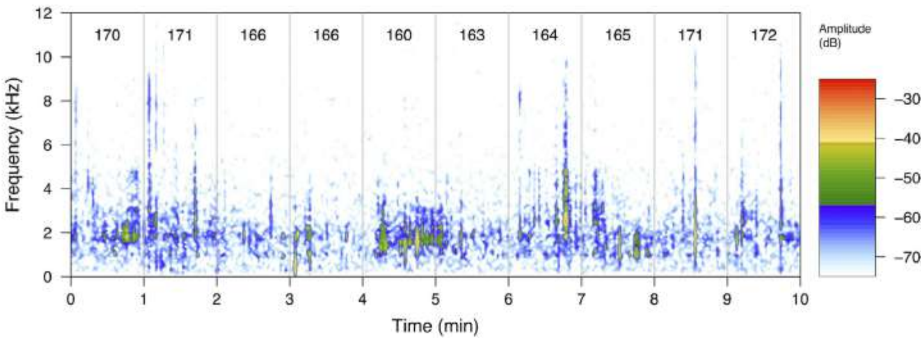

FIGURE 3 Full soundscape analysis. Spectrogram showing 10-min sound recording, divided into 1-min sections, each recorded in different locations around one pond. Acoustic Complexity Index (ACI) scores (range 159.9–171.8, mean 166.7) are indicated for each minute and are highest in minute 10, and lowest in minute 5. The spectrogram shows that most sound energy is centered around 1–3 kHz. Frequencies are displayed to a maximum of 12 kHz, although the recording included sounds up to 24 kHz. Spectrogram produced using package Seewave in R with an FFT size 512 and overlap = 50%. The R script for calculating the ACI scores for a recording, and producing this figure, is included in Data S1

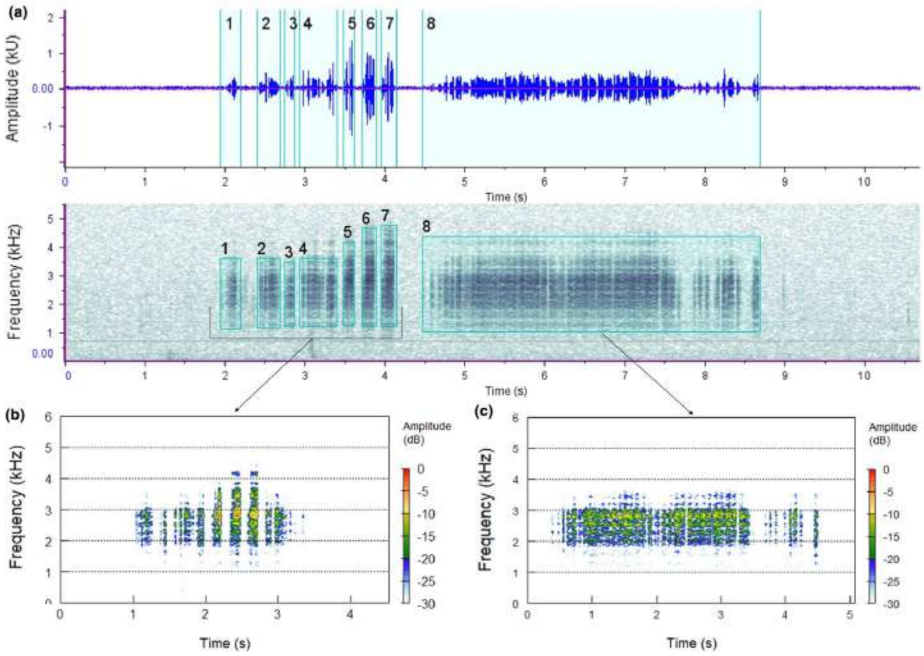

FIGURE 4 Single-species sound analysis. Analysis of the sound types of a Corixid species: (a) waveform and spectrogram of typical Corixidae call series. Numbers 1–8 represent sections of each call series measured in Raven Pro. (b–c) Spectrograms of each sound type using the package Seewave in R with an FFT size 2,048 and overlap = 50%; (b) sound type 4, (c) sound type 8

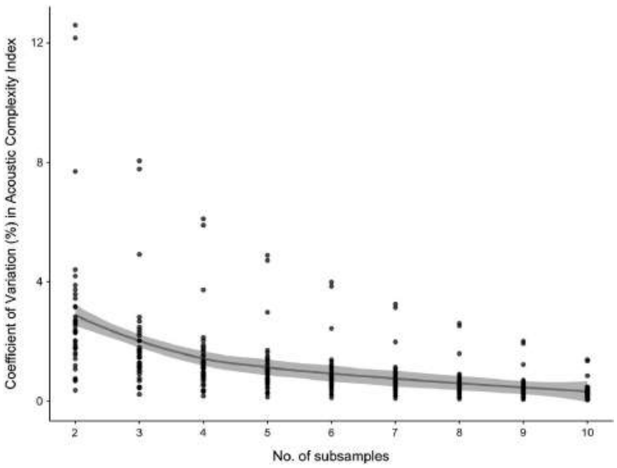

FIGURE 5 Coefficient of variation for Acoustic Complexity Index scores reduces substantially with the ten 1-min subsamples included in the PASS protocol

am.org/), the R package seewave (Sueur, Aubin, et al., 2008), and Raven Pro 1.5 (https://ravensoundsoftware.com/software/raven-pro/). These software applications also allow the user to compute a wide range of acoustic parameters, such as mean frequency or peak amplitude, which can then be exported for use in statistical analyses (Rountree & Juanes, 2020). This type of feature is demonstrated below (Figure 4), where the sounds produced by a water-boatman have been highlighted, to allow sound parameters to be extracted and analyzed. Such signal detection and feature extraction can be done manually or automatically using signal processing such as machine learning (Browning et al., 2017).

4 | TESTING THE PASS

During April 2020 to March 2021, we collected PASS recordings and metadata at 24 ponds across the UK. Although this was a limited pilot study, it is to our knowledge, the largest dataset yet published for pond ecoacoustics in terms of the number of sites covered. We tested the data in two ways: (1) calculating the percentage Coefficient of Variation (CV%) in an acoustic index score for the 10-min sample and (2) comparing derived acoustic indices to the Habitat Suitability Index (HSI) for each pond.

Acoustic Complexity Index (ACI) scores were calculated using the seewave package in R (Sueur, Aubin, et al., 2008) for each 1-min subsample. The CV% of the ACI score was then calculated for increasing numbers of subsamples, up to the full 10-min recording in the sample (Figure 5). This analysis, over 33 PASS samples, shows that CV% declines substantially with ten subsamples, indicating that variation in ACI is effectively captured using the proposed recording length.

Environmental data collected at each PASS site was combined with a review of Ordnance Survey mapping to calculate the HSI (Oldham et al., 2000) for each pond. The HSI combines parameters such as pond area, shading, and macrophyte cover into a single value and is a well-established metric of pond habitat quality, indicating amphibian species occupancy and abundance (Unglaub et al., 2018). A range of acoustic indices (ACI, ADI, AEI, BI, NDSI) were calculated for each site and compared with the HSI scores. Significant positive correlations were found between HSI and both ACI and the Bioacoustic Index (BI; Figure 6). This suggests that acoustic data recorded using PASS is likely to be related to a range of measurable environmental parameters and can be effectively used to assess pond habitat condition.

5 | CONCLUSION AND OUTLOOK

The PASS offers a new and highly valuable method for consistent acoustic sampling of small waterbodies. This sampling scheme is likely to enable the rapid assessment of pond quality and condition for ecological studies and conservation management. Further development in understanding the links between the sound characteristics of ponds and their ecology is certainly needed and will require the collection and analysis of data from a large number of sites. We believe that the availability of a standard protocol for data gathering will support comparisons between studies, data sharing, and the establishment of coherent "gold-standard" datasets. This would aid scientific research to evaluate the promising potential of ecoacoustics as a monitoring technique in small waterbodies, and better conservation action for vitally important pond habitats.

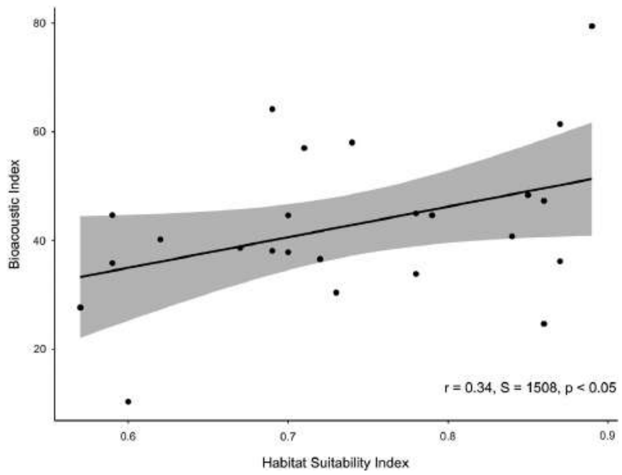

FIGURE 6 Bioacoustic Index compared with Habitat Suitability Index for 24 ponds

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTION

Carlos Abrahams: Conceptualization (lead); Methodology (equal); Visualization (lead); Writing-original draft (equal); Writing-review & editing (equal). **Camille Desjonqueres:** Methodology (equal); Visualization (supporting); Writing-original draft (equal); Writing-review & editing (equal). **Jack Greenhalgh:** Methodology (equal); Visualization (supporting); Writing-original draft (equal); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

Audio recordings and metadata are archived at Zenodo: [https://zenodo.org/communities/pass] https://doi.org/10.5281/zenodo.3954852.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Abrahams C, Desjonquères C, Greenhalgh J. Pond Acoustic Sampling Scheme: A draft protocol for rapid acoustic data collection in small waterbodies. *Ecol Evol*. 2021;00:1–12. https://doi.org/10.1002/ece3.7585

Chapter 4

SCIENTIFIC IMPACT

The citation history of the published works is one way to demonstrate their scientific impact. An assessment of this impact is given below, by reference to the publications that have built upon the published works (all references used in this section have cited the published works). In addition, evidence is provided of impact facilitated by other types of engagement with the scientific and conservation communities, indicating how the published works have informed ongoing research, guidance and policy in related disciplines. The sequence of papers in this section follows the thematic order of the thesis, originally set out in the Introduction and Figure 1.1.

Abrahams, C. & Nash, D. J. (2018). Do we need more evidence-based survey guidance? In Practice, 100, 53–56.

One citation, 332 reads on ResearchGate.

The thesis research was motivated by recognizing the ongoing need for improved methods of ecological data collection, given the demands of the biodiversity crisis, and the potential offered by new technologies. Better and 'bigger' ecological data are needed to both understand environmental problems and to monitor the success of policies and management interventions. For example, the implementation of urban green infrastructure projects, such as parks and wildlife areas, requires effective evaluation during and after development (Callway et al., 2019). Although this evaluation should typically be embedded in the development process, to enable good decision-making, it is often not undertaken properly. Callway et al. (2019) recognised the need to test and establish effective monitoring approaches, and cited Abrahams & Nash (2018) as an example of research examining the validity of ecological methods that might be used for such evaluations.

Abrahams, C. & Denny, M. J. H. (2018). A first test of unattended, acoustic recorders for monitoring capercaillie *Tetrao urogallus* lekking activity. Bird Study, 65, 197–207.

Seven citations, 85 reads on ResearchGate.

