Critiquing the use of Passive Acoustic Monitoring frameworks to support evidence-informed conservation for British bats

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Abstract

It is widely acknowledged that robust and accessible ecological evidence is required to underpin solutions to the current global biodiversity crisis. Reliable data are vital to inform conservation action, but can be challenging to obtain for some taxa, particularly those that are nocturnal, crepuscular, or cryptic. In the United Kingdom, one quarter of the mammal species found nationally are perceived to be at risk of extirpation, yet many species lack sufficient data to enable robust assessment of their distributions and the status of their populations.

This thesis examined passive acoustic monitoring frameworks for surveying and monitoring bat species in the United Kingdom, considering their ability to collect reliable data and to provide insights into species ecology, and evaluated their application to ecological research and practice.

Passive acoustic bat surveys were found to be most optimal when conducted for full nights, and in the absence of moonlight and/or heavy rain. Moreover, they were found to be more effective in recording comprehensive species assemblages, when compared to active acoustic surveys. Empirical testing of different detectors used in Passive Acoustic Monitoring (PAM) frameworks for bats, found that lower cost, open-source devices can serve as a viable alternative for commercial equipment in certain scenarios (dependent on target species and habitat), and when enough devices are deployed for a sufficient duration. The analysis of large PAM datasets was also examined, finding pairwise disagreement between popular automated bat classifiers, and supporting the recommendation that analysis should not, at present, be fully automated.

These findings contribute to the development of best practice and demonstrate the key advantages of PAM approaches, primarily in their potential to aid the up-scaling of both local, and national bat monitoring schemes.

Declaration

I declare that the work in this thesis was carried out in accordance with the regulations of the University of Gloucestershire and is original except where indicated by specific reference in the text. No part of the thesis has been submitted as part of any other academic award. The thesis has not been presented to any other education institution in the United Kingdom or overseas.

Any views expressed in the thesis are those of the author and in no way represent those of the University.

Signed: [redacted] Date: 28/08/2024

Dedication

For Mum & Dad, for everything

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Dissemination of research findings

The dissemination of the research presented in this thesis through scientific journal articles or conference presentations, are listed on the relevant cover page for each chapter.

CHAPTER ONE: Introduction

Post passive acoustic monitoring equipment set up for bats at Croome Park
August 2022

This chapter introduces the threats currently faced by biodiversity globally, and how the requirements for species surveying and monitoring form a key component of international targets and national legislation to address ongoing biodiversity loss. The state of nature in the United Kingdom is introduced, with particular regard to its bats and wider mammalian fauna. The broad methods used in surveying and monitoring of mammals in the region are outlined, including both traditional and novel techniques, and those relating primarily to bats are discussed in detail. Finally, the overall research aims of this thesis are defined, along with the thesis structure and the scope of each chapter.

1.1 Evidence-led biodiversity conservation

Halting the current rate of biodiversity decline is one of the foremost existential challenges faced by humanity across the world. The planet is in the midst of a biodiversity crisis, with notable reductions in species abundances and spatial distribution, and increases in human-accelerated species extinctions (Cowie *et al.*, 2022). It is generally accepted that the planet is undergoing its sixth mass extinction event (Barnosky *et al.*, 2011; Ceballos and Ehrlich, 2023), with the observed extinction rates estimated to be 100-1,000 times greater than the natural background rate of 0.1-1 E/MSY (extinctions per million species per year) (Lamkin and Miller, 2016). The International Union for Conservation of Nature's (IUCN) Red List states that upwards of 45,300 (28%) of the species assessed are currently threatened with extinction (IUCN, 2024). The drivers behind the elevated extinction rates are considered to be predominantly anthropogenic in origin (Ceballos *et al.,* 2015; Jaureguiberry *et al.*, 2022). Species are primarily threatened by climate change, habitat loss and non-native species introductions, as well as habitat fragmentation, the impact of pollution and eutrophication, agricultural intensification, and unsustainable harvesting or poaching (Mittermeier *et al.,* 2011; Dudley and Alexander, 2017; Groh *et al.*, 2022; Hald-Moretensen, 2023). The process of land use change has resulted in increasingly few areas escaping direct anthropogenic modification (IPBES, 2019; Jaureguiberry *et al.*, 2022). Indeed, Theobald *et al.* (2020), estimated that 14.6% of the Earth's land had been subjected to direct anthropogenic modification as of 2017. This is further compounded by the indirect effects of global or ultra-widescale pressures of climate change, atmospheric pollution, and ocean warming and acidification. Anthropogenic threats have implications not only on the intrinsic value of species and habitats within the biosphere, but also for humanity as a result of impacts on the range of ecosystem services upon which humanity depends (Ceballos *et al.,* 2015).

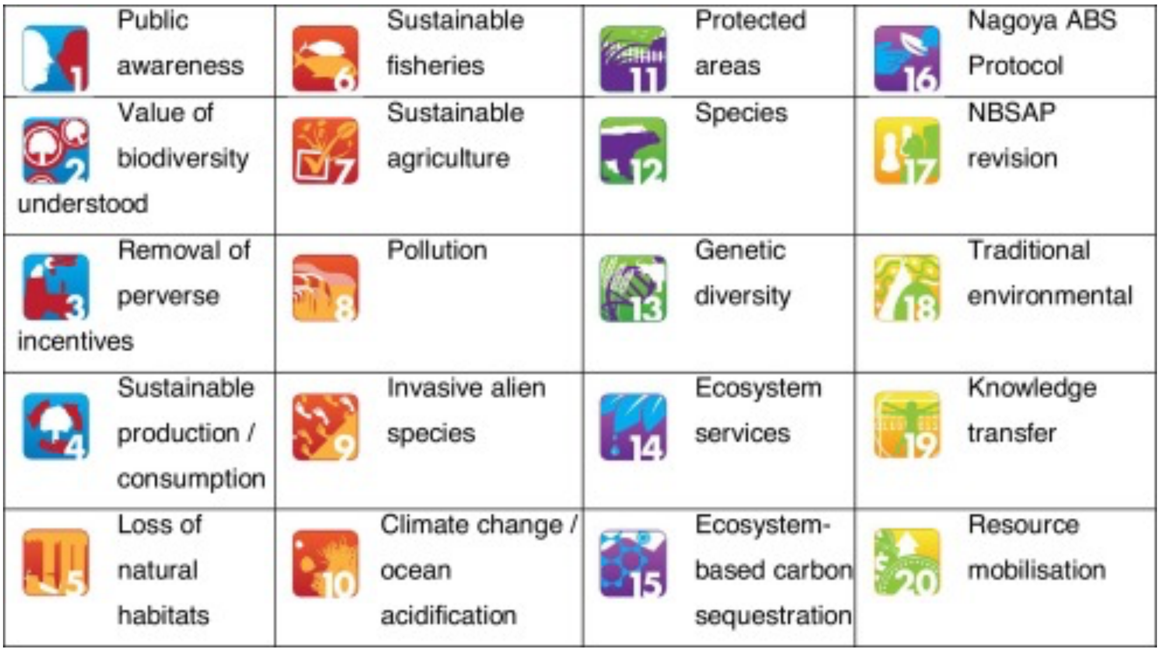
The concept of ecosystem services, used to describe the links between ecological and economic systems, was formally explored in the Millennium Ecosystem Assessment (2005) and the TEEB project (2007) (Braat and de Groot, 2012). The former defines ecosystem services as “the benefits people obtain from ecosystems”. The assessment divided these services into four categories: regulating, supporting, provisioning, and cultural. It has been argued that those in the former two categories essentially act as mechanisms to obtain the services listed in the latter two categories (Wallace, 2007). Regulating and supporting services include processes driven by mobile organisms that forage at a landscape scale and distribute seeds (Lundberg and Moberg, 2003), as well as pollination by organisms including insects (Allsopp *et al.*, 2008), bats (Kunz *et al.,* 2011) and birds (Paton and Ford, 1977), all of which are vital to both natural and agricultural systems (Kremen *et al.,* 2007). Essential regulating and supporting ecosystem services are also provided by sessile organisms, especially plant species that regulate hydrogeological cycles, remediate contaminated water, and facilitate soil formation and retention (Asbjornsen *et al.,* 2013). The resulting provisioning and cultural ecosystem services include food, fresh water, recreation and aesthetic value (Wallace, 2007). The provision of these vital services is becoming increasingly under threat as ecosystems are subjected to perturbations from land use change (Hasan *et al.*, 2020), climate change (Weiskopf *et al.,* 2020), and biodiversity loss (Bullock *et al.,* 2011, Le Provost *et al.*, 2023).

1.1.1 International efforts to conserve biodiversity

The significance of preserving biodiversity is recognised in the majority of countries globally. This is the first step along a complex pathway towards slowing the rapid rate of species loss and preserving natural processes (Rands *et al.,* 2010). The key to achieving the end goal lies in producing evidence that leads to the detection, measurement and monitoring of change (Field *et al.*, 2005), an understanding of the impacts of different anthropogenic actions (Mihoub *et al.*, 2017), support for the development of conservation action and practice, and allows the identification of priorities (Pullin *et al.,* 2004). An international approach to tackling biodiversity loss was first initiated in the late 1980s, with the formation of the United Nations Environment Programme (UNEP) working group, whose aim was to compile evidence to establish the requirement for an international convention relating to conserving biodiversity. At the historic Earth Summit in Rio de Janeiro in 1992, 168 nations signed the first Convention on Biological Diversity (CBD) thereby recognising the need, and obligation, to conserve global biodiversity in international policy for the first time (CBD, 2024).

In response to the Rio Summit, many countries opted to devise Biodiversity Action Plans (BAPs) (e.g. United Kingdom, New Zealand, Australia) or Species Recovery Programmes (e.g. United States) to focus conservation efforts on priority species and habitats (Goodenough and Hart, 2017). Commitments were reaffirmed in 2002 at the Johannesburg summit, and 190 countries committed to achieving a significant reduction in biodiversity loss at global, regional and national scales by 2010 (Balmford et al., 2005).

The next significant renewals of agreements were made at the 2010 Convention on Global Biodiversity in Nagoya, Japan, where the Strategic Plan for Biodiversity was adopted for the forthcoming decade, ending in 2020 (McCarthy *et al.,* 2012). This ten-year plan included five strategic goals, supported by twenty targets for global biodiversity that were originally known as the Aichi targets (Figure 1.1). However, a mid-term analysis undertaken by Tittensor *et al.* (2014) indicated that although there had been a marked upward trend in the prioritisation of biodiversity in policy and implementation of conservation action, it would likely be insufficient to meet the targets by 2020. Furthermore, the initial publication of the official report for the CBD, Global Biodiversity Outlook 5, released in June 2020, predicted that despite the action taken by the signatories, the majority of the agreed targets would be missed at a global scale (Secretariat of the Convention on Global Biodiversity, 2024).



1 Public awareness	6 Sustainable fisheries	11 Protected areas	16 Nagoya ABS Protocol
2 Value of biodiversity understood	7 Sustainable agriculture	12 Species	17 NBSAP revision
3 Removal of perverse incentives	8 Pollution	13 Genetic diversity	18 Traditional environmental
4 Sustainable production / consumption	9 Invasive alien species	14 Ecosystem services	19 Knowledge transfer
5 Loss of natural habitats	10 Climate change / ocean acidification	15 Ecosystem-based carbon sequestration	20 Resource mobilisation

Figure 1.1: *The 20 Aichi targets (Sumalia et al., 2017).*

The current, post-2020 Global Biodiversity Framework (GBF), was adopted at CBD COP15 (Montreal, Canada) in December 2022, and sets out global biodiversity goals for the decade up to 2030 (CBD, 2022). The framework aims to put forward measurable and verifiable objectives, with a tangible target of first achieving no net loss of biodiversity, before striving for net gain by the end of the decade (Milner-Gulland *et al.,* 2021).

1.1.2 Surveying and monitoring

Within ecology, the terms “surveying” and “monitoring” tend to be used interchangeably, however, there are marked differences. Surveys are generally used to collect primary data and ascertain the ecological conditions at a given place and time. For example, this might include determining species presence (or likely absence) and estimating species richness. This differs from a census, whereby the species/taxa identified in a survey are counted to assess population size. Surveillance and monitoring, on the other hand, involve repeated survey effort over an extended time period and, if appropriate, a wider geographical range (Goodenough and Hart, 2017). Ecological monitoring usually aims to answer a specific scientific question (Spellerberg, 2005), whereas surveillance typically involves long-term data collection, which may cover multiple species and locations. The aim of ecological surveillance is to detect and measure change from the baseline conditions, for example, in identifying the introduction of an invasive species (Jarrad *et al.,* 2011) or disease (Walton *et al.,* 2016).

Long-term conservation and effective species management depends on robust data from rigorous surveying and monitoring (Roberts, 2011). The monitoring of both species and habitats is essential in providing the data required to establish baseline ecological conditions, initiate and inform conservation action, and evaluate and compare the long-term efficacy of such action in attaining the desired outcome (Nichols and Williams, 2006; Burns *et al.*, 2018). Monitoring data to map species distributions and densities are also vital in designating priority areas for conservation (Jenkins *et al.*, 2013). This could be in the form of protected areas or nature reserves, where targeted management can be undertaken (Gaston *et al.*, 2006). Moreover, long-term monitoring and surveillance programmes aim to identify trends from the outset, whether they be positive or negative. Where negative, this enables the appropriate action to be taken to understand and address the cause, before the impacts become severe and potentially irreversible. In addition to directly informing conservation efforts, surveying and monitoring also form a key component of ecological research (Goodenough and Hart, 2017). Furthermore, ecological surveys frequently play a key role in legislation compliance and informing Ecological Impact Assessments (EcIAs) within the planning and development sector (Sutherland, 2008). The data from such surveys ensure that relevant environmental and wildlife law, such as that concerning protected species and habitats, is adhered to (Drayson *et al.,* 2015). Additionally, surveys inform mitigation/compensation strategies which strive to prevent development and land use change from resulting in biodiversity losses (Treweek, 2009).

Ecological surveying and monitoring can focus on species, habitats, or parameters within wider ecosystems or landscapes. Species specific monitoring tends to be question-driven and uses rigorous methodology to gain valuable insights into the population dynamics of the species concerned. Habitat monitoring is generally broader in approach, using spatial techniques to map and monitor habitat distribution and quality (Lengyel et al., 2008). Monitoring of habitat processes and wider ecosystems frequently focuses on selected indicator species; for example studying plant communities to study ecological succession (Goodenough and Hart, 2017). Additionally, data relating to environmental parameters, such as water quality and soil chemistry, are used to build robust assessments and monitor temporal changes in the quality of the environment (Spellerberg, 2005).

1.1.2.1 Resourcing ecological surveying and monitoring

Ecological surveying and monitoring often requires substantial resources, both in terms of the economic cost and the time and effort required by surveyors (Spellerberg, 2005). The drivers behind funding and conducting ecological surveying and monitoring, therefore, can generally be divided into two categories: those that support conservation and habitat management, including national schemes, and those that exist to ensure legislative compliance, concerning protected species and habitats, and requirements for biodiversity net gain. Under the CBD, all countries have an international obligation to conserve biodiversity, with those who are able making funds available for conservation action and the ecological monitoring schemes which underpin such actions (Coad *et al.*, 2019). Effective management of key habitats and species requires the use of well-established baseline information, which can only be obtained by ecological surveying. Furthermore, perturbations, whether natural or anthropogenic, are generally long-term and/or cumulative and synergistic. Being able to detect and manage the impact of such perturbations effectively, therefore, requires ecological monitoring over extended time periods (Lindenmayer and Likens, 2010). In the case of legislation compliance, the local authority or developer has a legal obligation to fund ecological surveys, as appropriate, to ensure laws regarding protected species and habitats are upheld. This involves both the collection of baseline data prior to any development/land-use change and longer-term monitoring to confirm that the proposed mitigation and/or compensation is sufficient in preventing ecological harm (Treweek, 2009).

1.1.2.2 Designing effective ecological monitoring schemes

Despite the need for ecological surveying and monitoring at local, national and international scales, surveying and monitoring efforts vary widely in extent and effectiveness. A review undertaken by Lindenmayer and Likens (2010), concluded that successful monitoring actions share a number of characteristics, including clear questions, a conceptual understanding of the species population or ecosystem concerned, and seamless collaboration between scientists, managers and policy makers. However, ecological monitoring has often faced criticism. For example, surveys undertaken for localised EcIAs, were found to be deficient in recommendations for, or evidence of, repeated survey effort to serve as follow up monitoring in order to document the ecological response to development (Drayson *et al.*, 2017). Moreover, national scale monitoring schemes have faced particular criticism from within the scientific community. In this instance, the main failing is considered to be a lack of focus or development of specific scientific questions within their design. This lack of focus can lead to those species that are less abundant, and often most in need of conservation action, going undetected (Nichols and Williams, 2006). Furthermore, Yoccoz et al. (2001) also agree that schemes can lack the effective collaboration between scientists and managers, which is essential in designing monitoring schemes that are effective both in terms of scale and cost.

Question-driven monitoring, such as that carried out for research purposes, is often able to give valuable insights into the population dynamics of the target species, and most often has sufficient rigour to identify emergent trends and potential drivers. However, this approach can be difficult to apply across the geographic scales required by the mandated monitoring, initiated for legislation compliance (e.g. national and international biodiversity targets).

Monitoring schemes that cover wider landscape or that are national or international in scope, have seen some success in detecting temporal changes within populations but are largely too broad to identify the drivers behind the observed trends (Lindenmayer and Likens, 2010). Therefore, the key challenges in undertaking effective ecological monitoring are: (1) adopting a focused approach with defined questions and objectives, (2) utilising the appropriate methods for both the target species and the spatiotemporal scale required, and (3) ensuring that the necessary support is in place, from scientists and policy makers, to confirm that the monitoring is suitably targeted to meet the relevant objectives (Stout, 1993).

1.1.3 The state of nature in the United Kingdom

Following the Rio Convention in 1992, the United Kingdom (UK) became the first country to develop and implement a series of nationwide BAPs (Ruddock *et al.,* 2007) for what ultimately became 1,150 priority species and 65 priority habitats (Joint Nature Conservation Committee (JNCC), 2024). Despite such efforts towards conserving biodiversity in the UK, the most recent State of Nature Report (State of Nature Partnership, 2023), revealed that, overall, the abundance of 753 terrestrial and freshwater species has decreased by an average of 19% since 1970, and that 16.1% of the taxa for which sufficient data are available (10,008), are currently threatened with extirpation (Figure 1.2).

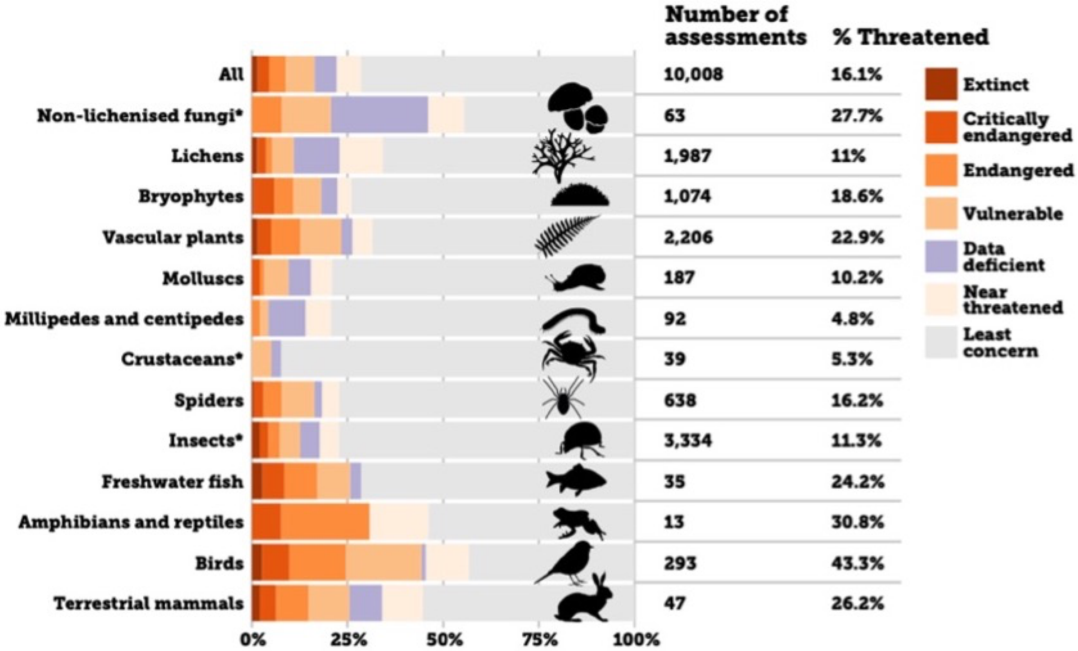


Figure 1.2: *Great Britain Red List Assessment by taxonomic group. *Only 17% of insect species, 10% of crustaceans and <1% of fungi have been assessed (State of Nature Partnership, 2023).*

Habitat loss and degradation, pollution, and insufficient policy are considered to be among the primary drivers behind the observed declines in the UK (Burns *et al.* 2016). Further pressures include agriculture, which has intensified significantly since the middle of the 20th Century (Matson *et al.,* 1997; Firbank *et al.,* 2008; McKay *et al.,* 2019), with mechanisation and increasing demand for food production leading to habitat loss and dramatic modification of the landscape (Boatman *et al.*, 2007). Global climate change is also being seen to have additional and synergistic impacts on national level species abundance, distribution, ecology and life history parameters, with average temperatures rising by approximately 1.1°C since the late 19th Century (Intergovernmental Panel on Climate Change (IPCC), 2023).

The UK's sixth National Report to the CBD, published in May 2019, predicted that the country was on track to meet only a quarter of the twenty Aichi targets by 2020 (JNCC, 2019a). Policy and funding are now focused on renewed global commitments to halting biodiversity declines by 2030 (State of Nature Partnership, 2023). This has included actions such as committing to the 30 by 30 target to conserve a minimum of 30% of land and sea for biodiversity by 2030 (Natural England, 2023). Moreover, national Agri-Environment Schemes (AES) were reformed after the UK departed the European Union (Baldock and Cam, 2024). The introduction of the new Environmental Land Management scheme (ELMs) offers financial incentives to promote sustainable farming practices, and to encourage conservation activities on farmland (Hurley *et al.*, 2022). Additional government funding has included the UK Nature for Climate Fund, which pledged £640 M for habitat restoration (Seddon *et al.*, 2020). Furthermore, the legal protections afforded to many species under former European legislation were upheld in national law under the Conservation of Habitats and Species Regulations (2017). This ensured a continuation of the protections for European Protected Species (EPS) found in the UK after Brexit, along with the financial and custodial penalties incurred for committing an offence.

1.1.4 Monitoring approaches and obligations in the United Kingdom

The UK has an obligation to undertake species monitoring under agreements and legislation made at both international and national levels. However, despite agreed targets, many species populations in the UK are vulnerable, with challenges in carrying out effective monitoring, resulting in data on many species being scarce (Battersby and Greenwood, 2004; Burns *et al.*, 2018; Coomber *et al.*, 2021). These pitfalls in the country's monitoring schemes are not due to a lack of surveyor effort. The 2019 State of Nature report estimated that 18,700 professional and volunteer naturalists were involved in formalised species monitoring schemes, reflecting a long-standing interest in natural history and wildlife recording (State of Nature Partnership, 2019). This report also revealed that the commitment to nature within the country was continuing to grow, with both the amount of time invested by volunteers and non-governmental organisation (NGO) spending increasing over the past decade. These figures were not updated in the recent 2023 report (State of Nature Partnership, 2023).

A significant proportion of the monitoring undertaken nationally, therefore, relies on valuable input from volunteers. Volunteer records broadly fall into two categories: structured and unstructured. Structured records are obtained through rigorously designed, co-ordinated, and repeated surveys, involving standardised methodology. This produces high quality datasets, which are statistically analysed to study population trends over time. The data obtained through these schemes are frequently utilised within scientific research. Examples include the British Trust for Ornithology's Breeding Bird Survey (Greenwood, 2003) and the Bat Conservation Trust's (BCT's) National Bat Monitoring Programme (NBMP) (Barlow et al., 2015). Unstructured records, on the other hand, include records submitted to the Biological Records Centre (BRC) or Local Environmental Records Centres (LERCs), which are usually acquired independently of any formal monitoring activities. The principal caveat associated with such records, is the potential for bias, stemming from inconsistencies in survey methods and locations. However, these records span a wide range of taxa and the ability to account for bias in statistical analysis, makes such records invaluable. They are currently collated by the BRC, along with data from formalised monitoring schemes. When both types of records are combined, biological recording is estimated to involve 70,000 surveyors annually (Pocock et al., 2015).

1.2 Mammals in the United Kingdom

The anthropogenic alteration of the landscape in the UK has profound implications for the country's mammalian fauna. Fragmentation of the landscape into smaller, more isolated habitat patches restricts population sizes, prevents genetic exchange, and inhibits dispersal to other patches of suitable habitat (Scopes *et al.,* 2024). Where populations already exist at low densities, or have a limited ability for dispersal, habitat fragmentation increases the likelihood of local extirpation (Bright, 1993). The Mammal Society lists 59 volant and von-volant terrestrial mammal species as present in the UK across six taxonomic orders: Eulipotyphla, Lagomorpha, Rodentia, Carnivora, Artiodactyla, and Chiroptera. Of these, 48 species are considered native. More than 50% of the country's native mammals are afforded at least basic protection under the Wildlife and Countryside Act (1981), with those that are rarer, declining, disturbance sensitive, or where the UK holds a substantial proportion of the global population being afforded additional protection, both under the Wildlife and Countryside Act (1981) and/or the Conservation of Habitats and Species Regulations (2017). Despite such provisions, the most recent national red list issued by the Mammal Society (2020), which assessed 47 native or formally native species, indicated that one quarter of the country's mammal species are at risk of extirpation. This included six species in the order Chiroptera.

The Mammal Society has been instrumental in coordinating national mammal recording efforts since the 1950s, with a number of targeted schemes yielding valuable insights and leading to successful conservation action (Flowerdew, 2004). This included identifying the loss of hazel dormice (*Muscardinus avellanarius*) at the northern extent of their range (Bright *et al.,* 1996) and determining the abiotic factors affecting the distribution of yellow-necked mice (*Apodemus flavicollis*) (Marsh *et al.*, 2001). The Mammal Society were also the primary NGO coordinating national bat monitoring efforts, prior to the formation of the BCT in 1990 (Flowerdew, 2004). However, many of the country's mammal species have historically lacked sufficient data, either spatially or temporally, to determine the status of populations (Battersby and Greenwood, 2004). As a result, assessing changes in populations and distributions to inform national Biodiversity Framework actions cannot be made with reasonable confidence for the majority of bat species and some terrestrial mammals, such as harvest mice (*Micromys* minutus) (Mathews *et al.,* 2018). This highlights the importance of well-designed and robust monitoring schemes, both to establish a clear baseline for data deficient species and monitor trends throughout the course of any ensuing management action, in order to safeguard against further losses.

Developing effective monitoring schemes to study the UK's mammal fauna is of prime importance. Owing to its early separation from continental Europe, the UK supports a relatively limited number of mammal species compared to mainland Europe. Additionally, limited prey and the impacts of numerous non-native and invasive species has resulted in populations of several native mammals becoming extremely fragile, and thus at risk from even minor perturbations and stochastic processes. Appropriate conservation therefore relies heavily on targeted management action, informed by rigorous monitoring data (Harris and Yalden, 2004).

Mammal conservation and monitoring in the UK face a number of challenges, particularly when compared to other taxa. Bird monitoring has a history of being rigorous and highly co-ordinated, largely as a result of a large pool of volunteer surveyors (Greenwood, 2007). Mammal monitoring, however, tends to attract fewer volunteer surveyors, principally owing to the specialist skills and field equipment required to survey a large number of mammal species. In comparison to birds, small mammals in particular are difficult to observe and survey techniques are difficult to standardise, with specific methods required to effectively survey for individual species (Battersby and Greenwood, 2004).

As technology has become more accessible in terms of economic cost and capability, researchers have successfully piloted the use of technology-based techniques, such as bioacoustics and camera traps, in surveying and monitoring increasing numbers of species. This includes smaller or otherwise elusive mammals, including bats and hazel dormice, for which monitoring data are often lacking. Technology therefore has the potential to establish rapid and non-invasive methods to monitor some of Britain’s most vulnerable mammals (Mills *et al.,* 2016). Moreover, such methods support recent calls to move monitoring techniques from invasive to non-invasive through the 3Rs principals for animal research: Replace, Reduce and Refine (Zemanova, 2020).

1.2.1 Methods of surveying and monitoring mammals

Mammal surveys can take a number of forms, depending on the target species, the question posed, and the primary data required. For example, surveys may be used to establish mammalian species richness, or a census may be used to quantify population sizes of one or more specific species (Sutherland, 1996). Alternatively, survey data can be used to map species distributions or to infer abiotic parameters using biological indicator species (Goodenough and Hart, 2017). Data can be obtained directly or indirectly, observationally or invasively and may also be collected across a range of spatial scales, from site level to landscape level or even national scale.

Mammal surveys are carried out by a wide variety of surveyors, from licenced professionals to citizen scientists and volunteers. Many species require specialist knowledge and skills for surveyors to legally be permitted to be in close proximity to, or handle individuals. This primarily relates to species protected by some form of national legislation, such as hazel dormice, where a licence is required to complete nest box checks (Bright et al., 2006). In these instances, only suitably qualified persons will be able to conduct surveys, although unlicenced individuals are often able to observe, or work under the supervision of the licenced surveyor (Natural England, 2025). Where surveys can be undertaken less invasively, either without the need to handle the species directly or where specialist licences are not required, a wider range of surveyors can become involved. This includes students, early career researchers or volunteers undertaking surveys under direct or indirect guidance of experienced individuals. A key example is the National Harvest Mouse Survey, which engages a wide range of volunteers to conduct surveys looking for distinctive harvest mouse nests (Clifton, 2024). Moreover, surveys that gather data exclusively using distanced observation or field signs can be carried out by almost anyone, with little or no supervision, but after appropriate training. This approach is frequently employed by large-scale citizen science projects, involving a variety of surveyors, often distributed across a wide geographic range (Dickinson et al., 2010).

The techniques used to survey and monitor mammals across the country can be grouped into four broad categories: observational, interventional, indirect and remote. Observational surveys include walked transects, with surveyors recording individuals seen/heard along a particular route (Smart *et al.,* 2003). Interventional surveys include live trapping, usually with the intention of marking individuals for capture, mark, recapture studies (Sutherland, 1996). Indirect surveys include footprint tunnels (Bullion and Looser, 2019) and hair tubes (Gurnell *et al.,* 2009), whereby surveyor efforts are focused on deploying and maintaining equipment to gather evidence of species presence, as opposed to direct observation. Finally, remote surveys, such as camera trapping (Kilshaw *et al.,* 2014) and remote ultrasonic recording (Gibb *et al.,* 2019), require little surveyor input once deployed, and automatically gather data over extended time periods.

Indirect and remote survey techniques have the potential to fill the gaps in surveying and monitoring efforts using observational or interventional methods (Mills *et al.,* 2016). Mammals can be particularly challenging and labour intensive to study (Battersby and Greenwood, 2004), especially through observational and interventional techniques, with protected species licences often required. Consequently, population monitoring data are severely lacking for many species (Flowerdew, 2004). There is, therefore, rapidly growing interest in the use of novel indirect survey techniques and the application of increasingly accessible technological approaches, in mammal surveying. Technological approaches can offer the potential to gather data on a fully- or semi-automated basis, often over extended time periods and with reduced levels of surveyor effort (Silveira *et al.,* 2003). However, many such techniques are yet to be widely used in the UK and methods regarding their use remain unstandardised, or with guidance for their use in the early stages of development. The following sections briefly outline the broad categories of mammal survey techniques commonly undertaken to survey and monitor mammals in the region; these are then summarised in Table 1.1.

1.2.1.1 Observational surveys

Observational surveys are those which involve direct observation by the surveyor, whether it be sight or sound. Direct observational survey methods for mammals fall into three broad categories: transect sampling, point sampling and mapping (Goodenough and Hart, 2017). Although transects and point counts are commonly used to survey other taxa, for example, birds (Newson *et al.,* 2005), for mammals, their use tends to be restricted to larger and readily observable mammals (Sutherland, 1996; Smart *et al.,* 2003). However, when supplemented with technology e.g., thermal imaging equipment and/or ultrasonic detection equipment, they can have wider application, primarily in surveying bats (Collins, 2023) (section 1.3). Such methods are also used within wider mapping surveys, such as mapping distributions and abundance of species using Geographic Information Systems (GIS).

Perhaps the most novel observational mammal surveying technique currently being used in the United Kingdom is that of employing specially trained Conservation Detection Dogs

(CDDs). This methodology employs the dog's olfactory senses (Bennett *et al.,* 2019), and has grown principally from using the technique to locate missing persons and in law enforcement and military applications (Beebe *et al.,* 2016). This technique has since been proved successful in detecting both live mammals (Bearman-Brown *et al.,* 2020) and bat carcasses (Mathews *at al.,* 2013). Moreover, numerous studies to date have found CDDs to be more effective in species detection, when directly compared to alternative methods (Beebe *et al.,* 2016), for example in detecting hedgehogs (*Erinaceus europaeus)* (Bearman-Brown *et al.*, 2020).

1.2.1.2 Interventional surveys

When individuals cannot be directly observed, or where additional data are needed, interventional trapping surveys may be necessary. These surveys usually involve some form of temporary trapping and restraint of the survey species. A key example of mammal trapping surveys undertaken in the UK is the use of Longworth traps for small terrestrial mammals (mice, voles, shrews) (Flowerdew et al., 2004; Gurnell and Flowerdew, 2006). Longworth traps are typically deployed along mammal runs (Sutherland, 1996), and are particularly effective for capture-mark-recapture (CMR) studies to determine species distributions and abundance (Sutherland, 1996; Goodenough and Hart, 2017; Jung *et al.,* 2020). The ability to take individuals into the hand enables biometric data (weight, sex, age) to be collected in order to assess population structure and health (Flowerdew *et al.,* 2004). Moreover, trapping surveys are also essential in studying species movements and home ranges (Bontadina et al., 2001) whereby tracking devices, such as PIT tags, need to be fitted (Marsh *et al.*, 2022).

1.2.1.3 Indirect surveys

Some mammal survey methods are entirely indirect and do not require any direct observation of the target species, instead relying on the documentation of evidence pertaining to species presence indirectly. These could be indicators of a species' physical presence in the survey area such as hair and skeletal remains, evidence of their behaviour such as footprints and refuges, or evidence of a species' physiological processes, including feeding remains and faeces (Goodenough and Hart, 2017). These techniques are of particular value in establishing the presence of small, nocturnal or otherwise elusive species. Indirect methods often involve the use of equipment to "harvest" indirect evidence. Examples include the use of footprint tunnels to study hedgehogs (Yarnell *et al.,* 2014) and arboreal mammals (Bright, 2006; Mills *et al.,* 2016), or hair tubes to establish the presence of red squirrels (*Sciurus vulgaris*) (Mortelliti and Boitani, 2008). Hair samples are analysed under the microscope to identify species with the aid of a reference collection or key (Teerink, 2003). Moreover, if the root of the hair is present, hairs can further be used for DNA analysis, allowing the identification of individuals in some cases (Sheehy *et al.*, 2018). Other indirect methods may involve simply noting indirect evidence based on observation alone (e.g., the presence of distinctly gnawed hazelnuts (Bright *et al.,* 1996)). Alternatively, comparatively more novel techniques can be used to ascertain species presence, including Conservation Detection Dogs (CDDs) being used to detect scat and living quarters (e.g., roosts and dens) (McKeague *et al.,* 2023), and sampling for environmental DNA (eDNA) in the soil and in waterbodies (Sales *et al.,* 2020; Broadhurst *et al.,* 2021).

1.2.1.4 Remote surveys

Over the past few decades, digital technology, particularly in the form of devices that generate and store data, are becoming increasingly widely used in surveying and monitoring of many species worldwide (Besson *et al.,* 2022). Such technological advances have enabled the development of a number of remote methods, whereby surveyors are able to gather data on their study species passively, often over extended time periods, without needing to be in the field directly (Rovero and Zimmermann, 2016). In the UK, several remote, technology-based techniques have been applied to mammals. Firstly, camera traps proved successful in studying medium and large terrestrial mammals, for example the Scottish Wildcat (*Felis silvestris silvestris*) (Kilshaw *et al.,* 2015), with more recent advances enabling the study of smaller and even arboreal taxa, including hazel dormouse (Mills *et al.,* 2016). Secondly, thermal imaging devices have proved valuable in surveying crepuscular and nocturnal mammals, for example elusive European hedgehogs (Bearman-Brown *et al.*, 2020). Finally, bioacoustic techniques, whereby recording devices are used to remotely capture mammal vocalisations, have been piloted for a range of terrestrial mammals from deer to shrews (Middleton *et al.,* 2023).

Although the initial cost of equipment required to undertake remote surveys can be substantial, they have the potential to provide much less labour intensive and cost-effective surveying while keeping ecological disturbance to a minimum and improving accuracy of data collected (Silveira *et al.,* 2003). Moreover, technological survey methods are predominantly non-invasive and can be widely undertaken without the need for species specific survey licences (Rovero and Zimmermann, 2016). This could prove invaluable for vulnerable species, which are otherwise challenging to study. Efficient and reliable analysis of the extensive datasets typically produced by remote methods remains a key area of research. Artificial Intelligence (AI) technologies continue to become more capable and accessible, unlocking the potential for automated identification of species present in camera trap (Falzon *et al.,* 2019) and thermal imaging (Keery, 2024) footage/images, and within acoustic recordings (Linhart *et al.,* 2022). The use of remote techniques to study bats specifically, is discussed in greater depth in section 1.3

Table 1.1: *A summary of mammal surveying and monitoring techniques undertaken within the field of applied ecology.*

Survey Type	Examples	Advantages	Disadvantages
OBSERVATIONAL	Point counts, transects, mapping	• Rapid form of faunal assessment • Uses sight/sound/smell – no need for trapping • Minimal ethical/legal considerations	• Individuals/species can easily be missed • Frequently underestimate population sizes
INTERVENTIONAL	Capture-mark-recapture, Longworth trapping, mist nets, harp traps	• Accurate species identification • Can provide a more in-depth assessment of population structure/health • Provides an opportunity to fit equipment for further remote surveys	• May require specialist licences/skills • Time consuming • Individuals may be trap-happy or trap-shy, impacting population estimates
INDIRECT	Hair tubes, footprint tunnels, feeding remains, scat, eDNA	• Enables data to be obtained for hard to observe species e.g. nocturnal/crepuscular • Effective in establishing species presence	• Limited ability to calculate species abundance – no live individuals seen. • Individual species can be difficult to decipher e.g. multiple footprints on footprint trap
REMOTE	Camera trapping, passive acoustic monitoring	• Non-destructive and non-invasive. • Time efficient – little surveyor input needed whilst the survey is underway • Ability to obtain records undetectable by direct observation or verify indirect evidence • Potential to study species presence/abundance over extended time periods/larger areas • Inclusion of night vision/infra-red thermography to study nocturnal species	• High equipment costs • Potential for technical errors/equipment failure • Camera resolution may limit which species can be detected with sufficient detail to be identified. • Considerable time investment needed to process footage and extract data

1.3 Bats in the United Kingdom

With >1,000 species globally, bats (Chiroptera) form the second largest order of mammals, accounting for approximately one fifth of all mammal species (Simmons, 2005). The Chiroptera are divided into two sub-orders: Megachiroptera (megabats), and Microchiroptera (microbats). Apart from Antarctica, Microchiroptera are found on every continent on Earth, with eighteen species present in the UK.