Capercaillie monitoring techniques, to date, have either been based on transect surveys or on lek counts, during which a survey is undertaken at dawn from hides placed in the centre of the lekking area (Aleix-Mata et al., 2021). Such lek counts have been criticized for underestimating the number of individuals, and recording fewer birds than transect surveys, especially when vocal activity is low. In addition, environmental conditions during lek counts can affect bird behaviour and surveyor performance, e.g. by wind noise in the hide reducing the audibility of displays and thereby decreasing detection distances (Aleix-Mata et al., 2021). Discussion of these constraints is supported by reference to Abrahams & Denny (2018), particularly in relation to environmental effects on the detectability of birds at lek sites.

Abrahams & Denny (2018) and Abrahams (2019) investigated the timing of vocal displays at lek sites through the dawn period. In their subsequent study on capercaillie song timing, Summers et al. (2021) recognised that this acoustic research identified a clear gap in scientific knowledge regarding the timing of male displays at leks. Such knowledge is needed to improve the reliability of all lek surveys, whether acoustic methods, point counts, or transects are used, by correctly including the peak of singing activity, which may change on a daily basis (Aleix-Mata et al., 2021).

Due to issues over varying environmental conditions and the timing of lek activity, as described in Abrahams & Denny (2018) and Abrahams (2019), traditional count methods only provide an imperfect index of abundance and occupancy (Aleix-Mata et al., 2021). This can be addressed with acoustic recorders, which have scope for determining lek occupancy, temporal patterns in song, and the effects of long-term environmental change, as recognised by Summers et al. (2021). Standard protocols for acoustic recorders have therefore been produced for Tengmalm's owl *Aegolius funereus* (Guixé & Florensa, 2020 a) and capercaillie (Guixé & Florensa, 2020 b), with reference to Abrahams & Denny (2018) as informing sound analysis and a model for the recommendations made in their guidance.

Abrahams & Denny (2018) has also influenced studies beyond the capercaillie species context. Sugai et al. (2019) cite it as an example of a study that has enabled new scientific insights due to its simultaneous use of recorders at multiple sampling locations. Brooker et al. (2020) also recognise the study's use of a software recogniser for sound data analysis to determine site occupancy and activity levels, demonstrating the effectiveness of this approach, for which there had been little previous evidence in the published literature.

Abrahams, C. (2019). Comparison between lek counts and bioacoustic recording for monitoring Western Capercaillie (*Tetrao urogallus* L.). Journal of Ornithology, 160, 685–697.

Sixteen citations, 263 reads on ResearchGate.

Following the Abrahams & Denny (2018) study on capercaillie, this publication compared the results from the bioacoustics approach with existing lek count methods as conducted by surveyors. The paper has been widely cited as a novel example of an integrated field method and analysis approach that allowed vocal activity rates to be correlated with bird abundance, inferring population density at a sampling location (Pérez-Granados et al., 2019; Rosten, 2020; Pérez-Granados & Traba, 2021; Sumitani et al., 2021; Nugent et al., 2022). Parallels have been found in subsequent studies on bird and mammal species, for example Dupont's lark *Chersophilus duponti* (Pérez-Granados et al., 2019), Neotropical white-tipped dove *Leptotila verreauxi* (Pérez-Granados & Schuchmann, 2020) and howler monkeys (Pérez-Granados & Schuchmann, 2021).

The key benefit of bioacoustics in enabling monitoring for long time periods, as demonstrated by recording over a month in this paper, has been recognised by other authors (Pérez-Granados et al., 2019; Chhaya et al., 2021). In particular, the extended recording period used has highlighted the capacity to detect and compensate for large temporal variations in vocal activity related to seasonality, weather conditions and the mobility of the birds around deployment sites. These benefits have been recognised in subsequent studies and guidance (Pérez-Granados et al., 2019; Marin-Cudraz, 2019; Aleix-Mata et al., 2020; Summers et al., 2021). Such long monitoring periods, and the potential to revisit and review field recordings, have also been recognised to enhance the potential to record rare or cryptic species, which are infrequently detected by other methods (Darras et al., 2019; Marin-Cudraz, 2019; Goodwin & Gillam, 2021).

For rare species, non-invasive methods for census and monitoring are critical. The finding in Abrahams (2019) that traditional count methods can reduce vocal activity at leks, is a key source of evidence in a number of publications (Teixeira et al., 2019; Marin-Cudraz, 2019; Aleix-Mata et al., 2020; Diepstraten, 2020; Aleix-Mata et al., 2021; Goodwin & Gillam, 2021). As a result of this work, it is considered that acoustic methods reduce observer biases and provide data that better represent actual field conditions. In addition, the paper presents evidence for the utility of automated signal recognition software in correctly recognizing a high proportion of target species vocalizations (81% for capercaillie). This capability has helped establish the use of recognizer software as an effective tool in monitoring a range of species (Pérez-Granados & Schuchmann, 2021 a; Pérez-Granados & Schuchmann, 2021 b).

I presented the results of this study at the Chester University conference on 'Future Directions in the Management of Small Populations' in April 2018, and at the British Ecological Society Annual Meeting December 2018 in a session on 'Novel methods in biodiversity and ecosystem monitoring'. The published works on capercaillie have resulted in invitations for me to contribute to studies on capercaillie vocal individuality and lek abundance with Richard Policht (Czech Republic) and David Guixe (Spain), and to collaborate on studies of bird vocal activity rates with Cristian Pérez-Granados (Spain/Brazil).

Abrahams, C. & Geary, M. (2020). Combining bioacoustics and occupancy modelling for improved monitoring of rare breeding bird populations. Ecological Indicators 112, 106131

Six citations, 98 reads on ResearchGate.

This study analysed bioacoustic data within an occupancy modelling framework, to produce occupancy and detectability estimates for three heathland bird species of conservation concern. The study identified that acoustic methods, combined with occupancy modelling, enable effective characterisation of population density, with reduced observer bias and greater consistency in data collection. The research was an innovation project funded by Natural England, the statutory nature conservation organisation, to develop methods that could improve monitoring of target bird species at internationally protected Special Protection Areas. The journal article was preceded in 2019 by a detailed technical report and presentation I prepared and delivered to Natural England and the Thames Basin Heaths Joint Planning Board, allowing these organisations to better understand the status of the species and the sites that they are responsible for managing. The project also won the Chartered Institute of Ecology and Environmental Management (CIEEM) national award for Best Practice: Innovation in 2020 due to its novelty, scale, value and repeatability (https://cieem.net/awards-2020-winners-spotlight-best-practice-innovation/).

The paper has been cited as evidence that passive acoustic recording is being increasingly used to monitor and assess changes in vocalising taxa, including bird communities (Brinley Buckley et al., 2021; Qi et al., 2021; Wu et al., 2021). It is also recognised internationally as illustrating how acoustic monitoring can effectively assess the occupancy and spatial distribution of hard to detect species (Chhaya et al., 2021; Jahn et al., 2022), and how this task is enabled by consistent data capture over repeated surveys (Rosten, 2020). The research has been included as a case study in a CIEEM webinar (http://events.cieem.net/Events/EventPages/10052019000000UsingBioacousticsforFieldSurvey.aspx) and training workshop on bioacoustics. I have also delivered the research as oral presentations for the British Ecological Society, UK Acoustics Network, and at the British Ornithologists Union 'Developments in monitoring science' conference. This study, and the capercaillie work (Abrahams & Denny, 2018; Abrahams, 2019), was also featured in a Birdwatching magazine (www.birdwatching.co.uk) article in November 2020, developing interest from amateur ornithologists in the use of acoustic methods for bird study. Interest in the project has also continued at the study sites, with Surrey Wildlife Trust aiming to implement the approach at further locations in the Thames Basin Heaths Special Protection Area.

Docker, S., Lowe, A. & Abrahams, C. (2020). Identification of different song types in the European nightjar *Caprimulgus europaeus*. Bird Study, 67, 119–127

No citations, 318 reads on ResearchGate.

This study was the first to identify that two distinct song types are used by male European nightjars, with relative levels of their use changing through the breeding season, indicating a possible link to paired status. The unattended survey afforded by acoustic recording methods minimizes disturbance during assessment of the number of breeding pairs of this species of concern. The study also highlights that acoustic data can advance understanding of bird behaviour and its links to ecology and conservation status.

This paper has not been cited yet (at 1/1/22), but has had considerable online engagement, with 300 reads on ResearchGate, 940 views on its journal webpage and 77 tweets on Twitter from 9 countries. Details from this study have also been presented alongside the Abrahams & Geary (2020) paper at the conferences listed above.

Abrahams, C. (2018). Bird bioacoustic surveys - developing a standard protocol. In Practice, 102, 20–23.

Seven citations, 3,150 reads on ResearchGate.

This article provided the first guidelines for the applied use of bird bioacoustic methods within consultancy and conservation practice, covering survey design, hardware options, recorder settings, data storage and analysis software. Building upon published scientific research and questionnaire responses from workshop delegates at the UK's first conference on bird bioacoustics, organised by the author in 2017, it reviewed the benefits and constraints of bioacoustic methods for bird surveys, in providing useful and robust data on avian distribution and ecology.

The protocol has been successful in knowledge transfer from scientific studies to applied ecology and environmental management, and has reached a global audience through delivery at conferences and training events. The article has been cited in reviews of acoustic methods for bird surveys (Darras et al., 2018; Zwerts et al., 2021), as providing best practice recommendations for using autonomous sound recorders, and also for allowing acoustic data to be compared effectively with point counts (Guixé & Florensa, 2020 a; Guixé & Florensa, 2020 b). Other citing studies have recognized the advantages identified for acoustic methods, including the larger temporal and spatial scales possible, while using fewer surveyors (Darras et al., 2018; Speck, 2019; Marin-Cudraz, 2019). The recommendations have also guided the specification of audio files used for analysing bird song data (Silva-Jr et al., 2021).

The article has achieved over 3,000 reads on ResearchGate and has prompted invitations for me to contribute to workshops by the Joint Nature Conservation Committee/Centre for Ecology and Hydrology, and the UK Acoustic Network (UKAN), and to lead production of the bioacoustics section of the new national Bird Survey Guidelines for professional ecologists (at https://birdsurveyguidelines.org/803-2/). I have also presented the protocol at the following events, to over 200 delegates:

- Training for Natural England staff, February 2021
- UKAN Ingleborough Soundscapes bird bioacoustics training, March 2020
- Wildlabs.net Tech Tutors Series: Tech Tutors: *How do I perform automated recordings of bird assemblages?* webinar, July 2020 (https://wildlabs.net/community/thread/923#post-3698)
- Institute of Acoustics Senior Members Group bioacoustics webinar, July 2020
- CIEEM *Bioacoustics for Field Survey* webinar, May 2019
- CIEEM *Bioacoustics for Field Survey* training course, April 2019

Abrahams, C., Desjonquères, C., Greenhalgh, J. (2021) Pond Acoustic Sampling Scheme: A draft protocol for rapid acoustic data collection in small waterbodies. Ecology & Evolution 11, 7532–7543.

One citation, 156 reads on ResearchGate.

In proposing the Pond Acoustic Sampling Scheme (PASS), this paper set out a protocol allowing standardised acoustic samples to be collected rapidly from small waterbodies, alongside environmental and methodological metadata. The protocol is intended to allow access to a wide range of participants and can be incorporated into a variety of survey designs. An online Zenodo repository (https://zenodo.org/communities/pass) has been created to allow joint archiving of data and metadata by participants, to enable collaboration within the expanding freshwater ecoacoustic community.

Vella et al. (2022) cite this paper in recognition of the lack of reference libraries and repositories for soundscape recordings that could be used to compare and characterise different ecosystems.

A 'PASS Day 2021' was organised with my co-authors, and contributions to the associated Zenodo repository were received from five participants. This archive currently holds 46 PASS recordings (at 22 February 2022). The PASS methodology and Zenodo archive were also highlighted at the 2021 Ecoacoustics Congress by my co-authors, and were featured in training to freshwater ecologists in a course I delivered for Edinburgh Napier University.