Bats are extremely sensitive to disturbance and land use change, and are thus considered to be particularly susceptible to the pressures faced by nature across the country, as outlined in section 1.1.3. Bats are afforded full legal protection under the Wildlife and Countryside Act (1981), and additional, more specific, protection under the Conservation of Habitats and Species Regulations (2017). However, six species are considered to be at risk from extirpation from the region according to the national red list issued by the Mammal Society (2020), with a further three species listed as data deficient. The species present in the UK, along with their conservation status and legal protections, are summarised in Table 1.2.

Table 1.2: *Bat species resident in the UK (conservation status: N/A=not assessed, DD=Data Deficient, LC=Least Concern, NT=Near Threatened, VU=Vulnerable, EN=Endangered, CR=Critically Endangered), (legal protection: WCA5=Wildlife and Countryside Act (1981) – Schedule 5, WCA6=schedule 6, CHSR=The Conservation of Habitats and Species Regulations (2017) – Schedule 2).*

Common name	Scientific name	Global Red List status (IUCN)	National Red List status (GB)	Native	Legal protection
Greater horseshoe bat	*Rhinolophus ferrumequinum*	LC	LC	✓	WCA5, WCA6, CHSR
Lesser horseshoe bat	*Rhinolophus hipposideros*	LC	LC	✓	WCA5, WCA6, CHSR
Alcathoe bat	*Myotis alcathoe*	DD	DD	✓	WCA5, WCA6, CHSR
Whiskered bat	*Myotis mystacinus*	LC	DD	✓	WCA5, WCA6, CHSR
Brandt’s bat	*Myotis brandtii*	LC	DD	✓	WCA5, WCA6, CHSR
Bechstein’s bat	*Myotis bechsteinii*	NT	LC	✓	WCA5, WCA6, CHSR
Daubenton’s bat	*Myotis daubentonii*	LC	LC	✓	WCA5, WCA6, CHSR
Greater mouse-eared bat	*Myotis myotis*	LC	CR	✓	WCA5, WCA6, CHSR
Natterer’s bat	*Myotis nattereri*	LC	LC	✓	WCA5, WCA6, CHSR
Serotine bat	*Eptesicus serotinus*	LC	VU	✓	WCA5, WCA6, CHSR
Leisler’s bat	*Nyctalus leisleri*	LC	NT	✓	WCA5, WCA6, CHSR
Noctule bat	*Nyctalus noctula*	LC	LC	✓	WCA5, WCA6, CHSR
Common pipistrelle bat	*Pipistrellus pipistrellus*	LC	LC	✓	WCA5, WCA6, CHSR
Soprano pipistrelle bat	*Pipistrellus pygmaeus*	LC	LC	✓	WCA5, WCA6, CHSR
Nathusius’ pipistrelle bat	*Pipistrellus nathusii*	LC	NT	✓	WCA5, WCA6, CHSR
Barbastelle bat	*Barbastella barbastellus*	NT	VU	✓	WCA5, WCA6, CHSR
Brown long-eared bat	*Plecotus auritus*	LC	LC	✓	WCA5, WCA6, CHSR
Grey long-eared bat	*Plecotus austriacus*	LC	EN	✓	WCA5, WCA6, CHSR

1.3.1 Non-acoustic bat survey methods

Microbats such as those present in the UK, are notoriously challenging to study (Barlow *et al.,* 2015), being small, volant, and nocturnal. The use of acoustic techniques to detect and record echolocation calls is often imperative. However, interventional trapping techniques, indirect signs, and Night Vision Aids (NVAs) can yield valuable insights, and are frequently used to supplement acoustic surveys. The principal non-acoustic bat survey techniques used in the UK, are discussed in more detail in the following sections.

1.3.1.1 Observational: Roost counts

Although low light levels hinder direct observational techniques, observation is important within roost surveys to establish presence of bats, and perform direct counts with the aid of artificial light, low-light videography, or Light Detection and Ranging (LIDAR) laser scanners (Azmy *et al.,* 2021), or to observe/count emerging and swarming bats at dusk and dawn (Warren and Witter, 2002; Collins, 2023). As disturbance to roosting bats is normally illegal, counts of individuals undertaken within roosts using torches and endoscopes must be carried out by licensed surveyors (Froidevaux *et al.,* 2020).

Bats can also be observed and counted directly on emerging from the roost at dusk, or when swarming prior to returning to the roost at dawn. Here, light levels are often sufficient for direct observation of earlier-emerging species, however, such surveys are typically supplemented by acoustic detectors (Collins, 2023). Unlike counts within the roost, these counts are not a licensed activity and can therefore be undertaken by a wider range of surveyors. Such counts form a key part of the methods undertaken largely by volunteers for the National Bat Monitoring Programme (NBMP), which contributes valuable monitoring data (Barlow *et al.,* 2015).

1.3.1.2 Interventional: Live trapping

Live trapping for bats was traditionally undertaken using mist nets, similar to those used to capture birds. However, since the invention of the harp trap in the 1950s, this has become the preferred choice for bats, as such traps are more efficient (Berry *et al.,* 2004) and limit any stress experienced by captured animals (Kunz and Kuta, 1988). Trapping bats and examining them in the hand, enables definitive species identification that cannot always be ascertained through bioacoustics (section 1.3.2) alone (Collins*,* 2023). Some species, such as those in the genus *Myotis* are inseparable when conducting visual roost counts (Barlow *et al.,* 2015), or using acoustics, therefore, trapping may be necessary where rarer species within the genus are suspected to be present. Furthermore, as with terrestrial mammals, live trapping bats allows for the collection of biometric data (Walters *et al.,* 2013) or tissue samples for genetic studies (Rossiter *et al.,* 2002). Trapping of bats, however, is a licenced activity, and can only be carried out by trained surveyors.

1.3.1.3 Indirect: Scat and DNA

In addition to non-volant mammals (outlined in section 1.2.1.3 above), indirect surveys are also valuable in surveying bats. The presence of scat/droppings is an effective means of establishing the presence of roosting bats, and are frequently encountered during Preliminary Roost Assessments (PRAs) of buildings and potential roosting structures (Froidevaux *et al.,* 2020). Moreover, bat droppings can be sent for DNA analysis in order to determine the species present, which can be advantageous for species such as those in the genus *Myotis*, which are challenging to identify to species level in acoustic surveys (Collins, 2023).

1.3.1.4 Remote: Night Vision Aids and camera traps

Night Vision Aids (NVAs), based on either thermal imaging (mid and long wavelengths) or infrared thermography (IRT) (short wavelength) technology, take precise measurements of infrared radiation to determine surface temperature (Mccafferty, 2007). NVAs display the observed variations in temperature into a digital signal. Data output is in the form of a thermogram, generated by either the device itself or a computer from the signal, to give a visual representation of the observed radiation (Fawcett-Williams, 2019). The application of NVAs in the fields of ecology and zoology, has enabled valuable insights into the activity and health of both bats (Hristov *et al.,* 2008), and an array of other mammal taxa, including burrowing species (Boonstra *et al.,* 1994), terrestrial mammals (Dunn *et al.,* 2002) and large sea mammals (Perryman *et al.,* 1999). Cameras can be used terrestrially, both at close range and from a distance, with larger mammals successfully detected from a distance upwards of 1000m (McCafferty, 2007) and aerially, with even early aerial studies being able to count groups of large mammals from altitudes of 300m in uncluttered environments (Graves *et al.,* 1972). Furthermore, NVAs can either be used in live view, to take user defined photographs (Goodenough *et al.,* 2018), or record video footage for post hoc analysis (Hristov *et al.,* 2008).

NVAs have huge potential to assist in both active and remote monitoring of mammal species, with a key advantage being able to observe diurnal and nocturnal species, including bats, that are otherwise challenging to observe (Cilulko *et al.,* 2013). Standard methods to study such animals are susceptible to visibility bias, arising from reduced detection ability as levels of visible light decline (Havens and Sharp, 2016). However, the costs involved in purchasing or hiring equipment, and the level of skill and knowledge required to successfully carry out surveys, remain significant barriers to the widespread use of the technology within ecology. Despite the large initial costs when used as a standalone method, thermal imaging cameras can effectively replace one or more surveyors, reducing the amount of night-time working required to carry out surveys (Fawcett-Williams, 2019).

Although not previously widely used, the ecological application of thermal imaging in the UK is growing, primarily owing to its ability to aid in surveying and studying bats (Figure 1.3), both in activity surveys, and when locating roosts in trees and buildings (Fawcett-Williams, 2019).

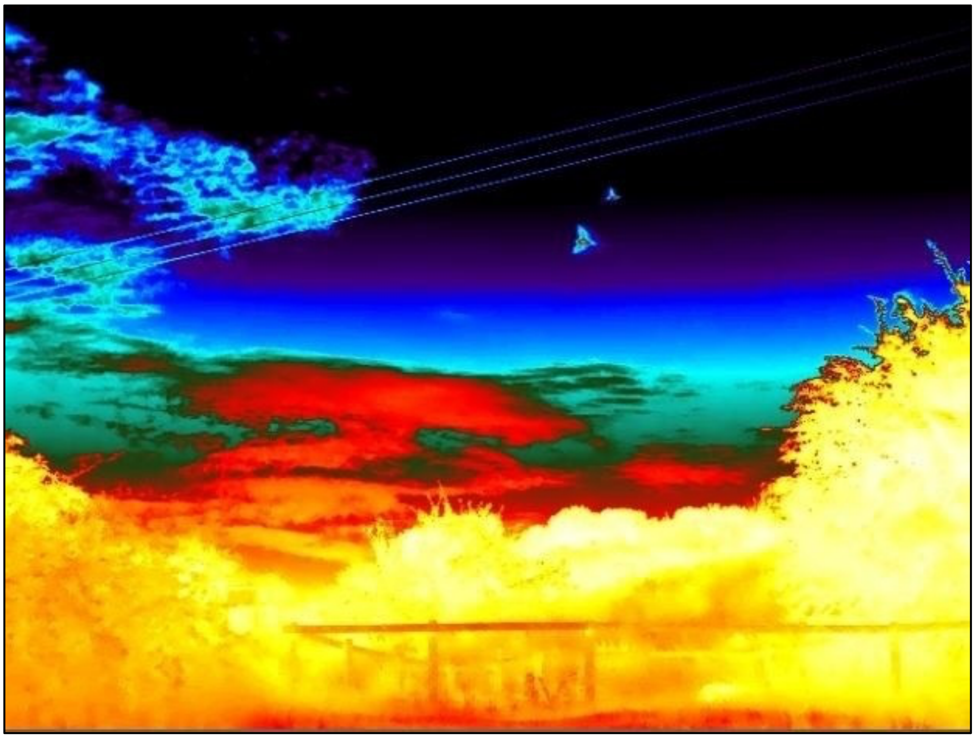


Figure 1.3: *Bats in flight, observed through a thermal imaging camera (Fawcett-Williams, 2019)*

Ensuring accurate species identification from NVA footage remains an ongoing challenge, both in the case of large mammals, especially when counted from a distance (Goodenough *et al.,* 2018) and smaller mammals, including bats (Darras *et al.,* 2022). In the case of bat surveys, NVAs can be used in tandem with acoustic bat detectors, and bioacoustics can be used to verify the species of bats present within the thermal imaging footage (Collins, 2023). The Bat Conservation Trust has recently integrated protocols for the use of NVAs into their bat survey guidelines (Collins, 2023), with further guidelines for a broader range of species in development (Inside Ecology, 2018).

Although standard ‘trail camera’ style camera traps are not typically suited to capturing images of fast-moving bats, Rydell and Russo (2015) successfully piloted a custom, remote-triggered camera set up to capture high quality images of bats drinking. The species richness recorded was comparable to that of mist netting, and highlighted the value of such techniques in recording species that are typically infrequently recorded in acoustic surveys as a result of minimal echolocation.

1.3.2 Acoustic bat survey methods

Bioacoustic monitoring is a rapidly developing field, offering the potential to non-invasively gain insights into the ecology of rare and cryptic species (Teixeira *et al.*, 2019), in addition to devising cost effective and reliable monitoring schemes to study species populations and communities at scale (Gibb *et al.*, 2019). Analysis of animal sound has been applied to biological studies since as early as the 18th Century, with the earliest research focusing on identifying birdsong (Rose *et al.*, 2022). The use of mammal sound in scientific research soon followed, with ultrasound having been used in the study of bats since the 1930s, following the work of Galambos and Griffin (1942) examining echolocation. At present, a range of weatherproof bioacoustic sensors are used, including sound recorders, ultrasonic detectors, and hydrophones, often on an automated basis, to gather sound data from animals and their environment (Gibb *et al.*, 2019). In addition to bats (Sugai *et al.,* 2019), this technique has been successfully applied to the study of birds (Pérez-Granados, 2021), amphibians (Desjonquères, 2020), Orthoptera (Newson *et al.*, 2017), and both marine (Mellinger *et al.,* 2007) and terrestrial mammals (Enari *et al.*, 2019). In the UK, bioacoustic monitoring is frequently used in the surveying of bats (Collins, 2023), but has additionally been piloted for birds (Abrahams, 2018), and small terrestrial mammals (Newson *et al.,* 2020).

As a taxonomic group that is otherwise incredibly difficult to observe, acoustic monitoring of ultrasonic bat calls has revolutionised bat ecology. Initially, ultrasonic bat calls could only be captured by heterodyne bat detectors. This technology was first tested in the 1950s, with the first commercial detectors becoming available in 1963 (Zamora-Gutierrez *et al.*, 2021). These detectors require manual tuning to the desired frequency, and detected sound is converted into lower frequency within human hearing range, with an output in the form of audible clicks. The ability to listen to bat echolocation calls provided valuable insights into species identification, ecology, and their spatiotemporal distribution (Russ, 2012). The technology developed to enable bat calls to be recorded, initially onto cassette tape, for further post hoc analysis. Handheld units continued to advance, with modern units offering full spectrum recording capabilities, inclusive of visual spectrograms, directly onto memory cards. The technology to enable Passive Acoustic Monitoring (PAM) of bats is a more recent development, starting with memory efficient zero crossing and frequency division detectors in the 1980s (Corben, 2004). Full spectrum, passive bat detectors were introduced to the market even more recently, with their first use documented in 2009 (Zamora-Gutierrez *et al.*, 2021). Passive detectors enabled bat surveys to be conducted over full nights and over several consecutive nights, increasing the temporal sampling range compared to transect surveys, carried out by surveyors with handheld detectors, during a set time period, on a given night (Goodenough *et al.,* 2015).

Bioacoustics shares many of the same key advantages as other remote methods (e.g., camera trapping), in that it can be used to monitor populations at scale, whilst being non-invasive and automated (with the exception of transect bat surveys). However, whilst identifying individual species from camera trap images/videos relies on animals entering the camera's field of view, microphones are typically omnidirectional and can capture sounds that carry across the landscape (Larsen *et al.*, 2022).

Species classification of sound recordings remains a key challenge facing wider application of bioacoustics, as post-hoc analysis of sound recordings can be time consuming and fraught with inaccuracies (Barré *et al.*, 2019). Advances in machine learning and AI have begun to offer algorithms for automating analysis as the pool of training data available widens (Stowell, 2022), but at present much uncertainty surrounds their reliability (Mac Aodha *et al.*, 2018; Barré *et al.*, 2019). Moreover, financial costs incurred in the purchase of both hardware and analysis software still represent a barrier to the accessibility and scalability of bioacoustic methods. Despite falling costs, commercial acoustic detectors remain substantially more expensive than equivalent camera traps (Gibb *et al.*, 2019). However, the recent development of open-source acoustic loggers, has provided opportunities to access bioacoustic monitoring at a much lower price point (Hill *et al.,* 2017) (Figure 1.4).

Figure 1.4*: A commercial (bottom) and open source (top) acoustic detector deployed in the field, targeting bats.*

1.4 Research Outline

The research contained in this thesis investigates the effectiveness of passive acoustic techniques to survey and monitor British bats in field conditions. Although protocols for open-source acoustic loggers have been piloted by researchers and some are now becoming more widely used, many have yet to be empirically tested. Research questions remain regarding their performance when tested against commercial detectors, variation between different habitats, and how the quality of the data impacts analysis. Moreover, regardless of the devices used, there remain gaps in knowledge around the impacts of abiotic factors on acoustic bat surveys, and how best to optimise the methodology based on the aims of the survey.

The research focuses on PAM for bats, considering the influence of abiotic variables on data collection, comparing data from different methods (walked transects versus automated fixed-point) and detector types (cost; data compression), and the analysis of acoustic data including use of automatic classifiers. Overall, therefore, this research will empirically test, critique and evaluate the relative benefits and caveats of methods used in the field for collecting optimal monitoring data, how they contribute to furthering knowledge of species ecology and behaviour, and how they can be effectively applied in ecological research and conservation practice. The **importance and originality of this research** centres on developing, testing, refining and improving survey techniques to enable the collection of robust data in quantity and as cost-effectively as possible.

This thesis is modular, with each data chapter concerning each specific research aim. These are set out in **section 1.4.1** with **section 1.4.2** introducing the research sites and data types used throughout the research and **section 1.4.3** detailing publications arising from this work completed during PhD study.

1.4.1 Thesis structure

This research comprises several linked studies on different focal mammal species and/or guilds, with technological approaches to ecological surveying being the linking theme. The thesis is divided into seven chapters. This chapter (**Chapter One**) has introduced the scientific and legislative requirements for biological surveying and monitoring, both globally and in the UK. It has also summarised the methods used for surveying and monitoring, both generally and with emphasis on those used widely for mammals in the UK, along with their strengths and caveats. Chapters Two to Five focus on the use of bioacoustics technology to survey and monitor bats. **Chapter Two** tests the influence of spatiotemporal and abiotic factors on bat activity recorded using passive acoustic monitoring and examines the benefits and caveats of this methodology in practice. **Chapter Three** evaluates the benefits and caveats associated with two widely used acoustic bat survey techniques; passive fixed-point monitoring and walked transect surveys. **Chapter Four** focuses on addressing some of the knowledge gaps associated with designing and financing passive bat surveys in relation to the type of detectors used and the number deployed (and how this differs according to habitat). The final data chapter, **Chapter Five** examines the analysis of the data collected in Chapter Four, comparing the performance of a suite of automated classifiers on data collected using different detectors. **Chapter Six** summarizes the key findings of the preceding data chapters, considers their implications for applied ecological practice, and suggests potential avenues for future research.

1.4.2 Thesis research sites and data types

The research is primarily based on primary data collected from sites in Gloucestershire and Worcestershire including parkland at Croome managed by the National Trust (52°05’48”N , 002°10’13”W) and private farms/estates. Additional secondary data were used in two data chapters (Chapters Two and Three). These data were collected from sites across the south of England as being representative of sites typically encountered in ecological consultancy settings. The author, who at the time was a seasonal fieldworker for an ecological consultancy company, was involved in equipment set-up and carrying out surveys at the majority of these sites, and undertook all acoustic data analysis before commencing PhD studies. These data, which were essentially secondary data in the context of the PhD despite having been collected by the author, were used with consent from the owner, and all field sites were accessed with full permission from the landowner/manager. The locations of all field sites are shown in Figure 1.5. The acoustic data collected and used throughout this research were collected exclusively under field conditions. Axiomatically, therefore, classifications, whether manual or determined by automated classifiers, could not be verified and are thus subject to error despite careful use of industry standard methods. Lack of ‘ground truthing’ bioacoustic data is a challenge faced by all practitioners undertaking bat surveys, especially where data are collected passively, and thus the level of uncertainty inherent in the data used in this PhD is representative of real-world data. This is acknowledged openly throughout this research, with acoustic data analysis workflows incorporating automated classification forming the focus of **Chapter Five**. For consistency, throughout this research the term ‘pass’ is used to denote an acoustic recording containing bat vocalisations, and ‘call’ to denote an individual bat vocalisation.

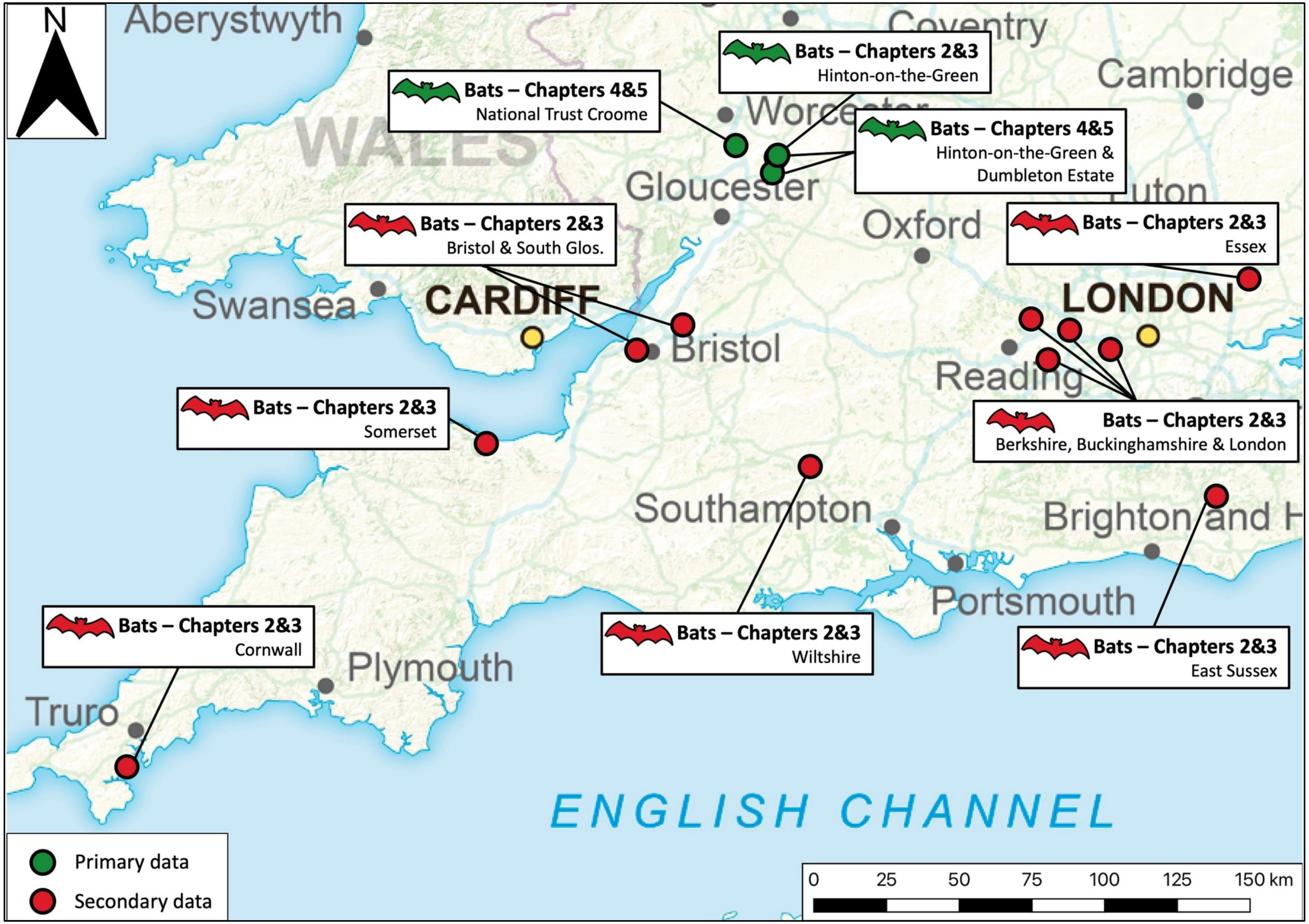


Figure 1.5: *Locations of the field sites within the south of the UK used for data collection according to thesis chapter. The secondary data were collected in a development context and exact locations are not appropriate to disclose, therefore, the locations shown are approximated.*

1.4.3 Publications arising from this PhD

Chapters Two and Three have been published in peer-reviewed journals during PhD study in 2020 and 2021, respectively. The material has been reformatted for inclusion in this thesis to provide consistency across the chapters and align with the University of Gloucestershire's thesis requirements, and additional summaries have been written at the start and end of each chapter to set the chapters within the thesis context, but have not otherwise been amended. Chapter Four was presented in-progress as a poster at the British Ecological Society Annual Meeting in 2023. Content from Chapters Four and Five is intended to be published in peer-reviewed journals in due course.

CHAPTER TWO: The influence of abiotic and spatiotemporal factors on the detectability of bats in passive acoustic surveys

Full moon over Bredon Hill – July 2021

Bat activity surveys are essential in the contexts of scientific research, conservation, assessment of ecosystem health, monitoring progress towards sustainable development goals, and legislative compliance in development and infrastructure construction. However, environmental conditions have the potential to influence bat activity and, in turn, their detectability in acoustic surveys. Here, 3,242 hours of acoustic survey data from 323 nights of bat monitoring at 14 sites over a 4-year period, are used to explore the influence of spatiotemporal factors, lunar phase, and weather conditions on bat activity.

Publications arising from this chapter:

Perks, S. J. and Goodenough A.E. (2020) 'Abiotic and spatiotemporal factors affect activity of European bat species and have implications for detectability of acoustic surveys'. *Wildlife Biology,* 2020(2), pp.1-8.

The material has been reformatted for inclusion in this thesis to provide consistency across the chapters and align with the University of Gloucestershire's thesis requirements, with summaries at the start and end of each chapter to set the chapters within the thesis context, but have not otherwise been amended. The data used for this chapter are explained in relation to the PhD process in Section 1.4.2.

2.1 Introduction

Bats (Chiroptera) are the second largest mammalian order with 1,100 species worldwide (Kunz and Lumsden, 2003; Simmons *et al.,* 2008). They have diversified over the past 52 million years to inhabit numerous habitats and utilise a range of food sources and foraging techniques (Patterson *et al.,* 2003). Insectivorous species, such as those found in Europe, are nocturnal and typically use echolocation to catch prey by aerial hawking (e.g. *Pipistrellus*) or from the surface of water (e.g. *Myotis*), as well as for navigation.

Although the broad-scale biogeographical ranges of most species are widely documented, and habitat requirements are reasonably well understood, at least for roost sites, there remain considerable gaps in knowledge regarding the factors that influence local-scale foraging activity both spatially and temporally (Barclay, 1991; Walsh and Harris, 1996a; 1996b; Erickson and West, 2002; Ciechanowski *et al.*, 2007). Given that acoustic bat surveys depend on detecting echolocation during foraging (and when bats are commuting between roost and feeding grounds), understanding the spatiotemporal and abiotic factors that influence detection is key to obtaining robust survey data (Hayes, 1997). This is of particular importance given the use of bat surveys in conservation contexts (Barlow *et al.,* 2015) and to quantify ecosystem health (Jones *et al.*, 2009), as well as when surveys of legally-protected species are a statutory obligation in infrastructure and development planning (Collins, 2016). In Europe, bats are protected under the European Protected Species licensing framework to ensure compliance with the EC Habitats Directive (92/43/EEC), with countries implementing this via their own national legislation (e.g. Wildlife and Countryside Act 1981 and Conservation of Habitats and Species Regulations 2010 in the UK).

Bats are not spatially uniform in occurrence. Habitat suitability for foraging is largely determined by insect prevalence and foraging opportunities. High-quality foraging habitat includes broadleaf woodland, water and linear vegetation corridors (Walsh and Harris, 1996a) whereas arable land and improved grassland are generally less favoured (Walsh and Harris, 1996b). Some species have particular habitat requirements for foraging. For example, Daubenton's bats (*Myotis daubentonii*) forage over water (Rydell *et al.,* 1999, Russ, 2012), greater horseshoe bats (*Rhinolophus ferrumequinum*) are often associated with cattle (Ransome, 1996), while brown long-eared bats (*Plecotus auritus*) depend on areas where there is suitable vegetation for gleaning (Rydell, 1989a, Anderson and Racey, 1991). Distribution of foraging sites also fundamentally depends on the location of roost sites and the distance individuals commute to their feeding grounds. For British bats, commuting distance can range from as little as <1km (e.g. Bechstein's bat *Myotis bechsteinii*) to up to 14km (e.g. Leisler's bat *Nyctalus leisleri*) (Hundt, 2012).

Temporal factors can also affect bat foraging and feeding behaviour, and thus their detection on bat surveys. Seasonality affects the presence of foraging temperate bats as they typically hibernate overwinter or migrate to other areas. Females are most active in early summer due to the high energy demands of pregnancy and lactation (Racey and Speakman, 1987, Ciechanowski *et al.*, 2007). Late in the summer, young bats increase the size of the population foraging (Erickson and West, 2002). This, together with the fact that adults often spend more time away from the roost after weaning, typically increases observed activity levels from late July to September (Maier, 1992). Different bat species also have different circadian rhythms and emerge at different times post-sunset (Jones and Rydell, 1994) both relative to one another and potentially also in response to night duration.

Abiotic factors also have the potential to affect bat activity and thus detectability in acoustic surveys. Light levels, including moonlight duration and intensity, could be especially important. A global meta-analysis by Saldaña-Vazquez and Munguia-Rosas (2013) combined results of multiple studies to research the effects of moonlight on bats. Their analyses found a significant negative relationship between moonlight intensity and levels of bat activity, indicating that some species were lunar phobic. The strongest effect was found in tropical frugivorous species, for example Neotropical fruit bats (*Artibeus*) (Morrison, 1978), and in Neotropical species that forage over water, such as the greater bulldog bat (*Noctilio leporinus*) (Börk, 2006). The limited research on the effect of moonlight on insectivorous bats in at higher latitudes is less conclusive. Negraeff and Brigham (1995) found no indication of lunar phobic behaviour based on work in Canada. This is possibly because bats at higher latitudes have lower nocturnal predation risk than those in the tropics (Karlsson *et al.*, 2002). However, even if predation pressures in temperate bats are low, there remains the potential for impacts on emergence times and bat activity patterns, both spatially and temporally (Lima and O'Keefe, 2013). In the Pacific northwest, Erickson and West (2002) suggested that variation in insectivorous bat activity might relate to moonlight intensity but did not explicitly test this hypothesis. The phenomenon has not been extensively studied for European species. Weather conditions can also influence bat activity. As small, endothermic mammals, bats use a large proportion of their energy to thermoregulate (Lewis, 1993). Lower air temperatures and rainfall require the bats to utilise more energy to maintain suitable body temperature, such that foraging in these conditions may be unfavourable. Insect prey may also be less abundant in poor weather (Racey and Speakman, 1987). Although weather conditions can cause bat activity to differ substantially on consecutive nights (Hayes, 1997), it does not account for all within- or between-night variation. Moreover, a study by Erickson and West (2002) showed that rain and temperatures accounted for 37% of the variation in insectivorous bat activity.

Here we explore the influence of spatiotemporal and abiotic variables on bat activity using data from automated monitoring from 14 sites over a four-year period (3,242 survey hours over 323 nights). This encompassed both overall bat activity, as well as species- and genus-specific trends in relation to site, nocturnal emergence patterns, duration of moonlight, and weather variables. Understanding the effect of these multifaceted and interlinked factors on the activity of different bat species is a vital step in ultimately developing maximally effective survey protocols, which, in turn, will improve the reliability of conservation and planning decisions made using survey data.

2.2 Methods

2.2.1 Data collection

Data were collected between 2014 and 2017 across 14 sites in the south of England. The sites represented a range of habitat types. Most of the sites (n = 9) comprised agricultural land with dividing hedgerows. The remaining sites were rural sites with heterogeneous habitat including well established treelines, woodland, and/or watercourses (n = 3), or were green spaces within urban areas (n = 2). An Anabat Express bat detector unit (Titley Scientific, Ballina, Australia) was deployed at the study sites in rotation to record data across the sites for a total of 323 nights between sunset and sunrise. Deployment and positioning was carried out in a consistent manner at all sites with units mounted about 1.75 m above the ground adjacent to a suitable hedgerow or treeline to ensure detection of commuting and foraging activity along linear features. The units recorded data directly onto an SD card. Post fieldwork, all data from the bat detectors were downloaded for sonogram analysis. The analysis was performed in AnalookW software (Titley Scientific, Ballina, Australia) developed specifically for Anabat detectors. Initially recordings were processed on a night-by-night basis and then data were subdivided into hourly units relative to sunset. This gave a total of 3,424 hours of survey data over 323 nights, with each night of data being from a single site (i.e. sites were sampled independently not concurrently). Survey effort (number of survey nights per month and per site) is given in Table S1. Species identification was carried out by assessment of the range and peak frequency, together with shape of each sonogram in terms of pitch and amplitude over time (Russ, 2012).

Data relating to temporal and abiotic factors were collected for use as explanatory factors in statistical modelling. The variables are explained in Table 1. Sunset, sunrise and lunar data were taken from Time and Date AS (www.timeanddate.com). Weather data were obtained via BBC (www.bbc.co.uk/weather) for the nearest town or using Time and Date AS using the nearest available weather station.

2.2.2 Statistical analysis

To examine whether there were significant deviations from a uniform distribution of bat passes throughout the night, Kolmogorov-Smirnov two-sample tests were used as per Milne *et al.* (2005) for Australian bat species.

To explore the influence of spatiotemporal and abiotic factors on bat activity, Generalised Linear Mixed Models (GLMMs) were constructed. Models were developed for overall bat activity (total number of bat passes per hour regardless of species: n = 3424) and also the activity of each of the four most prevalent species/genus groups; common pipistrelle (*Pipistrellus pipistrellus*), soprano pipistrelle (*Pipistrellus pygmaeus*), *Myotis* spp. and *Nyctalus* spp. (specific bat passes per hour: n = 3424). In all cases, a full model was constructed whereby the factors listed in Table 2.1 were entered as continuous fixed factors (hour post sunset, temperature, wind speed) or categorical fixed factors (illumination, rainfall). Two random factors were also entered: site (coded 1-14 with no underlying rationale for the order and thus entered as a categorical random factor) and month (April to October). Because the dependent variable of bat activity (total or species-specific) used count data (number of bat passes per hour), a Poisson distribution was used with a log link function: this gave the lowest Akaike's Information Criterion (AIC) value (Akaike, 1971) relative to other options for count data of Poisson with identity link, negative binomial with log link, and negative binomial with identity link. For the random factors, a scaled identity covariance type was specified as this covariance structure was associated with the lowest AIC score. To ascertain the effect of the fixed factors in explaining bat activity, marginal r^2 was calculated. To ascertain the effect of both fixed and random factors, conditional r^2 was calculated. The relative importance of the random factors can be inferred from the difference between conditional and marginal r^2.

Table 2.1: *Temporal and abiotic data collected for use in statistical analyses. All data were hourly (n = 3,242)*

Name	**Details**	**Data type**
Time post sunset	Bat survey hour relative to sunset, whereby 1 was the first hour post sunset, 2 was the second hour post sunset etc. The number of full survey hours varied between 8 and 14 depending on the length of night, with a modal duration of 10 hrs.	Continuous
Illumination	Illumination based on moon presence taking into account moonrise and moonset times, as well as cloud cover. Note that depending on the lunar phase, on some nights moonrise was at/before sunset (such that potential moonlight was at the start of the night) but that on other nights moonrise was after sunset (such that there was no potential moonlight for the first part of the night). The moon was potentially present for part of the night on all survey nights. Lunar timing information was combined with hourly cloud cover to give a ranking scale whereby: 0 = no illumination (no moon present for any part of the survey hour and/or overcast skies; 56.9% of cases); 0.5 = partial illumination (moon present for part of the hour only and/or patchy cloud; 30.3% of cases); and 1 = full illumination (moon present for full survey hour and clear skies; 12.8% of cases). None of the 14 survey sites was subject to artificial illumination.	Categorical
Temperature	Measured in degrees Celsius (°C). Min = 1°C; max = 27°C; mean = 13.2°C	Continuous
Wind speed	Average miles per hour (mph). Min = 0 mph, max = 30 mph; mean = 7 mph.	Continuous
Rainfall	Ranking scale of: 1 = none (63.4% of cases), 2 = intermittent and/or light (18.6% of cases) , 3 = persistent and/or heavy (18.0% of cases).	Categorical

Once full models had been computed for bat activity, reduced models were tested by dropping different combinations of fixed factors to establish whether the full model was optimal or whether a simpler model might better balance explanatory power and parsimony. Competing models were compared using delta (Δ) AIC on the basis that models with ΔAIC ≤ 2 had essentially have the same support and models with ΔAIC of 3-4 had strong support; models with AIC ≥ 5 were considered to have substantially less support and were discounted (Burnham and Anderson, 2002). In all cases the full model was optimal and hence only full models are reported. All statistical analysis was carried out in IBM SPSS Statistics (version 24).

2.3 Results

In total, 52,628 bat passes were recorded over 3,242 survey hours between sunset and sunrise across 323 nights. The majority of passes were: common pipistrelle = 29,657, soprano pipistrelle = 13,034, *Myotis* spp. = 7,146 and *Nyctalus* spp. = 831. The remaining 1,960 passes were split between serotine (*Eptesicus serotinus*), brown long-eared (*Plecotus auritus*), greater horseshoe (*Rhinolophus ferrumequinum*), lesser horseshoe (*Rhinolophus hipposideros*), barbastelle (*Barbastella barbastellus*) bats: these species were encountered too infrequently for meaningful statistical analysis. As common pipistrelle or soprano pipistrelle overlap in call frequency, there were also some *Pipistrellus* calls between 50 and 51 kHz that could not be definitively identified. As per Russ (2012), we classified *Pipistrellus* calls with a maximum energy (peak) frequency <50.2 kHz as common pipistrelle and *Pipistrellus* calls with a maximum energy (peak) frequency >50.6 kHz as soprano pipistrelle, while those between 50.2 and 50.6 were discounted from analysis unless they were part of a series of calls that had already been identified definitively to species level. The mean number of bat passes per hour for total activity and the four specific taxa are given in Table S2.1 on a per month, per site basis.

2.3.1 Temporal distribution

Two sample Kolmogorov-Smirnov tests demonstrated that passes of all species/genera differed significantly from a uniform distribution ($P \leq 0.046$ in all cases). The majority of bat passes, regardless of species, occurred in the first hour post sunset and then decreased as the night progressed, with a small increase in activity towards dawn that made the overall activity distribution slightly bimodal (Figure 2.1a). Both pipistrelle species also showed higher activity in the hours immediately following sunset (Figure 2.1b-c), however, soprano pipistrelle alone showed an additional peak in activity towards dawn (Figure 2.1c). The temporal distribution of *Nyctalus* passes (Figure 2.1d) was the most sporadic, with higher peaks in activity occurring haphazardly throughout the night. However, this species was recorded much less frequently than pipistrelle species or *Myotis* spp. and thus the variability in passes, as shown by the standard error bars, was considerably higher. *Myotis* passes were relatively infrequent in the first hour post sunset (Figure 2.1e), but increased thereafter, peaking in the third hour post sunset and then decreasing, with a small peak in activity prior to dawn.

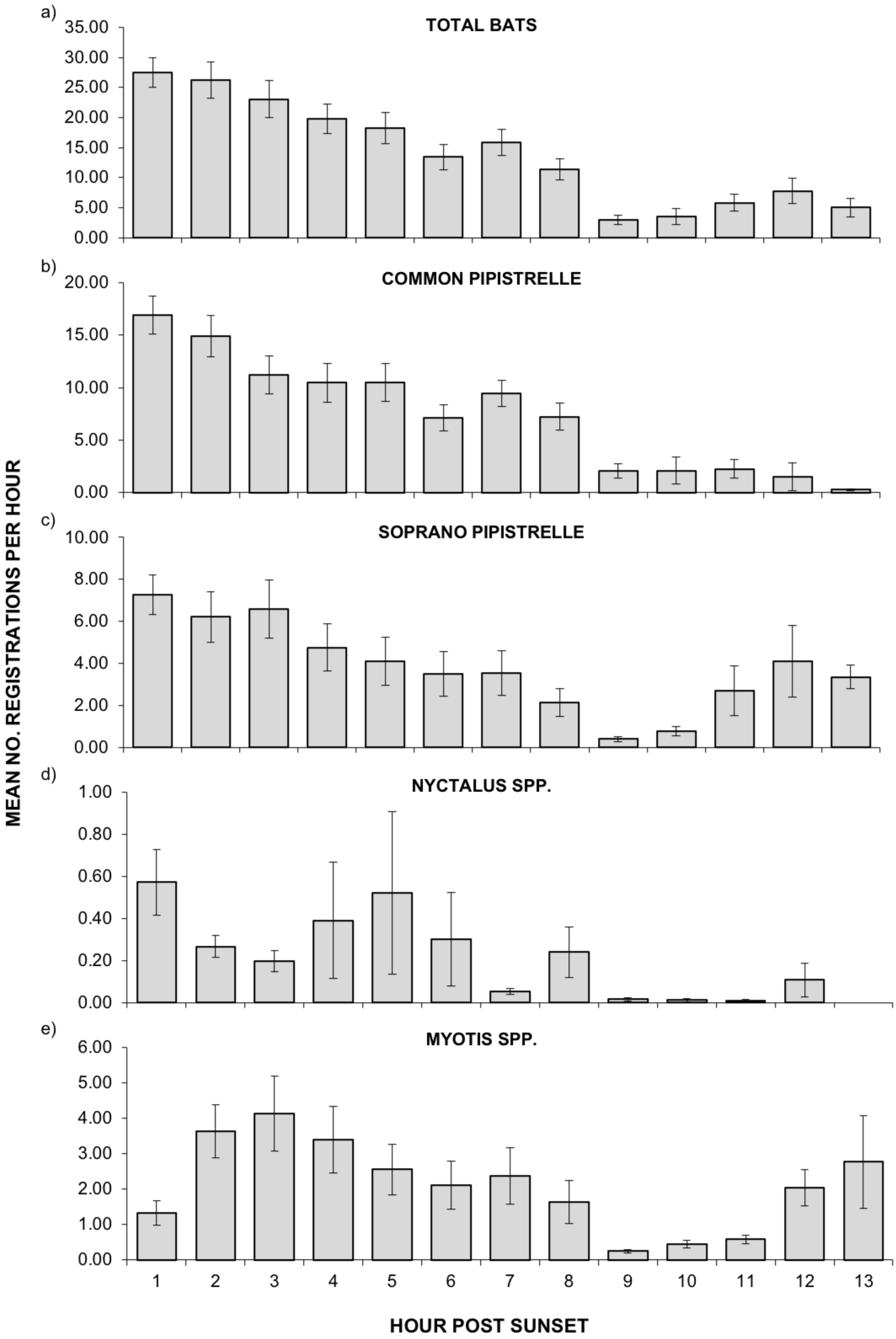


***Figure 2.1:** Mean number of passes in each hour post sunset for total bats and within species/genus. Error bars show SEM (±1se).*

2.3.2 Spatiotemporal and abiotic influences on bat activity

Hour post sunset, temperature, wind speed, illumination and rainfall all had a significant effect on overall bat activity (bat passes per hour regardless of species) and the activity of the four focal taxa; the single exception was temperature for soprano pipistrelle, which was not significant (Table 2.2).

Hour post sunset was significantly negatively related to overall bat activity: bat passes per hour decreased by 0.147 per hour (± 0.002 SEM) as the night progressed. Similar negative relationships were seen for activity in all four specific taxa, with gradients varying between -0.051 ± 0.017 (*Nyctalus*) and -0.176 ± 0.004 (common pipistrelle). These relationships largely reflect the temporal pattern of bat activity decreasing throughout the night (Figure 2.1), with the shallower gradients being for species with a notable pre-dawn peak in activity (soprano pipistrelle) or species whose activity was sporadic throughout the night (*Nyctalus*).

The relationship between temperature and overall bat activity was weakly positive, with bat activity increasing by 0.015 bat passes per hour (± 0.002 SEM) for each °C increase in temperature. A similar pattern was seen for common pipistrelle (0.022 ± 0.003), with a stronger positive relationship being found for *Nyctalus* (0.383 ± 0.017). A weak negative relationship was observed between temperature and *Myotis* (-0.029 ± 0.006). There was a significant positive relationship between bat activity and wind speed for overall bat activity and for activity of common pipistrelle, soprano pipistrelle and *Myotis*: all relationships were comparatively similar with bat passes per hour increasing by ~0.067 (± ~0.002 SEM) for each additional mile per hour in wind speed. The exception was *Nyctalus* where bat passes decreased by 0.111 (± 0.011 SEM) for each additional mph in wind speed.

Table 2.2: *Generalized linear mixed models exploring the influence of temporal and abiotic factors on overall bat activity (bat passes per hour) and activity for four specific taxa (n = 3,242 survey hours across a total of 323 nights and 14 sites). The models used a Poisson distribution with a log link function. For the three continuous fixed factors – hour post sunset, temperature, and wind speed – the gradient of any significant relationship with bat activity is given with the standard error below in parentheses. For the two fixed factors – illumination and rainfall – the estimated marginal mean (EMM) is given with the standard error below in parentheses. In all models, site (n = 14) and month (n = 7) were included as random factors. The importance of the fixed factors in explaining bat activity can be assessed using the marginal r squared value (r^2_m), while the additional importance of the random factors can be assessed using the difference between r^2_m and the conditional r squared value (r^2_c). For more details of the variables, including the categories for illumination and rainfall, please see Table 2.1.*

	Overall model		Hour post sunset			Temperature			Wind speed			Illumination					Rainfall				
	r^2_m	r^2_c	F	P	Gradient	F	P	Gradient	F	P	Gradient	F	P	EMM None	EMM Partial	EMM Full	F	P	EMM None	EMM Light	EMM Heavy
Total Activity	0.369	0.474	6798	<0.001	-0.147 (0.002)	61	<0.001	0.015 (0.002)	2822	<0.001	0.067 (0.001)	208	<0.001	4.838 (0.054)	4.002 (0.044)	2.934 (0.044)	393	<0.001	5.668 (0.063)	5.114 (0.057)	2.628 (0.029)
Common Pipistrelle	0.286	0.347	2986	<0.001	-0.176 (0.002)	78	<0.001	0.022 (0.003)	2402	<0.001	0.071 (0.002)	18	<0.001	2.390 (0.030)	2.222 (0.032)	2.203 (0.032)	71	<0.001	2.791 (0.040)	2.614 (0.038)	1.606 (0.023)
Soprano Pipistrelle	0.423	0.478	2406	<0.001	-0.133 (0.004)	1	0.592	N/A	589	<0.001	0.065 (0.003)	128	<0.001	0.214 (0.006)	0.163 (0.005)	0.127 (0.004)	314	<0.001	0.280 (0.009)	0.257 (0.009)	0.062 (0.002)
Myotis spp.	0.282	0.513	962	<0.001	-0.133 (0.005)	20	<0.001	-0.029 (0.006)	322	<0.001	0.067 (0.004)	57	<0.001	0.131 (0.005)	0.096 (0.003)	0.120 (0.004)	29	<0.001	0.139 (0.005)	0.109 (0.004)	0.100 (0.004)
Nyctalus spp.	0.354	0.357	11	0	-0.051 (0.015)	518	<0.001	0.383 (0.017)	111	<0.001	-0.111 (0.011)	4	0.020	0.055 (0.002)	0.068 (0.003)	0.053 (0.002)	13	<0.001	0.117 (0.005)	0.043 (0.002)	0.040 (0.002)

Bat activity, both overall and for each of the four focal taxa, was significantly lower in heavy rain. In the case of overall activity, bat passes per hour were fairly consistent in dry conditions and in light rain (5.668 and 5.114 bat passes per hour, respectively), but decreased substantially in heavy rain (2.628 bat passes per hour). This notable decrease in activity in heavy rain also occurred for both pipistrelle species. In contrast, *Myotis* declined linearly as rain intensified, while *Nyctalus* activity dropped substantially between dry conditions and light rain with activity levels in light and heavy rain being approximately equal.

The impact of moon illumination on bat activity was more varied between taxa. Overall bat activity was significantly lower in instances of full illumination (2.934 bat passes per hour), than in partial or no illumination (4.002 and 4.838, respectively). The effect of moonlight on activity of both common and soprano pipistrelle was more gradual but remained negative. The effect of moonlight on *Nyctalus* and *Myotis* bats was less clear: partial illumination was associated with peak activity of *Nyctalus* and lowest activity of *Myotis*.

The random factors of site and month increased the amount of variance in total bat activity explained by the GLMM ($r^2_m = 0.369$ versus $r^2_c = 0.474$; a difference of 0.105). This demonstrates the importance of site-specific factors and seasonality on overall bat activity. For specific taxa, site and month varied in how much they influenced bat activity, with the difference between conditional and marginal r^2 values being negligible for *Nyctalus* (0.003) and low for soprano and common pipistrelle (0.055 and 0.061, respectively), but substantially higher for *Myotis* (0.231). It is important to note that the fixed factors (hour post sunset, temperature, wind speed, illumination and rainfall) together accounted for substantially more variation in bat activity than did the random factors of site and month in all cases.

2.4 Discussion

2.4.1 Spatiotemporal factors

Bat populations differ across time and space suggesting that resource partitioning is important in facilitating the co-existence of multiple species (Arlettaz, 1999). Within the United Kingdom, such partitioning has been observed previously between Pipistrelle species, which differ in foraging locations and feeding times (Nicholls and Racey, 2006). Here, we found that random factors of site and month typically accounted for 12-22% of the variation in bat activity but were particularly important for *Myotis*, where they accounted for 45% of the variation explained by the GLMM model. This is likely driven by Daubenton's bats (*Myotis daubentonii*), which are associated with water as they glean insect prey from the surface of lakes and ponds (Jones and Rayner, 1988; Russ, 2012) and were thus present in large numbers at some sites and absent from others. Seasonality (accounted for here by adding month as a random factor) is also likely to impact observed levels of activity. Temperate bats in the United Kingdom are most active during the summer months, foraging regularly to prepare for, or to recover from, the high energy demands of raising young (Racey and Speakman, 1987; Ciechanowski *et al.,* 2007). All bats remain active for the remainder of the summer and into early autumn to ensure they have sufficient energy reserves for winter hibernation (Speakman and Racey, 1989). The time at which bats enter and emerge from hibernation is primarily dependent on temperature. They enter torpor when energy demands are higher than can be met by decreasing insect densities (Speakman and Racey, 1989). Depending on ambient temperature, bats typically become active in April and seek out hibernation sites in late September as temperatures drop.

Bat activity was not uniform throughout the night, as shown by the clear patterns in the temporal distribution of activity across the night and reinforced by hour post sunset being significant in each GLMM. Bats emerge at different times (Russ, 2012) and also commute different distances, at different speeds, between roosts and foraging areas. Some bats return to their roost part way through the night and then re-emerge for a pre-dawn feed and this likely explains the increase in bat activity shown towards sunrise shown here for soprano pipistrelle and *Myotis*. This has been seen to vary between nights and seasons (Anthony *et al.,* 1981) and may be influenced by peaks in insect densities at dusk and, to a lesser extent, at dawn (Rydell *et al.,* 1996). Ultimately different temporal patterns in activity levels between species, as demonstrated here, plays an important role in niche partitioning in multi-species assemblages of insectivorous bats (Milne *et al.*, 2005; Ciechanowski, *et al.,* 2007).

2.4.2 Weather

Temperature was weakly positively correlated with bat activity both overall and for common pipistrelle (i.e. more passes in warmer conditions). This was expected given that bat activity tends to peak in the summer months, when temperatures are usually highest. The weak negative relationship between temperature and bat activity for *Myotis* and *Nyctalus* was more surprising. However, as surveys were undertaken between April and early October, when it is typically warm enough for bats and their insect prey to be active, one explanation is that temperature is important as a threshold, rather being linearly related to activity levels (Rydell, 1989b). The notable pre-dawn peak for *Myotis*, when nightly temperatures are usually at their coldest, might also be a partial driver for this finding (and may also provide an explanation as to why there was no significant relationship between temperature and activity of soprano pipistrelle; the other species with a pre-dawn peak in activity). Rainfall was negatively correlated with bat activity in all cases (i.e. more passes in dry conditions). This is consistent with previous findings that rain imposes an additional energetic cost and decreased prey abundance (Erickson and West, 2002; Downs and Racey, 2007). Wind speed was positively correlated with bat activity in all cases with the exception of *Nyctalus.* This finding is surprising given the potential for additional energetic costs posed by flight in strong winds (Norberg, 1990). However, insectivorous bats, and specifically pipistrelles, are known to utilise linear features such as treelines and hedgerows to provide shelter when foraging in windy conditions (Verboom and Spoelstra, 1999; Russ *et al.*, 2003). This spatial shift in foraging activity might account for the increase in detected echolocation calls as the detectors used in this study were predominantly placed along linear features as is common in automated surveys (Collins, 2016). In this way, automated survey results might be affected by the three-way relationship between the presence of linear features, detector placement, and wind conditions.

2.4.3 Moon illumination

Previous studies on the effects of moonlight on bats have shown mixed effects. For example, Lang *et al.* (2006) found that activity of some insectivorous bats such as the white-throated round-eared bat (*Lophostoma silvicolum*) in Panama to be lower on moonlit nights, while Appel *et al.* (2017) found bat activity was positively correlated with moonlight for Parnell's mustached bat (*Pteronotus parnellii*) and lesser sac-winged bat (*Saccopteryx leptura*) in Brazil. Here, we found that moon illumination was negatively related to bat activity. This agrees with work by Adams *et al.* (1994) on the Virginia big-eared bat (*Corynorhinus townsendii virginianus*) in the US but contrasts with previous work on non-

British *Myotis* species, which did not find a link between activity and moonlight (Negraeff and Brigham, 1995; Hecker and Brigham, 1999) - although it is notable that neither of these studies included the modifying effect of cloud cover on illumination.

Although it has been suggested previously that bats at higher latitudes are exempt from the predation pressures that impact tropical species (Karlsson *et al.,* 2002), predation risk on bright nights could still be an important modifier of activity in temperate species (Lima and O'Keefe, 2013). It has also been suggested that temperate insectivorous bats may seek more enclosed (shaded) habitats when foraging in bright moonlight (Reith, 1982; Erickson and West, 2002), such that an apparent decrease in activity in open areas nights might actually be a repositioning of foraging activity spatially. We therefore suggest that the bats in our study might be avoiding bright moonlight conditions because of an increased risk of predation, either real or perceived. Moreover, it is notable that *Myotis* and *Rhinolophus* bats in Europe have previously been found to have an aversion to artificial illumination (Rydell, 1992; Stone *et al.*, 2009), which again was provisionally attributed to predation risk.

2.4.4 Implications and recommendations

Bats comprise an important, and legally-protected, part of mammal fauna in the UK. Surveying and monitoring is important in the contexts of scientific research, conservation, assessment of ecosystem health, monitoring progress towards sustainable development goals, and in compliance with legislation on development planning and infrastructure construction (Jones *et al.,* 2009; Barlow *et al.*, 2015; Collins, 2016). It is thus vital that the factors which underpin bat activity, and thus detectability in acoustic surveys, are clearly understood. Bat surveys are notoriously difficult to standardise in terms of timing and the abiotic conditions under which they are conducted and only with robust understanding of optimal foraging conditions is it possible for this to be achieved.

We recommend that automated fixed-point surveys are undertaken throughout the night where possible (where this is not possible, they should be conducted for 4 hours post-sunset and 2 hours pre-sunrise to ensure peak activity times for all species are covered). As long as bats are active, temperature is largely immaterial but nights with heavy rainfall should certainly be avoided. Wind speed should also be taken into account, as linear features might be preferred habitat when shelter is sought from the wind, potentially increasing estimates of activity if detectors are placed close to such features. Surveying during high summer gives the simultaneous advantages of higher activity and greater concentration of activity as nights are shortest. We recommend that given increasing urbanization, the effect of light on bats should be further investigated, and that such research take cognisance of cloud cover as well as lunar phase (Stone *et al.*, 2009; Russo *et al.*, 2017). Given that the findings of this research indicate that overall bat activity decreases when the moon is unobscured by cloud, there remains potential for light from artificial sources to also impact bat activity. Passive monitoring of light levels in the field during surveys might be particularly helpful in such research.

2.5 Chapter summary

1. *Within-night bat activity was not uniform, with peaks in overall activity found in the 3-4 hours post sunset, and again shortly before dawn for particular taxonomic groups (soprano pipistrelle, Myotis spp.).*

2. *Further spatiotemporal factors of site and month were found to driving 45% of the observed variation in activity for Myotis spp.*
3. *Rainfall was negatively correlated with bat activity in all cases.*
4. *Moonlight was also negatively correlated with bat activity, suggesting "lunar phobia" or a spatial shift in activity on moonlit nights.*
5. *Results from this chapter inform the methods used for primary data collection in Chapters Four and Five by ensuring data collection occurred throughout the night in suitable weather conditions and sites being surveyed in rotation to mitigate the influence of seasonal patterns.*

2.6 Supplementary material

***Table S2.1:** Number of survey nights at each site (1-14) within each month (April-October). The mean number of bat passes per hour are given for total bat activity and for four specific taxa, both per month, per site and overall.*

			Mean bat passes per hour				
Site	Month	Nights Surveyed	Total Activity	Common Pipistrelle	Soprano Pipistrelle	*Myotis* spp.	*Nyctalus* spp.
1	April	3	17.63	9.99	4.29	2.38	0.28
	May	9	17.58	9.96	4.27	2.73	0.28
	June	-	-	-	-	-	-
	July	-	-	-	-	-	-
	August	-	-	-	-	-	-
	September	23	15.67	8.63	3.86	2.29	0.22
	October	15	15.49	8.49	3.83	2.28	0.22
2	April	-	-	-	-	-	-
	May	17	17.15	9.65	4.21	2.32	0.28
	June	-	-	-	-	-	-
	July	-	-	-	-	-	-
	August	-	-	-	-	-	-
	September	16	15.59	8.59	3.83	2.28	0.22
	October	-	-	-	-	-	-
3	April	-	-	-	-	-	-
	May	7	18.81	9.55	3.95	2.33	0.28
	June	-	-	-	-	-	-
	July	-	-	-	-	-	-
	August	-	-	-	-	-	-
	September	-	-	-	-	-	-
	October	-	-	-	-	-	-
4	April	-	-	-	-	-	-
	May	-	-	-	-	-	-
	June	3	18.44	10.48	4.33	2.56	0.31
	July	-	-	-	-	-	-
	August	-	-	-	-	-	-
	September	-	-	-	-	-	-
	October	-	-	-	-	-	-

5	April	-	-	-	-	-	-
	May	-	-	-	-	-	-
	June	-	-	-	-	-	-
	July	-	-	-	-	-	-
	August	-	-	-	-	-	-
	September	2	15.66	8.88	3.72	2.16	0.25
	October	-	-	-	-	-	-
6	April	-	-	-	-	-	-
	May	6	18.39	10.45	4.33	2.56	0.31
	June	10	18.19	10.28	4.30	2.56	0.31
	July	20	17.95	10.11	4.26	2.54	0.30
	August	-	-	-	-	-	-
	September	-	-	-	-	-	-
	October	-	-	-	-	-	-
7	April	-	-	-	-	-	-
	May	-	-	-	-	-	-
	June	-	-	-	-	-	-
	July	13	17.91	10.05	4.27	2.54	0.30
	August	-	-	-	-	-	-
	September	-	-	-	-	-	-
	October	-	-	-	-	-	-
8	April	-	-	-	-	-	-
	May	-	-	-	-	-	-
	June	5	19.78	10.95	4.82	2.85	0.32
	July	-	-	-	-	-	-
	August	-	-	-	-	-	-
	September	6	16.00	9.03	3.77	2.25	0.26
	October	-	-	-	-	-	-
9	April	-	-	-	-	-	-
	May	-	-	-	-	-	-
	June	-	-	-	-	-	-
	July	-	-	-	-	-	-
	August	-	-	-	-	-	-
	September	12	15.98	9.04	3.76	2.25	0.26
	October	-	-	-	-	-	-

10	April	-	-	-	-	-	-
	May	-	-	-	-	-	-
	June	-	-	-	-	-	-
	July	-	-	-	-	-	-
	August	9	16.64	9.43	3.91	2.34	0.27
	September	-	-	-	-	-	-
	October	-	-	-	-	-	-
11	April	-	-	-	-	-	-
	May	-	-	-	-	-	-
	June	1	17.96	10.11	4.29	2.56	0.27
	July	-	-	-	-	-	-
	August	7	16.75	9.38	3.92	2.34	0.25
	September	8	15.98	9.02	3.79	2.26	0.24
	October	-	-	-	-	-	-
12	April	16	13.33	11.74	0.58	0.34	0.08
	May	18	2.06	1.06	0.28	0.22	0.20
	June	23	3.71	2.47	0.19	0.42	0.21
	July	22	11.30	9.32	1.68	0.11	0.06
	August	-	-	-	-	-	-
	September	18	6.14	3.23	0.16	1.48	0.23
	October	11	3.08	1.77	0.14	0.74	0.10
13	April	-	-	-	-	-	-
	May	-	-	-	-	-	-
	June	-	-	-	-	-	-
	July	-	-	-	-	-	-
	August	1	15.71	8.69	3.81	2.29	0.22
	September	7	15.68	8.68	3.80	2.29	0.22
	October	-	-	-	-	-	-
14	April	-	-	-	-	-	-
	May	-	-	-	-	-	-
	June	-	-	-	-	-	-
	July	-	-	-	-	-	-
	August	15	50.00	40.27	1.11	0.17	0.01
	September	-	-	-	-	-	-
	October	-	-	-	-	-	-
Total		**323**	**16.27**	**9.15**	**4.02**	**2.20**	**0.26**

CHAPTER THREE: Comparing acoustic data from transect and automated bat surveys

Hand-held detector on a transect survey versus passive detector on an automated survey

***Chapter Two** investigated the effect of spatiotemporal and abiotic factors on the bat activity (recorded in automated fixed-point bat surveys via passive acoustic monitoring). However, acoustic bat surveys can also be conducted via activity surveys using walked or driven transects. Transect surveys are typically performed for two hours commencing around sunset, where automated, fixed-point, surveys record continually between sunset and sunrise, often over multiple consecutive nights. Here, a subset of the fixed-point data used in **Chapter Two** are supplemented by transect data collected at the same sites totalling 2,349 survey hours over a 3-year period (some of the earlier data used in the previous chapter did not correspond with a transect survey). These data are used to investigate the relative effectiveness of walked activity transects and automated fixed-point methods for 12 species of European bats.*

Publications arising from this chapter:

Perks, S. J. and Goodenough, A. E. (2021) 'Comparing acoustic survey data for European bats: do walked transects or automated fixed-point surveys provide more robust data?'. *Wildlife Research*, 49(4), pp.314-323.

The material has been reformatted for inclusion in this thesis to provide consistency across the chapters and align with the University of Gloucestershire's thesis requirements, with summaries at the start and end of each chapter to set the chapters within the thesis context, but have not otherwise been amended. The data used for this chapter are explained in relation to the PhD process in Section 1.4.2.

3.1 Introduction

There are approximately 1400 species of bats globally (Bat Conservation International, 2021), many of which are declining due to natural and/or anthropogenic processes (Hutson *et al.*, 2001; O'Shea *et al.*, 2016). Direct causes of mortality include disease and extreme weather events, which often differ spatially: for example, White Nose Syndrome is a major cause of mortality in North America while extreme heat is a major cause of mortality in Australia (O'Shea *et al.*, 2016). Indirect threats are often more varied and affect bats through loss of, or disturbance to, roosts or feeding grounds (Walsh and Harris, 1996b; Hutson *et al.,* 2001). For example, bats are extremely sensitive to habitat change and fragmentation, agricultural intensification, and deforestation or sub-optimal forest management (Walsh and Harris, 1996a; 1996b; Willig *et al.*, 2007; Lintott *et al.,* 2016; O'Shea *et al.,* 2016; Alder *et al.*, 2020). Climate change is likely to become an increasing threat worldwide (Jones *et al.,* 2009), while pesticides and pollutants can also pose substantial threats to regional or national populations (O'Shea and Johnston, 2009).

Bat data are important in establishing species' distribution, quantifying population metrics, and understanding ecological relationships, as well as assessing temporal trends in relation to environmental change and conservation initiatives (Hutson *et al.,* 2001; Walsh *et al.*, 2004; Barlow *et al.*, 2015). Because of the ecological importance of bats and the ecosystem services they provide, as well as their vulnerability to anthropogenic processes, bats can be a useful bioindicator of habitat quality and climate change (Jones *et al.,* 2009; Russo and Jones, 2015). Population change is thus often used as an indicator of ecosystem health (e.g. in the USA: Treanor *et al.,* 2019; throughout Europe under EUROBATS scheme) and to monitor progress towards sustainable development (e.g. UK: JNCC, 2019b).

In addition to monitoring bats spatially and temporally through national-level initiatives, such as the North American Bat Monitoring Programme and EUROBATS, site-level bat surveying is often undertaken in research contexts and, in parts of the world where bats are legally protected, site-level survey data are often required to allow planning authorities to make informed decisions on infrastructure development (Drayson *et al.,* 2015; Goodenough and Hart, 2017). For example, in Europe, a considerable amount of bat survey effort is driven by the need for compliance with the EC Habitats Directive (92/43/EEC) and European Protected Species licensing framework, as well as national legislation through which these are implemented (Goodenough *et al.,* 2015). Site-based bat surveys are thus often undertaken within mandatory Ecological Impact Assessments (EcIAs) to quantify bat presence and abundance, assess potential development impacts, and devise suitable mitigation and compensation measures (Treweek, 2009; CIEEM, 2018), as well as to support license applications to permit work around bat roosts that would otherwise be illegal (Mitchell-Jones, 2004).

Bat surveys can involve counting bats visually (roost counts: Barlow *et al.,* 2015; Warren and Witter, 2002) or trapping bats in flight (harp traps or mist netting: Law *et al.,* 1998; O'Farrell and Gannon, 1999). However, non-invasive acoustic surveys are commonly undertaken whereby ultrasonic devices are used to detect echolocation calls. Acoustic surveys typically involve either: (1) automated fixed-point ultrasonic detectors to record bats continually between sunset and sunrise or (2) transect surveys using ultrasonic detectors in real-time (Collins, 2016). Automated fixed-point surveys are used worldwide, including throughout Europe, North America and Oceania, but also increasingly in Asia and Africa (Sedlock *et al.*, 2014; Weier *et al.,* 2020). In contrast, transect acoustic survey methodologies vary between countries. Where activity is typically monitored across large geographic scales, such as in the USA and Canada, ultrasonic detectors may be fitted to vehicles to enable transects to be driven (Braun de Torrez *et al.,* 2017a; D'Acunto *et al.,* 2018). However, throughout Europe, walked transects with handheld detectors are more commonly used (Russo and Jones, 2003; Ciechanowski *et al.,* 2007; Stahlschmidt and Bruhl, 2012; Henkens *et al.,* 2014; Goodenough *et al.*, 2015; Collins, 2016). Outside of Europe, walked transects are used in Oceania (O'Donnell, 2000; O'Donnell and Sedgeley, 2001; Scanlon and Petit, 2009; Lavery *et al.*, 2020), Africa (Bambini *et al.*, 2006; Taylor *et al.*, 2013; Musila *et al.*, 2019), and Asia (Pottie *et al.,* 2005; Lee *et al.,* 2017; Mullin *et al.,* 2020). In addition to use in formal surveys for research, legislative complacence, and long-term monitoring, walked transects are increasingly being used in citizen science or volunteer-led bat surveys, for example in the Bat Walks Programme by Bat Conservation International and the National Bat Monitoring Programme in the UK. Better insight into how such survey data compare to data derived from more formal automated fixed-point surveys would thus be beneficial.

For any form of monitoring to be effective, underpinning data must be collected in a consistent and rigorous manner appropriate to the aim of the survey (Collins, 2016). Survey methods need to be logistically-feasible, robust, and comparable (Balmford *et al.,* 2003; Collins, 2016) and account for the influence of spatiotemporal and abiotic factors (Perks and Goodenough, 2020; Chapter Two). This is particularly important in applied settings when legally-protected species are affected by resulting actions, either through conservation interventions (Barlow *et al.*, 2015) or development decisions (Mitchell-Jones, 2004). In fixed-point detection, spatial coverage is limited to a (very) few points per site, but temporal coverage is extensive with detectors usually recording sunset to sunrise for 5-21 consecutive nights. This allows the entire nocturnal period to be sampled over multiple nights as per the recommendations of Law *et al.* (1998) and Hayes (1997). In the case of transects (walked or driven), coverage is restricted temporally – often to a two-hour period commencing at or near sunset (O'Donnell, 2000; Goodenough *et al.,* 2015; Braun de Torrez *et al*., 2017a) – but a much wider spatial area is covered.

Although the need to monitor bat populations is recognised (Barlow *et al.*, 2015), and there are commonly-used acoustic techniques to achieve this, there have been few attempts to either compare the efficacy of different acoustic surveys or determine whether data from different survey types are directly comparable. This is important because although both transect and fixed-point methods are commonly used and industry-standard techniques, it is common for just one method to be used to survey bats at a specific site. Published evidence that has focused on comparing automated fixed detection with transects surveys is limited to Tonos *et al.* (2014) in Indiana, USA, and Braun de Torrez *et al.* (2017a) in Florida, USA. Work to date, therefore, has compared automated detection and *driven* transects on American Chiropteran guilds. In this study, we empirically compare automated fixed-point acoustic surveys with *walked* transect acoustic surveys for a European Chiropteran guild.

We examine overall bat activity as well as species-specific activity for 12 European bat species and two wider genera (*Myotis* sp. and *Nyctalus* sp.) at the same sites to determine: (1) differences between the survey methods over exactly the same time period (i.e. walked transect acoustic surveys starting two hours post sunset with automated fixed-point acoustic surveys over the same two hour window) and (2) differences between the survey methods over a longer timeframe (i.e. one two-hour walked transect acoustic survey that commenced at sunset compared with whole-night automated fixed-point acoustic surveys for multiple nights within a 21 night window). Undertaking both comparisons enables full exploration of the ability to passively monitor bats whole and consecutive nights, as opposed to the traditional survey window of two hours post sunset. We also use the automated data to quantify hourly bat activity patterns, to explore how peak levels of activity varies throughout the night and how this related to the two-hour walked survey transect period. Our conclusions and recommendations are necessarily related primarily to European bat species, but we also make tentative broader comments relating to walked bat transects in other geographical regions, and for other species, with appropriate caveats.

3.2 Methods

3.2.1 Data collection

We used a paired survey design whereby data were collected from 14 sites across the south of England, encompassing a range of habitat types. Most of the sites (n = 9) comprised agricultural land with dividing hedgerows, but other sites included high quality rural habitat or lakeside (n = 3) and green spaces within more urbanised areas (n = 2). At each site, the bat community was surveyed in two ways: (1) walked transect acoustic surveys, and (2) automated fixed-point acoustic surveys.

Walked transect acoustic surveys were conducted in accordance with the Bat Conservation Trust Guidelines (Collins, 2016) using Anabat SD1 detectors (Titley Scientific, Ballina, Australia). These two-hour surveys commenced at sunset and were carried out by two surveyors; either walking in opposite directions around a single perimeter transect (n = 7 sites), or walking separate transects on larger sites (n = 7 sites). Automated fixed-point acoustic surveys were conducted using Anabat Express Units (Titley Scientific, Ballina, Australia). Deployment and positioning of these units was carried out in a consistent manner at all sites with units mounted about 1.75m above the ground adjacent to a suitable hedgerow or treeline to ensure detection of commuting and foraging activity along linear features. The SD1 detectors enabled audio allowing fieldworkers to identify the bats present *in situ*, whereas the Express units were weatherproof and had long battery life and facilitated extended periods of automated recording of sound files to a memory card where sound output was unnecessary. In both cases, the default or recommended settings were used (data division ratio = 8 on both SD1 and Express; sensitivity = 6 on SD1 and 8 on Express): both units had identical frequency ranges.

In total, 24 walked transect acoustic surveys were carried out across the 14 sites. These surveys were matched with data from automated fixed-point acoustic surveys from multiple (minimum of 3) nights within a 21-night window. The 21-night window was set to ensure that seasonality did not confound method comparison analyses. This gave 24 cases where walked transect data (for two hours post sunset on a single night) were matched to automated fixed-point data (encompassing the entire period between sunset and sunrise over several nights) at the same site at the same time of year. This is henceforth referred to as the multi-night dataset. A subset of 14 transects coincided exactly with automated fixed-point surveys so that there were data from the same two-hour window, on the same night, at the same site, from the two different methods. This gave 14 cases of directly-matched data, which are henceforth referred to as the concurrent dataset.

Post fieldwork, all data, which were in zero crossing format, were downloaded from internal SD cards in the bat detectors for sonogram analysis. Sonogram analysis was performed using AnalookW software version 4.1z (Titley Scientific, Ballina, Australia) developed specifically for Anabat detectors. Initially recordings were processed on a night-by-night basis and then data were subdivided into hourly units relative to sunset. Species identification was carried out by assessment of the frequency range and peak frequency, together with shape of each sonogram in terms of pitch and amplitude over time using information in Russ (2012). As is typical for acoustic surveys (Russ 2012), *Myotis* bats were challenging to identify to species level. Where possible, Daubenton's (*Myotis daubentonii*) and Natterer's (*Myotis nattereri*) bats were identified as separate species. Brandt's bat (*Myotis brandtii*) and whiskered bat (*Myotis mystacinus*) were generally distinguishable from other *Myotis* bats but not from one another and were grouped accordingly. Indistinguishable *Myotis* bats were grouped at genus level. In most cases, noctule (*Nyctalus noctula*) bats could be distinguished to species level but some calls could not be differentiated from Leisler's (*Nyctalus leisleri*) and were thus grouped at genus level.

3.2.2 Statistical analysis

To compare overall species richness recorded in exactly the same two-hour window at the same site via the two different survey methods (i.e. the concurrent data), paired sample t-tests were used for the comparison of mean values between matched samples. This approach was also used to compare total activity of bats (regardless of species) and species-specific or genus-specific activity when there was sufficient data and for species that were recorded in both survey types. To undertake these analyses, walked transect survey data and automated fixed-point survey data were converted to mean bat passes per hour and then log transformed (*ln*+1). Parametric assumptions were met for these transformed data (i.e. the difference between the mean bat passes per hour for the two survey types – the difference scores – were normally distributed in all cases). To compare species richness, total activity, and species-specific activity of bats recorded via the walked transect surveys compared to multi-night data from automated fixed-point surveys, the same paired-sample approach was used. This was adopted on the basis that although the data were not exactly matched in time, they were still exactly matched in space and very similar in time. Again, data were converted to mean bat passes per hour and then log transformed (*ln*+1) to meet parametric assumptions.

To explore nightly activity patterns, trends in bat activity across the night were examined for each species using the automated fixed-point data from the multi-night dataset. Data were grouped on an hourly basis and graphed. Significant deviations from a uniform distribution throughout the night were tested using Kolmogorov-Smirnov two-sample tests. This allowed better understanding of possible differences between walked transect data (which were temporally restricted) and automated fixed-point data (which spanned the entire night). All statistical analysis was carried out in IBM SPSS version 24.

3.3 Results

Data were collected on 223 nights of automated fixed-point acoustic recording and 24 walked transect acoustic surveys giving a combined sample size of 2,349 hrs of bat recording data summarising 47,915 individual bat passes.

3.3.1 Species richness

Over the entire study, more species were detected using automated fixed-point surveys (n = 11 species plus *Myotis* sp. and *Nyctalus* sp.) than using walked activity surveys (n = 8 species plus *Myotis* sp. and *Nyctalus* sp.). However, mean species richness per hour was significantly higher in the walked transect acoustic surveys compared to the automated fixed-point acoustic surveys when considering both the concurrent data (2.89 ± 0.29 SEM versus 1.96 ± 0.31 species per hour, respectively: paired samples t-test t= 3.501, n= 14 pairs, *P* = 0.004) and the multi-night data (2.92 ± 0.22 SEM versus 1.32 ± 0.12 SEM species per hour, respectively: paired samples t-test t= 9.338, n= 24 pairs, *P* <0.001).

3.3.2 Species prevalence

In the concurrent dataset, lesser horseshoe bats (*Rhinolophus hipposideros*) were only detected in automated fixed-point acoustic surveys. Common pipistrelle (*Pipistrellus pipistrellus*), soprano pipistrelle (*Pipistrellus pygmaeus*), noctule (*Nyctalus noctula*), serotine (*Eptesicus serotinus*), brown long-eared (*Plecotus auritus*) and Natterer's bats, in addition to bats identified at *Myotis* and *Nyctalus* genus level only, occurred on both survey types but were more prevalent in the walked transect acoustic surveys (Figure 3.1a). Conversely, Brandt's/whiskered (*Myotis* spp.) and barbastelle (*Barbastella barbastellus*) occurred on both survey types but were more prevalent in the fixed-point acoustic surveys (Figure 3.1a). Greater horseshoe (*Rhinolophus ferrumequinum*) and Daubenton's bats (*Myotis daubentonii*) were absent in both survey types.