Chapter 5

DISCUSSION

5.1 Introduction

This chapter provides an integrated discussion of the published works, addressing the overall aim of the thesis, synthesizing research findings, interpreting the scientific contributions made, and demonstrating the implications of the research (Lewis et al., 2021). Strengths and limitations of the research are discussed, policy and practice implications outlined, and recommendations made. Broad conclusions are then highlighted in Chapter 6.

The overarching aim for this thesis was to investigate acoustic methods for ecological research and monitoring, enabling animal populations, habitat quality and conservation status to be characterised. It therefore sought to develop a greater scientific understanding of how biological sounds reflect the ecology of individuals, populations, species and communities. This understanding can be used to improve data collection and its application, and to advance scientific research, conservation assessment and management.

To address the stated aim of this thesis, the published papers have quantified bird populations at local scales using vocal activity rates (Abrahams & Denny, 2018; Abrahams, 2019), and have employed occupancy modelling to determine population status across wider areas (Abrahams & Geary, 2020). The papers have established the potential for using different song types in the assessment of bird breeding status (Docker et al., 2020). The research has also investigated the influence of environmental conditions on vocal activity, occupancy, detectability and acoustic indices (Abrahams & Denny, 2018; Abrahams, 2019; Abrahams & Geary, 2020; Abrahams et al., 2021). This thesis has, therefore, enabled new insights into the use of acoustic methods for ecology, informing their implementation as novel sources of data for research and conservation management. The reported studies have advanced the discipline in new species, habitat and geographical contexts. In so doing, the case studies have indicated that traditional survey methods may be replaced or supplemented by acoustic approaches, to provide a range of benefits. The scientific research has been combined with practical fieldwork recommendations to establish good practice guidelines for avian and freshwater habitat acoustic surveys (Abrahams, 2018; Abrahams et al., 2021), addressing the need for evidence-based survey guidance (Abrahams & Nash, 2018).

The main scientific insights that have emerged from the research are:

- Bird vocalisations can be effectively classified to species level using a combination of unsupervised software and manual analysis/verification.
- Bird vocal activity rates vary significantly by time, date, location, and in relation to environmental variables. The effects of these parameters, detected using acoustic methods, have general implications for bird survey and monitoring.
- Vocal activity rates, as demonstrated by capercaillie, can be correlated with the number of birds at a lek (a location where males perform competitive displays) — and so are indicative of local population size. Vocal activity rates decline due to disturbance when human surveyors are present at capercaillie leks, while bioacoustic methods are non-invasive.
- Occupancy models can be effectively built upon bioacoustic data, to provide insights into the presence, distribution and population density of bird species.
- High-resolution habitat data are needed to link environmental factors and bioacoustic outputs at the local (sampling site) level.
- Bird species differ widely in their detectability using both bioacoustic and traditional survey methods, reflecting their vocalisation amplitude and behaviour, as well as the habitats in which they are surveyed.
- Occupancy modelling has highlighted negative and positive habitat relationships between heathland bird species and habitat characteristics, indicating species associations with woodland, heather grassland and wetland.
- The European nightjar has two distinct song types, which change through the breeding season and are therefore likely to be indicative of breeding status.
- Freshwater acoustic recordings can be used to calculate acoustic indices that indicate environmental quality, can capture species-specific sounds (such as insect

stridulations), and can be related to habitat characteristics.

Below, the findings of the publications are integrated and discussed in terms of their contributions to the disciplines of bioacoustics and ecoacoustics, and their current and potential impacts on conservation management practice. The sections cover the five research questions laid out in the Literature Review (section 2.8).

5.2 How do vocal activity rates relate to bird abundance?

Conservation practitioners require effective methods to infer animal density/abundance and evaluate conservation management practices. Potential acoustic approaches include the use of microphone arrays to locate individuals in time and space (Sebastián-González et al., 2018; Rhinehart et al., 2020), but such methods are analytically complex and difficult to implement without considerable technological and statistical skill (Marques et al., 2013; Pérez-Granados et al., 2019; Pérez-Granados & Traba, 2021). In contrast, the use of vocal activity rates (VAR) allows a simple analytical process that can be related to the behaviour and numbers of a target species, enabling a scalable and efficient approach to assessing the population status of soniferous animal species (Borker et al., 2014; Pérez-Granados et al., 2019).

Abrahams & Denny (2018) and Abrahams (2019) assessed whether VAR could indicate site-specific bird abundance. The data analysis process in Abrahams & Denny (2018) classified 758 capercaillie song phrases, with 0–272 phrases recorded at each of the four sampling locations. This considerable variation in the detected VAR was presumably due to the differences in bird numbers as well as activity levels at each site. However, no comparison with bird counts was made, due to the limited number of leks covered and the lack of synchronous count data. Abrahams (2019) resolved this limitation by comparing VAR and male bird abundance recorded by observers at the lek, and found a significant positive correlation between the two. This identified that VAR could be used to indicate population size.

Similarly to the two capercaillie studies, Abrahams & Geary (2020) found considerable variation in vocalisations between sample sites for the target heathland bird species, reflecting the distribution of birds according to habitat preferences. Although analysis of VAR across the 44 sampling sites was not described in the scientific paper, this information (summarised in Figures 5.1 and 5.2) was provided to Natural England, as it demonstrated fine-scale variation in species distribution and could be used to inform conservation management within the Special Protection Area designated sites.

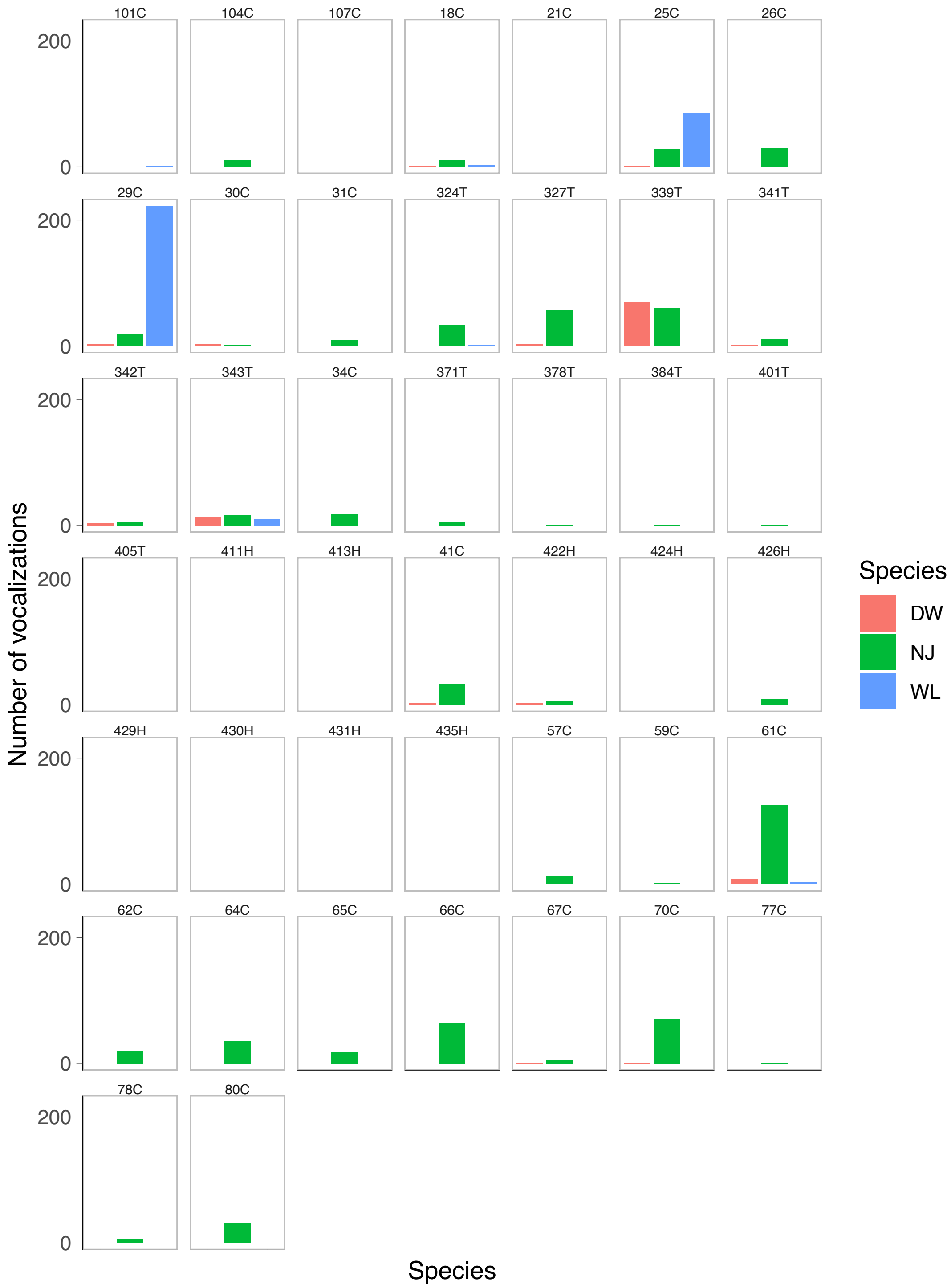

Figure 5.1: Total numbers of target species vocalisations recorded over six days at each sampling location during the Abrahams and Geary (2020) study. Each facet panel represents a different sampling location, with the numbers of Dartford warbler (DW), nightjar (NJ), and woodlark (WL) song phrases indicated. Figures 5.2 and 5.3 show the distribution of sampling locations across the study sites.

The findings from Abrahams & Denny (2018) and Abrahams (2019) support those from previous avian studies, which have established that VAR can be used as a proxy for population abundance, i.e. more calls are produced due to a greater number birds (Laiolo et al., 2011; Borker et al., 2014; Oppel et al., 2014; Knight et al., 2017). In particular, for lekking species such as hummingbirds, flycatchers and manakins, VAR is positively correlated with the number of birds present at the lek (Atwood et al., 1991; Westcott, 1992; Pizo & Aleixo, 1998; Cestari et al., 2016). However, Abrahams & Denny (2018) and Abrahams (2019) indicate that this relationship may not be a simple linear correlation. Call rates, and the amount of time dedicated to singing, may vary significantly amongst males, determining their ability to hold territories and attract mates at the lek (Pizo & Aleixo, 1998). In addition, the competitive function of song rates means that efforts by dominant males increase in response to the presence of other singers, such that overall display effort at leks increases disproportionately with lek size (Atwood et al., 1991; Laiolo et al., 2011; Cestari et al., 2016).

Alongside these behavioural factors, environmental parameters affect call rates over short timescales. Such factors need to be considered when interpreting correlations between VAR and bird numbers. Abrahams (2019) demonstrated a significant link between VAR and the numbers of males birds present at a lek — but only over an extended sampling period, i.e. weeks. There was no such correlation between daily VAR and bird numbers. This shows the importance of sampling over extended periods when using VAR to assess population size, to account for large daily variations in vocal activity (Abrahams & Denny, 2018; Abrahams, 2019). The same principle of extended sampling periods can also be used to track seasonal changes in VAR, as shown in Abrahams & Denny (2018), which detected a declining trend in vocal activity towards the end of the lekking period.