In the multi-night dataset, common pipistrelle, soprano pipistrelle, noctule, serotine, brown long-eared, Brandt's/whiskered, barbastelle and Natterer's bats, in addition to bats identified as *Myotis* and *Nyctalus* genus level occurred in both survey types, but were more prevalent in walked transect acoustic surveys (Figure 3.1b). Two species that were not detected in the concurrent data (greater horseshoe, Daubenton's) were detected in the multi-night dataset in the automated fixed-point surveys only. Lesser horseshoe, which was detected at very low levels in the automated fixed-point surveys in the concurrent dataset, increased in prevalence marginally (<1%) in the multi-night dataset. The three species that only occurred in the automated fixed-point surveys (greater and lesser horseshoe and Daubenton's) were present in <10% of the total recording hours.

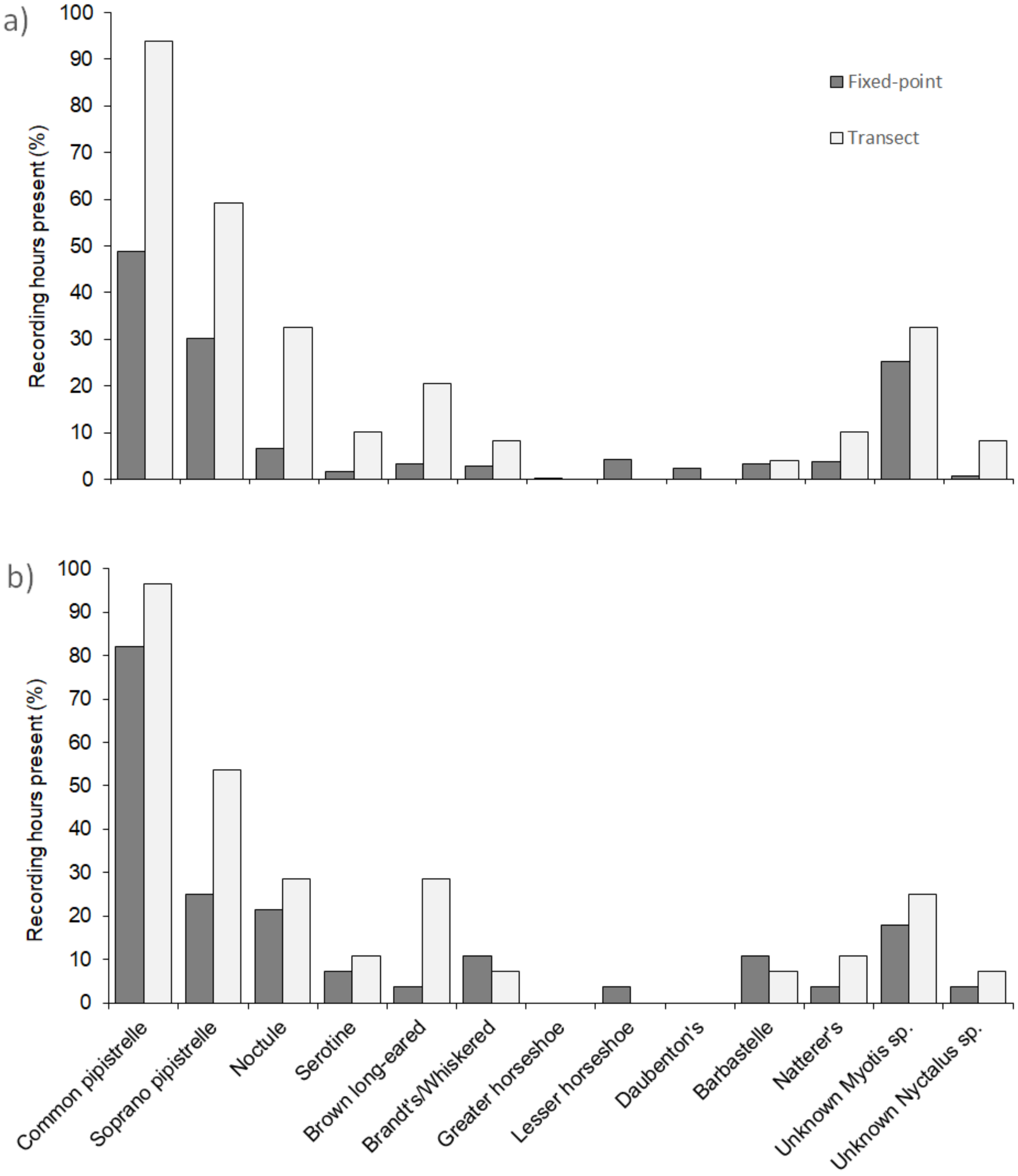


Figure 3.1: *Prevalence of each species/genus in acoustic automated fixed-point and acoustic walked transect surveys (a) within the same two-hour window post-sunset whereby data are directly paired; and (b) using fixed-point data from multiple (minimum of 3) nights*

3.3.3 Species activity

Within the concurrent data, there was no significant difference in overall bat activity between automated fixed-point surveys and walked transect surveys (19.86 ± 5.65 SEM and 24.18 ± 7.91 SEM, respectively; paired samples t-test: t= 0.870, n= 14 pairs, P= 0.400). However, there was a significant difference between these survey types over multiple nights, with walked transect surveys recording higher overall mean activity (17.53 ± 5.93 SEM, 24.09 ± 5.66 SEM; paired samples t-test: t= 2.610, n = 24 pairs, P= 0.016). Moreover, there were significant species-specific differences between survey methods. Within the concurrent data, the mean number of brown long-eared bat passes per hour was significantly higher in the walked transect surveys (paired samples t-test: t = 2.235, n = 14 pairs, *P* = 0.044; Figure 3.2a). In the multi-night dataset, the mean number of brown long-eared bat passes per hour was also significantly higher during the walked transect surveys than fixed-point surveys (paired samples t-test t = 2.275, n = 24 pairs, *P* = 0.033: Figure 3.2b). For common pipistrelle, there was no significant difference between survey methods within the concurrent data, however, within the multi-night data, the mean number of passes per hour was significantly higher during the walked transect surveys, than was recorded in the fixed-point surveys (paired samples t-test: t = 2.777, n = 24 pairs, P = 0.011). For soprano pipistrelle, walked transect surveys recorded a significantly higher number of passes per hour in both the concurrent and multi-night data (t = 2.228, n = 14 pairs, P = 0.044; t = 2.159, n = 24 pairs, P = 0.042, respectively).

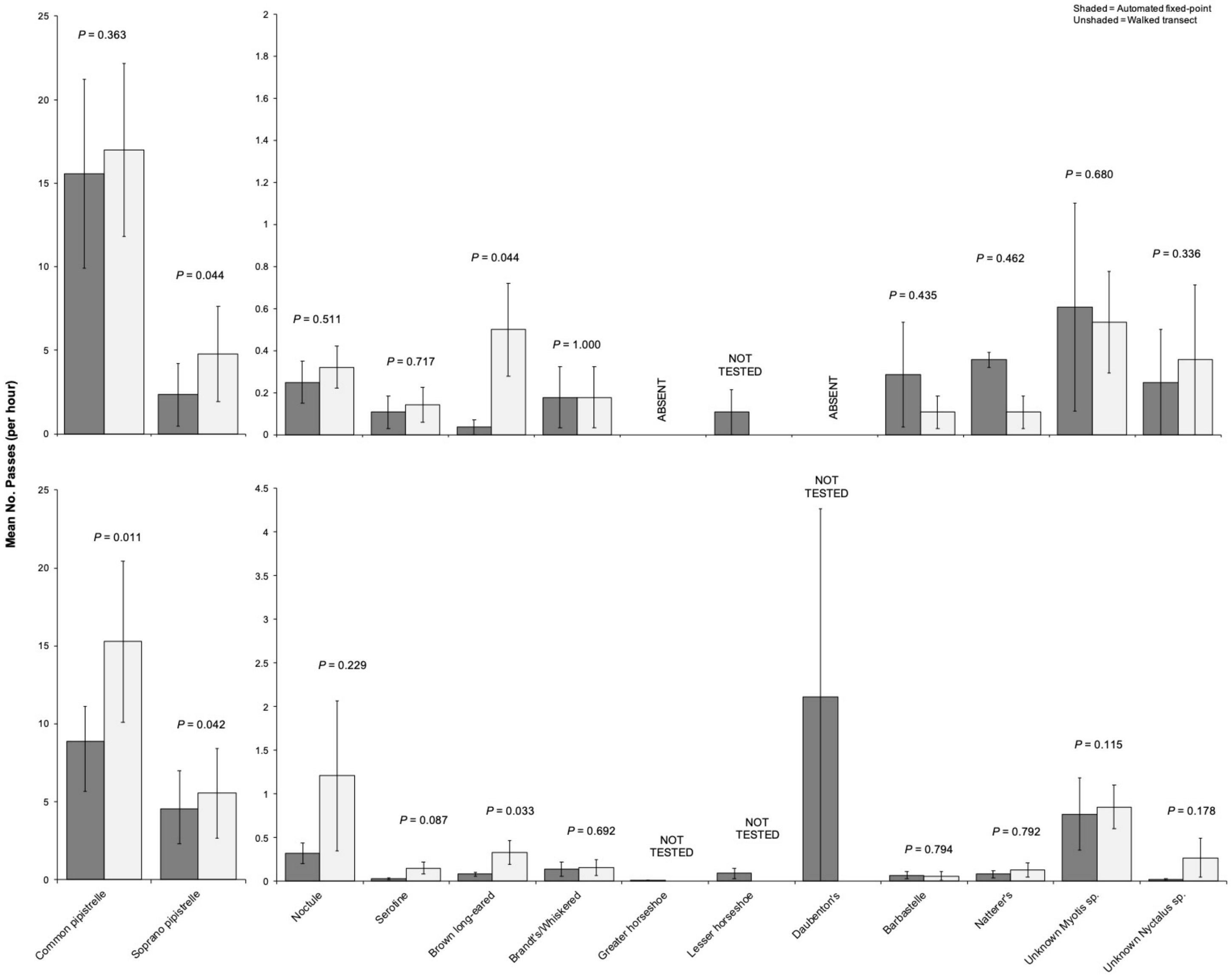


Figure 3.2: *Mean number of bat passes per hour from acoustic automated fixed-point and acoustic walked transect surveys (a) within the same two-hour window post-sunset whereby data are concurrent (significance values from paired samples t-tests undertaken on log-transformed data); and (b) using fixed-point data from multiple (minimum of 3) nights within a 21-night window using the multi- night dataset (significance values from paired samples t-tests undertaken on log-transformed data). Error bars show SEM (±1se).*

3.3.4 Temporal distribution

Analysis of the temporal distributions of each species/genus in relation to hour post sunset is shown in Figure 3.3. Two sample Kolmogorov-Smirnov tests demonstrated that the activity of all species/genera differed significantly from a uniform distribution ($P \leq 0.046$ in all cases). Most species were detected throughout the night, including within the walked transect survey window (the first two hours post sunset). The exception was the greater horseshoe bats, which were detected in low numbers from 4 hours post sunset onwards. Moreover, although Daubenton's and lesser horseshoe bats were detected in the initial two hours post-sunset they were recorded as frequently (lesser horseshoe) or more frequently (Daubenton's) later in the night. Both pipistrelle species showed a tendency towards being more active in the earlier period of the night, however, the distribution for soprano pipistrelle showed a slight increase in the hours before dawn, making the distribution slightly bimodal.

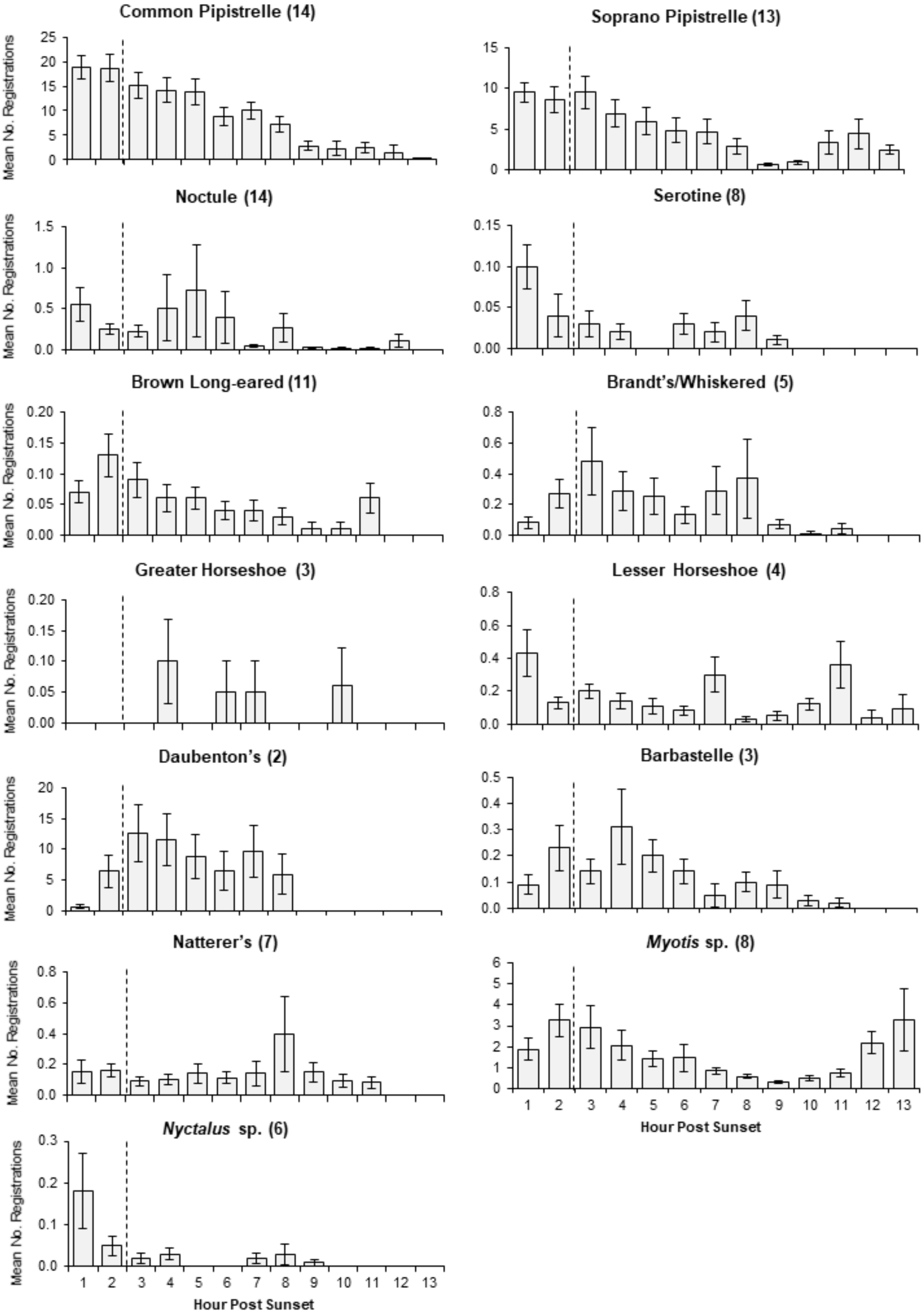


Figure 3.3: *Temporal distribution of each bat species/genus based on mean passes per hour post sunset using automated fixed-point survey data. Number of sites at which species were encountered shown in brackets, the normal transect survey window (two hours post sunset) is shown by the dashed lines. Error bars show SEM (±1se).*

3.4 Discussion

This study found that, for a European bat guild, although more species were recorded via automated fixed-point acoustic surveys than walked transect acoustic surveys in the entire dataset, species richness per hour was substantially and significantly higher in transect surveys. This finding was significant in both the paired dataset (2 hr post sunset) and the multi-night dataset (which fully exploited the recording abilities of the automated method) where per-hour species richness found using walked transects was almost double that found using automated fixed-point acoustic surveys.

Three species - greater horseshoe, lesser horseshoe and Daubenton's - were not detected on the walked transect surveys, which reduced the species community detected using this method relative to the automated fixed-point surveys. This means that while the walked transects often detect more bat passes, both overall and for some specific species, fixed-point surveys provide a more comprehensive overview of the bat community. Interestingly, the three species not detected on the walked surveys occurred as often (lesser horseshoe), more often (Daubenton's) or exclusively (greater horseshoe) after the two hours post-sunset window when walked transects took place. Greater horseshoes typically emerge late relative to sunset (Collins, 2016) and can travel up to 8 km to reach favourable foraging habitat (Billington, 2003a; 2003b; Billington, 2004), both of which might mean detection is unlikely during the standard two-hour survey window post sunset as the likelihood of detecting the species on transects will depend largely on roost proximity. This highlights the importance of secondary data in identification of known roost locations, particularly to target on-ground surveys for legislative compliance in development contexts. Bat mitigation guidelines recommend extending the duration of walked transect acoustic surveys to 3 hours, on sites within commutable distance (4 km) to greater horseshoe roosts (Mitchell-Jones, 2004). This aims to account for bat commuting time and minimizes the potential risk of the species being wrongly assumed as absent. However, in this study, greater horseshoes were only detected >4 hrs post sunset, which suggests that this species could still be missed especially if the site constitutes a rich feeding ground that could attract bats from up to 8 km away. Lesser horseshoe bats were detected throughout the night, including within the two-hour transect survey window, but only in the automated fixed-point acoustic surveys. They were always recorded in low densities, probably because they tend to forage within closer proximity to their roosts (Bontadina *et al.,* 2002) and can move easily between roost and foraging grounds throughout the hours of darkness. Given this nocturnal pattern and the comparative rarity of lesser horseshoes, automated fixed-point surveys covering the entire night would be more likely to detect this species. Daubenton's bats were also recorded throughout the night, although they were much more abundant after the end of the transect survey window. Daubenton's roost predominantly in close proximity to the waterways on which they forage (Dietz *et al*., 2006) and are a later emerging species (Collins, 2016), which likely explains their absence from the walked transect acoustic surveys. The decline of activity in both common and soprano pipistrelle throughout the night is also likely responsible for the higher activity of these species in walked transect data compared to fixed-point acoustic data.

The absence of key species from walked transect data emphasises the key advantage of recording for the entire nocturnal period, and over several nights, when surveying bat communities at specific sites: it increases the likelihood of encountering locally rare species or species that emerge (or arrive at foraging grounds) after the widely-used transect survey window two hours post sunset. This is much easier to achieve using fixed-point (passive) surveying, where a fieldworker need not be present, rather than transects. It is not surprising to find different temporal patterns in different bats as multi-species assemblages of insectivorous bats frequently use niche partitioning by selecting different prey, different habitats, or different activity times (Rydell *et al.,* 1996; Milne *et al.*, 2005; Ciechanowski *et al.,* 2007). A similar result was found for US bats whereby three rare species were detected on whole-night automated surveys in Florida, but not on two-hour driven transects that commenced 30 minutes after sunset (Braun de Torrez *et al.,* 2017a). Tonos *et al.* (2014) also found a higher overall species richness on fixed-point surveys relative to driven transects in Indiana. This suggests that although our study has focused on European species and walked transects, this finding is potentially relevant in other bat guilds and for other types of transect including driven and even boat transects (Weier *et al.,* 2020).

Walked transect data and automated fixed-point data were also notably different for the brown long-eared bat. This species was not particularly abundant in either of the acoustic survey methods, despite being fairly common in the UK (Russ, 2012), but was detected significantly more often in the walked transect data. This finding was consistent regardless of whether paired data or multi-night data were analysed. Brown long-eared bats are principally gleaners rather than aerial hawkers and thus usually take moth and beetle prey directly from plants (Swift and Racey, 1983; Russ, 2012). Foraging is often undertaken visually or using sound directly (Anderson and Racey, 1991; Eklöf and Jones, 2003) as echolocation is not always useful in close proximity to vegetation when hunting (Simmons *et al.,* 1979). Any echolocation sounds they do produce, therefore, are short and quiet (Russ, 2012) and have historically been almost impossible to pick up using an ultrasonic detector

(Anderson and Racey, 1991). Although technological advances have now made it possible to detect echolocation from a distance of around 5m (Russ, 2012), brown long-eared bats would still have to echolocate very close to the detector to be recorded, which is potentially less likely to occur if the detector is fixed. Moreover, an advantage of walked transect surveys is that light levels at the start of the survey often permit brown long-eared bats to be identified visually (Russ, 2012); the surveyor can also manually orient the detector to obtain a clear recording for sonogram analysis, which can significantly improve detection rates as shown by Milne *et al.* (2004) for Australian bats. Failure to undertake walked surveys might lead to this species being under-represented in data (Russo and Voigt, 2016).

3.4.1 Conclusions and recommendations

Compared to walked transect surveys, automated fixed-point surveys are sometimes considered to be a more effective acoustic survey method (Stahlschmidt and Bruhl, 2012), primarily because walked transect surveys are difficult to standardise and can miss activity patterns even in homogenous landscapes. However, our study indicates that the survey types have different strengths and different weaknesses, certainly for European bats and potentially for other bat guilds too. This highlights the value of using a combination of the two methods to collect bat activity data, either for specific sites (e.g. for research, legislative complacence, or conservation) and for national monitoring programmes. While this study has focused on comparing data from paired surveys, examining whether multi-year walked transect and automated fixed-point surveys show the same temporal trends in bat activity would be a useful avenue for future research.

Walked surveys that occur in the standard window of two hours post sunset are likely to under-record rare species, especially those that emerge from roosts late and/or travel a considerable distance to foraging grounds. In Europe, if relying on walked activity surveys, especially in legislative compliance contexts, the survey window for at least one site visit should be extended to 4 hours post sunset by conducting two back-to-back transects to maximise the chances of encountering greater and lesser horseshoe bats, especially if the site is within 8 km of a known horseshoe roost.

In terms of specific recommendations for European bat surveys, we suggest:

- Walked transect acoustic surveys should be used if the aim is to obtain initial baseline data on bats at a specific site, since these are effective in recording high levels of activity, and species richness, in a very time-effective way. Gauging differing activity levels across the whole site also aids in determining its ecological value to bat populations spatially, particularly in heterogenous landscapes.
- Automated fixed-point acoustic surveys should be used if the aim is to catalogue the complete bat species assemblage at a site. As this approach provides data over a longer time period, both throughout the night and over several consecutive nights, issues of temporal niche partitioning and different nocturnal activity patterns between species are negated. This method also allows for differences in activity due to different environmental conditions on different nights.
- Fixed-point surveys are likely to under-record brown long-eared bats, probably because of infrequent and quiet echolocation as a result of their highly-specific foraging strategy. In Europe, walked activity surveys should be conducted where this species is the target (research contexts) or where habitat is favourable and

determining presence conclusively is important for legislation compliance or informing conservation decisions. Pending specific research in other geographical areas, it is suggested that where species are known to undertake infrequent or quiet echolocation, or for species known to glean as their main foraging strategy rather than being primarily aerial insectivores (e.g. Gould's long-eared (*Nyctophilus gouldi*) and Lesser long-eared (*Nyctophilus geoffroyi*) bats in Australia (Grant 1991); African yellow-winged bat (*Lavia frons*) in sub-Saharan Africa (Vaughan and Vaughan 1986)), transect surveys are undertaken to complement any fixed-point surveying.

- Walked activity and automated fixed-point acoustic surveys are combined where possible for site assessments, and certainly for national monitoring programmes to ensure that data, and any decisions made on those data including in bioindicator metrics or sustainable development indicators, to be comprehensive, valid and robust.

3.5 Chapter summary

1. *The fixed-point surveys recorded the highest species richness overall, however, the walked transects recorded a higher mean species richness per hour.*
2. *Three species: greater horseshoe, lesser horseshoe and Daubenton's bat, were only recorded in the fixed-point surveys, possibly because the survey window encompassed the entire night rather than the period immediately after sunset.*
3. *The number of brown long-eared bat detections was significantly higher in the walked transect surveys, suggesting that this method of surveying is optimal for such species which glean prey, thus emitting infrequent or quiet echolocation calls.*
4. *The strengths of automated surveys, as highlighted in this chapter, and the subsequent expansion in their use, informed the decision to evaluate automated*

fixed-point detectors in a Passive Acoustic Monitoring (PAM) framework in Chapters Four and Five.

CHAPTER FOUR: Evaluating Passive Acoustic Monitoring (PAM) protocols for bats in lowland habitats in the UK

Field sites used for PAM data collection: riparian, woodland, arable, wood pasture (clockwise)

*As discussed in **Chapters Two and Three**, acoustic bat surveys are vital methods of collecting data to inform bat research, conservation, and mitigation. **Chapter Three** (published as Perks and Goodenough, 2021) investigated the relative effectiveness of using fixed-point detectors in a passive acoustic monitoring (PAM) framework and found these to be superior overall and for all species except brown long-eared relative to using handheld detectors on walked activity transect surveys at dusk, although the results of **Chapter Two** demonstrated the need to allow for abiotic factors and seasonality when collecting data in this way. This chapter builds on this work by exploring differences in PAM devices and settings on the bat data collected.*

Publications arising from this chapter:

Perks, S. J., Goodenough, A. E. and O'Connell, M. Evaluating Passive Acoustic Monitoring (PAM) protocols for bats in lowland habitats in the United Kingdom. British Ecological Society Annual Meeting, Belfast, 12th-15th December 2023 [POSTER]

4.1 Introduction

Passive Acoustic Monitoring (PAM) is becoming increasingly widely used in site-level species and community surveys, as well as in longer-term monitoring schemes at regional and national levels. PAM methods have the potential to be scalable, standardisable, and financially viable, while also being substantially less labour intensive than traditional methods (Gibb *et al.,* 2019), especially if workflows can harness Artificial Intelligence (AI). The PAM approach is developing rapidly as it is adapted and piloted for a wide range of taxa, including terrestrial mammals (Enari *et al.*, 2019), birds (Pérez-Granados, 2021), amphibians (Desjonquères, 2020), and insects (Newson *et al.*, 2017); hydrophones also enable the technology to be used within marine environments, particularly for cetaceans (Mellinger *et al.,* 2007). However, despite wide taxonomic potential, bats are the primary species group to which PAM is applied in the terrestrial environment (Sugai *et al.,* 2019). Unlike surveying bats using traditional walked transect surveys, which are labour intensive and temporally restricted (Collins, 2023; Perks and Goodenough, 2021; Chapter Three), collecting bat data using passive detectors requires little to no surveyor input once deployed. Detectors also automatically record bat activity for whole nights, and for several consecutive nights, vastly improving the temporal sampling range when compared to transect surveys (Gibb *et al.*, 2019). This increased temporal sampling range increases the likelihood of detecting both later emerging bats, as well as species that are locally less prevalent (Perks and Goodenough, 2021; Chapter Three).

Bat detectors used in PAM frameworks were first developed in the late 1980s. Initially they were simple units, adapted from heterodyne detectors used for walked transects, that recorded bat calls onto cassette tape. Purpose-built detectors emerged onto the market in the early 2000s, expanding the capability of acoustic surveys considerably (Browning *et al.,* 2017). Such detectors comprise a fully waterproof housing, similar in design to a camera trap, typically with an omnidirectional microphone fitted either directly to the detector, or indirectly via an extension cable. However, storing the quantity of data generated over extended survey periods presented an initial challenge. Recording ultrasound at the high sampling rates needed to study bats in full spectrum produces large waveform audio (.wav) files, the storage of which, even temporarily within the units, needs considerable memory (Frick, 2013).

The design of passive bat detectors has evolved as the technology has advanced. Among the key attributes that continue to improve are unit size (becoming smaller) together with data storage capacity (larger) and battery life (longer) (Merchant *et al.*, 2015). Detectors are now manufactured by multiple companies, with the specifications of models available, often varying substantially (Adams *et al.*, 2012). Frequency division and zero crossing (zc) devices, such as those within the Anabat range (Titley Scientific, Australia) launched in the 1990s, were the first to offer a solution to prohibitive data storage limitations by reducing the amount of call information written, initially to cassette tape, and later on to a memory card (Corben, 2004). This allowed multiple nights of data to be stored on a single memory card. The Anabat Express system, launched in 2014, then provided a second breakthrough in device power by prolonging battery life for approximately two weeks (Titley Scientific, 2023). Further developments in storage capacity of memory cards have recently made recording in full spectrum for extended periods possible. This means that most passive detectors currently available record in full spectrum, either exclusively or with the surveyor having the choice between full spectrum and zc formats. However, hardware costs remain a limiting factor in many applied ecology contexts as commercial PAM devices remain substantially more expensive than camera traps. This has thus far hindered the scalability of PAM, towards the use of multi-device networks at large spatial scales (Gibb *et al.*, 2019). At the time of writing, passive bat detectors available to purchase in the UK range from approximately 700 GBP for the Batlogger S2 (Elekon, Switzerland) to >7000 GBP for the Batmode 2S+ system (bioacoustic technology, Germany) for remotely monitoring bat activity at wind turbines (Wildcare, 2024). Comparatively, camera traps typically range from 55 GBP up to 600 GBP per unit (NHBS, 2024).

The introduction of open-source acoustic loggers, such as the AudioMoth (Hill *et al.*, 2019), has created opportunities for researchers and practitioners to access PAM at a much lower price point. AudioMoths are currently available to purchase at approx. 75 GBP per unit (LabMaker, 2025). Despite this, however, they do not represent a 'silver bullet' to the high financial costs associated with PAM. The microelectromechanical systems (MEMS) microphones used are not as efficient as those used in commercial ultrasonic detectors, and data quality, therefore, is not as high (Gibb *et al.*, 2019). Very recent developments have led to the release of configurable amplitude and frequency triggers for AudioMoth, however, their reliability and how they compare to the sophisticated built-in triggering ability of commercial units has yet to be rigorously tested. In the absence of a trigger, AudioMoth users configure the devices to either record continuously (Revilla-Martin *et al.,* 2020; López-Bosch *et al.*, 2022), which is demanding in terms of battery life and data storage, or using sleep and wake on a pre-configured cycle (e.g. Bota *et al.,* 2023; Kunberger and Long, 2023; Starbuck *et al.,* 2024). The latter allows more nights of data collection without the need for surveyor intervention but decreases the amount of data recorded per night, which risks missing species. The former provides more data overall, but the surveyor time associated with frequent maintenance visits to download data or replace memory cards and batteries contributes to survey costs in ways that are not always considered when simply comparing per unit price (Gibb *et al.,* 2019). Finally, there is still uncertainty regarding the recording quality (Kunberger and Long, 2023) and detection capability of ultrasonic sound (Brinkløv *et al.*, 2023) compared to commercial units. Poor recording quality could have implications for data analysis and accurate identification of species, especially those that echolocate at higher frequencies (e.g. *Rhinolophus* spp.) or with low energy calls (e.g. *Plecotus* spp.). This could be a substantial issue, especially when data processing is undertaken using automated classifiers (Barré *et al.*, 2019).

There is a longstanding need to both optimise and standardise passive acoustic sampling schemes for bats in relation to habitat and target species, as well as available funds and resources (Froidevaux *et al.*, 2014). In the UK, the Bat Conservation Trust (BCT) bat survey guidelines (Collins, 2023) set out specific recommendations in relation to conducting passive bat surveys, typically for commercial applications, such as impact assessments. The level of survey effort (number of detectors, number/duration of surveys) recommended is determined by surveyor assessment of habitat suitability for bats. A minimum monitoring period of five days in suitable weather conditions is specified, regardless of habitat type, with the number of replicates required dependent on adjudged habitat quality. This ranges from three seasonal replicates (spring, summer, and autumn) for sites with habitat assessed as low quality, to seven replicates (monthly between April to October) for sites with habitat assessed as medium or high quality. Additionally, habitat suitability for bats was originally used to subjectively determine the number of locations within each site that should be sampled. In the previous edition of the guidelines (Collins, 2016), this ranged from one location for low quality up to three locations for high quality. In the latest edition (Collins, 2023), this was updated to state that detector locations should instead provide a representative sample of the habitats present within the site. This remains somewhat subjective, and does not specifically consider the overall size of individual sites, or differing requirements for the habitats found in heterogeneous sites, and how this might impact the efficacy of passive surveys. Moreover, as PAM technology available continues to become both more accessible and capable, a wider range of protocols for surveying and monitoring are becoming feasible for practitioners, many of which are yet to be empirically tested and compared to established protocols. It should also be noted that any updated recommendations should allow for the fact that “optimisation” of PAM frameworks is multifaceted as it involves considerations around detectors (type, settings, and number) and deployment (duration and replicates) that affect both the amount and quality of data, and survey costs (Figure 4.1).

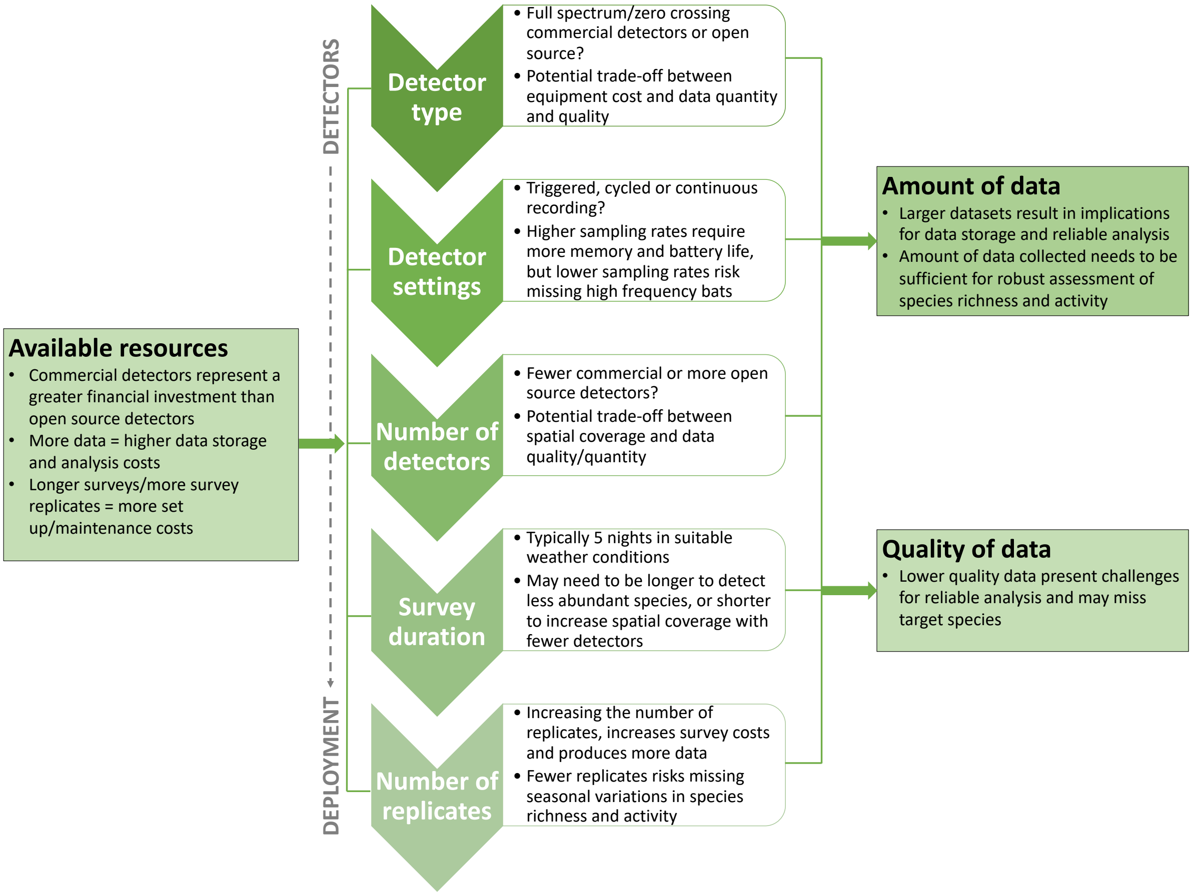


Figure 4.1: *Elements of passive acoustic bat survey design that need to be considered when optimising sampling schemes.*

This chapter empirically tests three types of passive acoustic detectors in surveying bats: full spectrum commercial detectors (Anabat Swift, approx. £1000), zc commercial detectors (Anabat Express, approx. £700), and open-source acoustic loggers (AudioMoth) to investigate: (1) their comparative performance in different habitats when deployed simultaneously at the same location, (2) variation in detections made by co-located AudioMoths using different sampling rates to further explore the trade-off between data storage and data quality, and (3) how the use of multiple detectors at the same site (simultaneously deployed, multiple temporal replicates, or surveying being undertaken in different parts of the site) affects the data collected.

4.2 Methods

Bat activity was recorded for a total of 112 nights between mid-June and mid-October 2022, across four sites, each representing a different habitat type (riparian, woodland, wood pasture and arable). To provide an element of (semi-independent) spatial replication, each site was split into two geographically-separated sub-sites. Monitoring was undertaken over a seven-day period in rotation thus: the first sub-site of each of four sites was monitored over data collection weeks 1-4, followed by the second sub-sites over weeks 5-8. To provide an element of temporal replication, a compete second survey of all habitats and sub-sites was then undertaken from weeks 9-12 and 13-16 (Table 4.1). A seven-night recording period was undertaken to mitigate any nights of poor weather unsuitable for bats within the survey period. Only five nights of data were carried forward for analysis for any replicate of any sub-site as per the current bat survey guidelines in the UK (Collins, 2023).

Table 4.1: *Monitoring schedule for each site and sub-site across the 16-week study period (1=riparian, 2=woodland, 3=wood pasture, 4=arable)*

Week	Date	Site	Sub-site	Replicate
1	16/06/22 – 23/06/22	Riparian	1	1
2	24/06/22 – 01/07/22	Woodland	1	1
3	01/07/22 – 08/07/22	Wood pasture	1	1
4	08/07/22 – 15/07/22	Arable	1	1
5	15/07/22 – 22/07/22	Riparian	2	1
6	22/07/22 – 29/07/22	Woodland	2	1
7	29/07/22 – 05/08/22	Wood pasture	2	1
8	05/08/22 – 12/08/22	Arable	2	1
9	12/08/22 – 19/08/22	Riparian	1	2
10	19/08/22 – 26/08/22	Woodland	1	2
11	26/08/22 – 02/09/22	Wood pasture	1	2
12	02/09/22 – 09/09/22	Arable	1	2
13	12/09/22 – 19/09/22	Riparian	2	2
14	19/09/22 – 26/09/22	Woodland	2	2
15	26/09/22 – 03/10/22	Wood pasture	2	2
16	03/10/22 – 10/10/22	Arable	2	2

4.2.1 Detector types

Three types of ultrasonic bat detectors were used to record bat echolocation call sequences: Titley Scientific (Australia) automated bat detectors (n=4) and Open Acoustic Devices (United Kingdom) AudioMoth full-spectrum acoustic loggers (n=10). The Titley Scientific devices comprised Anabat Swift full-spectrum bat detectors (n=2) and Anabat Express zero-crossing (zc) bat detectors (n=2). Both Anabat models were housed in weatherproof cases, designed for extended periods of deployment, and were deployed in lock boxes or fixed into position with cable ties. The AudioMoth devices were not weatherproof. Only three proprietary AudioMoth waterproof cases were available from the stockist at the time of the study, so deployment used a combination of these and seven modified electrical junction boxes (Figure 4.2).

***Figure 4.2**: Passive acoustic bat detectors: Anabat Swift (highlighted in yellow), Anabat Express (highlighted in white), AudioMoth in proprietary case (highlighted in blue), and AudioMoth in junction box case (highlighted in red).*

Manufacturing delays impacted the ability to acquire the necessary number of AudioMoths. Therefore, three AudioMoths were used in the first replicate at each sub-site (weeks 1-8), with an additional seven detectors arriving in time to be integrated into the study design for the second replicates (weeks 9-16) to enable testing of two different sampling rates: 250 kHz (low) and 384 kHz (high). AudioMoths configured with a 250 kHz sampling rate are hereby referred to as Low Frequency AudioMoth (LFAM), and those configured with a 384 kHz sampling rate as High Frequency AudioMoth (HFAM).

All the detectors were powered by AA batteries, renewed at the end of each recording period to prevent any battery failures. Detectors recorded data onto either SD cards (Anabat Swift = 64GB + 32 GB, Anabat Express = 32 GB) or microSD cards (LFAM = 32GB, HFAM = 64GB)). All data were downloaded, and the cards erased, before redeployment.

4.2.2 Detector configuration

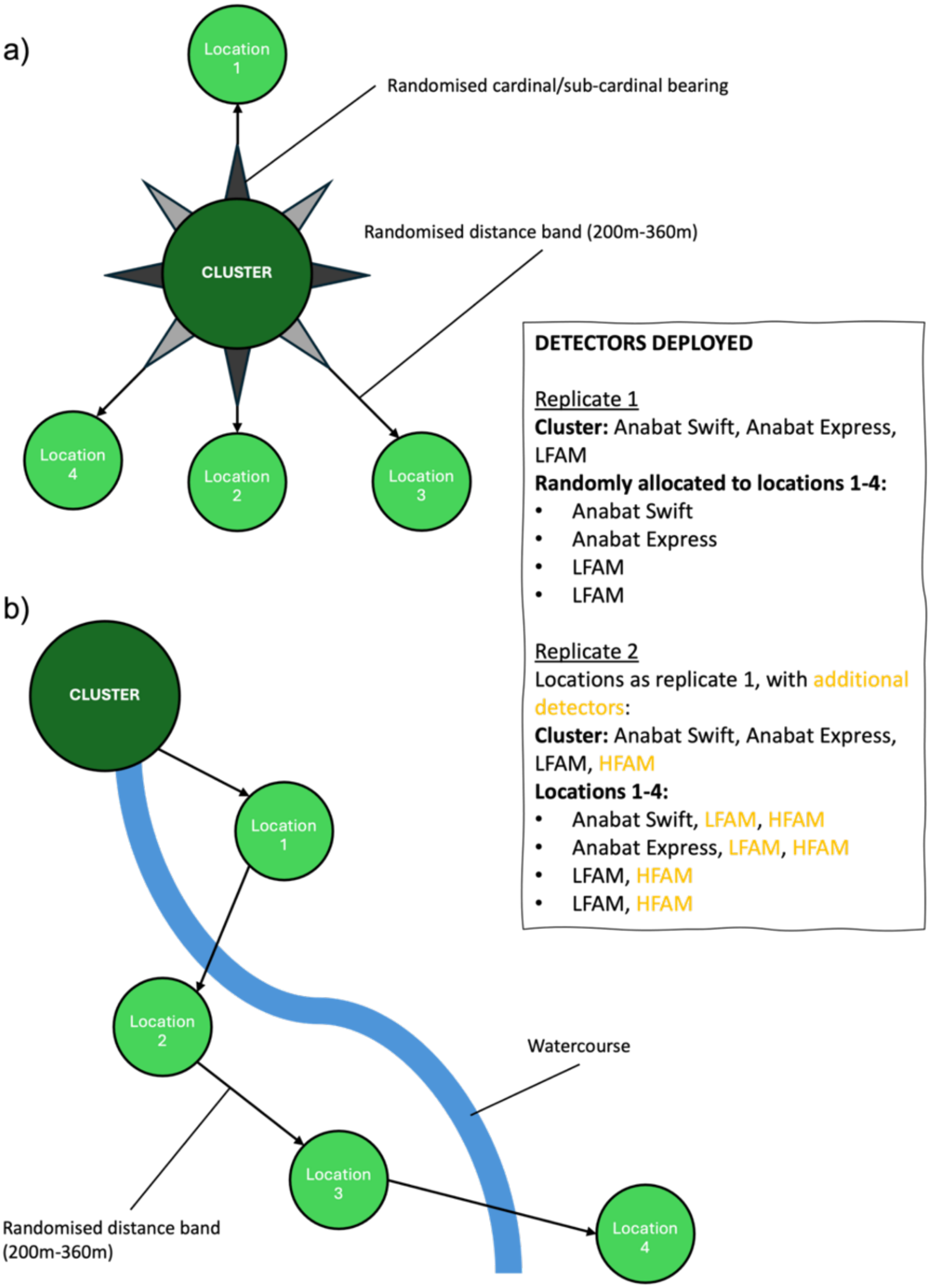
The Titley Scientific detectors were configured to use their standard on-board trigger, so that only sounds that met the pre-programmed criteria based on known parameters for bat calls, were recorded. They were configured to record all night at their standard sampling rate of 500 kHz, and to automatically switch on 30 minutes prior to sunset and switch off 30 minutes after sunrise, with these times determined via a GPS fix for the deployment location. At the time of this study, the AudioMoth did not feature a reliable trigger specifically for bats, so these detectors were configured to record all sound based on a pre-determined sleep:wake cycle. The times at which the detectors were to switch on and off were configured at set-up: starting recording 30 minutes before sunset and stopping 30 minutes after sunrise, according to the sun times for the longest night of the each seven-day recording period. To facilitate storing seven nights of data onto each 32GB microSD card supplied with the detectors, the LFAMs were configured to record on a five-second record, 15-second sleep cycle, for the first replicates. For the second replicates, the LFAMs were configured on a five-second record, 25-second sleep cycle (the longer sleep period relative to LFAM settings in replicate one was necessary to facilitate data collection throughout the longer nights later in the survey season), and the HFAMs, configured on a five-second record, 20-second sleep cycle. The HFAMs utilised larger 64GB microSD cards, which were supported by the more recent AudioMoth units.

4.2.3 Detector location

For each recording replicate at each sub-site, the detectors were deployed at five locations. To enable a direct comparison of detectors, there was one single “cluster” that comprised one of each detector type (Anabat Swift, Anabat Express and LFAM for replicate one; Anabat Swift, Anabat Express, LFAM, and HFAM for replicate two). The location for the cluster within each sub-site was chosen subjectively, both to maximize the likelihood of recording bats (as would typically happen within ecological consultancy) and to act as a centralised location for the deployment of the four additional detectors (replicate one) or 10 additional detectors (replicate two). In non-linear habitats (woodland, wood pasture, arable) the four additional detector locations were situated around the central cluster based on three levels of random allocation. Firstly, the eight cardinal and sub-cardinal bearings radiating from the central cluster were allocated a number (1-8), and four bearings selected using a random number generator. If a bearing wasn’t accessible within the area of the sub-site, or had already been used, random numbers continued to be generated until four feasible bearings had been selected. Secondly, the position of the detector along the bearing was also randomised after allowing for appropriate inter-detector distances. Titley Scientific specifies that lower frequency calling bats (e.g. noctule) can be detected by their Swift and Express devices from a distance of up to 100m (Titley Scientific, 2024). Although the detection distances for the AudioMoth are still largely unresearched, it was concluded these were unlikely to exceed that of the Swift and Express units, especially considering the lower quality of the MEMS microphone. Thus, to ensure that detections made by each of the devices outside the cluster were truly independent both in relation to one another and to the cluster, a minimum distance of 200m between all locations was used. Successive numbered “zones”, each 20 m in length were laid out along each bearing starting at 200 m from the cluster to a maximum of 360 m (based on logistical constraints). The location at which the detector would be located along the bearing was determined randomly. The third and final step was a random allocation of the specific detector type to each location. A similar process was used in linear (riparian) habitats, whereby the additional locations were located one side (upstream or downstream) of the main cluster, with distances (but not bearings) and detector allocation per location randomly determined as for non-linear habitats. In all cases, minor adjustments were made in the field as necessary based on location of trees or fence posts upon which to mount the detectors.

Detectors were deployed at least 1 m above the ground using suitable features, most commonly trees, shrubs, and fences, with microphones orientated towards open space to increase the likelihood of ultrasonic sound reaching the microphone. Where appropriate, the microphone extension cable was used to facilitate the placement of the Titley Scientific detectors, either where vegetation was not substantial enough to secure the detector at a suitable height from the ground, or at sites with a high public presence, for better concealment.

The number of detectors (but not the number of locations in which detectors were placed) differed between replicates. During the first replicates, one of each detector type; Anabat Swift (full-spectrum), Anabat Express (zero-crossing) and AudioMoth (full-spectrum) were deployed together at the cluster location to conduct a direct comparison between detector types. The remaining four detectors; Anabat Swift (n=1), Anabat Express (n=1) and AudioMoth (n=2) were deployed individually at the remaining four locations to increase spatial coverage. During the second replicates, the Anabat detectors remained at the same locations as in the first, but two AudioMoths (LFAM and HFAM) were deployed at each of the five locations. This is summarised in Figure 4.3, which also illustrates the spatial arrangement of detector locations described above.



DETECTORS DEPLOYED

Replicate 1

Cluster: Anabat Swift, Anabat Express, LFAM

Randomly allocated to locations 1-4:

- Anabat Swift
- Anabat Express
- LFAM
- LFAM

Replicate 2

Locations as replicate 1, with additional detectors:

Cluster: Anabat Swift, Anabat Express, LFAM, HFAM

Locations 1-4:

- Anabat Swift, LFAM, HFAM
- Anabat Express, LFAM, HFAM
- LFAM, HFAM
- LFAM, HFAM

Figure 4.3: *Determination of monitoring locations in relation to the "cluster" location and detector allocation in (a) non-linear and (b) linear habitats. Gold text details detectors added for the second replicates.*

4.2.4 Site-specific setup

The four field sites were situated within a 20 km radius in the south Worcestershire/north Gloucestershire region of the UK. All sites were split to encompass two adjacent sub-sites. Figure 4.4 below illustrates the broad areas within each site determined as being suitable for detector deployment, for each of the sub sites. The individual monitoring locations within each, and the detectors allocated, were then determined following the methods set out in section 4.2.3.

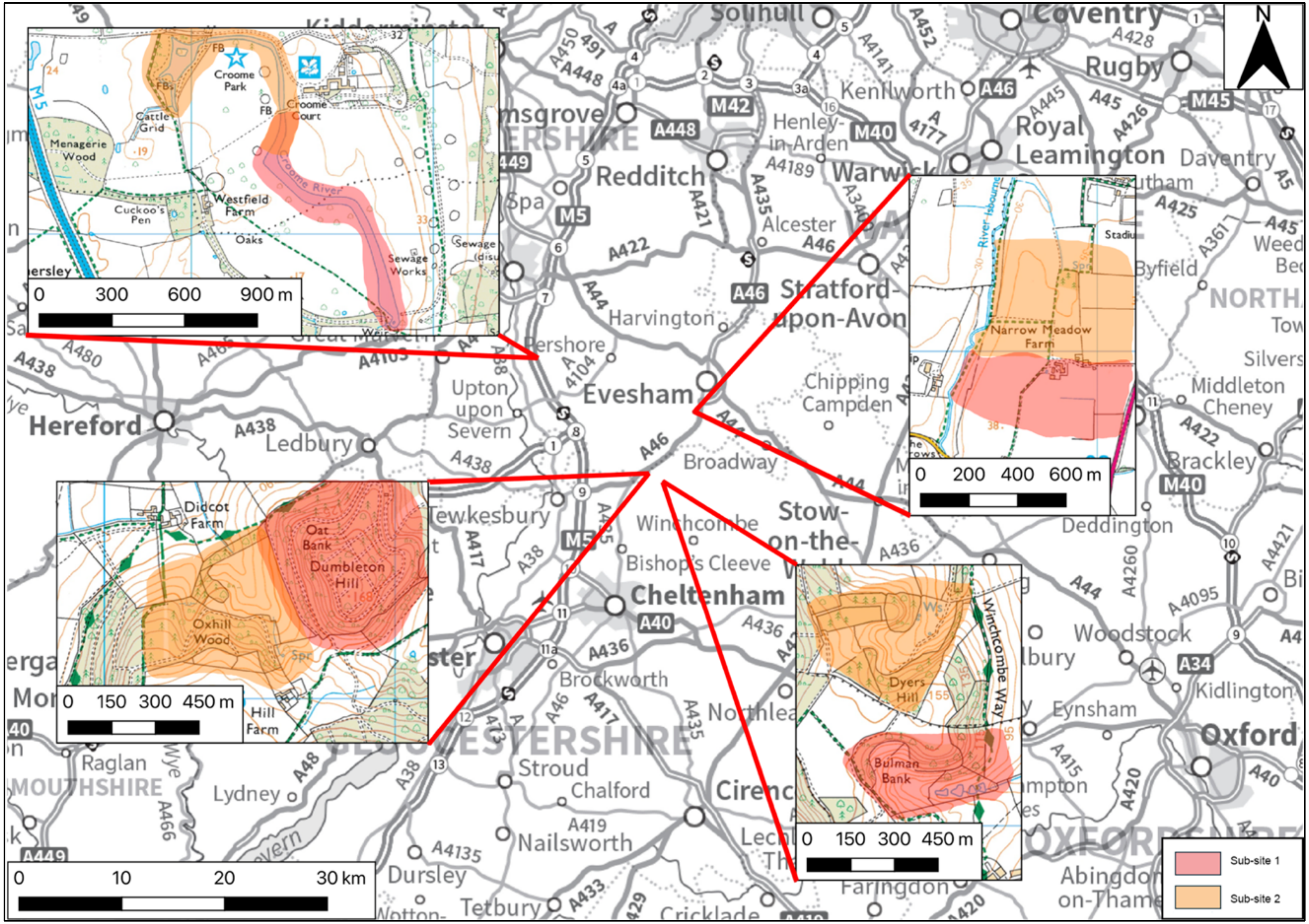


Figure 4.4: *Locations of the four study sites within the Worcestershire/Gloucestershire area of the UK. Anti-clockwise from top left: riparian, woodland, wood pasture, arable farmland. Overlay indicates broad areas suitable for detector deployment, for each sub-site.*

4.2.1.1 Riparian

The riparian site was situated within the estate at Croome Court, south Worcestershire, 5.6km west of Pershore, centred on 52°05’51”N, 002°10’08”W. The estate occupies approximately 270 ha and has been managed by the National Trust since 2007. The Croome River, a 1.7 km long artificial watercourse inclusive of a lake at its northern extent, transects the parkland. The southern end of the Croome River was used as the first sub-site, and the northern end, including the lake, as the second (Figure 4.5), with the cluster locations situated at each extent. The randomised distances between each monitoring location, necessitated a slight overlap between sub-sites, at the centre of the watercourse, but these were never monitored at the same time such that the sub-sites were semi-independent rather than fully independent but that, crucially, there was no pseudoreplication within each sub-site replicate.

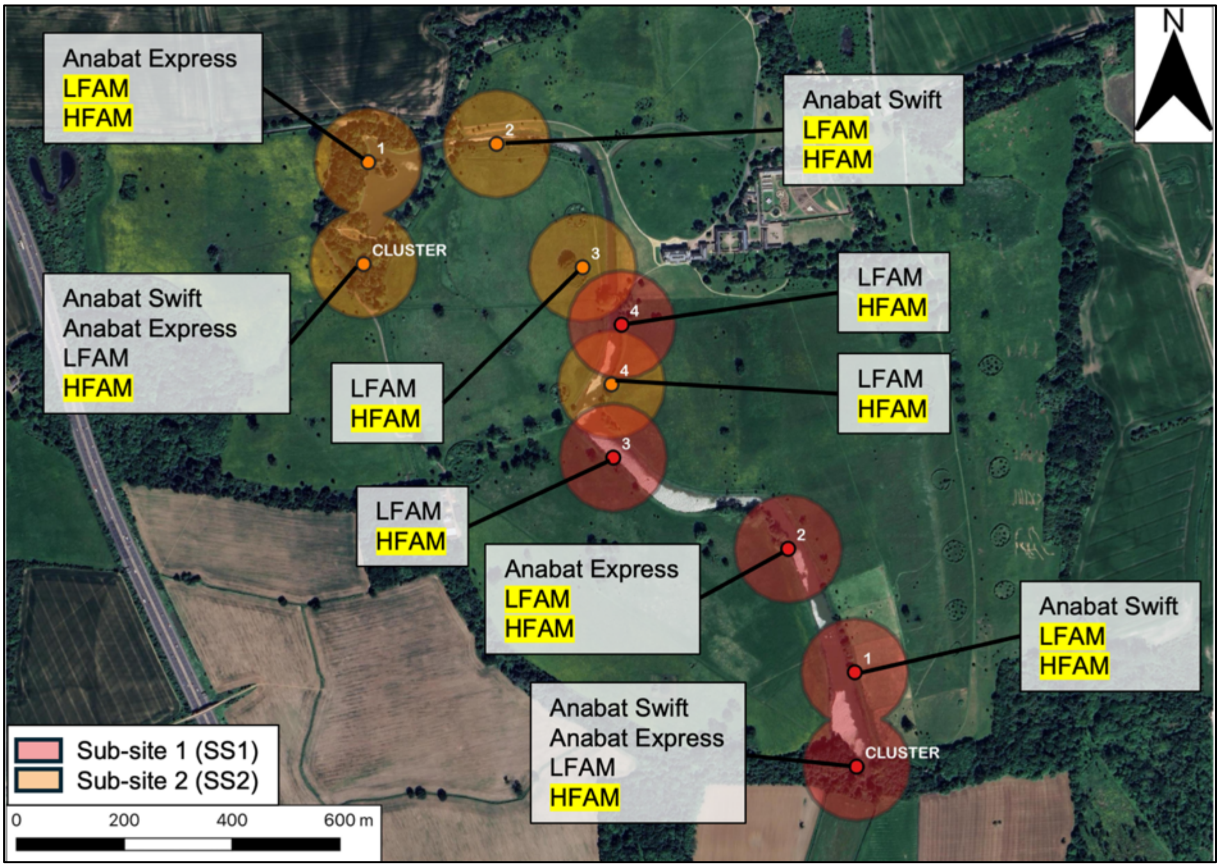


Figure 4.5: *Monitoring locations within the two sub-sites, within the riparian site (detectors highlighted in yellow added for the second replicate). Sub-site overlay shows a 100m buffer around the monitoring locations within each sub-site, as an indication of the maximum spatial extent covered by each detector.*

4.2.1.2 Woodland and wood pasture

The woodland and wood pasture sites were situated within the Dumbleton Estate in north Gloucestershire, approximately 12 km east of Tewkesbury. The estate is managed under middle tier Countryside Stewardship (CS), with all woodland areas subject to woodland management plans. Woodland to the north of the estate was selected to represent woodland habitat (Figure 4.6). The two parcels of woodland on the northern edge of the estate, Oxhill Wood to the west and the woodland on Dumbleton Hill to the east, were used as the two sub-sites, with each cluster location positioned on opposite sides of the open valley between the two. Similarly to the riparian site, the randomised distances and bearings resulted in a slight overlap between sub-sites, but these were monitored at different time periods.

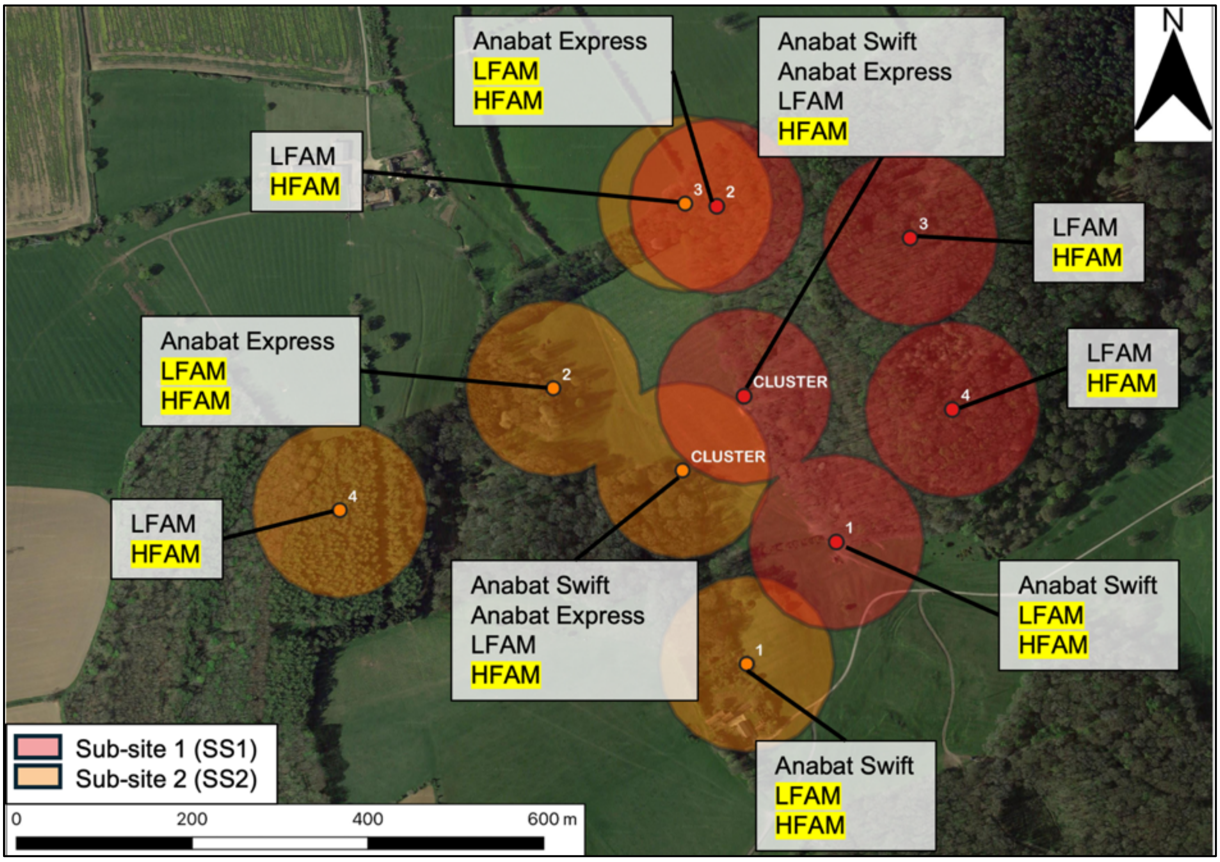


Figure 4.6: *Monitoring locations within the two sub-sites, within the woodland site (detectors highlighted in yellow added for the second replicate). Sub-site overlay shows a 100m buffer around the monitoring locations within each sub-site, as an indication of the maximum spatial extent covered by each detector.*

More open areas of sheep-grazed pasture and parkland, with areas of young woodland and scrub to the south of the estate, were used to sample high quality wood pasture habitat (Figure 4.7). The first sub-site was situated within and around the deep valley enclosed by Bullman Bank to the south. The valley leading up to Dyers Hill to the north, was adopted as the second sub-site.

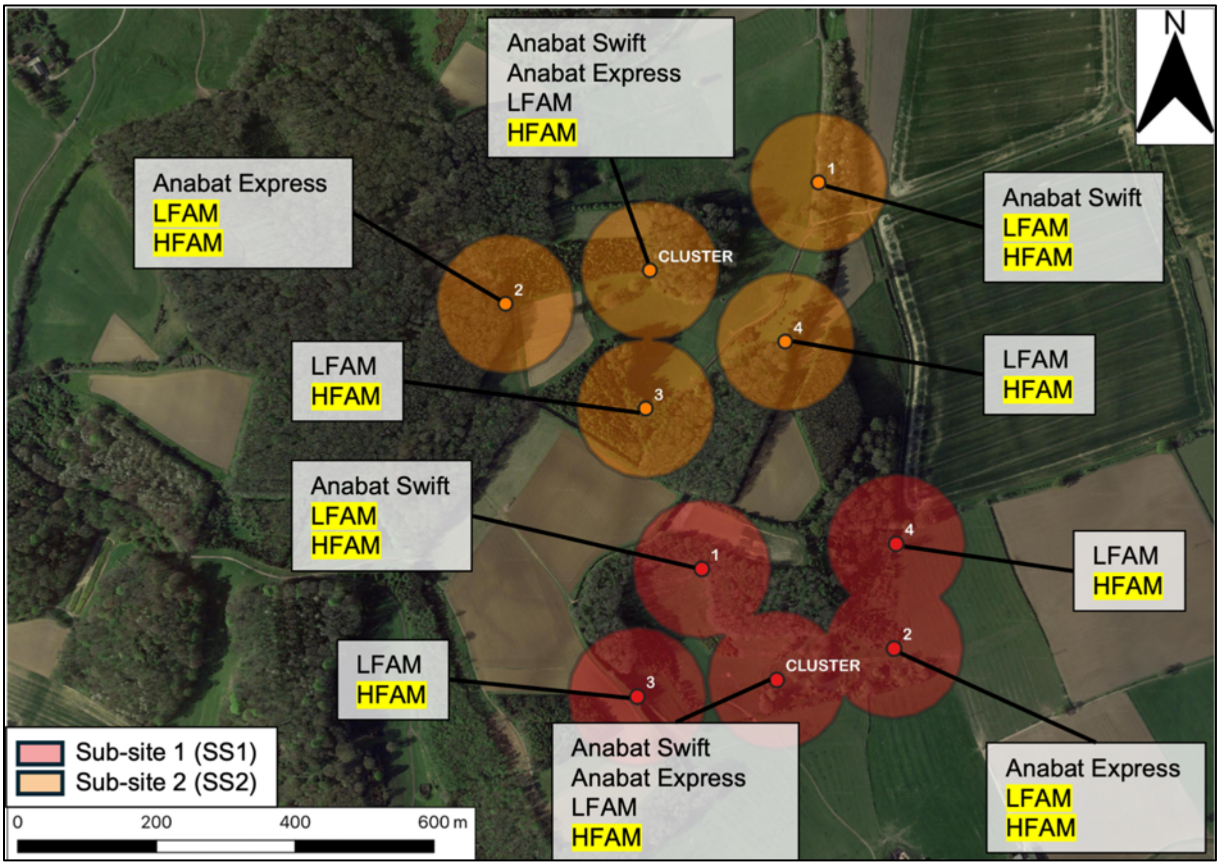


Figure 4.7: *Monitoring locations within the two sub-sites, within the wood pasture site (detectors highlighted in yellow added for the second replicate). Sub-site overlay shows a 100m buffer around the monitoring locations within each sub-site, as an indication of the maximum spatial extent covered by the detectors*

4.2.1.3 Arable

The arable farmland site was situated in Hinton-on-the-Green, South Worcestershire, approximately 4 km south of Evesham. The site comprises arable farmland, situated between the A46 trunk road to the east, and the river Isbourne to the west. At the time of the study the land was planted with either wheat, or a meadow grassland mix for hay, and was not managed under any CS options. The farm was broadly divided in two, with fields in the southern half forming the first sub-site, and fields to the north, forming the second sub-site (Figure 4.8).

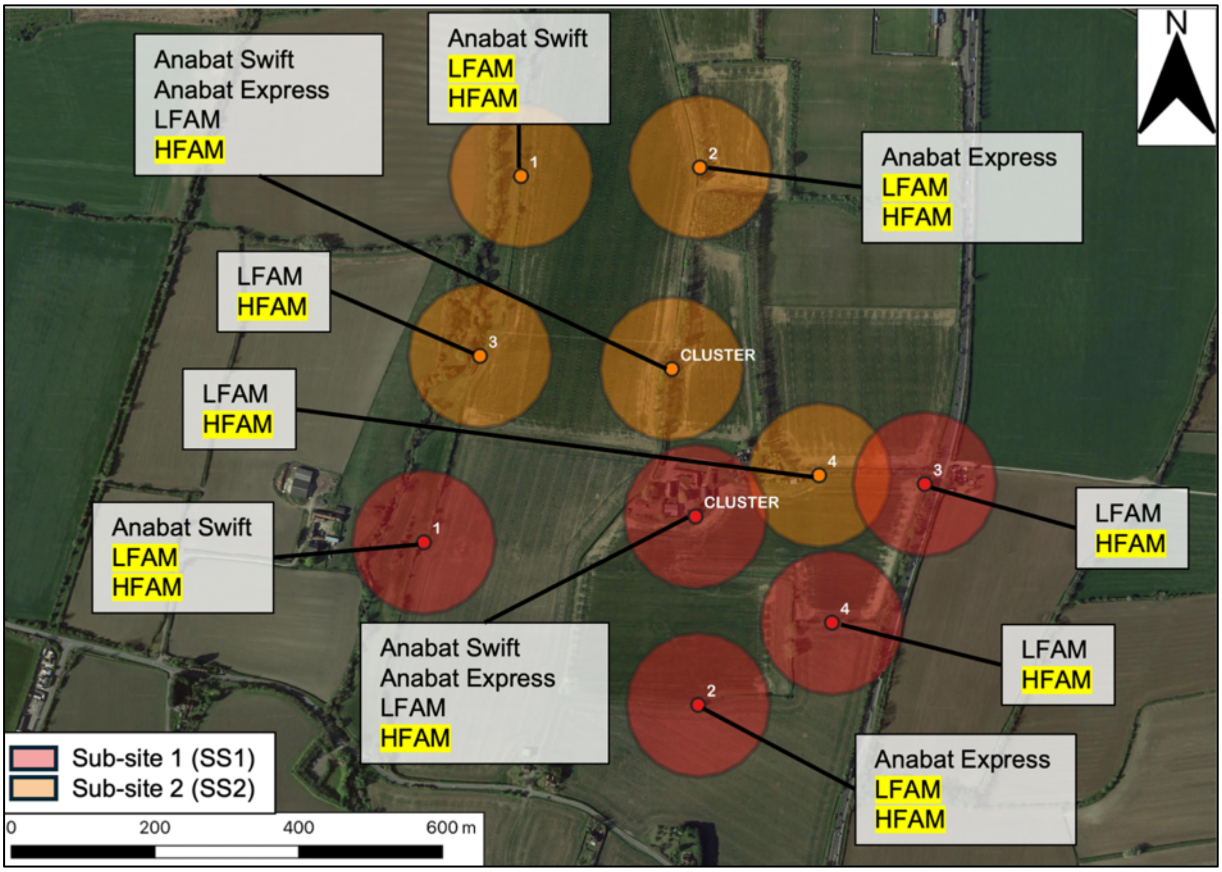


***Figure 4.8**: Monitoring locations within the two sub-sites, within the arable farmland site (detectors highlighted in yellow added for the second replicate). Sub-site overlay shows a 100m buffer around the monitoring locations within each sub-site, as an indication of the maximum spatial extent covered by the detectors.*

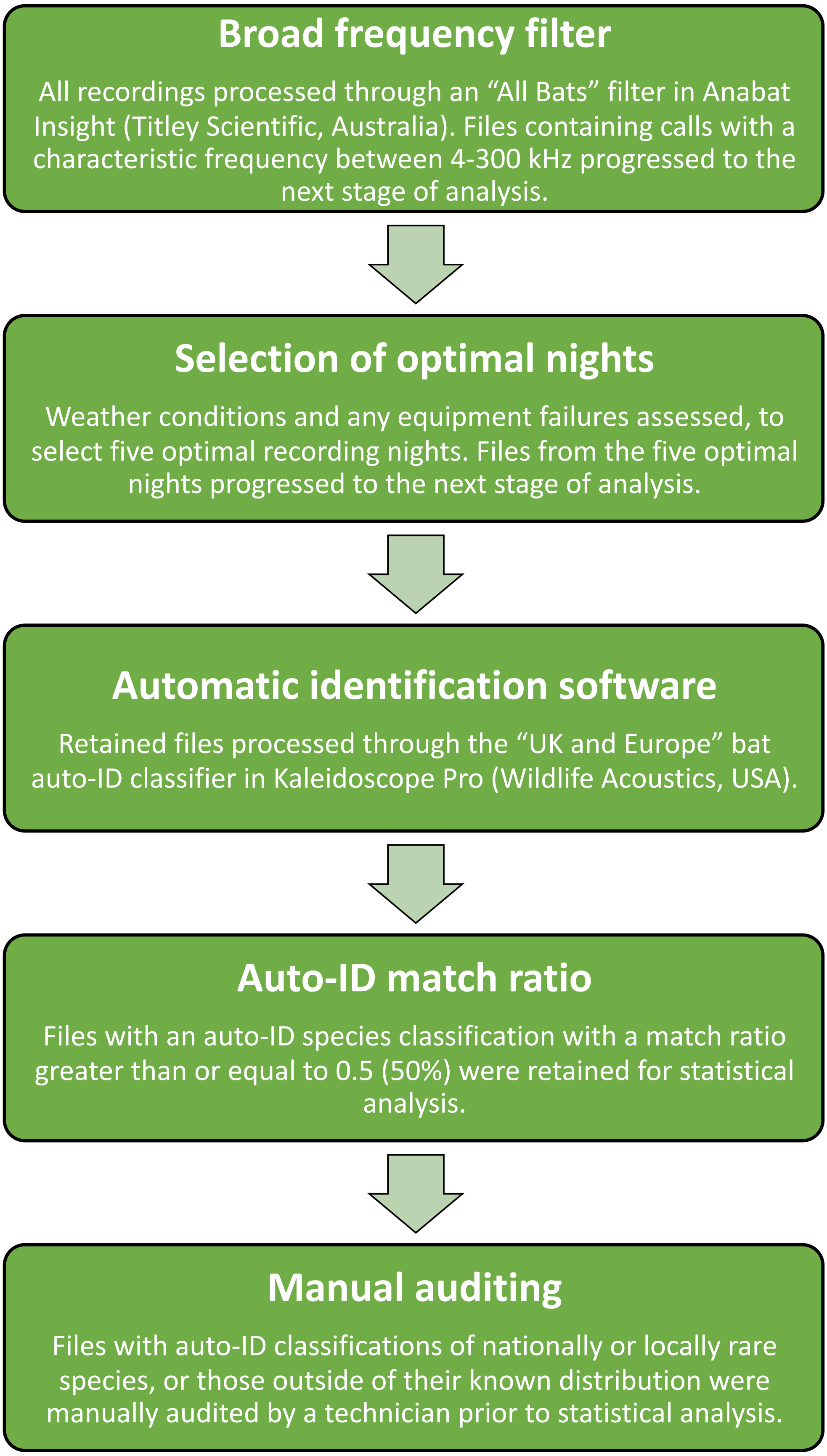
4.2.4 Acoustic data processing

At the end of each 7-day monitoring period all data recorded were transferred onto a central hard drive and the memory cards erased ready for the next monitoring period.

To assist data storage, particularly with the AudioMoth detectors that recorded continually when “awake”, a broad frequency filter (“All bats” in Anabat Insight) was used initially to necessitate only storing those recordings likely to contain bat calls. Recordings which did not contain sound with a characteristic frequency within a generous range for bats (4-300 kHz) were not retained for further processing. Next, the weather conditions for each recording period were assessed. The first five nights of data for each recording period were carried forward, except in the event of poor weather or equipment failure, whereby the affected night or nights were substituted for more optimal consecutive nights later in the recording period.

Five nights of acoustic bat data for each monitoring period was processed through Kaleidoscope Pro’s bats of Europe (v. 5.4.0) auto-ID classifier, to remove recordings of noise and obtain species classifications. Kaleidoscope’s auto-ID classifier analysed each call within a recorded sequence and compared them to an extensive reference library for the region, before making a single species classification for the sequence and reporting the match ratio. To minimise false positives, Barré *et al.* (2019) recommend only retaining classifications with a reported confidence score greater than or equal to 0.5 (50%). The match ratio reported by Kaleidoscope Pro is often used as a measure of self-reported classifier confidence (Braun de Torrez *et al.*, 2017b; Springall *et al.*, 2019; Smith *et al.*, 2021; Taille *et al.*, 2021). Therefore, only those recordings with a match ratio greater than or equal to 0.5 (50%), were carried forward for statistical analysis. Once the automated classifications were obtained, classifications for species challenging to differentiate acoustically were grouped: Brandt’s bat (*Myotis brandti*) and whiskered bat (*Myotis mystacinus*) were grouped, and grey long-eared bat (*Plecotus austriacus*) classifications were grouped with those of brown long-eared bat (*Plecotus auritus*) to form a single ***Plecotus*** group. Records for grey long-eared are scarce, but cannot be distinguished from the much more widespread brown long-eared bat on acoustics alone (Crawley *et al.*, 2020).

A random sub-set of recordings from each classification species/group were manually audited to verify classification plausibility and verify species presence. After manual auditing, recordings classified as Alcathoe bat (*Myotis alcathoe*) and Bechstein's bat (*Myotis bechsteinii*), were not carried forward for statistical analysis. Both species are relatively sparsely distributed and challenging to discern from other *Myotis* species acoustically. Recordings classified as greater horseshoe bat (*Rhinolophus ferrumequinum*) were also discounted as none of the audited files were found to contain greater horseshoe calls. Finally, recordings classified as Nathusius' pipistrelle (*Pipistrellus nathusii*) were discounted from statistical analysis. Although geographically widespread, few colonies have been identified nationally, calling into question the reliability of the classifications. All remaining species classifications were carried forward following manual auditing of a subset of recordings. A summary of the workflow adopted to process these raw acoustic data is shown in Figure 4.9.



Broad frequency filter

All recordings processed through an “All Bats” filter in Anabat Insight (Titley Scientific, Australia). Files containing calls with a characteristic frequency between 4-300 kHz progressed to the next stage of analysis.

Selection of optimal nights

Weather conditions and any equipment failures assessed, to select five optimal recording nights. Files from the five optimal nights progressed to the next stage of analysis.

Automatic identification software

Retained files processed through the “UK and Europe” bat auto-ID classifier in Kaleidoscope Pro (Wildlife Acoustics, USA).

Auto-ID match ratio

Files with an auto-ID species classification with a match ratio greater than or equal to 0.5 (50%) were retained for statistical analysis.

Manual auditing

Files with auto-ID classifications of nationally or locally rare species, or those outside of their known distribution were manually audited by a technician prior to statistical analysis.

Figure 4.9: *Workflow adopted to store and process acoustic data.*

4.2.5 Statistical analysis

All statistical analyses were carried out in R 4.2.2 (R Core Team, 2022). To test how co-located passive bat detectors differed in performance in different habitats, multiple Friedman tests were used to explore variations in total bat activity and individual species/taxon activity from 20 (Swift, Express, LFAM) or 10 (HFAM) nights of recording per habitat using data from the central cluster where all detector types were co-located. It is recognised that bat activity is difficult to determine by passive acoustic techniques alone because sequences recorded by a particular species may be the result of a single bat remaining in close proximity to the microphone, or a larger number of individuals passing the detector. For consistency with Chapters Two and Three, in this study, bat “passes” were adopted as a metric of activity levels with a “pass” defined as a call sequence file as defined by the detector.