Abrahams & Denny (2018), Abrahams (2019) and Abrahams & Geary (2020) build upon the results from other studies that demonstrate that acoustic monitoring can document local bird populations and their temporal dynamics (Buxton et al., 2013; Oppel et al., 2014; Cook & Hartley, 2018; Arneill et al., 2019; Pérez-Granados et al., 2019). VAR may provide an index of population size within the area local to the recording unit, but this relationship is likely to vary, due to changes in breeding status, dominance hierarchies between individuals, site attendance patterns, and aspects of behaviour such as seasonality (Abrahams, 2018). This range of factors will generate differences in the acoustic outputs at a site (Stiffler et al., 2018). Methods-based issues, such as detection rates declining as distance from the recorder increases, may also cause biases. This was clearly demonstrated in Abrahams & Denny (2018), where microphones only 50 m apart detected widely varying numbers of capercaillie song phrases. Aspects of the environment, such as vegetation density, anthropogenic noise levels and weather conditions will alter how well signals are received at a recording device (i.e. the signal:noise ratio) (Borker et al., 2014; MacLaren et al., 2018; Pérez-Granados et al., 2019). The results of Abrahams & Geary (2020) showed how vegetation type, and distance from roads, affected detectability of the heathland bird species. Weather conditions were found to affect capercaillie VAR in Abrahams & Denny (2018), but not in Abrahams (2019). An improved analytical framework is needed to account for such variability, by calibrating vocal activity rates based upon how the local soundscape properties affect signal detectability and predictions of abundance (Borker et al., 2014). Variability in vocal activity can also be simply addressed by calculating average call rates for data collected over extended periods. This approach was used in Abrahams (2019), allowing a significant correlation to be identified between lek counts and call activity measured over a month, demonstrating the benefits that automated acoustic sensors can bring for long-term fieldwork capability (Borker et al., 2014).

In assessing the use of VAR, Abrahams (2019) compared acoustic data with the numbers of birds determined by human observers using a 'traditional' census technique (Alquezar & Machado, 2015; Leach et al., 2016; Vold et al., 2017). Such comparisons rely on both effective acoustic recording and traditional survey data, the latter which is critically affected by the observers' ability to detect individuals during fieldwork (Johnston et al., 2014; Zwart et al., 2014; Darras et al., 2018). This point is clearly reinforced by the daily fluctuations in VAR in Abrahams & Denny (2018) and Abrahams (2019), showing that greater understanding is needed on how both detectability and temporal variations in occupancy influence estimations of bird abundance in all types of avian studies (Cayford & Walker, 1991; Sadoti et al., 2016; Fremgen et al., 2018; Pérez-Granados et al., 2019).

5.3 How can acoustic recordings enable the development of effective species occupancy models?

Taking a different approach to population assessment than VAR, Abrahams & Geary (2020) assessed the potential for presence/absence information from acoustic recordings to inform the development of effective occupancy models. The paper used repeat observations from each sampling location to estimate occupancy and detectability for three target species — Dartford warbler, European nightjar and woodlark — allowing assessments of both species distribution and population density (Figure 5.2) (MacKenzie et al., 2002). Abrahams & Geary (2020) thus demonstrated that occupancy modelling is suitable for monitoring rare and threatened bird species (Campos-Cerqueira & Aide, 2016; Stiffler et al., 2018). The results of the occupancy modelling were also shown to be comparable with data collected by traditional survey methods for the same sites. This demonstrates that suitable data can be provided by bioacoustic methods, with reduced surveyor biases and resourcing costs, enabling site managers to employ evidence-based site management practices more efficiently and consistently.

Reducing the acoustic dataset into daily detection/non-detection encounter histories for occupancy modelling makes the analysis and interpretation of the data easier, and reduces the potential influence of false positives or negatives that might be introduced during the classification of individual bird vocalizations (Furnas & Callas, 2015). As a result, the development of a simple encounter history is less reliant on detailed acoustic analysis than VAR or the identification of different vocalization types, as employed in Abrahams & Denny (2018), Abrahams (2019) and Docker et al. (2020).

Abrahams & Geary (2020) combined the occupancy models with environmental covariates from satellite imagery and land cover mapping. Previous occupancy modelling studies on birds have found significant relationships between occupancy/detectability and parameters such as elevation, vegetation structure, proximity to water and wetland salinity (Furnas & Callas, 2015; Campos-Cerqueira & Aide, 2016; Furnas & McGrann, 2018; Stiffler et al., 2018; Metcalf et al., 2019). Incorporating the environmental covariates for heathland study sites in Abrahams & Geary (2020) expanded on this previous work, and identified positive relationships between nightjar occupancy and tree cover density, and between woodlark occupancy and heather grassland cover. These findings correspond to respective associations with woodland (Bright et al., 2007; Conway et al., 2007), and tall/dense heather or grass (Mallord et al., 2007), found in previous heathland studies. A negative relationship was also found between Dartford warbler and heather grassland land cover, whereas this species has previously been associated with gorse heath (Bibby & Tubbs, 1975).

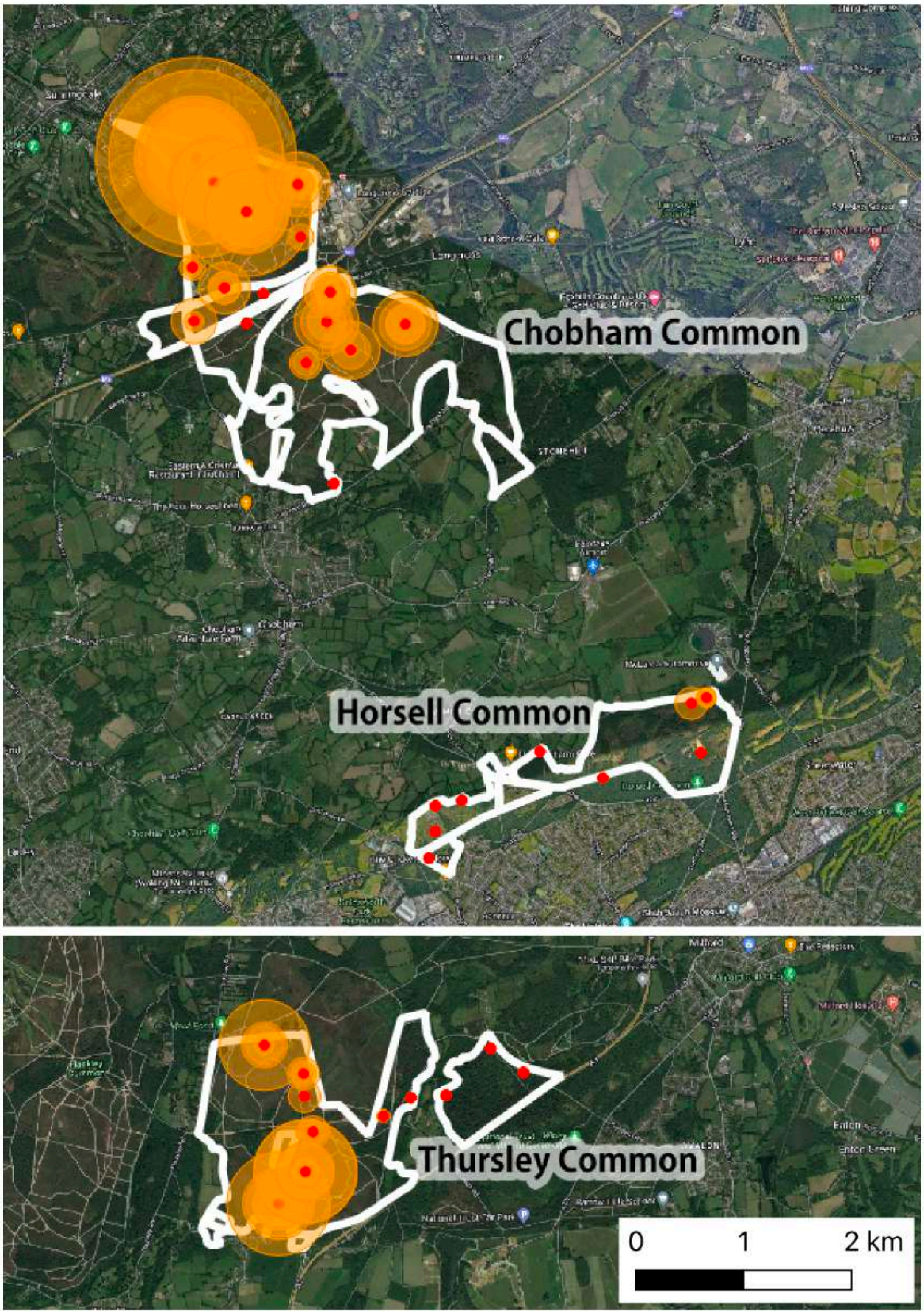

Figure 5.2: Nightjar vocalisations per night at Chobham, Horsell and Thursley Commons. Red dots indicate recorder sampling locations. The size of the orange circles indicates the numbers of songs recorded per night, with data overlaid for all six survey nights.

These apparent contrasts in habitat preferences require further work to confirm and understand fully. However, the benefit of the bioacoustics occupancy modelling approach in quantifying detectability may be critical in accurately determining such species-habitat associations. Using traditional methods, detecting enough individuals of rare and cryptic species to correctly infer habitat selection is difficult. The detectability of a species during traditional surveys is also likely to vary significantly based upon vegetation density and composition, and so the habitat type is likely to bias conclusions over species habitat preferences and potentially mask real relationships (Johnston et al., 2014). The use of automated acoustic recorders and occupancy modelling can address these problems by enabling consistent, repeated and observer-independent sampling, providing the detailed detection histories required to effectively relate occupancy to habitat (Bobay et al., 2018). For example, Campos-Cerqueira & Aide (2016) redefined the assumed habitat preferences for the Elfin Woods warbler, discovering that it preferred Palo Colorado forest, rather than Elfin Woods vegetation.

Abrahams & Geary (2020) assessed the detectability of the three heathland bird species, by analysing presence/absence data from the six sampling days. This provided detectability estimates of 0.73 for nightjar, 0.49 for woodlark and 0.26 for Dartford warbler. The high detectability of nightjar shows the utility of the bioacoustic approach for this species, as found by Zwart et al. (2014), especially when compared to its 0.30 detectability figure from the standard Breeding Bird Survey transect method (Johnston et al., 2014). In comparison, the Dartford warbler results from Abrahams & Geary (2020) indicate that bioacoustic surveys of this species may suffer from low detectability, due to its indistinct song, similar to standard surveys for this species (Bibby, 1978). This could be effectively counteracted by increasing the number of sampling days within the study (MacKenzie & Royle, 2005). Such a change is easily accomplished when using automated acoustic recorders, and should be considered in future studies for this species, or others with expected low detection rates.

Abrahams & Geary (2020) highlighted the effects of temporal and environmental parameters on detectability, finding that survey date, combined with habitat characteristics including wetland, woodland and heather cover, explained detectability and improved occupancy model performance. The effects of survey date and the environment on detectability correspond with previous studies (Furnas & Callas, 2015; Furnas & McGrann, 2018; Stiffler et al., 2018), with higher detection probabilities often reported for more open habitats such as non-forested areas and flat riparian habitats (MacLaren et al., 2018; Metcalf et al., 2019; Sugai et al., 2019). Abrahams & Geary (2020) found that detectability declined with proximity to roads for Dartford warbler. Cooke et al. (2019)

showed this effect for many species, with the strongest negative associations found in smaller-bodied birds (such as warbler species). Differences in detectability between species and among habitat types, therefore, indicate the need to consider detection probabilities in greater depth when interpreting results from any survey method.

Novel aspects of the Abrahams & Geary (2020) study were the application of acoustic methods to heathland bird species, the use of study sites outside of forest habitats, and being the first study in Europe to combine bioacoustic survey with occupancy modelling. The research demonstrated the wider potential of occupancy modelling for species with different vocalisation parameters, and in a habitat type (heathland, rather than forest) with previously untested sound propagation characteristics. To maximise the potential of this research to influence future studies and conservation management practice, issues highlighted within the published works need to be considered when using automated recorders with occupancy modelling. These include appropriate study design, accommodation of detection probability, misclassification errors in species identification, and the closure assumption that individuals are relatively static within their territories during the survey period (Furnas & Callas, 2015). Study methods that take these into account will enable occupancy modelling methods to provide valuable new data streams, at scales that are unmatched using other survey and analysis techniques.

5.4 Can the breeding status of bird pairs be assessed by the identification of different song/call types?

As an aspect of population assessment, the determination of mating status of birds within a site, such as a nature reserve, is vitally important. This information is needed to assess the breeding success of target bird species, understand population dynamics and deliver adaptive conservation management (Christoferson & Morrison, 2001; Hoodless et al., 2008; Buxton & Jones, 2012). Breeding status can be assessed through aspects of behaviour, such as territorial singing by male birds. In this respect, different song types (Nemeth, 1996; Staicer et al., 2006; McKillip & Islam, 2009; Bessert-Nettelbeck et al., 2014) and the use of accented or unaccented endings (Morse, 1966; Kroodsma et al., 1989; Catchpole & Slater, 2008), have been linked to male pairing status for a number of bird species.

Using spectrogram analysis, Docker et al. (2020) demonstrated — for the first time — that European nightjar, a migrant species of conservation concern, has two distinct song types. These are: song type I, a sequence of approximately two minutes length, that ends abruptly and is very rarely accompanied by non-vocal wing claps; and song type

II, a shorter song of around one minute, which concludes with a distinctive terminal phrase and is normally accompanied by wing claps. Docker et al. (2020) suggest that shorter, accented, songs are likely to be associated with a paired nightjar male or interactions with a female, as found for other species such as great reed warbler (Catchpole, 1983) and chestnut-sided warbler (Byers, 1996). This song type could therefore help define the spatial distribution and number of breeding pairs in an area, so that conservation management can be effectively targeted, for example, preventing recreational disturbance and enhancing habitat quality in appropriate locations (Lowe et al., 2014).

In Docker et al. (2020), the use of song type II was concentrated later in the breeding season, when most male birds are in established pairs. However, a link between individuals with confirmed breeding status and those using song type II was beyond the scope of this study. Further studies are needed to characterise the use of the two song types by individuals of known breeding status. Such studies could use data obtained from other technologies such as camera traps, radio or GPS tracking (e.g. Rebbeck et al., 2001; Spray, 2006). Alternatively, the use of song types by birds with different breeding status could be investigated by identifying individuals from their own particular vocal characteristics. This has been achieved for species including nightjar (Rebbeck et al., 2001; Chang et al., 2018; Raymond et al., 2020) and capercaillie (Hart et al., 2020), amongst other species (Peake et al., 1998; Policht et al., 2009; Cornec et al., 2014), and would provide a non-invasive option for gathering high-resolution data on breeding pairs.

5.5 How do environmental conditions, such as habitat structure and weather, affect acoustic data?

Environmental parameters, relating to habitat structure, weather conditions and time of day/year, affect animal behaviour, potentially determining occupancy at a particular site and detectability during surveys. For example, bird occupancy, as detected in bioacoustic studies, varies in accordance with spatial environmental parameters such as latitude, elevation and habitat type (Furnas & Callas, 2015; Sadoti et al., 2016; Campos-Cerqueira et al., 2019). Adverse environmental conditions, such as extreme temperature/precipitation or impenetrable vegetation, can also affect fieldwork operations by limiting surveyor access or the effective use of survey equipment. This can significantly alter the results of field-based surveys, including acoustic recording methods (Storch, 1997; Walsh et al., 2004; Mollet et al., 2015; Raynor et al., 2017; Fremgen et al., 2018; Abrahams et al., 2021). An understanding of these environmental factors is therefore critical to the interpretation of study findings, such as population estimates, for monitored species (Cayford & Walker, 1991; Drummer et al., 2011; Sadoti et al., 2016; Priyadarshani et al., 2018).

In the published works on capercaillie, VAR was inversely related to wind speed (Abrahams & Denny, 2018). This is likely to reflect, at least in part, reduced lekking activity in high winds, as noted for other grouse species (Drummer et al., 2011; Sadoti et al., 2016), and which may be related to noise sensitivity in the birds (Walsh et al., 2015). In addition, recording devices capture vocal activity less effectively in adverse weather (wind and rain), as the direction and strength of sound is affected, and there is increased masking by background noise (Digby et al., 2013; Klingbeil & Willig, 2015; La & Nudds, 2016). VAR and male abundance were both inversely related to elevation in Abrahams (2019), possibly as a proxy for weather exposure, despite the tested parameters showing no such correlation in that study. Lek attendance is considered likely to vary by elevation in a range of species (Sadoti et al., 2016), and capercaillie appear to prefer raised or elevated sites, such as ridgelines (Rolstad & Wegge, 1987; Saniga, 2002), although in Scotland hilltops are generally avoided (Haysom, 2013). Further investigations are therefore needed to characterise the relationship between VAR and bird abundance in different environmental conditions.

Habitat characteristics have a significant effect on lekking bird species, determining the location of lek sites and the distribution of birds around them. For example, *Mionectes* flycatchers (Pizo & Aleixo, 1998) and some hummingbird species (Atwood et al., 1991) have widely spaced male displays, similar to the 'exploded lek' described for capercaillie (Wegge et al., 2013; Abrahams & Denny, 2018). For such species, displaying males are audible to each other, but visual interactions are prevented or limited by distance, topography, or dense vegetation. The same is also often true for non-lekking species that display in a wider territorial context. For the heathland birds investigated by Abrahams & Geary (2020), the cover of trees, water/wetland (Figure 5.3), and heather grassland influenced detectability, and to a lesser extent, occupancy. The habitat covariates included in the models of Abrahams & Geary (2020) were not critical indicators of occupancy at the scale of the sampling sites, most probably due to the use of broad-scale habitat data. Higher resolution data, which could represent micro-habitat features not detectable at the scale of the field survey, and satellite and map data as applied here, could improve such site-based occupancy studies (Niedballa et al., 2015).

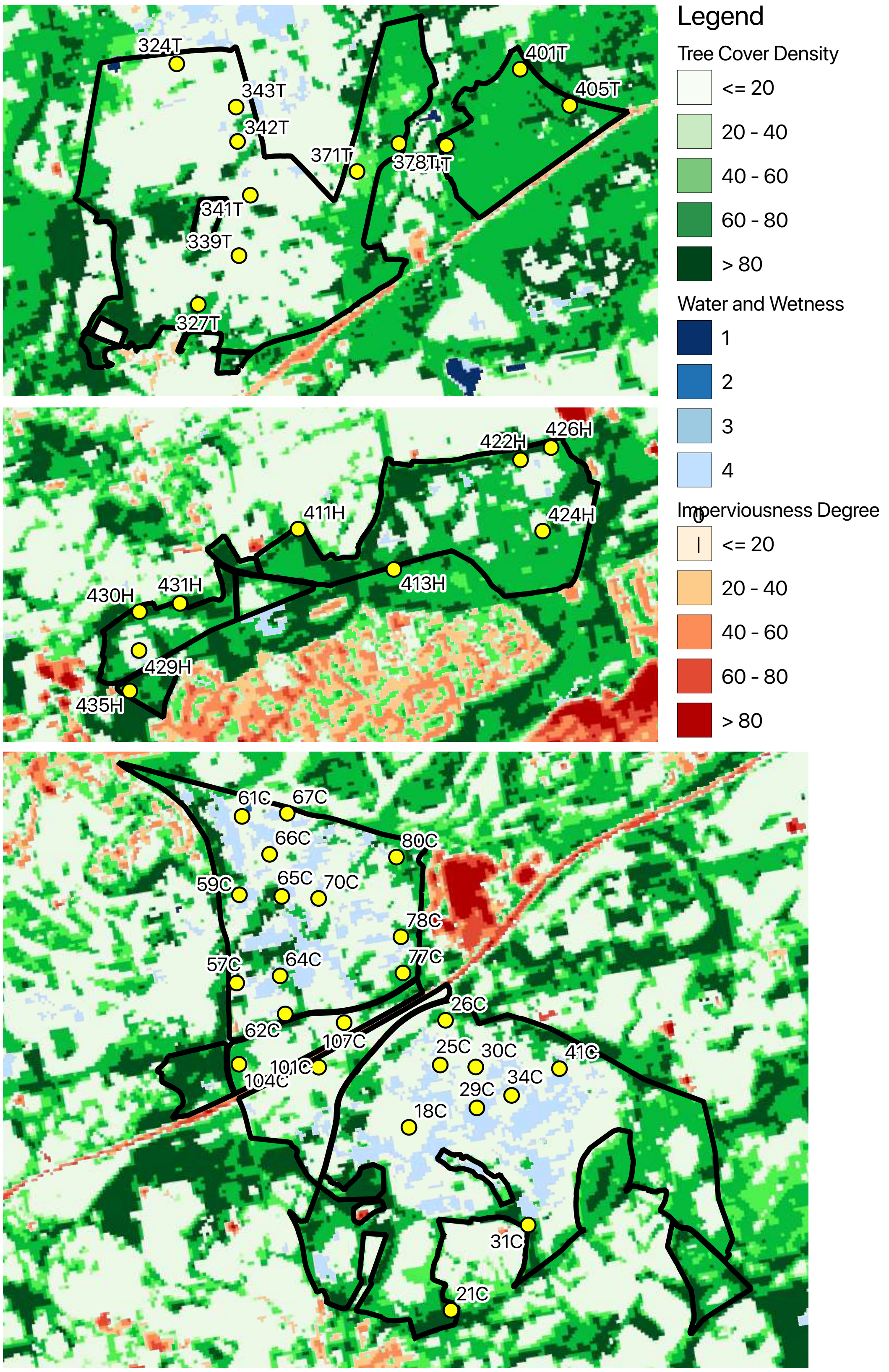

Figure 5.3: Processed satellite imagery accessed from Copernicus Pan-European High Resolution Layers, as used in Abrahams and Geary (2020). These layers provide raster information on tree cover density, water and wetness, and imperviousness degree, at a 20 m resolution. Yellow circles show acoustic recorder locations.

The collection and use of high-resolution covariate data was included in the protocol for the Pond Acoustic Sampling Scheme (Abrahams et al., 2021). This paper correlated acoustic indices derived from audio recordings across 24 ponds with the Habitat Suitability Index (Oldham et al., 2000). This metric of habitat quality combines parameters such as pond area, shading and macrophyte cover into a single value, and can indicate amphibian species occupancy and abundance (Unglaub et al., 2018). Future work could relate acoustic indices to the likelihood of recording a particular target species, based upon known relationships between occupancy levels and habitat condition as represented by measured environmental parameters. This application of acoustic data as an effective predictor of species presence or indicator of habitat quality would be a valuable tool in biodiversity monitoring and ecosystem management.