Analyses were conducted firstly on all data recorded by the four detectors each night, and secondly on two subsets of these data. Subset one included only those data recorded by the Express and the Swift when time-matched to the wake periods of the LFAM; subset two included only those data recorded by the Express and the Swift when time-matched to the wake periods of the HFAM. Analysis of these subsets was necessary to avoid the potential that differences between the AudioMoths and the Anabat devices might be driven by the latter having the ability to record all bats at any point throughout the night, whereas the AudioMoths were only able to record bats during their regular wake periods (two such subsets of the data were necessary, due to the LFAM and HFAM being configured on different recording cycles). Friedman tests, with paired Wilcoxon tests for post-hoc analysis, were firstly conducted on the overall species richness and total bat passes for each habitat, before conducting taxon specific analyses. To conduct meaningful statistical analysis all classifications in the genus *Myotis* were grouped into a single taxonomic group at genus level (***Myotis***). This approach was also taken to combine classifications from the genus *Nyctalus* with those of serotine, to form a single taxonomic group (***Nyctalus/Eptesicus***). The same analytical approach (Friedman tests with pairwise Wilcoxon undertaken as a form of post-hoc analysis) was used for these taxon-specific analyses. As seven species/taxonomic groups were analysed at each habitat, the significance values produced by these tests were Bonferroni adjusted to avoid family-wise error.

To test how co-located AudioMoths (one LFAM, one HFAM) recording at different sampling rates differed in performance in different habitats, Wilcoxon matched-pairs tests were used to explore variations in total bat activity, individual species/taxon activity and overall species/taxon richness, from ten nights of recording at each habitat. As multiple species/taxonomic groups were again analysed at each habitat, the results of the taxon-specific tests were Bonferroni adjusted.

To explore how having multiple units of each detector type, multiple sub-sites and multiple temporal replicates, affected the species richness recorded in different habitats, species accumulation curves were constructed using the function *specaccum* in R package *vegan* (Oksanen *et al.,* 2022). Data for detectors that were deployed for 20 nights at each site were used in the analysis (AudioMoth n=3, Swift n=2, Express n=2). Firstly, for the Anabat Swifts and Anabat Expresses, two accumulation curves were generated using cumulative species richness over successive nights for each habitat, the first using the combined data from two detectors (to simulate a situation when two detectors were deployed at a field site) and the second using the mean of the data from two detectors (to simulate a situation when one detector was deployed at a field site). Nightly data were added such that all data from the first sub-site represented nights 1-10, and data from the second-sub-site represented nights 11-20. As such, the second replicates at each sub-site commenced on nights six and 16 respectively, thus allowing both the effect of a second replicate, and a second sub-site, to be visualised. This approach was further applied to species richness data from 20-day monitoring periods at each habitat to examine the effects of multiple detectors, replicates and sub-sites on species richness for the AudioMoths, by plotting three accumulation curves (one detector, two detectors, three detectors).

4.3 Results

A total of 571,380 recordings made by all the detectors deployed across the duration of the fieldwork, passed the initial bat filter, and were carried forward for classification by Kaleidoscope Pro. Of these recordings, 108,228 were classified as bat passes by Kaleidoscope Pro, using a match ratio of ≥ 50%, with the split between the detector types shown in Table 4.2.

Table 4.2: *Percentages of recordings classified as bats by Kaleidoscope Pro, using a match ratio of ≥ 50%, for each detector type (LFAM = Low Frequency AudioMoth, HFAM = High Frequency AudioMoth).*

Detector type	Total no. recordings	No. bat passes (≥ 50% match ratio)	%
Anabat Swift	211,145	40,367	19.12
Anabat Express	101,491	28,161	27.75
LFAM (250 kHz)	177,655	29,700	16.72
HFAM (384 kHz)	81,089	10,000	12.33

A breakdown of the number of classifications made for each individual species is shown in Table 4.3. The majority of the classified bat passes were common pipistrelle (n=51,201) or soprano pipistrelle (n=33,519), followed by *Nyctalus* and serotine (n=14,201). After manual auditing, 538 bat passes were not carried forward for statistical analysis, being classified as Alcathoe bat (n=2), Bechstein's bat (n=46), Nathusius' pipistrelle (n=329), or greater horseshoe (n=61). See Methods for more detail.

Table 4.3: *Number of recordings for each species, carried forward for statistical analysis.*

Common name	**Scientific name**	**No. recordings**
Common pipistrelle	*Pipistrellus pipistrellus*	51,201
Soprano pipistrelle	*Pipistrellus pygmaeus*	33,519
Noctule	*Nyctalus noctula*	11,981
Daubenton's	*Myotis daubentonii*	3,780
Leisler's	*Nyctalus leisleri*	1,930
Brown long-eared/Grey long-eared	*Plecotus auritus/Plecotus austriacus*	1,578
Lesser horseshoe	*Rhinolophus hipposideros*	1,262
Barbastelle	*Barbastellus barbastellus*	929
Brandt's/Whiskered	*Myotis brandtii/Myotis mystacinus*	785
Natterer's	*Myotis nattereri*	435
Serotine	*Eptesicus serotinus*	290
Total		**107,690**

4.3.1 Co-located detectors

The detectors situated at the cluster location within each of the four sites recorded 46,428 bat passes in total: riparian = 17,650 (38.0%), woodland = 9,041 (19.5%), wood pasture = 16,537 (35.6%) and arable = 3,200 (6.9%).

4.3.1.1 Full dataset

Analysis of the full dataset found significant differences in the species richness and bat passes overall and per taxonomic group that were detected by the different detector types in all habitats (Table 4.4). Details of relative detector performance in the different habitats is given below, however, the general findings are: (1) there were few differences between the Anabat Swift and Anabat Express, (2) both Anabat detectors frequently performed better than either of the AudioMoths, and (3) the LFAM AudioMoth performed better than the HFAM.

Table 4.4: *Friedman test results comparing species richness or bat passes detected by the four detectors, conducted on the full dataset (df = 3 in all cases).*

	Riparian		Woodland		Wood pasture		Arable	
	χ^2	p	χ^2	p	χ^2	p	χ^2	P
Species richness	18.832	<0.001	29.234	<0.001	25.863	<0.001	24.469	<0.001
All bats	20.758	<0.001	30.000	<0.001	28.080	<0.001	25.948	<0.001
Common pipistrelle	19.653	0.001	26.196	<0.001	24.589	<0.001	18.582	0.002
Soprano pipistrelle	19.320	0.001	29.277	<0.001	25.024	<0.001	19.709	0.001
Plecotus	23.761	<0.001	23.543	<0.001	24.584	<0.001	19.800	0.001
Nyctalus/ Eptesicus	19.129	0.003	27.092	<0.001	22.055	<0.001	13.026	0.032
Myotis	23.761	0.002	23.761	<0.001	25.710	<0.001	23.062	<0.001
Lesser horseshoe	23.548	<0.001	27.710	<0.001	18.31	0.003	12.536	0.040
Barbastelle	2.000	1.000	27.903	<0.001	19.571	0.002	5.667	0.903

The best performing detectors for each of the species/taxonomic groups, at each habitat, are summarised below (Table 4.5) and are discussed in more detail below with reference to the supplementary figures at the end of the chapter.

Table 4.5: *Summary of best detector performance in analysis of the full dataset. Colour coding (key in column headings) indicates the superior detector type (where statistically significant, grey=no significant difference). Habitat codes: RI=Riparian, WL=Woodland WP=Wood Pasture, AR=Arable). See Figures S4.2-4.5 for details of values.*

	Express vs Swift	**Express vs LFAM**	**Express vs HFAM**	**Swift vs LFAM**	**Swift vs HFAM**	**LFAM vs HFAM**
Species richness	AR: Swift	RI: Express WL: Express AR: Express	**ALL HABS: Express**	**ALL HABS: Swift**	**ALL HABS: Swift**	RI: LFAM WL: LFAM WP: LFAM
All bats		AR: Express	RI: Express WL: Express AR: Express	RI: Swift WL: Swift AR: Swift	**ALL HABS: Swift**	RI: LFAM WL: LFAM
Common pipistrelle		AR: Express	WL: Express AR: Express	RI: Swift AR: Swift	RI: Swift WL: Swift AR: Swift	WL: LFAM
Soprano pipistrelle		AR: Express	RI: Express AR: Express	AR: Swift	RI: Swift AR: Swift	RI: LFAM
Plecotus	AR: Swift	RI: Express WL: Express WP: Express	RI: Express WL: Express WP: Express	WL: Swift WP: Swift AR: Swift	**ALL HABS: Swift**	RI: LFAM WL: LFAM WP: LFAM
Nyctalus/ Eptesicus	AR: Swift		AR: Express	AR: Swift	AR: Swift	RI: LFAM
Myotis		**ALL HABS: Express**	**ALL HABS: Express**	RI: Swift WP: Swift AR: Swift	**ALL HABS: Swift**	RI: LFAM WL: LFAM WP: LFAM
Lesser horseshoe		RI: Express WL: Express	WL: Express	RI: Swift WL: Swift AR: Swift	**ALL HABS: Swift**	
Barbastelle		RI: Express WL: Express	WL: Express WP: Express	WL: Swift WP: Swift AR: Swift	WL: Swift WP: Swift	

Post-hoc testing (plots are included as supplementary material at the end of this chapter) of species richness across the four habitats, emphasised the higher performance of the Anabat detectors which each having detected significantly higher mean number of species per night than either of the AudioMoths (LFAM or HFAM) in all habitats (Figure S4.1). However, the different Anabat units did not differ significantly from one another, in the riparian, woodland, and wood pasture habitats (Figure S4.1 a,d,g) in terms of species richness. Both Anabat detectors outperformed the AudioMoths within the arable habitat, however, the Swift detected significantly more species than the Express (Figure S4.1 j) in this instance.

In the riparian habitat (Figure S4.2), the Swift was the strongest of the four detectors, recording significantly more bat passes per night than the HFAM both overall and for all individual taxonomic groups except *Nyctalus*/*Eptesicus*. In this single exception, the only significant difference was that of the LFAM recording significantly more passes per night than the HFAM.

In the woodland habitat (Figure S4.3), post-hoc testing again highlighted the strengths of the commercial Swift and Express detectors. When considering passes recorded by all bat species, the Swift recorded significantly more bat passes per night than both the LFAM and the HFAM (Figure S4.3 a). The Express recorded significantly more bats than the HFAM, but no significant difference was found in the numbers detected when compared to the LFAM. The two commercial Anabat detectors did not differ significantly from one another. Moreover, the commercial detectors were each found to have recorded significantly more bat passes than either of the AudioMoths, for *Plecotus* (Figure S4.3 j), lesser horseshoe (Figure S4.3 s) and barbastelle (Figure S4.3 v). In contrast, and despite significant Friedman tests, no significant pairwise post-hoc comparisons were identified for soprano pipistrelle (Figure S4.3 g) or the *Nyctalus*/*Eptesicus* group (Figure S4.3 m).

In the wood pasture habitat (Figure S4.4), the Swift recorded significantly more bat passes per night than either of the AudioMoths for *Plecotus* (Figure S4.4 j), *Myotis* (Figure S4.4 p), and barbastelle (Figure S4.4 v). The Express also performed significantly better than either of the AudioMoths for these groups, except for Barbastelle. Additionally, the Swift recorded significantly more passes per night than the HFAM, for both all bats (Figure S4.4 a) and the lesser horseshoe group (Figure S4.4 s).

Finally, in the arable habitat (Figure S4.5), significantly higher numbers of bat passes were recorded by the Swift, which detected significantly more passes than both AudioMoths for all bats, and all taxonomic groups. Additionally, it detected significantly more passes than the Express in the brown long-eared (Figure S4.5 j) and *Nyctalus*/*Eptesicus* groups (Figure S4.5 m).

4.3.1.2 Temporally restricted datasets

Analysis of the two temporally restricted datasets (LFAM subset and HFAM subset), also found significant differences between the bats detected by the different detector types (Table 4.6). Significant differences were found extensively in the HFAM subset, but much less often in the LFAM subset, where the significant differences between detectors in both the species richness, and numbers of bat passes detected, were predominantly found in woodland.

Table 4.6: *Friedman test results comparing species richness or bat passes detected by the three detectors, for each of the AudioMoth (LFAM and HFAM) subsets (df = 2 in all cases).*

	LFAM								**HFAM**							
	Riparian		Woodland		Wood pasture		Arable		Riparian		Woodland		Wood pasture		Arable	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Species richness	4.831	0.089	7.420	0.025	4.906	0.086	3.397	0.183	10.316	0.006	18.200	<0.001	15.842	<0.001	17.684	<0.001
All bats	29.200	<0.001	24.700	<0.001	25.139	<0.001	15.158	<0.001	14.600	<0.001	2.811	<0.001	14.368	<0.001	15.744	<0.001
Common pipistrelle	22.354	<0.001	15.474	0.003	14.889	0.004	12.329	0.011	9.556	0.042	11.806	1.000	11.706	0.020	8.222	0.082
Soprano pipistrelle	21.641	<0.001	10.839	0.031	20.848	<0.001	4.333	0.573	14.000	0.005	12.560	0.019	10.207	0.043	14.774	0.003
Plecotus	7.2766	0.158	0.031	1.000	2.711	1.000	INSUFFICIENT DATA		13.000	0.008	7.189	0.013	8.539	0.098	INSUFFICIENT DATA	
Nyctalus/ Eptesicus	34.816	<0.001	24.514	<0.001	26.000	<0.001	7.404	0.123	8.267	0.016	11.200	0.192	7.294	0.183	9.769	0.038
Myotis	7.614	0.133	14.358	<0.001	1.793	0.317	1.857	1.000	7.1538	0.028	12.562	0.026	13.862	0.006	7.760	0.103
Lesser horseshoe	5.429	0.398	10.511	0.037	9.188	0.071	6.938	0.156	INSUFFICIENT DATA		11.812	0.013	5.546	0.437	3.500	0.869
Barbastelle	INSUFFICIENT DATA		9.418	0.063	0.696	1.000	INSUFFICIENT DATA		INSUFFICIENT DATA		18.200	0.019	5.765	0.392	INSUFFICIENT DATA	

The best performing detectors for each of the species/taxonomic groups, at each habitat, for each subset, are summarised below (Table 4.7)

Table 4.7: *Summary of best detector performance in analysis of the LFAM and HFAM subsets. Colour coding (key in column headings) indicates the superior detector type (where statistically significant, grey=no significant difference). Habitat codes: RI=Riparian, WL=Woodland, WP=Wood Pasture, AR=Arable).*

	LFAM subset			**HFAM subset**		
	Express vs Swift	**Express vs LFAM**	**Swift vs LFAM**	**Express vs Swift**	**Express vs HFAM**	**Swift vs HFAM**
Species richness					**ALL HABS: Express**	**ALL HABS: Swift**
All bats		RI: LFAM				WL: Swift AR: Swift
Common pipistrelle		RI: LFAM				
Soprano pipistrelle		RI: LFAM				RI: Swift AR: Swift
Plecotus					RI: Express	WL: Swift
Nyctalus/ Eptesicus		RI: LFAM AL: LFAM WP: LFAM				AR: Swift
Myotis				RI: Express	RI: Express WL: Express WP: Express	WL: Swift WP: Swift
Lesser horseshoe			WL: Swift		WL: Express	WL: Swift
Barbastelle					WL: Express	WL: Swift

Post-hoc testing (plots are included as supplementary material at the end of this chapter) of species richness across the four habitats did not find any significant pairs between detectors in the LFAM subset, despite an overall significant Friedman test result for the woodland habitat. Within the HFAM subset, the overall significant differences found, were seen to be driven by the AudioMoth detecting significantly fewer species at all habitats, a trend that was particularly pronounced in woodland (Figure S4.1 f). Moreover, no significant differences in species richness were found between the Swift and Express in analysis of the HFAM subset.

In the riparian habitat (Figure S4.2), significant differences in the numbers of bat passes recorded between detectors were found for the majority of the species/taxonomic groups in both subsets. Where significant differences were seen in analysis of the LFAM subset (all bats, common pipistrelle, soprano pipistrelle, *Nyctalus/Eptesicus*), the LFAM recorded significantly more bat passes than the Express in all cases. Conversely, the differences reported in all groups in analysis of the HFAM subset, were seen to be driven by either the Swift or the Express recording more bat passes than the HFAM, where significant pairs were found.

In the woodland habitat (Figure S4.3), analysis of the LFAM subset found few significant pairs, even for groups (all bats, common pipistrelle, soprano pipistrelle, *Myotis*) where the Friedman tests reported significant differences. In these cases, outlying nights with high numbers of passes appear to be driving these significant overall differences. Notably, the Swift detected significantly more passes for lesser horseshoe than the LFAM (Figure S4.3 t). Conversely, however, the LFAM recorded significantly more *Nyctalus*/*Eptesicus* passes than the Express (Figure S4.3 n). Post-hoc analysis of the HFAM dataset in woodland, found the Swift to have consistently recorded significantly more passes per night than the HFAM, both for all bats (Figure S4.3 c) and for *Plecotus* (Figure S4.3 l), *Myotis* (Figure S4.3 r), lesser horseshoe (Figure S4.3 u) and barbastelle (Figure S4.3 x).

In the wood pasture habitat (Figure S4.4), only a single significant pair was found in the LFAM subset, with the LFAM performing better than the Express, recording significantly more *Nyctalus*/*Eptesicus* passes (Figure S4.4 n). Moreover, few significant differences were found in analysis of the HFAM subset. The only significant pairs found in this subset, were the Swift and Express recording significantly more *Myotis* passes per night than the HFAM (Figure S4.4 r)

Finally, in arable habitat (Figure S4.5), no significant pairs were found in post-hoc testing of the LFAM subset, even in instances where the Friedman tests found an overall significant difference. Within the HFAM subset, for groups where overall differences were found; all bats (Figure S4.5 c), soprano pipistrelle (Figure S4.5 i), and *Nyctalus*/*Eptesicus* (Figure S4.5 o), these differences were found to be driven by the Swift detecting significantly more passes than the HFAM in all instances.

4.3.2 Co-located AudioMoths

The five pairs of AudioMoths, located at each of the five monitoring stations within each of the four sites for the second replicates, recorded 27,347 classified bat passes in total: riparian = 20,361 (74.5%), woodland = 2,533 (9.3%), wood pasture = 2,959 (10.8%) and arable = 1,494 (5.4%).

4.3.2.1 Species richness

There were significant differences in the richness of species detected by the AudioMoth pairs, across all four habitats. Across the pairs, the AudioMoths configured with a 250 kHz sampling rate (LFAM) detected significantly more bat species each night than those configured with a 384 kHz sampling rate (HFAM). This finding was consistent at all habitats: riparian (V=405, P<0.001), woodland (V=849.5, P<0.001), wood pasture (V=683, P<0.001), and arable (V=726, P<0.001). The mean species detected per night by each AudioMoth configuration, at each habitat, is shown in Figure 4.10.

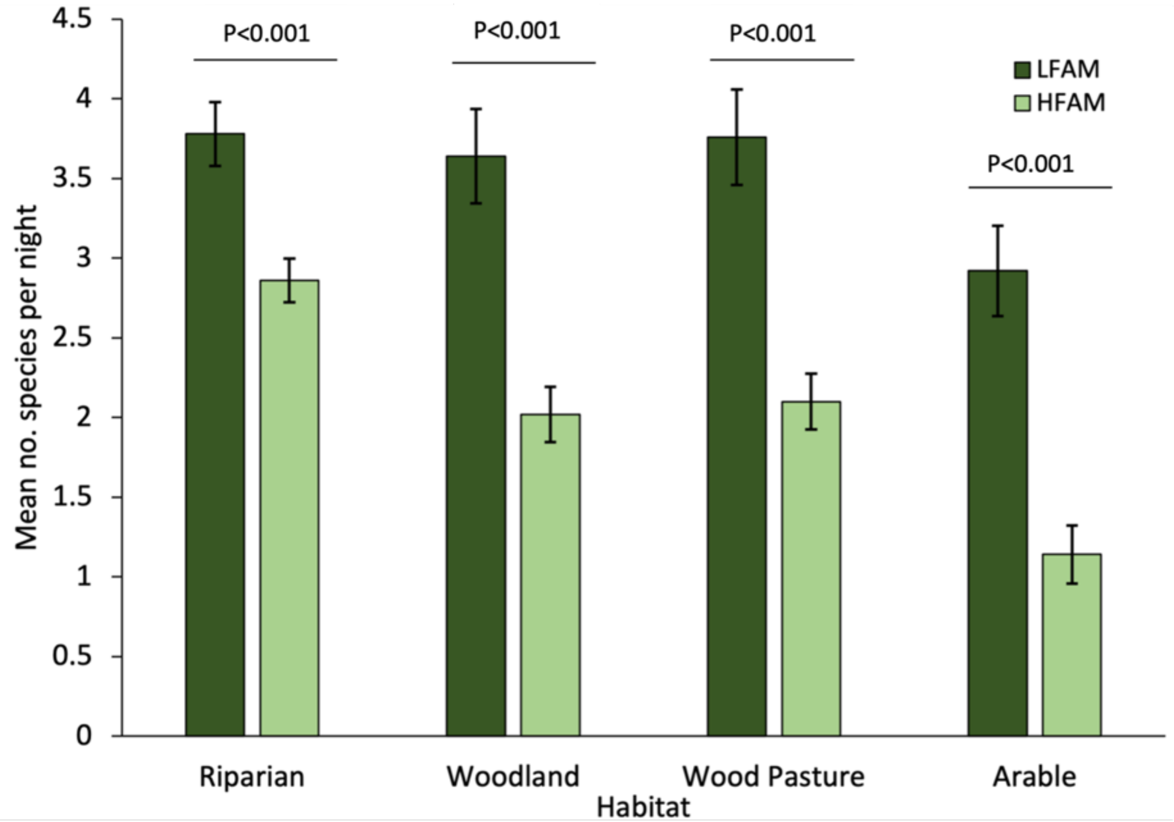


Figure 4.10*: Mean species richness detected by the AudioMoth pairs in each habitat (error bars show SEM (±1se)).*

4.3.2.2 Total bat activity

Significant differences were found between the mean number of bat recordings per night, with the LFAM having significantly more recordings found to contain bat calls, per night, compared to HFAM. This finding was again consistent for all four habitats: riparian (V=1144, P<0.001), woodland (V=811.5, P<0.001), wood pasture (V=958.5, P<0.001), and arable (V=925.5). The mean number of recordings containing bat calls, made by each of the AudioMoths, at each site, are shown in Figure 4.11.

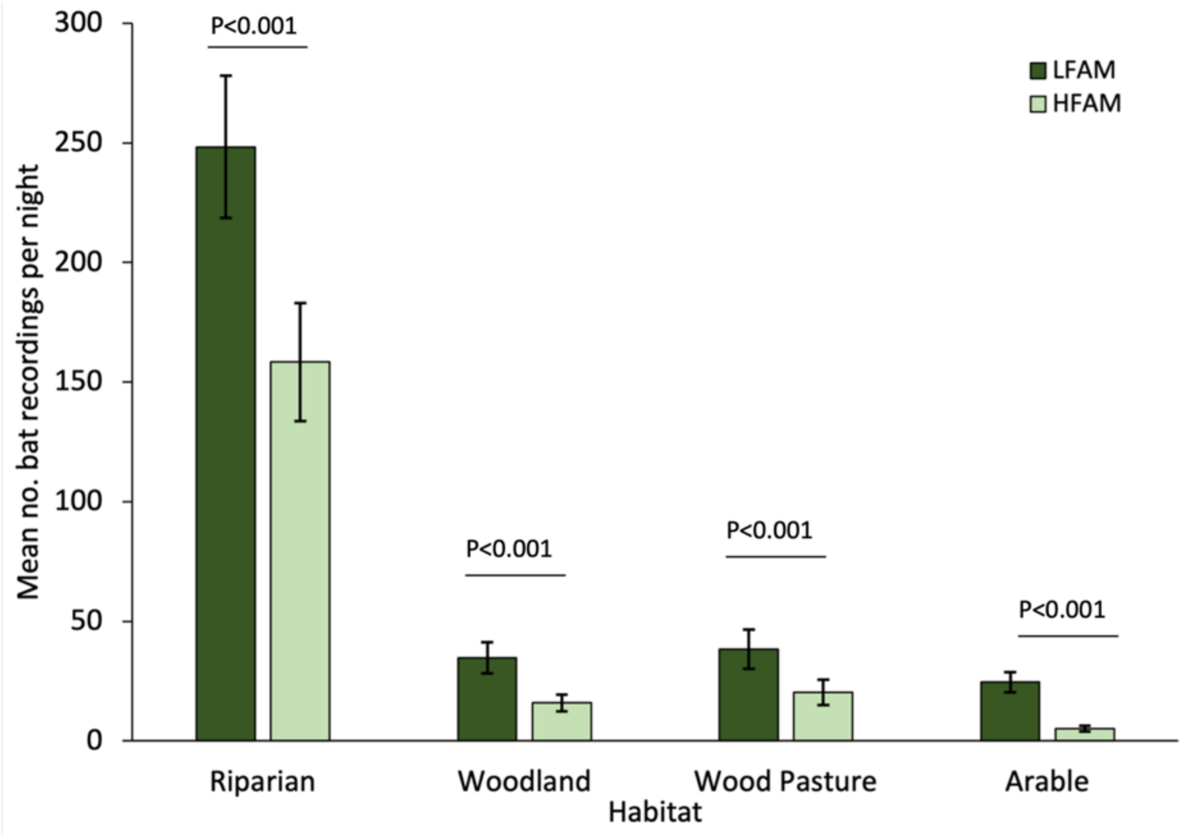


Figure 4.11*: Mean numbers of recordings containing bat calls made by the AudioMoth pairs in each habitat (error bars show SEM).*

4.3.2.3 Individual taxonomic groups

Notable differences were recorded in the numbers of recordings of individual taxonomic groups made by the AudioMoths in each pair. Firstly, within the riparian habitat, the LFAM made significantly more recordings for soprano pipistrelle (V=1108, P<0.001), *Plecotus* (V=66, P=0.014), and *Myotis* (V=66, P=0.013). In the case of the latter two groups, no recordings were made by the HFAM over the duration of the study (Figure 4.12).

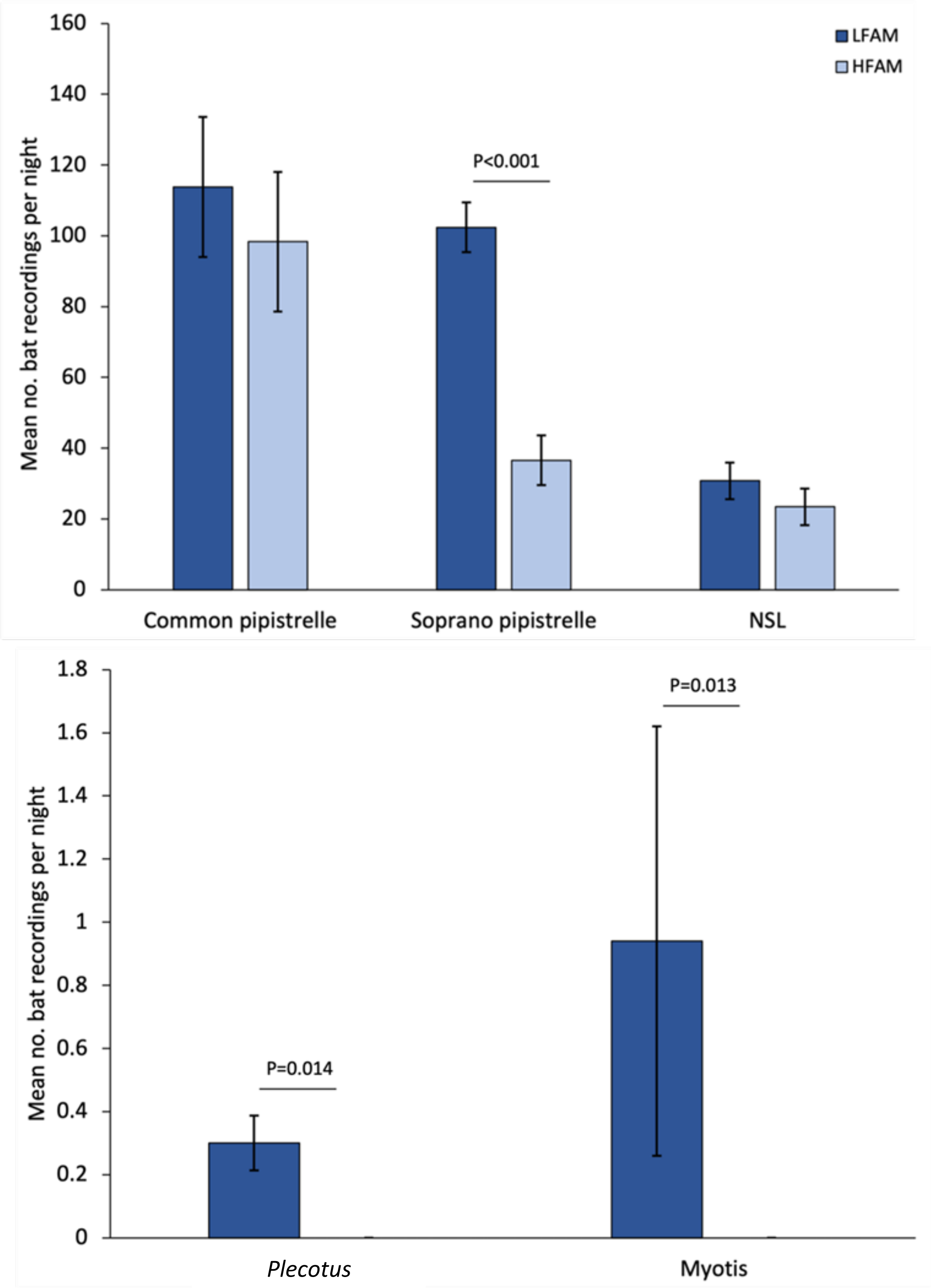


Figure 4.12: *Mean numbers of recordings containing bat calls of individual taxonomic groups, made by the AudioMoth pairs within the riparian habitat (error bars show SEM (±1se)).*

In the woodland habitat, significant differences were again found for soprano pipistrelle (V=558, P<0.001) and *Plecotus* (V=300, P<0.001), with the LFAM making insignificantly more recordings than the HFAM (Figure 4.13). Additionally, this effect was seen in the *Nyctalus/Eptesicus* group (V=741, P<0.001).

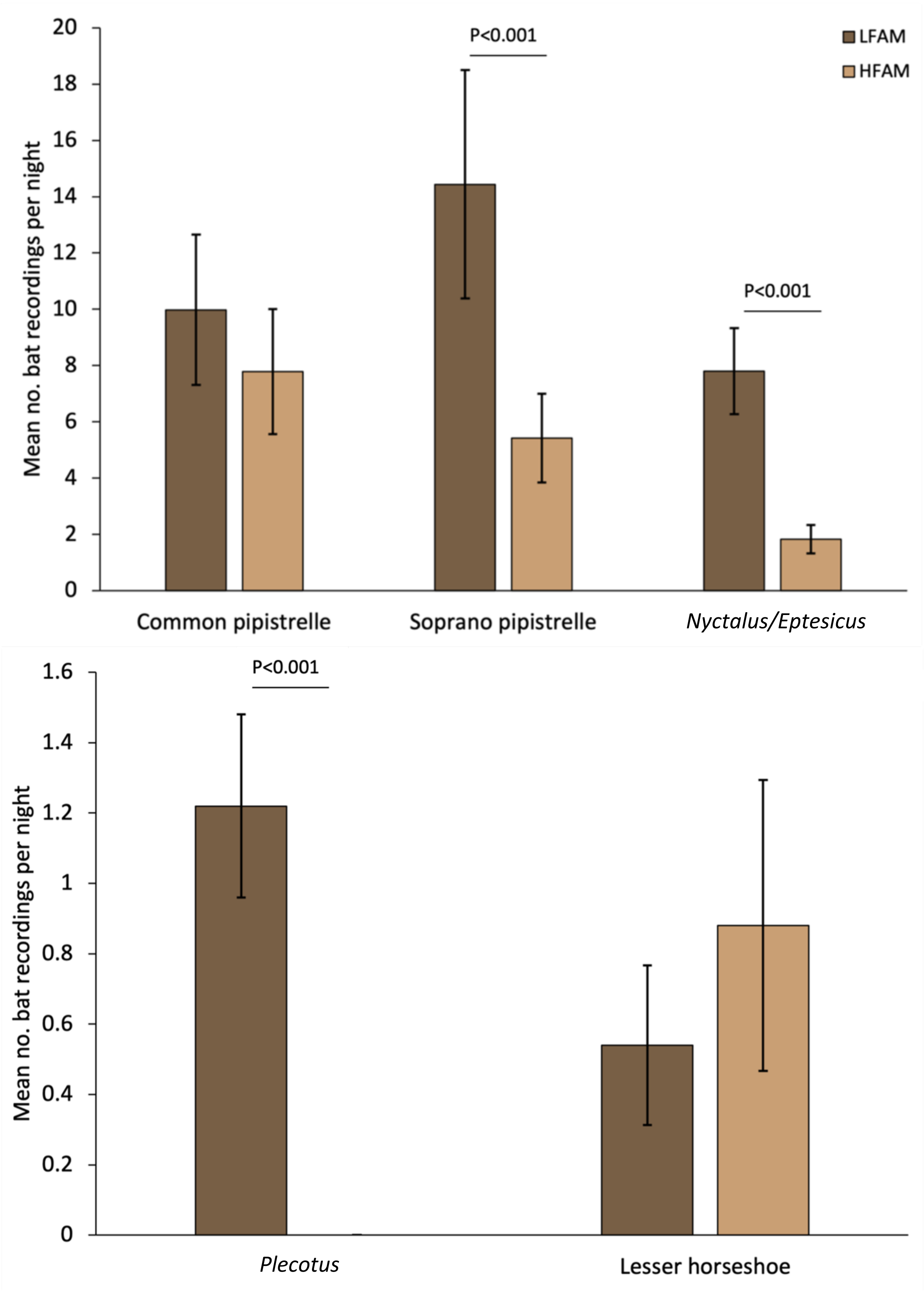


Figure 4.13: *Mean numbers of recordings containing bat calls of individual taxonomic groups, made by the AudioMoth pairs within the woodland habitat (error bars show SEM (±1se)).*

Thirdly, in the wood pasture habitat, the LFAM made significantly more recordings per night than the HFAM, for all the species groups where analysis was meaningful, with the exception of lesser horseshoe (Figure 4.14). The paired Wilcoxon tests were significant for common pipistrelle (V=644, P=0.002), soprano pipistrelle (V=650.5, P<0.001), *Nyctalus/Eptesicus* (V=810.5, P<0.001), *Plecotus* (V=105, P=0.005) and *Myotis* (V=66, P=0.021).

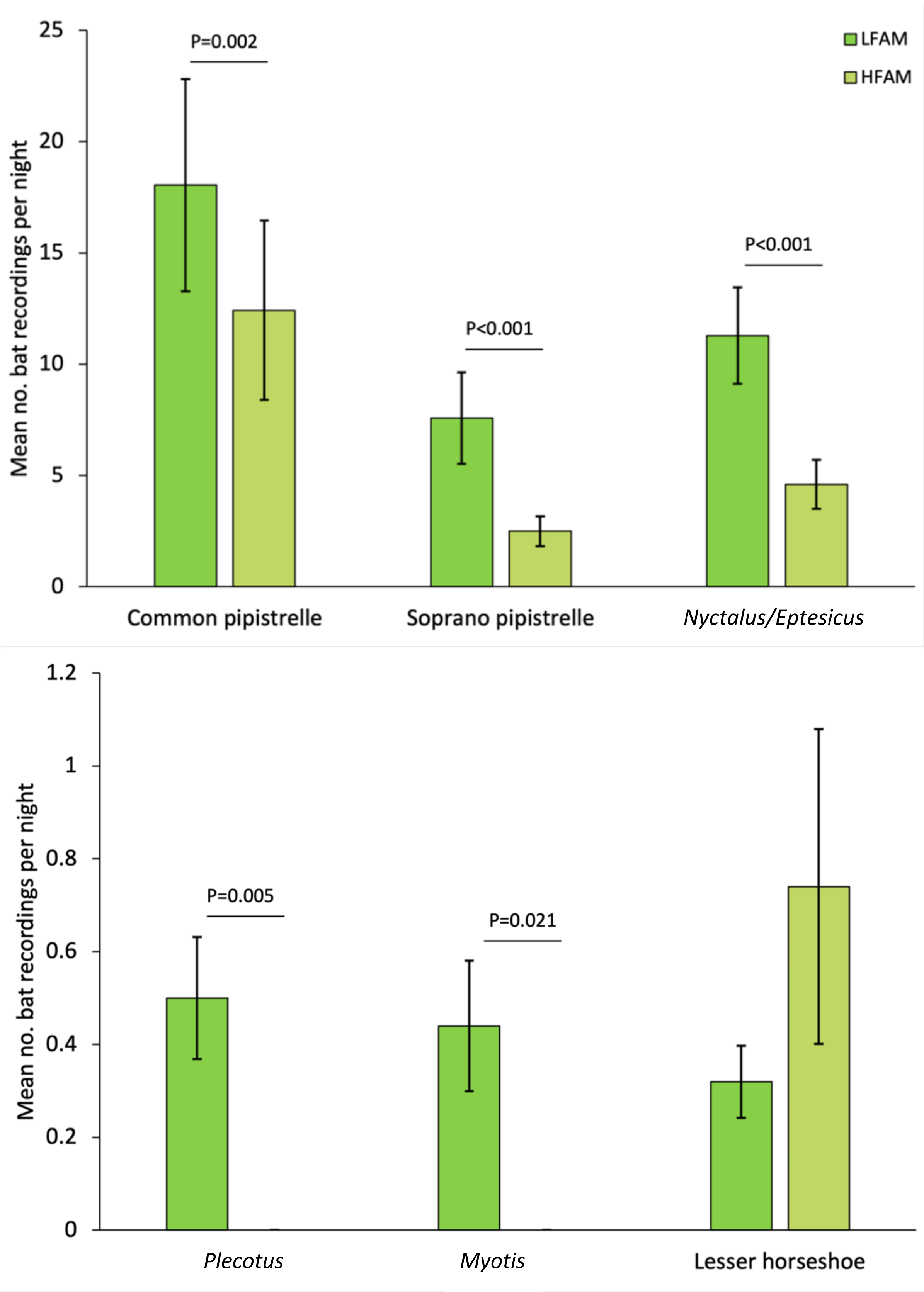


Figure 4.14*: Mean numbers of recordings containing bat calls of individual taxonomic groups, made by the AudioMoth pairs within the wood pasture habitat (error bars show SEM (±1se)).*

Finally, in the arable habitat, the LFAM again made significantly more recordings per night for those species groups with sufficient numbers to make statistical analysis meaningful, with the exception of lesser horseshoe (Figure 4.15). These groups were common pipistrelle (V=664.5, P<0.001), soprano pipistrelle (V=580, P<0.001), *Nyctalus/Eptesicus* (V=297, P<0.001), and *Myotis* (V=63.5, P=0.036).