Temporal parameters operating at yearly, seasonal and diel scales influence the state of ecosystems, due to variations in weather patterns, day/night length and species life-histories. This variability can be observed in acoustic recording data by quantifying the numbers of sounds or the values in an acoustic index within a time unit (Lellouch et al., 2014; Desjonquères et al., 2015; Farina et al., 2015; Linke et al., 2018). In the bird studies included here, the levels of daily vocal activity varied widely (Abrahams & Denny, 2018; Abrahams, 2019; Abrahams & Geary, 2020). The overall decline in vocal activity during the 13-day survey period in Abrahams & Denny (2018), likely reflected a reduction in display behaviour towards the end of the main lekking season. No such overall trend was observed in Abrahams (2019), with the peak in capercaillie vocal activity varying between mid-April and early May depending on recorder location. The shorter sampling periods in Abrahams & Geary (2020) and Docker et al. (2020) did not allow longitudinal trends to be investigated, but still showed considerable daily variation in the birdsong activity recorded. This phenomenon of daily variation in VAR is poorly investigated in the literature, which has often focussed on within-day dynamics, such as the timing of the dawn chorus, or on longer seasonal patterns (Atwood et al., 1991; Tremain et al., 2008; Moran et al., 2019; Pérez-Granados & Schuchmann, 2020). However, daily variability has clear potential to bias study results when sampling is short-term or sporadic (Abrahams, 2019), indicating the need for protocols that recommend multi-day sampling (Balestrieri et al., 2017; Franklin et al., 2021), such as the minimum six day period in Abrahams (2018).

Diel variation in vocal activity, for example, high levels of activity during the dawn chorus, can be easily detected in acoustic recordings. Abrahams & Denny (2018) recorded a clear dawn peak for capercaillie, while Docker et al. (2020) found that nightjar vocal activity took place throughout the night, but was concentrated around dusk and dawn, as in previous studies (Cadbury, 1981; Zwart et al., 2014). In addition, song type II (associated with paired birds) was most common around dawn, possibly linked to the holding of territory. The capercaillie studies found the highest number of song phrases at 0.5–1 hour before sunrise. Similar findings have been recorded by human surveyors for capercaillie (Summers et al., 2021) and black grouse (Cayford & Walker, 1991), with the highest counts of lekking birds obtained in the two hours around sunrise. However, there were significant differences in the timing of the dawn peak between different recorder locations in Abrahams & Denny (2018) and Abrahams (2019). This variation between leks is a novel finding and requires further investigation. It could reflect habitat differences, such as forest structure, aspect or altitude, and how these influence temperature and light levels (Farina et al., 2015) — or possibly be a behavioural response to human disturbance at some locations. This demonstrates, again, the value of the acoustic approach in being able to quantify such findings and highlight the potential implications for research projects and conservation management.

A critical outcome from Abrahams & Denny (2018) and Abrahams (2019) is the recognition that wide temporal variation in activity levels can cause biases in detectability, with consequent implications for survey results (Angelstam, 2004; Laiolo et al., 2011). Traditional survey methods often use single or few survey counts (Summers et al., 2021) to assess presence/absence and population numbers, but such infrequent sampling can clearly skew results, as species activity and detectability will be suppressed by factors such as weather conditions (Calladine et al., 2009; Johnston et al., 2014; Sadoti et al., 2016). Cayford & Walker (1991) found that daily variation in black grouse lek counts was substantial, with numbers varying by up to 80% depending on the survey time and date. The published works collectively demonstrate that the temporal dynamics captured by bioacoustic sampling methods are a key benefit of the approach (Pérez-Granados et al., 2019; Sugai et al., 2019). Repeated sampling is therefore recommended in the survey protocols for birds in Abrahams (2018), and ponds in Abrahams et al. (2021), which include wide coverage of seasonal and diel periods within an appropriate survey design, to effectively capture how the the soundscape changes through time (Kuehne et al., 2013; Farina et al., 2015; Gottesman et al., 2018; Decker et al., 2020; Karaconstantis et al., 2020).

Overall, the studies included here demonstrate that acoustic recordings can be effectively combined with environmental data from field surveys, weather records, or remote sensing approaches to elucidate the habitat preferences of studied species. Detailed analysis of temporal dynamics can also be undertaken to understand how short or long-term changes in environmental conditions and animal behaviour can affect sound production by sampled populations and communities, or the wider soundscape produced by an ecosystem (Abrahams et al., 2021). This is likely to be detectable in correlations between environmental parameters and acoustic indices that quantify the sound characteristics of a field recording.

5.6 How does the research inform the development of evidence-based acoustic survey and monitoring guidance?

The findings outlined above have been used to inform both both future scientifc research and the development of evidence-based practical guidance on acoustic survey and monitoring for the conservation of animal populations and habitats (Abrahams & Nash, 2018). The research in this thesis has therefore enhanced practice in both these contexts, by addressing the main development needs for acoustic methods as identified by Sugai et al. (2019). These are:

- standardised monitoring procedures
- protocols for determining sampling effort
- protocols for determining the spatial distribution of acoustic sensors
- protocols for recording schedules that capture the appropriate temporal resolution
- efficient solutions for acoustic data analysis
- guidelines to optimise the audio settings (e.g. sampling rate and gain) of acoustic recorders
- procedures to estimate species detectability

The key aspects of standardised survey design, spatial distribution of sensors, temporal recording schedules, and sound analysis methods are discussed further below.

Standardised survey design

Advice on how to plan and design acoustic surveys is scattered through the scientific literature, and coherent standard guidelines have generally been absent – with notable exceptions for bats (Collins, 2016) and marine mammals (Todd et al., 2015). Sampling designs have often been influenced by specific research aims related to particular target species and closely defined questions. This has resulted in a variety of specialised recording protocols, which are often not described in full, and are not necessarily transferable between different taxa, ecosystems and research goals (Sugai et al., 2019). For birds, specific methods have been produced for tropical bird assemblages (Lacher, 2008), Canadian forest birds (Saskatchewan Ministry of Environment, 2014) and Australasian bittern (O'Donnell & Williams, 2015), while for freshwater ecosystems, only general guidance has been provided (Linke et al., 2020). To address these limitations, the recommended recording protocols for bird assemblages and ponds set out respectively in Abrahams (2018) and Abrahams et al. (2021) provide fundamental good practice guidance for the implementation of standardised methods for scientific research and conservation management. This guidance enables studies that span a variety of spatial and temporal scales to be conducted to capture organism and ecosystem dynamics and heterogeneity (Kuehne et al., 2013; Hill et al., 2016; Gottesman et al., 2018; Decker et al., 2020; Karaconstantis et al., 2020; Linke et al., 2020).

Spatial distribution of acoustic sensors

In automated acoustic studies with fixed sampling locations, the spatial layout of recorders is a major influence on the data collected. Previous studies have ranged widely in the number and density of recorders used, from single to hundreds of units being deployed (Figure 5.4). A range of approaches for developing sensor layouts are discussed in Piña-Covarrubias et al. (2018) and Sugai et al. (2019). For occupancy modelling, where sampling should reflect expected population density, the spacing of recorders should correspond approximately to the territory size of the species being assessed (Niedballa et al., 2015). Recorder layout should also aim to prevent overlap in the detection radii around each sampling location, so that pseudoreplication is minimised. In Abrahams & Geary (2020), sampling locations had nearest neighbour distances of 466-608 m, and Docker et al. (2020) had distances of >450 m. Threshold distances of 350 m and 400 m separation between singing males have been previously applied to differentiate between territories of male nightjars (Conway et al., 2007) and wetland birds (Stiffler et al., 2018). On this basis, there can be reasonable confidence that no birds were double-counted in the published works. For general bird assemblage studies, the survey protocol of Abrahams (2018) recommends a sampling grid spacing of 250 m. However, additional refinement of recorder placement may be warranted to maximise coverage of sites, dependent on the vocal and territorial characteristics of the species being studied. For a desired detection threshold, careful selection of recorder placements, based on topography, vegetation and weather patterns may be most efficient (Piña-Covarrubias et al., 2018). The development of good practice guidance for these aspects of spatial deployment should be prioritised for future studies (Eyre et al., 2014; Pocock et al., 2015).

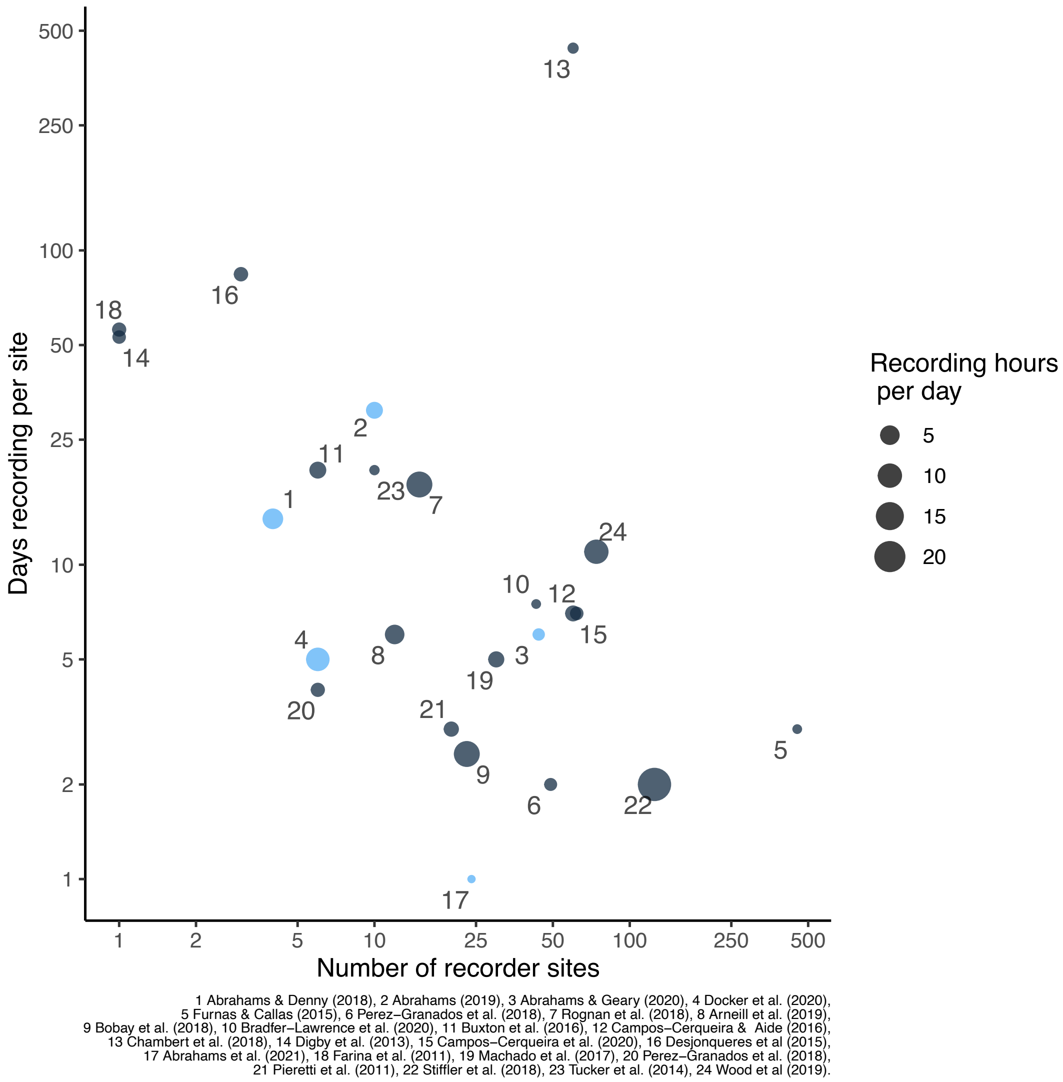

Figure 5.4: Examples of survey effort from 24 bioacoustic studies, indicating the number of recording days and the number of sampling sites. The hours of recording per 24-h period are proportional to point size. Blue points indicate the published works.

The characteristics of the recording environment and the response of microphones will affect sound transmission and recording quality. These environmental and equipment factors will therefore affect detection distances, potentially introducing biases to apparent bird occupancy and density. The published works presented on capercaillie and heathland birds (Abrahams & Denny, 2018; Abrahams, 2019; Abrahams & Geary, 2020; Docker et al., 2020) found that the numbers of calls recorded varied widely between recorder locations – potentially even over short distances (e.g. <50 m) (Figures 5.1 and 5.2). Other bioacoustic studies of forest birds have found bird call detection radii in the region of 50-100 m to be common, dependent on the species, ambient noise levels and microphone condition (Venier et al., 2012; Furnas & Callas, 2015; Sedláček et al., 2015; Turgeon et al., 2017; Yip et al., 2017). To make best use of bioacoustic methods for bird survey, greater understanding of the effects of distance on the detection of species and individuals is needed. This would, for example, enable biases in the assessment of abundance/density or species richness to be reduced. In particular, analysing the sound pressure level of recordings would enable a distance sampling approach to data analysis, similar to that employed in point counts by human observers (Tegeler et al., 2012; Darras et al., 2018; Pérez-Granados & Traba, 2021).

Recording schedules

Alongside spatial aspects of study design, the temporal schedules used for recording are critical to the taxa and questions being investigated. An infinite range of recording schedules is possible with modern programmable recorders, with the studies included in Figure 5.4 recording between 3 and 100 days per site. The data requirements of any survey will clearly vary, dependent on the objectives of the project and the detectability or life-history of the target species (Bayne et al., 2017; Abrahams et al., 2021). Continuous monitoring through the 24-hour period for several weeks may be preferable for increasing the likelihood of recording the full range of sound types within a site (Bradfer-Lawrence et al., 2019). This is especially the case if attempting to capture the sounds from rare, cryptic or transient taxa, as greater survey effort will generally increase detection probabilities (Sugai et al., 2019). Conversely, more resource-efficient protocols can be optimised by recording only within specific high activity periods of the target taxa, e.g. dawn and evening chorus times, offering practical benefits such as greater battery and memory card life, together with reduced data volume. This type of targeted recording protocol is hence the most common current practice for fieldwork applications, as shown by the data on recording hours in Figure 5.4 (Klingbeil & Willig, 2015; La & Nudds, 2016; Bayne et al., 2017; Sugai et al., 2019; Metcalf et al., 2020).

For occupancy modelling studies, the number of recording locations and the number of sampling events (e.g. days) affects the balance between the accuracy and precision of the occupancy and detectability estimates (Shannon et al., 2014; Sliwinski et al., 2016). Abrahams & Geary (2020) recorded for six days at 44 sites. This was an equivalent or longer deployment time than in previous bird occupancy studies (Furnas & Callas, 2015; Stiffler et al., 2018; Campos-Cerqueira et al., 2019; Wood et al., 2019) (Figure 5.4), but an increased number of survey days would have improved results for Dartford warbler, which had low detectability. In contrast, an increased number of sampling sites would have improved the modelling results for woodlark, which had low occupancy (MacKenzie & Royle, 2005; Banner et al., 2018). The Abrahams & Geary (2020) study therefore demonstrated a typical cost-benefit issue caused by species of varying ecology and limited study resources (as shown by the negative relationship between recording days and sampling sites in Figure 5.4). Modified sampling approaches could be developed for future studies to better target either of the two heathland species, but these would be likely to increase equipment, fieldwork and data analysis requirements (Wood et al., 2019).

Acoustic analysis methods

Once acoustic recordings have been collected from a fieldwork programme, analysis of the sound is required to generate ecological data. Rapid ongoing developments in the software tools for this task make it difficult to make standardised recommendations that remain current (Abrahams, 2018; Abrahams et al., 2021). The main procedure used to extract biological information from recordings, thus far, has been manual annotation and measurement of acoustic parameters (Sugai et al., 2019). However, acoustic data can also be analysed using automated species recognisers or the processing of signals using acoustic indices (Sueur et al., 2008; Wimmer et al., 2013; Fuller et al., 2015; Browning et al., 2017; Eldridge et al., 2018; Abrahams et al., 2021). These methods are being actively developed to either fully classify species vocalisations outright, or to group recordings into sound types so that manual checks can more easily be undertaken (Machado et al., 2017; Priyadarshani et al., 2018; Sugai et al., 2019).

A semi-automated approach was used in the published works (Abrahams & Denny, 2018; Abrahams, 2019; Abrahams & Geary, 2020), and is recommended in the draft bird survey protocol (Abrahams, 2018). Due to the acknowledged current limitations on identifying freshwater species acoustically (Greenhalgh et al., 2020), the PASS (Abrahams et al., 2021) is focussed on a rapid assessment approach, primarily using acoustic indices to indicate environmental quality (Sueur et al., 2008; Fuller et al., 2015; Eldridge et al., 2018). Such automated or semi-automated processing systems substantially reduce analysis time in comparison to manual methods (Knight et al., 2017; Shonfield &

Bayne, 2017). However, they can also introduce the potential for failures in call classification, resulting in fewer identified target sounds than manual analysis, and with more false-negative and false-positive errors (Swiston & Mennill, 2009; Zwart et al., 2014; Salamon et al., 2016; Knight et al., 2017; Campos-Cerqueira et al., 2019). These findings were confirmed by Abrahams & Denny (2018), Abrahams (2019) and Abrahams & Geary (2020), who demonstrated that low frequency and non-complex regular vocalisations, such as nightjar songs, can make it difficult for software algorithms to distinguish signals as they lack a distinctive audible or visual 'signature' (Swiston & Mennill, 2009; Sidie-Slettedahl et al., 2015; Knight et al., 2017; Bobay et al., 2018). Therefore, further software development is needed to accommodate the vocalisations of those species with less complex calls, to improve detection and classification of their signals.

Based upon the published works and other studies, the most effective current approach for species identification is likely to integrate automated and manual methods, combining the benefits of processing speed with the quality assurance of species classifications. Such an approach can help achieve high precision and recall rates (Digby et al., 2013; Knight et al., 2017; Chambert et al., 2018), which are particularly important for occupancy modelling, in which misclassification errors violate a major assumption of the models, and can lead to substantial errors in occupancy estimates (MacKenzie et al., 2006; Banner et al., 2018).

Chapter 6

CONCLUSION

The rapid development of bioacoustic and ecoacoustic approaches is providing valuable new tools for scientific research, species and ecosystem monitoring, and conservation management. This thesis has consistently demonstrated that the use of the acoustic approach within ecological research can generate new types of data, in large quantities, and with a temporal/spatial coverage not possible by human surveyors. In this respect, the acoustic approach shares benefits common with other new and developing technologies, such as remote sensing, genetic capture-recapture techniques and implementations of artificial intelligence (Jacob et al., 2010; Digby et al., 2013; Marvin et al., 2016; Berger-Tal & Lahoz-Monfort, 2018). The published works have shown that acoustic methods can eliminate or minimise observer biases by recording data in a standardised way and simultaneously across many sites. The studies on capercaillie, in particular, have demonstrated that the use of automated recorders can resolve practical fieldwork problems associated with surveying in pre-dawn darkness, at hard to access survey sites, and with the limited availability of expert field observers (Hobson et al., 2002; Celis-Murillo et al., 2009; Zwart et al., 2014). The use of automated recorders also reduces disturbance by surveyors, which is a particular benefit when working with sensitive, rare and threatened species (Abrahams, 2019).

The publications included in this thesis add vital evidence, previously lacking within the UK and wider European context, to demonstrate that acoustic monitoring can be highly effective in gathering field data for a range of species and habitats. The studies, for example, have covered a variety of birds with different vocal characteristics and habitat requirements and shown that the survey approach can accommodate these differences. The protocols produced for bird (Abrahams, 2018) and pond acoustic surveys (Abrahams et al., 2021) meet an identified need for improved, evidence-based survey methods (Abrahams & Nash, 2018). Following on from this work, further development of standard and consistent guidance on the applied use of acoustic methods is needed, widening implementation across an expanding range of habitat and taxa contexts (Marques et al., 2013; Browning et al., 2017; Sugai et al., 2019; Greenhalgh et al., 2020; Linke et al., 2020). Defined protocols for particular species or taxon groups will be required (Collins, 2016), and habitat-based guidance, such as the PASS, will aid the investigation of soundscapes, integrating data on biological, environmental and anthropogenic sounds (Pijanowski et al., 2011; Sueur & Farina, 2015; Abrahams et al., 2021). Bioacoustics and ecoacoustics therefore have great application potential, offering to fill significant methodological gaps in several areas of ecology and conservation (Dawson & Efford, 2009; Bardeli et al., 2010; Laiolo, 2010; Zwart et al., 2014; Shonfield & Bayne, 2017; Darras et al., 2018).

The publications included within this thesis have been published within and contributed to a period of very rapid development in the bioacoustic and ecoacoustic disciplines, during which new methodological approaches have been tested, and new ecological knowledge on species and ecosystems has been gained. The knowledge transfer work that has taken place alongside the publication of these works, such as the delivery of training courses and conference papers, has helped establish a wider awareness of how to apply these advances to real-world contexts. Together, they have prompted the implementation of the acoustic approach in new scientific research and the management of designated sites, habitats and species. As such, the acoustic approach will promote effective monitoring of species and ecosystems, thus enabling us to understand the changing global environment, and address the biodiversity and climate crises.

Chapter 7

APPENDIX - SURVEY METHODS

Bioacoustic field methods

Survey design

Like all ecological survey methods, the effective use of bioacoustic techniques depends on appropriate experimental design (Furnas, 2020). However, survey design for bioacoustic methods is still a poorly defined area, with a wide range of research methods being used and the limited guidelines available being scattered throughout the literature (Marques et al., 2013; Sugai et al., 2019). As bioacoustics becomes more established, efforts to systematically quantify sources of bias and standardize surveys are increasing (Sugai et al., 2019). Important topics for future research and development include: (i) how to choose the most effective detector hardware for a particular application; (ii) how best to deploy detectors in the field spatially and temporally; (iii) how to optimize recording autonomy and recording schedules; and (iv) how to store and process data and metadata (Gibb et al., 2018; Sugai et al., 2019). Establishing such standards for bioacoustics studies will improve the quality of research outputs and promote essential standardization between projects (Sugai et al., 2019).

Recorder selection and maintenance

The type of recorder to be used for a particular application will be driven by the kinds of animals or soundscapes being studied, as microphone elements are sensitive to a limited range of frequencies (Blumstein et al., 2011). Directional microphones can be used to capture acoustic information from specific orientations. However, most modern studies use omnidirectional microphones that sample sounds with more or less equal efficiency in all directions (Blumstein et al., 2011).

Modern digital recorders reproduce signals received by the microphone with good accuracy, low noise, flat frequency response, and no speed variation (Obrist et al., 2010). The ability of acoustic recording systems to accurately record sound is limited by their frequency range, dynamic range and system self-noise (Merchant et al., 2015). The maximum frequency that can be recorded is defined by half of the recorder sampling rate. The bit depth of the equipment defines the dynamic amplitude range that can be resolved - roughly equivalent to 6 dB per bit. Thus, a 16-bit 48 kHz recorder can record sound frequencies up to 24 kHz with dynamics of 96 dB (Obrist et al., 2010; Blumstein et al., 2011).

The dynamic range is the ratio of the highest to the lowest amplitude that can be measured by the microphone and recorder system. It can be scaled to higher or lower amplitudes by adding gain to the signal. If the gain is too low, quieter sounds may not be recorded, but if it is too high, loud sounds can distort the signal through clipping. System self-noise is noise generated by the recorder and microphone and can limit the ability of a system to record quieter sounds. It is therefore important to establish the required recorder specification and quality when planning and implementing studies.