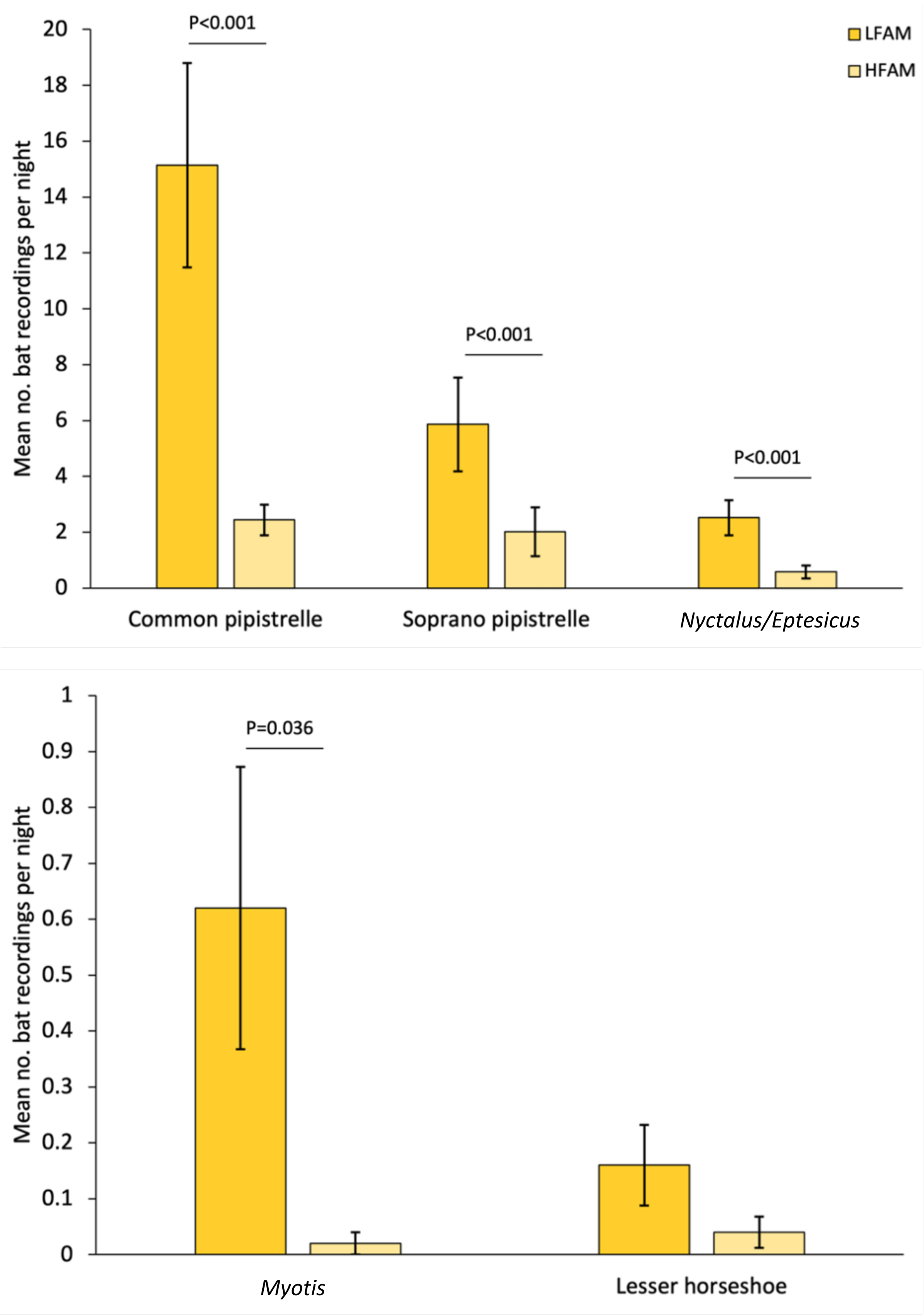


***Figure 4.15**: Mean numbers of recordings containing bat calls of individual taxonomic groups, made by the AudioMoth pairs within the arable habitat (error bars show SEM (±1se)).*

4.3.3 Species accumulation

Seven detectors were deployed for the full 20 nights at each site: Anabat Swift (n=2), Anabat Express (n=2), and AudioMoth (LFAM) (n=3). Recording nights were divided into 5-night recording periods, with nights 1-5 and 6-10 accounting for the first and second replicates at the first sub-site, and nights 11-15 and 16-20 accounting for the first and second replicates at the second sub-site, respectively. Kaleidoscope Pro classified 11 different species in the recordings from these detectors over the duration of the study.

4.3.3.1 Riparian

In the riparian habitat, the two Anabat Swifts combined had recorded the maximum richness within the first recording period, reaching maximum species richness on night three. However, the single Anabat Swift, on average, took six nights to record the maximum species richness, running into the second recording period at the first of the sub-sites (Figure 4.16a). The two Anabat Expresses combined also recorded the maximum richness of 11 species within the first five-night recording period, at the first sub-site, and the performance of two units was not superior to the performance of a single unit (Figure 4.16b). The three AudioMoths combined needed eight nights to record a lower maximum richness of ten species. However, using fewer detectors (one or two units rather than three) required not only two five-night recording periods at the first sub-site, but a further two five-night recording periods at the second sub-site to record the maximum richness. The use of two AudioMoths on average took until night 18 to reach maximum richness, with a mean species richness of 9.66 (± 0.33 SEM). The use of a single AudioMoth also took on average until night 18 to record a mean maximum richness of 8.33 (± 1.20 SEM) (Figure 4.16c).

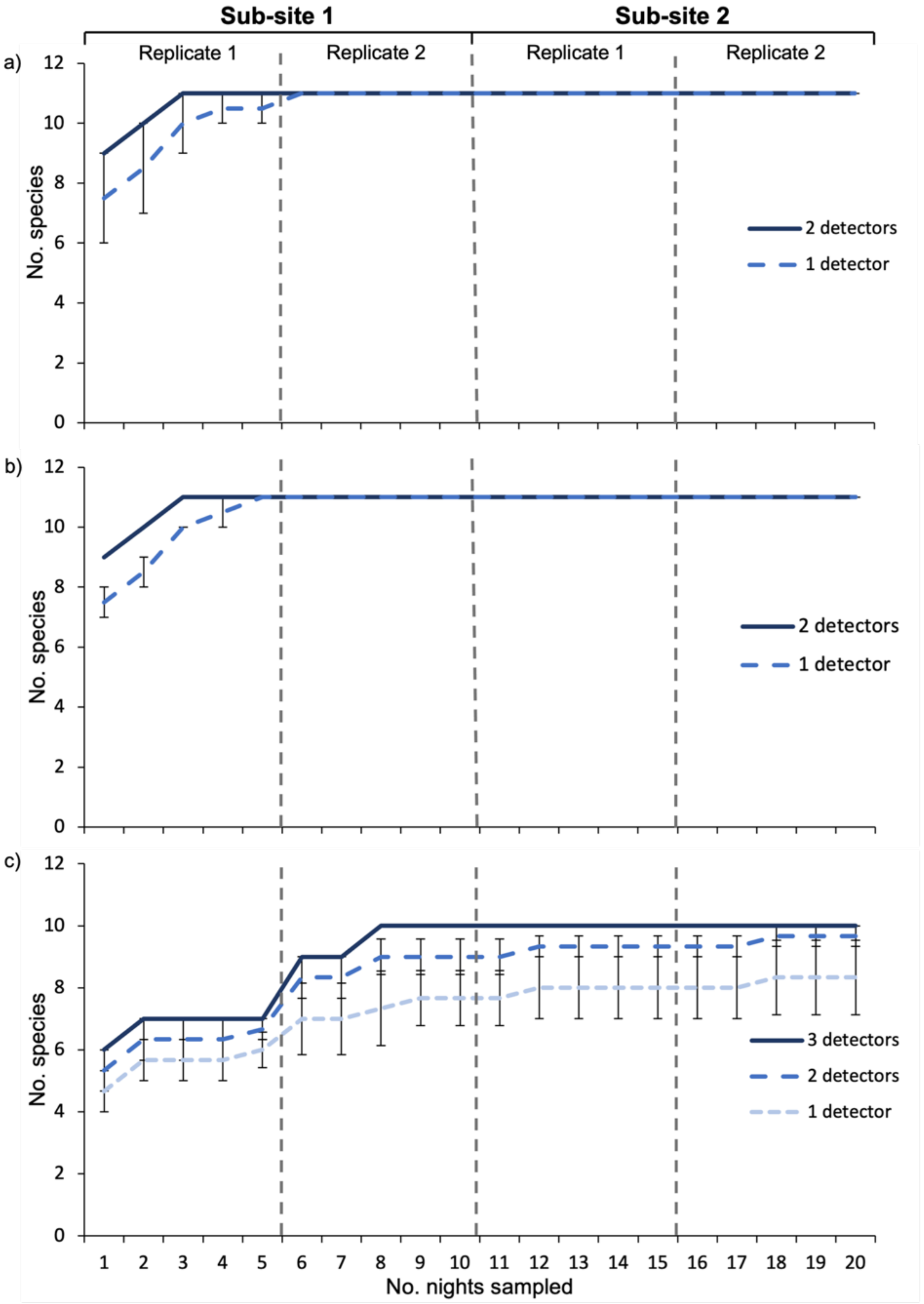


Figure 4.16: *Species accumulation curves within the riparian habitat for (a) Anabat Swift, (b) Anabat Express, and (c) AudioMoth (error bars show SEM (±1se)).*

4.3.3.2 Woodland

In woodland habitat, two Anabat Swifts combined took two five-day recording periods at the first sub-site to reach maximum richness, recording all 11 species by night seven. Reaching maximum richness was again slower for a single Anabat Swift, taking on average 12 nights (and, therefore, monitoring of the second sub-site) to record the same maximum richness as the two detectors combined (Figure 4.17a). The superiority of two detectors versus one was also seen for Anabat Express, although two detectors combined had recorded the maximum richness of 11 species by the end on the first five-day monitoring period (Figure 4.17b). Regardless of the number of detectors used, the AudioMoths required monitoring of both sub-sites to reach maximum richness. The three AudioMoths combined, had recorded the maximum 11 species by night 11. When using two detectors, it took 19 nights to reach the same species total. Using one detector also took an average of 19 nights for the number of species to peak, at a lower mean richness of 9.66 (± 1.33 SEM) (Figure 4.17c).

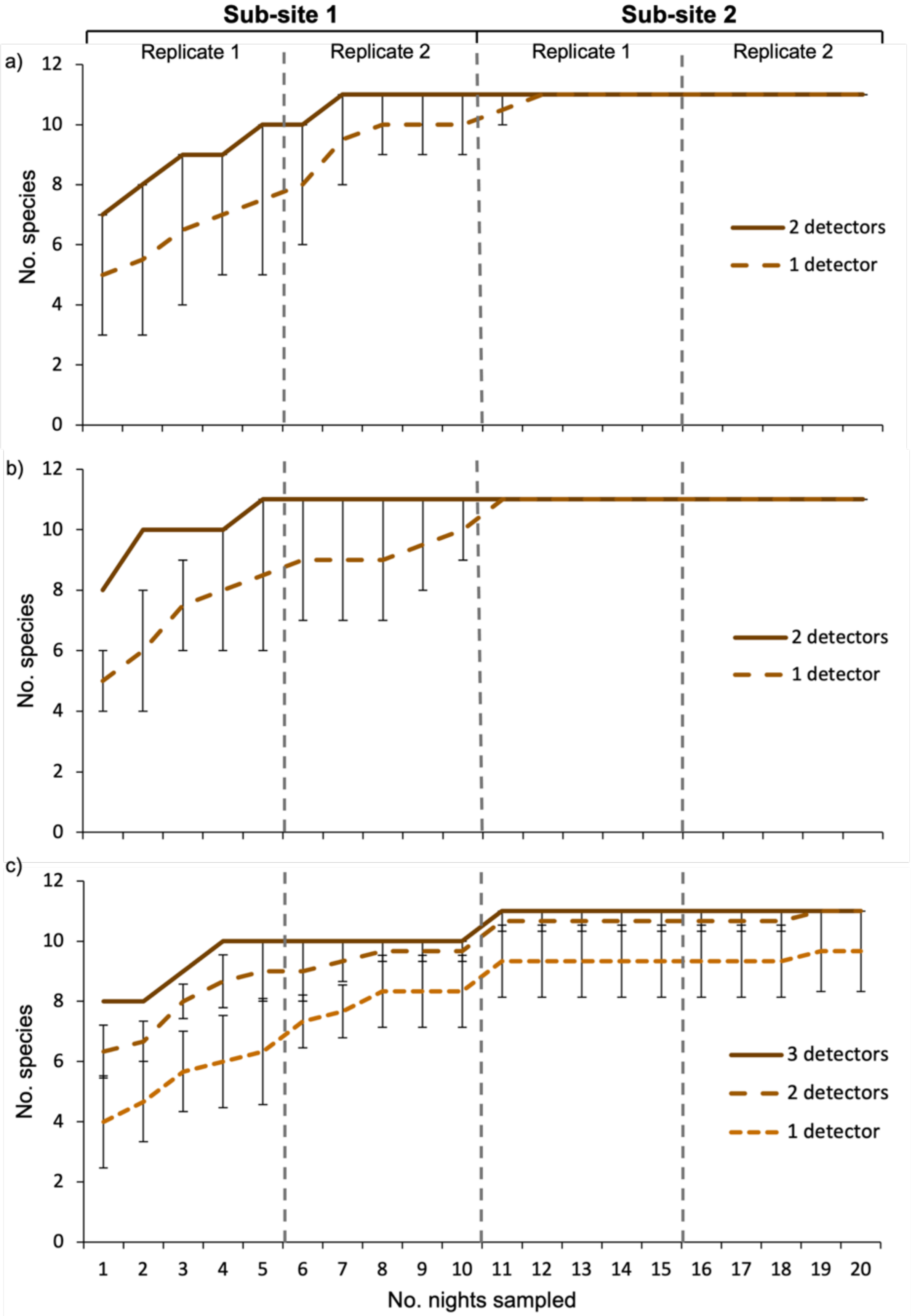


***Figure 4.17**: Species accumulation curves within the woodland habitat for (a) Anabat Swift, (b) Anabat Express, and (c) AudioMoth (error bars show SEM (±1se)).*

4.3.3.3 Wood pasture

In the wood pasture habitat, use of either one or two Anabat Swift detectors needed two monitoring periods to reach the maximum richness of 11 species at the first sub-site (Figure 4.18a). On the other hand, the two Anabat Express units in combination recorded the same maximum richness more quickly, with the number of species recorded peaking on night three, but using a single Anabat Express necessitated a second recording period at the first sub-site, with peak richness reached, on average, on night seven (Figure 4.18b). The difference observed between using two or three AudioMoths was negligible, with the maximum richness of eleven species being reached on nights eight and six, respectively, both within the second recording period at the first sub-site (Figure 4.18c). The use of a single AudioMoth, however, recorded a lower mean maximum richness of 10 species (± 0.58 SEM), which was reached on night 12, during monitoring of the second sub-site.

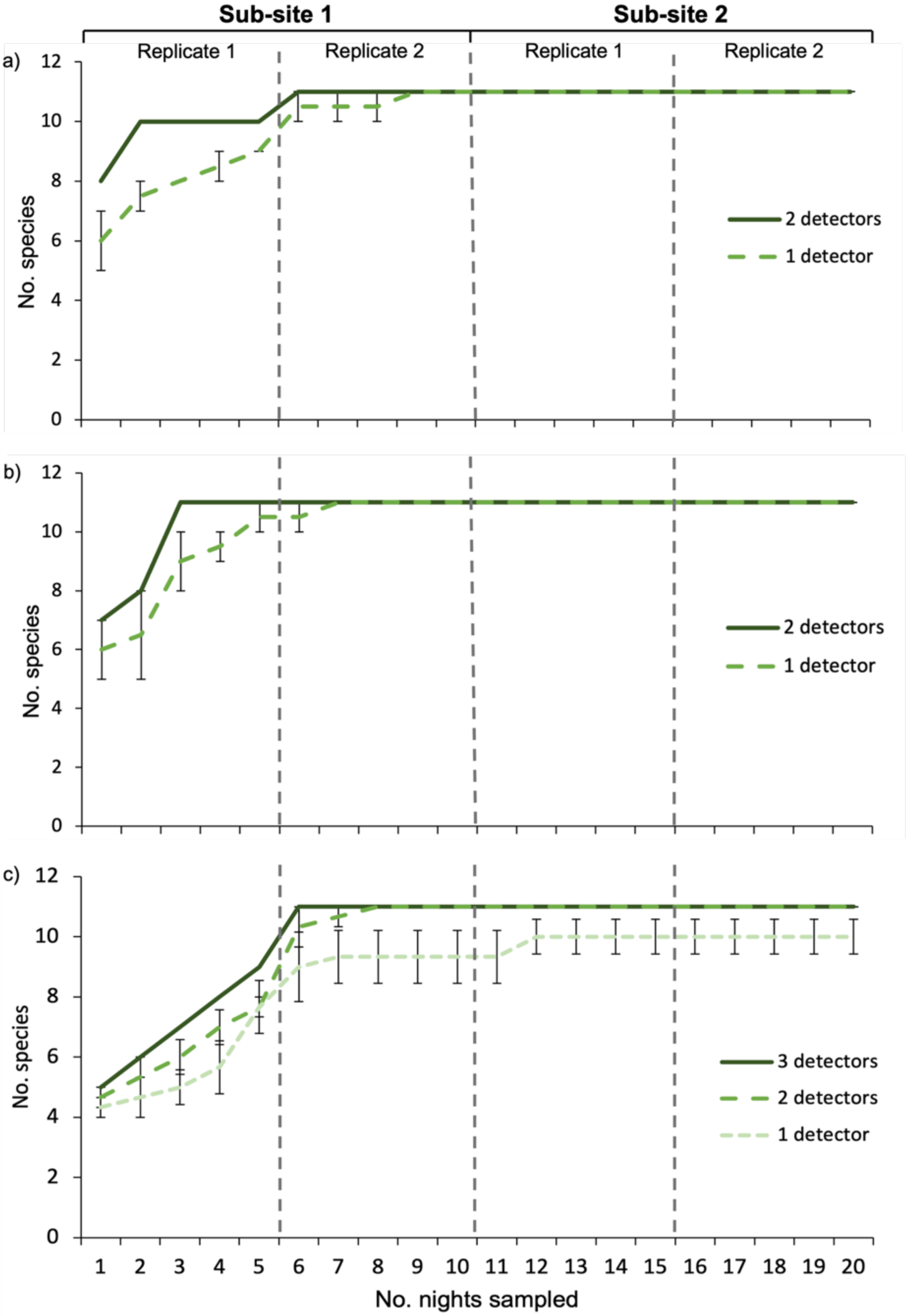


Figure 4.18: *Species accumulation curves within the wood pasture habitat for (a) Anabat Swift, (b) Anabat Express, and (c) AudioMoth (error bars show SEM (±1se)).*

4.3.3.4 Arable

In the arable habitat, the use of either one or two Anabat Swift detectors recorded the maximum richness of eleven species inside the first five-night recording period at the first sub-site (Figure 4.19a). The Anabat Expresses took comparatively longer; using two detectors didn’t reach the same maximum richness until night nine, towards the end of the second recording period at the first sub-site. Recording with one Anabat Express took longer again, with the maximum richness being reached by night 11 on average, requiring recording at both sub-sites (Figure 4.19b). Only monitoring the site with all three AudioMoths was sufficient to reach the same maximum richness as the Anabat devices, with all 11 species having been recorded by night eight. When using either one or two AudioMoth devices, the peak in species richness was not reached until the second recording period at the second sub-site. Moreover, the mean maximum species richness recorded was lower, with a mean species richness of 10.66 (± 0.33 SEM) being reached on night 16 for two AudioMoths, and 8.66 (± 1.22 SEM) for a single AudioMoth (Figure 4.19c).

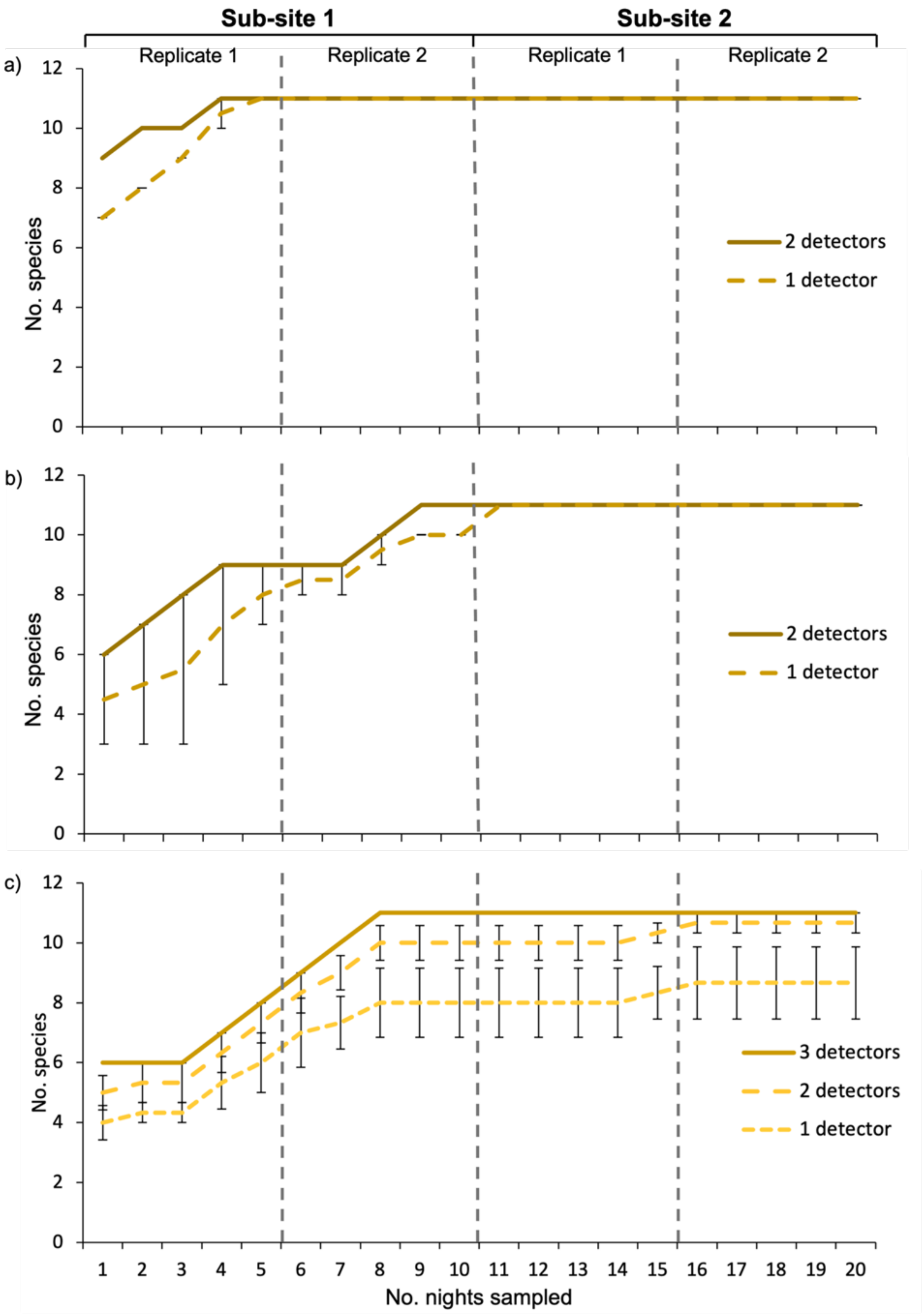


Figure 4.19: *Species accumulation curves within the arable habitat for (a) Anabat Swift, (b) Anabat Express, and (c) AudioMoth (error bars show SEM (±1se)).*

4.4 Discussion

The commercial Anabat detectors generally outperformed the open-source AudioMoths (LFAM and HFAM), both in terms of numbers of bat passes detected, overall species richness, and detecting the same number (or more) species faster, with fewer detector units, fewer replicate recording periods and fewer recording locations/sub-sites being needed. Fewer significant differences in bat passes detected were found when restricting analysis to the time periods in which the AudioMoths were awake and recording, with the LFAM detecting similar numbers of bats as the Anabat devices overall, and even detecting more bat passes than the Anabat Express for some taxonomic groups in certain habitats. Analysing both the full dataset and the time matched subsets was important to understand the differences in the detectors in both field conditions, as they are likely to be used by practitioners (full dataset), and scientifically under the same conditions (time matched subsets).

4.4.1 Comparative detector performance

In analysis of the full dataset, where significant differences between detectors were found, the Anabat detectors recorded a higher species richness or a greater number of bat passes than either of the AudioMoths. This finding highlights the major disadvantage in configuring the AudioMoths to record on a sleep/wake cycle, as bat activity is inevitably missed when the units are asleep. However, this was seen to have a bigger impact for *Myotis* and *Plecotus* bats, which can be classed as short-range echolocators (SRE) (Frey-Ehrenbold *et al.*, 2013; Froidevaux *et al.*, 2014) – this was also seen for brown long-eared in Chapter Three where more passes were recorded on walked transects than using PAM, again likely due to the influence of SRE. For *Pipistrellus* species, the LFAM only recorded significantly fewer bat passes than the Anabat Express in the arable habitat, even when only switching on to record periodically. Few previous studies have examined the difference in detections from different detector models, particularly to compare zero-crossing and full spectrum detectors. However, Adams *et al.* (2012) and Kaiser and O'Keefe (2015) both compared a zero-crossing detector (Anabat SD2) to at least one other full spectrum detector. The former study reported that although the Anabat devices performed similarly, in the majority of cases it recorded fewer bats than the full spectrum equivalents. Therefore, ability of the AudioMoth units to record in full spectrum may enable them to perform similarly to the Anabat Express for more abundant taxa, even when configured to sleep periodically. A firmware update introducing a frequency trigger for the AudioMoth was released in mid-2022 (Open Acoustic Devices, 2022a). It was not adopted here owing to the timing of the release and lack of empirical testing; however, future research should aim to assess if utilising triggered recording for AudioMoth yields more comparable results when compared to commercial equipment.

In the analysis of the time matched subsets, fewer significant differences between the detectors were seen, particularly when comparing the LFAM with the Anabat detectors. This perhaps emphasises the superior ability of full spectrum detectors to detect bats, alluded to in the analysis of the full dataset. On some occasions, the LFAM was found to have recorded significantly more passes than the Anabat Express in the data subset. Neither of the AudioMoths significantly outperformed the Anabat Swift in the subset analysis. These findings are consistent with those of a recent detector comparison conducted by Starbuck *et al.* (2024). The higher quality microphone in the Swift, is likely to be the principal driver behind their superior performance.

4.4.2 Comparison of AudioMoth configurations

Testing of the two AudioMoth sampling rate configurations yielded some perhaps unexpected findings with the lower sampling rate, 250kHz LFAM, frequently outperforming it's co-located 384kHz HFAM partner in the analysis of the paired AudioMoths. Moreover, the LFAM was therefore found to be closer in terms of performance to the two commercial Anabat detectors. Analysis of the LFAM subset found it was only significantly outperformed by the Anabat Swift in recording lesser horseshoe bats in woodland habitat. Configuring the AudioMoth with the highest possible (384kHz) sample rate to record bats is recommended by Hill *et al.* (2019) and has frequently been adopted in previous work using AudioMoth to study bats (Katunzi *et al.*, 2021; Lopez-Bosch *et al.,* 2022; Carvalho *et al.*, 2023). A recent detector comparison study in the USA used this configuration (Starbuck *et al.,* 2024), however, they also reported reduced performance compared to commercial equipment. Configuring the AudioMoths to use the highest possible sampling rate, does potentially have disadvantages. Firstly, the use of a higher sampling rate can result in greater amounts of self-noise from more frequent SD card writes, which may reduce recording quality. AudioMoths require ultra-high speed microSD cards, however, U1 (10MB/s write speed) cards will generate more noise than U3 (30MB/s write speed) cards, especially where higher sampling rates are used (*Pers. comm.* Alex Rogers, Open Acoustic Devices). Increased noise can result in calls being overlooked or less confidently identified by a classifier (Brinkløv *et al.*, 2023). In this study, only recordings classified with a match ratio of >0.5 were analysed, with the HFAM having the lowest percentage of recordings exceeding this threshold (12.33.%) of all the detector types. Secondly, in many cases the greater requirement in terms of memory for each recording at higher sampling rates (Browning *et al.,* 2017; Gibb *et al.*, 2019) may necessitate configuring the AudioMoth to record at less frequent intervals/for a shorter duration, to fit recordings from the required monitoring period, on to the memory card.

4.4.3 Species accumulation

The Anabat detectors were found to have accumulated the full species inventory in all habitats. When two detectors were used, the maximum accumulation was always reached by the end of the second replicate at the first sub-site (10 nights). This could also typically be achieved by using a single detector. However, on occasion, the use of a single detector necessitated further monitoring of the second sub-site most notably within the woodland habitat for both the Swift and the Express. In cluttered environments such as woodland, calls may become obscured, and higher frequency calls produced by bats in clutter are more easily attenuated (O'Keefe *et al.*, 2014). This finding highlights the need for sufficient spatial coverage in such habitats, even when using commercial detectors. Although the AudioMoths generally accumulated species more slowly, using multiple detectors was seen to have a positive impact. Using three AudioMoths enabled the full species inventory to be recorded within one sub-site at all of the habitats, except for in woodland. The lower purchase costs of the AudioMoths makes the necessity of using multiple detectors less of a limitation (Browning *et al.*, 2017), and doing so was shown here to be capable of recording as many species as the Anabat detectors, over a similar monitoring period.

4.4.4 Habitat effects

The riparian site saw the highest levels of overall activity, with the watercourse and riparian corridor likely providing plentiful foraging opportunities for a range of species (Smith and Racey, 2008; Scott *et al.*, 2010). Here, the AudioMoths were not able to record the same species inventory as the commercial detectors, and even the use of three units required a second replicate of recording before no new species were recorded. This finding differs from the other three habitats, where the use of three AudioMoths was eventually sufficient to record the same species richness as the other detectors. More heterogeneous, species rich habitats with high levels of activity, may present more of a challenge for the AudioMoth's lower quality microphone. The MEMS microphones are hypothesised to have a lower signal to noise ratio, therefore, environments with high levels of background noise and vocalisations from other species, may detract from the recording quality, and the subsequent ability for bat calls to be confidently identified (Gibb *et al.,* 2019).

The overall detected level of activity was lower at the woodland habitat compared to the riparian habitat. Bats produce quieter echolocation calls in cluttered environments (Russ, 2012), which can result in fewer detections, and calls which are more challenging to identify. As such, acoustic methods alone are not always sufficient to produce a complete species inventory (Lintott *et al.*, 2014). This was shown to impact the PAM protocols required to record the maximum species richness. A single Anabat Swift was still capable of recording the maximum observed species richness, however, unlike the other habitats, the use of the second sub-site was necessary to achieve this. Moreover, more significant differences between the detectors were found in woodland than any other habitat, with the Swift typically recording more bat passes. This emphasises that high quality detectors are best suited to robustly capturing bat activity and richness in these instances, and most efficiently.

4.4.5 Implications and recommendations

The findings presented here show that the full spectrum, commercial detectors (Anabat Swift) performed the most efficiently in all four habitats, recording the highest mean species richness and mean numbers of bat passes each night. Moreover, they were seen to accumulate the full species inventory at each site more quickly, and often with the use of fewer units. However, consistent with the findings of Starbuck *et al.* (2024), the AudioMoths were seen to be sufficiently capable in certain scenarios, and may serve as a viable alternative in instances where the purchase of commercial equipment is financially prohibitive. With adequate replicates, multiple AudioMoths were shown to be able to accumulate the same species inventory as the Anabat Swift in all habitats except riparian. For complex habitats, or those where species richness is anticipated to be high, commercial PAM equipment should still be strongly considered.

The reduced numbers of bat passes recorded by the AudioMoths does indeed suggest a trade-off between detector cost and recording quality (Gibb *et al.*, 2019), which needs careful consideration, especially if the analysis is to be partially or fully automated. These findings suggest a 250kHz sampling rate better preserves recording quality by potentially reducing self-noise generated by memory card writes. However, although high frequency bats (lesser horseshoe) were still detected at the lower sampling rate, there may be some reduction in microphone sensitivity at higher frequencies. Fully understanding the noise generated by different memory cards and how this is impacted by recording at different sampling rates will be of vital importance. Moreover, empirical testing of the updated AudioMoth firmware with configurable frequency triggers will enhance understanding of how these lower cost units compare to the commercial alternatives.

Optimising efficient and reliable workflows for the analysis of the large datasets produced by PAM is also of paramount importance. Manual auditing of these datasets is incredibly time consuming and remains a subjective process. It is important to acknowledge that the workflow adopted for this chapter was largely automated, with the degree of manual auditing undertaken proportionate to the resources available. With multiple classifiers and pipelines now available to process acoustic data, gaining an understanding of the relative reliability of these algorithms, and how this is influenced by variation in the quality of recordings from different detectors (**Chapter Five**), will be key in ensuring that PAM produces accurate and reliable data (Browning *et al.*, 2017; Gibb *et al.,* 2019; Sugai *et al.*, 2019).

Acoustic bat surveys are a vital component in the monitoring and assessment of bat populations and communities, for scientific research (Jones *et al.*, 2013), informing conservation action (Barlow *et al.*, 2015), and to ensure legal compliance under protected species legislation (Collins, 2023). With the ever-expanding availability of acoustic recorders capable of passively recording ultrasonic bat calls, it is of vital importance that the relative strengths and limitations of commercial and open-source recorders are fully understood. Ensuring that PAM protocols are empirically tested, will aid in allowing practitioners to make informed decisions when selecting the most suitable equipment and protocols for their specific research aims.