Environmental conditions have substantial impacts on the durability and reliability of acoustic sampling units. As recorders are repeatedly exposed to adverse environmental conditions, they will degrade in performance - especially exposed parts of the equipment such as microphones. Protection from temperature extremes, rain or humidity may therefore be required for both microphone and recording unit (Blumstein et al., 2011), and procedures for the regular inspection, maintenance and calibration of recording systems are needed to support field studies (Adams et al., 2012; Merchant et al., 2015; Turgeon et al., 2017).

Spatial deployment

Of the 460 studies reviewed by Sugai et al. (2019), only half (54%) of all studies completely described their sampling designs - an important shortfall in documenting survey protocols. For those studies with the relevant information, most (64%) focused on macro spatial scales with recorders greater than 20km apart. However, half of the studies only used between one and three acoustic recorders, with only 14% using more than 10 recorders. A single recorder per site was reported in 71% of studies, with recorders commonly being rotated between sites, especially when few recorders were used. Such rotation can help increase spatial coverage, but will preclude simultaneous recording across sites, and will reduce the number of monitoring days. Hence, bias may be introduced from seasonal and weather differences, and species detectability may be reduced (Sugai et al., 2019).

Presuming limited resources for a bioacoustics project, the spacing and locations of recorders should be optimized for data collection according to the requirements of the study (Piña-Covarrubias et al., 2018; Furnas, 2020). Single recorders arrayed along an environmental gradient or in different land-cover patches can be employed to assess the effects of habitat on target species or soundscapes (Depraetere et al., 2012; Campos-Cerqueira & Aide, 2016; Sugai et al., 2019). However, when this is done, it is important to be able to separate detectability issues from any conclusions over occupancy, as physical habitat structure (e.g., vegetation, water surface, topography) affects the transmission of sound through the environment, and hence alters the 'detection space' around a recorder (Darras et al., 2016). Higher species detectability has been recorded for non-forested areas and flat riparian habitats, with reduced detection spaces in dense forest and where topography blocks line-of-sight (MacLaren et al., 2018). Survey design therefore needs to consider how differences in habitat might affect detection of target species (Piña-Covarrubias et al., 2018), as well as potentially affecting species behaviour and population density. Pilot studies can inform the detection space (or distance) of sensors over the range of monitoring habitats, and this information can determine the appropriate spatial layout of recording sites (Sugai et al., 2019) .

Temporal deployment

Long-term acoustic monitoring allows the investigation of broad aspects of seasonal activity and population dynamics. The use of programmable automated recorders allows a wide variety of temporal sampling protocols to be selected according to the species/groups of interest and the research goals. The use of acoustic sensors is often optimized by focussing recording on those times of day or night when the target species are most vocally active, e.g. dawn for birds and after dusk for bats. This helps to prolong battery life and avoid data storage issues. The review of (Sugai et al., 2019) found that 70% of studies monitored specific periods during the day/night, rather than covering the full 24 h cycle, with 77% of studies using continuous recording during the monitoring period. Those studies using discontinuous recordings commonly used a single recording per hour (47%), of up to 3 minutes (59%).

Different combinations of recording length and the number of recordings will influence how well acoustic activity, temporal resolution and detectability is captured, with the optimum schedule likely to depend on the target taxa and/or habitat type (Pieretti et al., 2015; Bradfer-Lawrence et al., 2019; Sugai et al., 2019). Due to this variation between study options, pilot studies are recommended to assess the efficiency of distinct recording schedules and appraise survey effort for a given goal, prioritizing longer diel periods and continuous recordings (Bradfer-Lawrence et al., 2019; Sugai et al., 2019). When discontinuous recordings are used, the optimum schedule can be determined by first conducting continuous 24-h recordings, and then sub-sampling this data to test how different recording lengths and numbers of recordings influence species detectability or other biological parameters of interest (Cook & Hartley, 2018).

Bioacoustic data analysis methods

Bioacoustic data analysis

The widespread uptake and applicability of bioacoustics to conservation monitoring is currently limited by the methods and technologies available to handle and process sound data (Teixeira et al., 2019). Clear guidance on how best to analyse bioacoustic data is lacking (Merchant et al., 2015; Knight et al., 2017; Pérez-Granados et al., 2019). Standardised survey and analysis protocols required development, ideally developing the capabilities of open-source processing tools (Gibb et al., 2018).

Converting raw sound recordings into scientific data generally involves two main steps: signal detection, and signal classification (Blumstein et al., 2011; Gibb et al., 2018). The methods for signal detection and classification start, at their most basic, with human analysts listening to recordings and/or visually inspecting spectrograms. Advanced methods involve automated signal detection software, including machine-learning approaches based on the development of complex computer algorithms (Blumstein et al., 2011; Browning et al., 2017; Knight et al., 2017; Gibb et al., 2018). The output of most analysis workflows is an accurately detected and correctly classified data frame, annotated with appropriate information. This is typically a list of target sounds for a particular species or sound type, with attached metadata such as time, date and location (Gibb et al., 2018) .

The reliable detection of signals during analysis of sound data is an essential first step for automated processing, to identify that a sound of interest is present within a recording and worthy of further study. This involves the extraction of structured sounds of interest from the recordings, excluding quiet periods or random background noises, and thus allows the removal of large quantities of unnecessary and uninformative noise from the data recorded in the field (Blumstein et al., 2011). This filtering of the dataset, however, must not cut valuable data from the analysis workflow, and so most studies promote a balance towards false positive detections at this stage in the process, as these can be reduced later (Blumstein et al., 2011). Detection algorithms that provide a confidence or quality estimate for each detection can therefore be helpful, allowing data to be tested and the decision threshold to be adjusted as needed (Blumstein et al., 2011).

In field studies, the detection process frequently involves distinguishing large numbers of spectrally and temporally overlapping calls, emitted by multiple vocalising species in acoustically heterogeneous settings (e.g., birds in the dawn chorus, swarming bats). This is a challenging task for most current algorithms. The probability of successfully detecting a vocalising animal normally depends on its distance from the sensor, vocalising behaviour, call parameters, and site-specific environmental factors (Darras et al., 2016; Gibb et al., 2018). Although prior noise reduction filtering can improve accuracy, environmental, biotic, and anthropogenic sounds can mask the target sounds or generate false positives (Metcalf et al., 2020).

Once a signal of interest has been detected, it needs to be classified to a signal type, allowing it to be labelled as a biologically relevant sound, such as a call from a particular species, or individual. This may be done by listening to playback of the sound or by visual inspection of a spectrogram. Alternatively, automated classification methods can be used to assign the signal to a particular category (Blumstein et al., 2011; Villanueva-Rivera et al., 2011). Such automated classification methods can be either supervised, in which previously collected and expertly labelled recordings are used to train the system, or unsupervised, in which the structure of the sound data itself guides decision-making about the categories to be assigned (Blumstein et al., 2011; Gibb et al., 2018). As for detection, the classification process is sensitive to factors including source distance, background noise, and temporal overlap between calls. Species classifications may also be intrinsically difficult for taxa with highly variable vocal repertoires, such as birds (Gibb et al., 2018).

Each detection and classification method has advantages and limitations. Trained analysts can detect subtle cues and differences to discriminate relevant sounds in recordings, but this is time-consuming and subjective, and it is difficult to quantify biases related to the experience and accuracy of the analyst. Given the quantity of data frequently collected during acoustic studies, relying on human experts limits the analysis rate and is often, therefore, impractical. In contrast, automated recogniser systems can quickly and consistently apply classifications to large volumes of acoustic data and are hence critical in enabling long-term or large scale studies, with machine learning methods increasingly being applied to bioacoustic signal detection and classification (Gibb et al., 2018).

Recognizer/classifier performance

Automated classification methods have the potential to identify the species, sexes, age groups or individuals producing a sound, sometimes with extremely high success rates (e.g. greater than 95% accuracy), allowing for the reliable processing of data from acoustic studies. (Blumstein et al., 2011). However, the automated identification of sounds can often include significant numbers of false-negative or false-positive detections and classifications, as some sounds of interest will be missed, and detections will sometimes be registered in the absence of a signal of interest (Waddle et al., 2009; Digby et al., 2013; Zwart et al., 2014; Gibb et al., 2018). The performance of automated recognizers may depend upon the distance of the individual from the recorder, extraneous sources of sound such as the calls of other species, and the overall noisiness of the environment (Teixeira et al., 2019). To address this issue, any reporting of results from automated analysis systems should include information on how the recognizer algorithm was constructed and statistics on its classification performance. The statistics on classifier performance should include both precision (the number of true positive detections divided by the sum of true positive and false positive detections) and recall (the number of true positive detections divided by the sum of true positive and false negative detections) (Teixeira et al., 2019).

Calculation of recognizer performance is commonly undertaken by following the automated species identification by a human post-validation process to assess the levels of false negatives and positives in the results, and remove these from the analysis (Campos-Cerqueira & Aide, 2016). This post-validation need not check all the data within the dataset, as model accuracy can be improved significantly even when only a very small proportion (e.g. 1%) of data is manually validated (Chambert et al., 2018).

Importantly, recognizer development must consider the vocal variability within and between individuals, social groups, and populations. If the species being monitored has a large repertoire, efforts should be made to determine which vocalizations are of most use, and tailor the recognizer towards these (Elphick, 2008; Teixeira et al., 2019). If vocalizations are highly variable, training data for a supervised system must properly represent this variability, such as by using calls from several individuals or groups. For conservation programmes aiming to detect rare or cryptic species or behaviors, specificity should be low, so that more detections are returned, although this may include a high number of false positives, which then need to be excluded through manual verification. Conversely, for projects in which detecting every call is not necessary, then reducing false positives by increasing specificity will be more important. For this reason, recognizers should ideally be built to align with the specific aims of each project

(Teixeira et al., 2019)

Future developments in analysis

Three main challenges exist for the development of acoustic survey methods (Sugai et al., 2019). These are nonstandardized monitoring procedures, time-consuming acoustic analysis, and limited data curation and data sharing resources. Research to date has used a wide variety of acoustic recording protocols, and there has been little consolidation in practice on this issue. Some formalization of approaches for designing and employing acoustic survey programmes could include, for example, procedures to estimate species detectability, protocols for determining adequate recording schedules and sampling efforts, and guidelines to optimize the deployment of automated recorders (Brandes, 2008; Roch et al., 2016; Sugai et al., 2019).

A critical challenge is the handling and analysis of large amounts of acoustic data, especially for programs spanning wide temporal or spatial extents (Browning et al., 2017; Sugai et al., 2019). Currently, analyses of large bioacoustic datasets are usually semi-automated, involving time-consuming manual quality control to resolve ambiguous classifications (Llusia et al., 2011; Kasten et al., 2012; Gibb et al., 2018; Sugai et al., 2019). Further development is needed to facilitate more robust analysis approaches and allow analysis of large, multisensor datasets, and to address issues to do with variable species detectability in different habitats and over time (Gibb et al., 2018; Linke et al., 2018).

One of the main constraints to the development of accurate classification algorithms is the limited availability of sound archives that can be used for training data. Existing sound libraries are mostly focused on storing short individual recordings of particular species, rather than larger datasets from automated recording systems, and their infrastructure is often not suitable for transferring and storing this type of data (Sugai et al., 2019). A very useful development would be the creation and adoption of publicly-available data storage libraries that would allow the storage of appropriate data and metadata, to use as benchmarks for testing of new classification systems (Gibb et al., 2018; Linke et al., 2018).

Chapter 8

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