4.5 Chapter summary

1. *The Anabat Swift and Express typically detected a significantly higher species richness, and significantly more bat passes than the AudioMoths, over five-night PAM periods (non-temporally restricted).*
2. *Analysis of the temporal periods in which all detectors were able to record, showed the AudioMoth to be capable of recording significantly more bat passes than the Anabat Express, for taxonomic groups which call at lower frequencies (Eptesicus, Nyctalus and Pipistrellus species).*
3. *When comparing AudioMoth configurations, a 250kHz sampling rate was found to detect a significantly higher species richness than a 384kHz sampling rate, and always detected more bat passes for taxonomic groups where significant differences were found.*
4. *Three AudioMoths were able to record the same number of species as one or two AnaBats in all habitats except riparian, however, species accumulation typically took longer, and a second sub-site was required in the woodland habitat.*
5. *The analysis workflow used in this chapter incorporated an automated bat call classifier. Improving understanding of the reliability of the various classifiers and pipelines currently available is important to ensuring large PAM datasets can be analysed efficiently and accurately. The pairwise consensus between commonly used classifiers is investigated in Chapter Five.*

4.6 Supplementary material

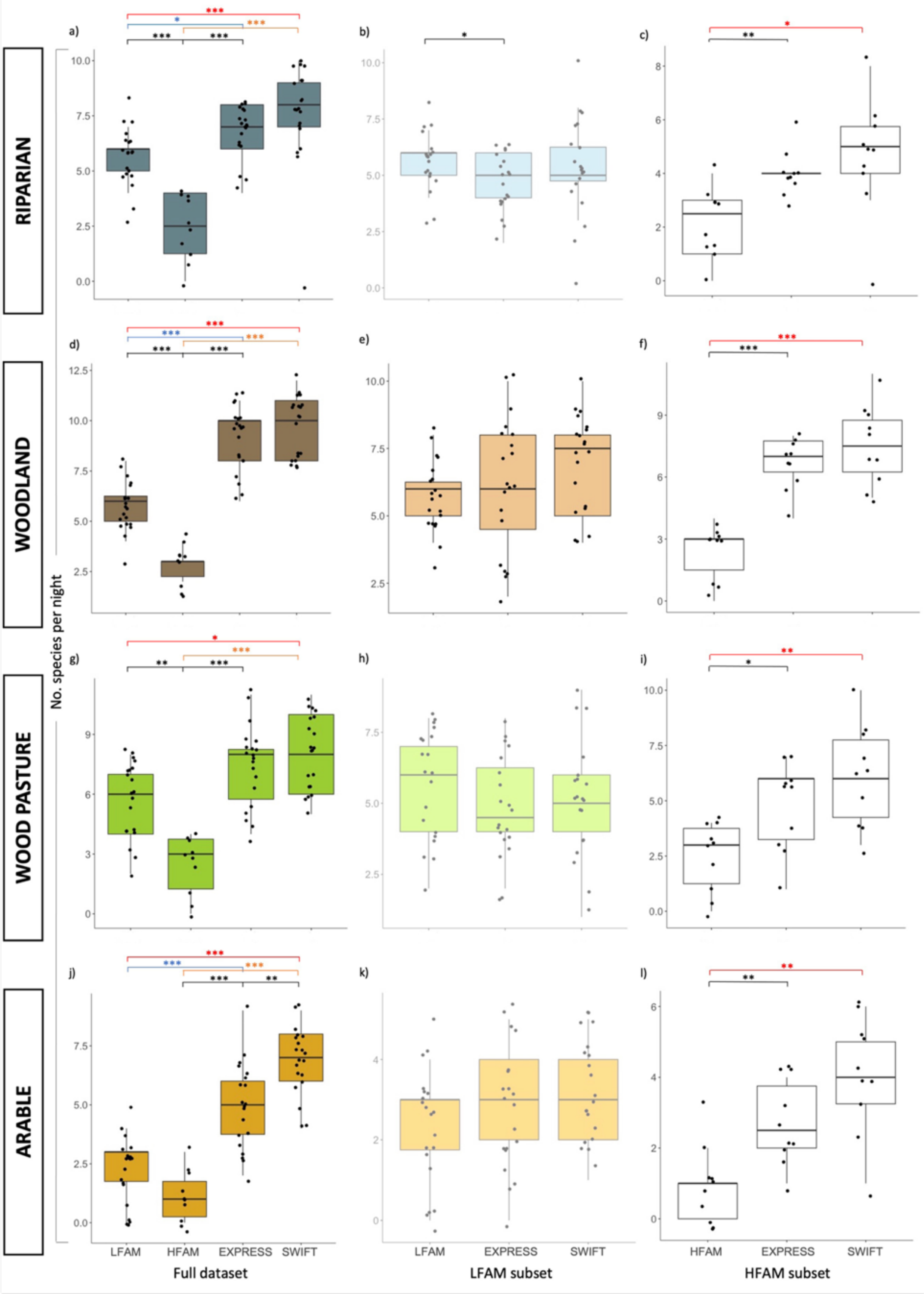


Figure S4.1: Differences in species richness between detectors. Significant post-hoc pairwise Wilcoxon results displayed with codes <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

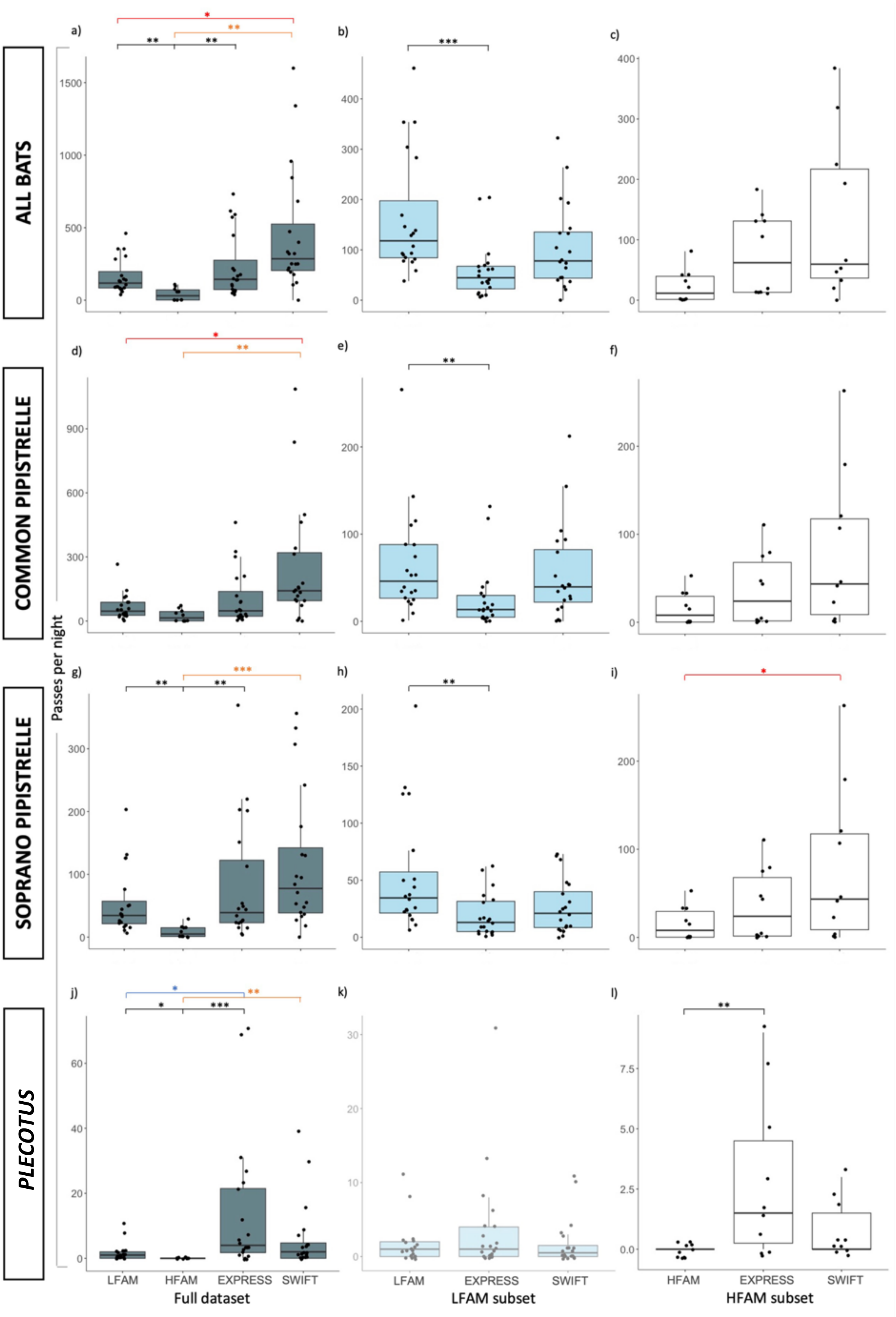


Figure S4.2.1: Differences in bat passes between detectors. Significant post-hoc pairwise Wilcoxon results displayed with codes <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

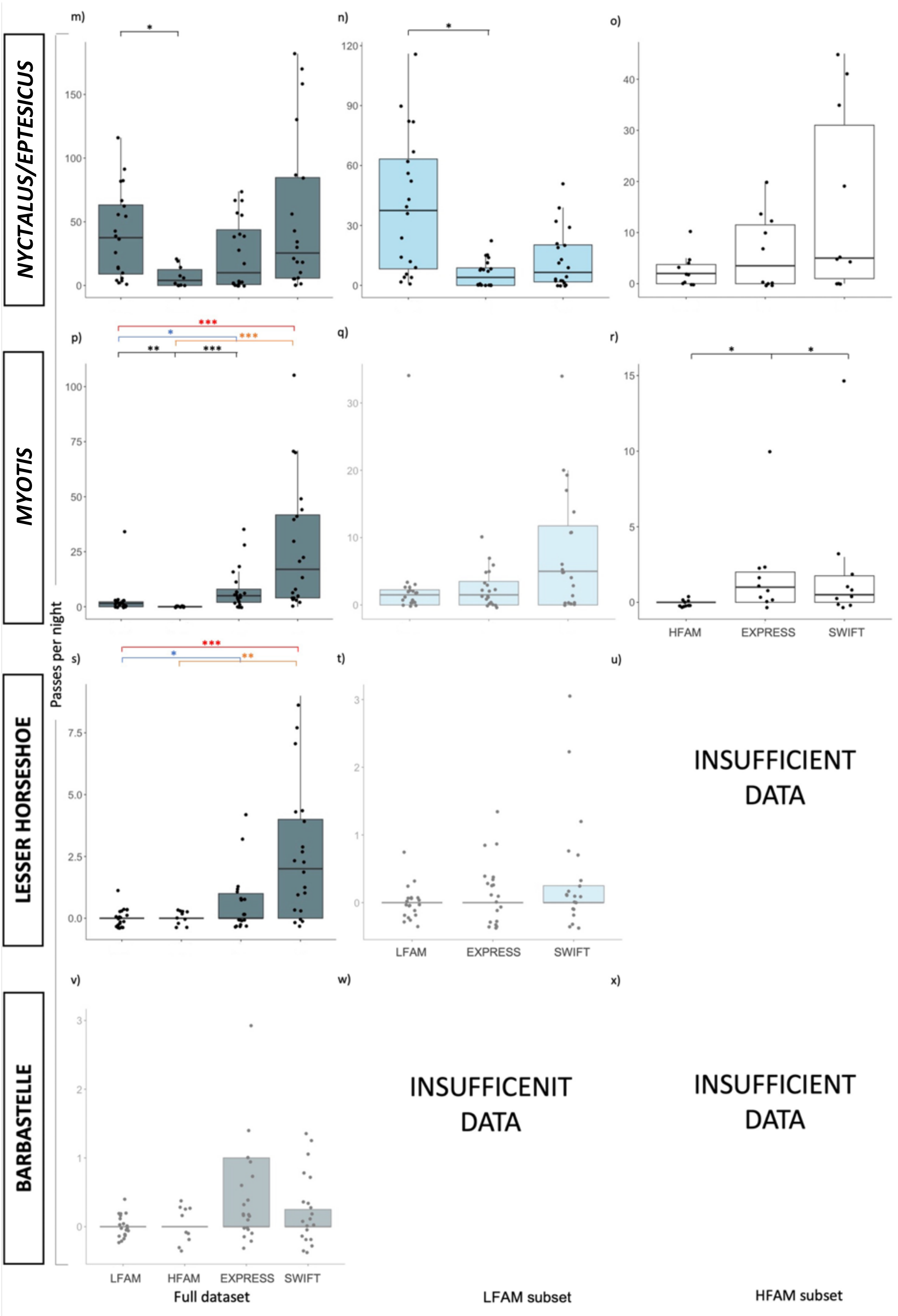


Figure S4.2.2: Continuation of figure 4.10.1. Significance codes: <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

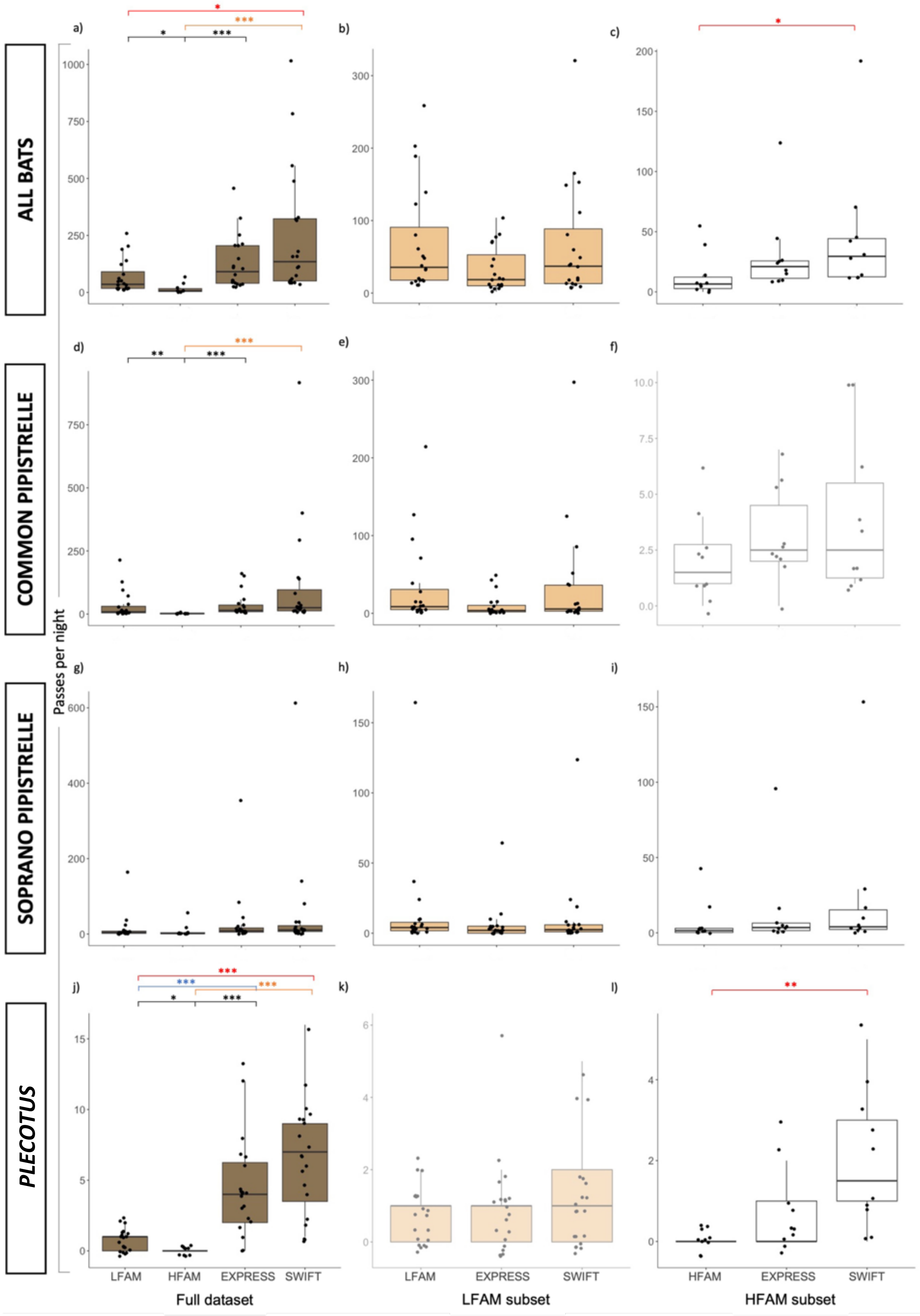


Figure S4.3.1: Differences in bat passes between detectors. Significant post-hoc pairwise Wilcoxon results displayed with codes <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

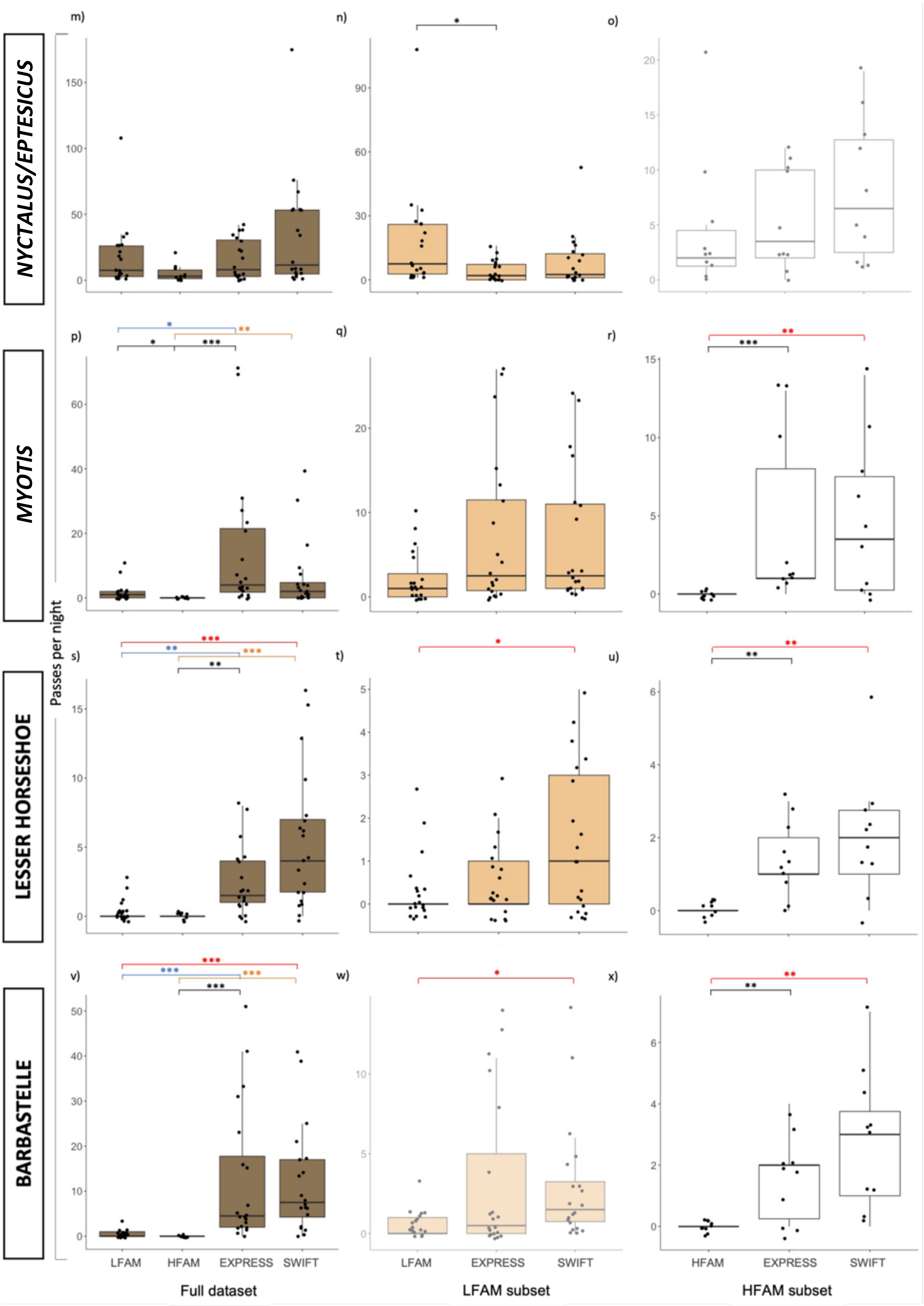


Figure S4.3.2: Continuation of figure 4.11.1. Significance codes: <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

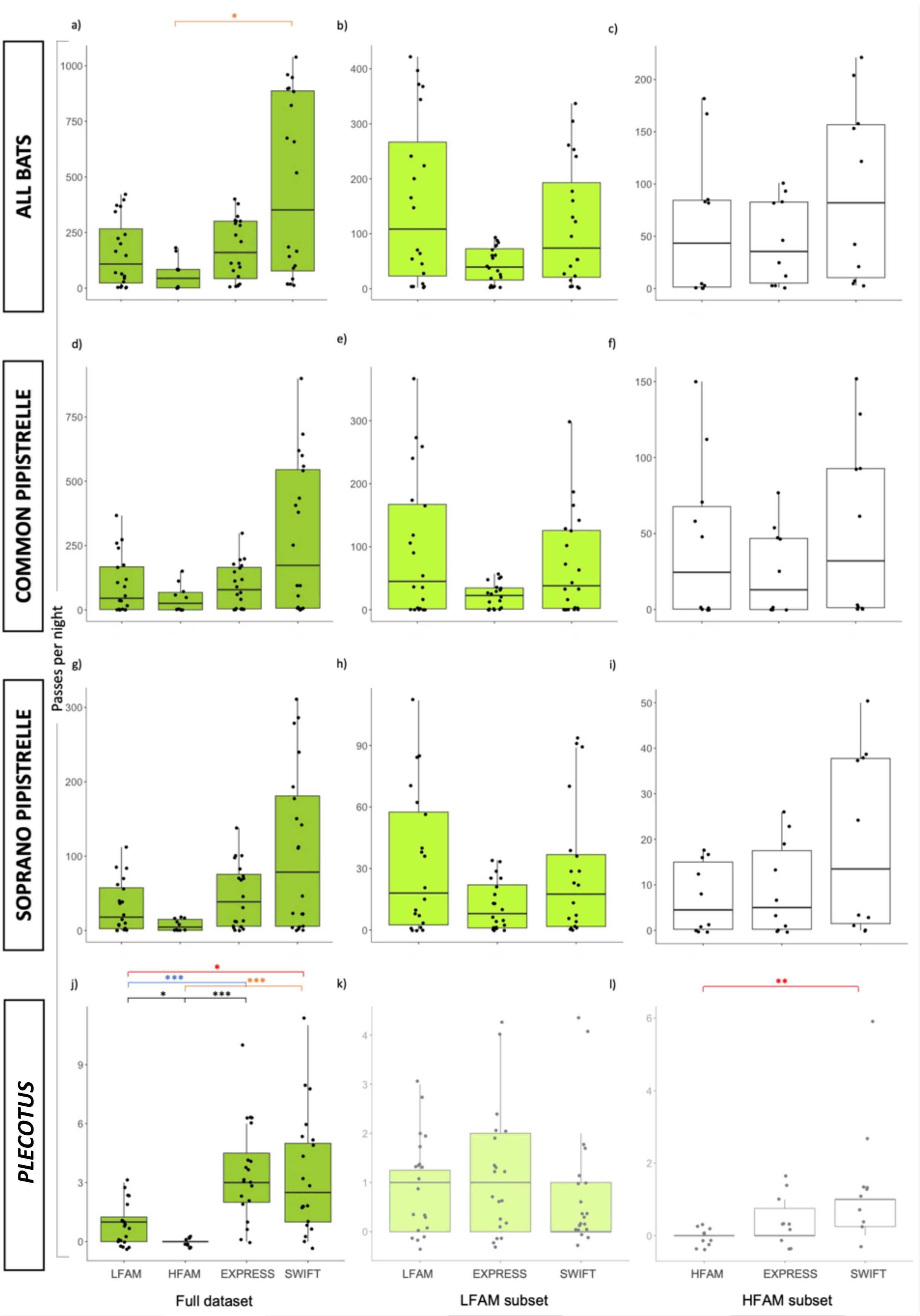


Figure S4.4.1: Differences in bat passes between detectors. Significant post-hoc pairwise Wilcoxon results displayed with codes <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

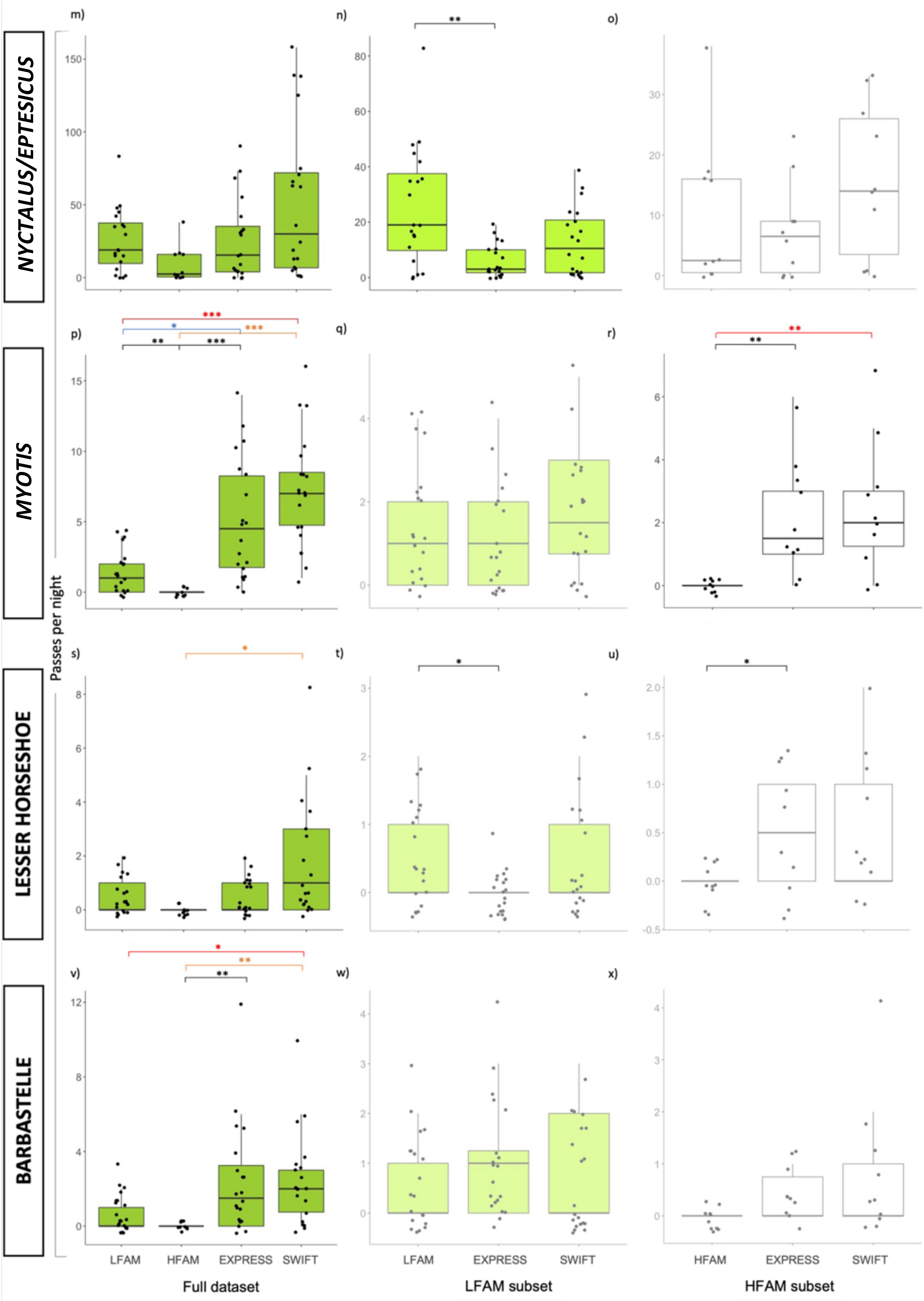


Figure S4.4.2: Continuation of figure 4.12.1. Significance codes: <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

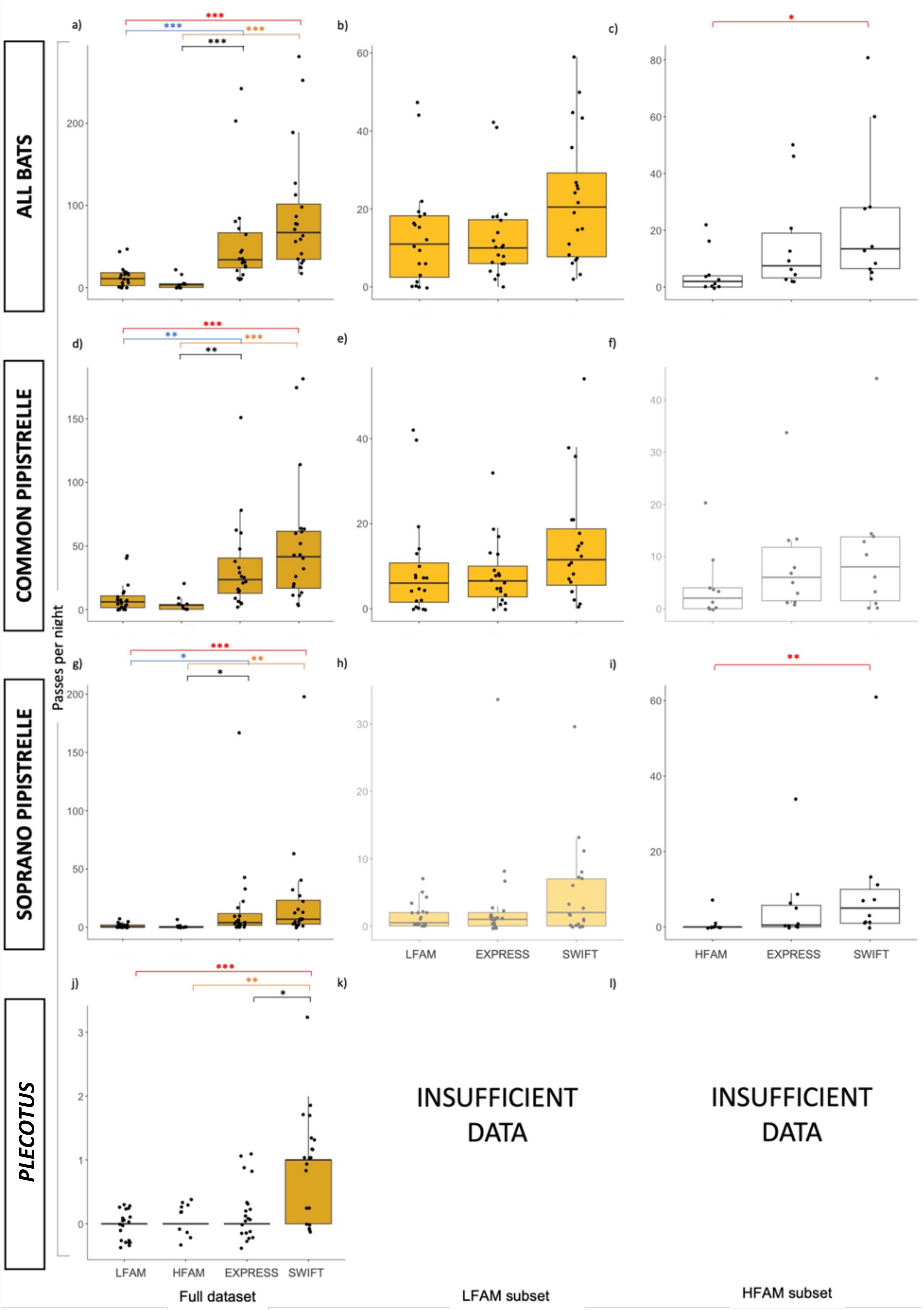


Figure S4.5.1: Differences in bat passes between detectors. Significant post-hoc pairwise Wilcoxon results displayed with codes <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

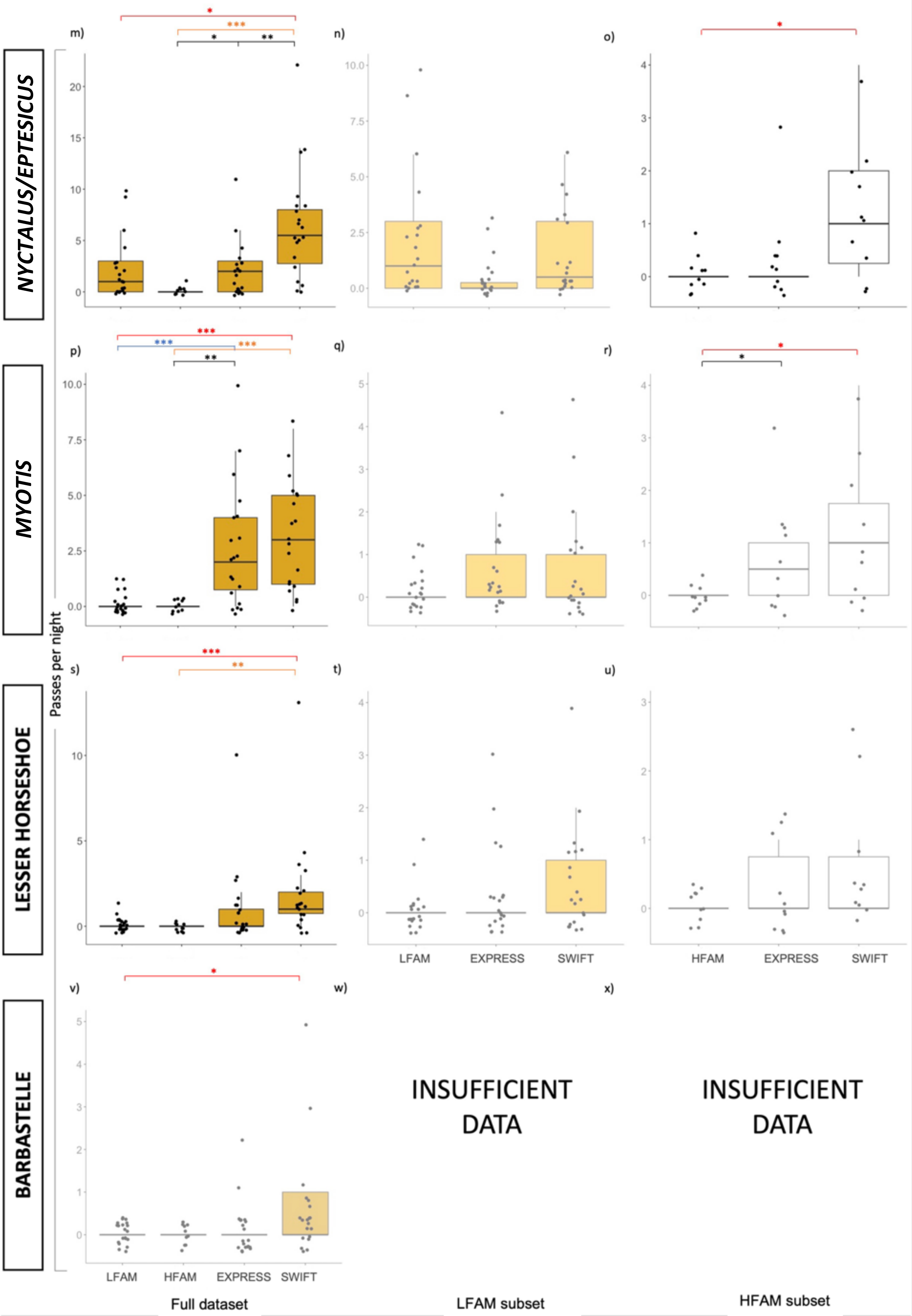
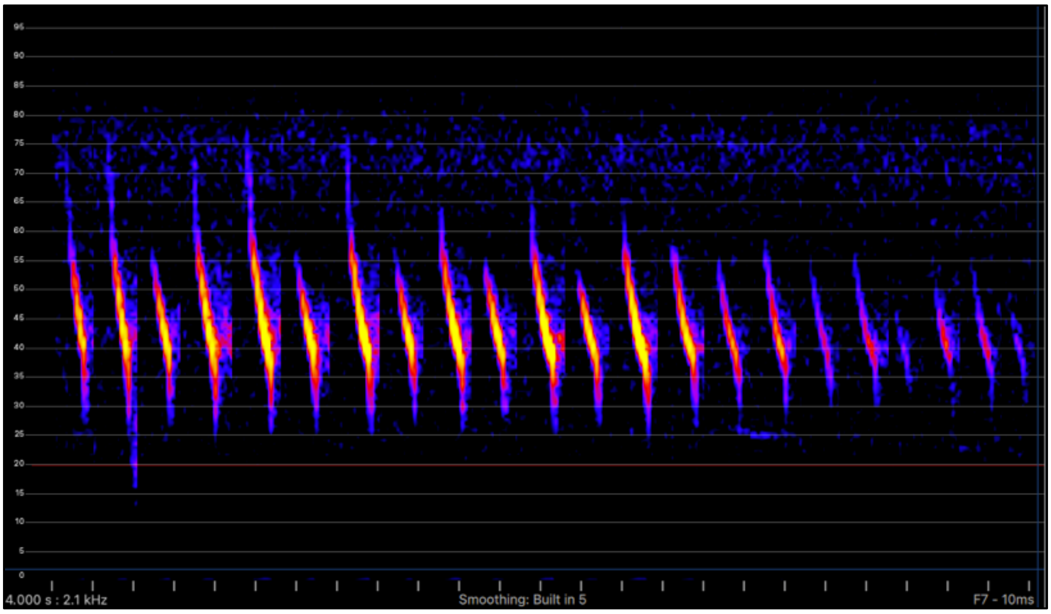


Figure S4.5.2: Continuation of figure 4.13.1. Significance codes: <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

CHAPTER FIVE: Comparing automated bat classifier agreement on Passive Acoustic Monitoring (PAM) datasets from Anabat Swift and AudioMoth



A bat call recorded by an Anabat Swift, classified by BatClassify as Brandt's/Whiskered bat with 61% confidence

As discussed in ***Chapter Four****, Passive Acoustic Monitoring (PAM) is becoming an increasingly popular means of conducting surveys and monitoring for bats for a range of applications, including scientific research, and commercial surveys for legislation compliance purposes. Although PAM protocols have the potential to be standardisable and scalable, they typically produce vast acoustic datasets, which require considerable resources to analyse manually. With the continually evolving capabilities of Artificial Intelligence (AI), multiple automated classifiers now exist to classify specific bat guilds, with the potential to streamline analysis workflows considerably. However, the reliability of such classifiers is poorly understood, particularly in how their outputs differ from one another, and how their performance is impacted by recordings of varying quality from different detectors. This chapter explores the level of agreement between pairs of commonly used classifiers on two PAM datasets; one produced using commercial bat detectors (Anabat Swift), and one produced by open-source acoustic recorders (AudioMoth) using a subset of the recordings collected for Chapter 4.*

5.1 Introduction

As discussed in **Chapter Four**, Passive Acoustic Monitoring (PAM) is developing rapidly as an increasingly important ecological method, with applications as diverse as surveying species presence and monitoring spatiotemporal change in ecological communities (Wrege *et al.*, 2017; López-Bosch *et al.*, 2022), researching evolution and behaviour (Teixeira *et al.*, 2019), and detecting anthropogenic threats (Tleimat *et al.*, 2022). As the technology develops and acoustic detectors become more financially viable, PAM has the potential to become ever more widely utilised to detect any species that produces sound. Ensuring effective data management, and conducting robust and reliable analysis of the large datasets created, however, remain key challenges (Browning *et al.*, 2017; Gibb *et al.,* 2019; Sugai *et al.*, 2019; Brinkløv *et al.*, 2023).

In the terrestrial environment, bats are the taxonomic group most frequently surveyed and monitored using PAM (Sugai *et al.,* 2019) (Chapters Two, Three, and Four). The high sampling rate required for recording ultrasonic sound results in large audio files, which typically generates larger datasets in terms of memory than those for other taxa (Frick, 2013). In order to reduce memory requirements when recording in the field (thus maximising survey duration) and facilitate post hoc data storage and analysis, passive bat detectors typically use a built-in trigger whereby audio is only recorded if it meets specific ultrasonic parameters consistent with bat echolocation frequencies (Browning *et al.*, 2017; Chapter Four). This system is common on most major commercial bat detectors, such as the Anabat Swift (Titley Scientifics, Australia) and the SM4 (Wildlife Acoustics, MA, USA). Whereas commercial detectors record only when triggered by ultrasonic sound, open-source devices, such as AudioMoths, are typically configured to record sound continuously or on a pre-programmed sleep:wake cycle. As discussed in Chapter Four, however, very recent developments have involved the launch of amplitude and frequency filters that are customisable in the configuration application and that function as triggers in a similar way to those used on commercial devices (Open Acoustic Devices, 2022b). However, the efficiency of these on-board filters is still very much in beta mode and needs to be empirically, and robustly, tested (Brinkløv *et al.*, 2023). Until this happens, many users are still opting for continuous recording (Revilla-Martin *et al.,* 2020; López-Bosch *et al.*, 2022) or use of sleep:wake cycles (e.g. Bota *et al.,* 2023; Kunberger and Long, 2023; Starbuck *et al.,* 2024), rather than using largely untested triggered configurations, despite the very large amounts of data these approaches generate.

Regardless of how recordings are collected in the field, manual processing and analysis of these large datasets can be incredibly time consuming. Moreover, even when processing is carried out by skilled technicians, it remains a subjective process, with the opportunity for user error that is challenging to quantify (Gibb *et al.*, 2019). Artificial Intelligence (AI) has the potential to revolutionise ecological monitoring for a range of taxa through automated analysis of large datasets produced by sensors, cameras and acoustic recorders in the field (Goodwin *et al.*, 2022). These approaches have been applied widely in the marine environment for cetaceans (Blount *et al.*, 2022), and have the potential to improve both the efficiency and reliability of automatically identifying animal vocalisation from within audio recordings, including ultrasonic bat calls (Stowell, 2022). Automated bat classification was first seen in the 1990s, with early exploration of decision trees and Artificial Neural Networks (ANNs), with continual development into random forest and deep learning based approaches (Zamora-Gutierrez *et al.*, 2021). Automated bat classifiers are a key component in analysing acoustic data from current national bat monitoring efforts in the UK, including a pilot study conducted by Forestry England and the Bat Conservation Trust (BCT) (Forestry England, 2024), and the BCT's national British Bat Survey (BBatS) (Bat Conservation Trust, 2024).

Bat classifiers typically utilise call parameter thresholds (e.g. amplitude, frequency) and reference sonograms to assess each sound file. The first stage of this process, often known as filtering, involves identifying and classifying the relevant sounds based on pre-defined criteria typically associated with bat calls (Mac Aodha *et al.*, 2018). Where a detector with an on-board threshold trigger is used, filtering is primarily done in the field, as sounds clearly outside the specified parameters are not recorded. However, all sounds within range will be retained, including some ultrasonic sounds not produced by bats, along with false triggers. Therefore, additional non-bat files may still need to be filtered out and excluded, either prior to, or during, automated analysis (Brinkløv *et al.*, 2023). Where a detector without an on-board threshold trigger is used, basic filtering is sometimes undertaken as part of initial data cleaning to streamline the dataset, before automated analysis commences. Once any filtering is complete, all remaining calls are identified by algorithms based on known call parameters for individual species or genus groups and/or using a pre-verified call library (Gibb *et al.*, 2019).

A number of auto-ID tools are becoming available to process and classify acoustic data. These are either integrated into analysis software (e.g. Kaleidoscope Pro, BatClassify) or are standalone pipelines (e.g. BTO Acoustic Pipeline). Some tools are free to access but are specific to the type of device used to collect the data, for example, BatClassify is available in the freeware version of Anabat Insight for files recorded on Anabat devices. Other tools, such as Kaleidoscope and the BTO Acoustic Pipeline, allow limited amounts of data to be processed for free regardless of the device used to collect the data, but require the purchase of a software licence or “credits” for long term access or to process large volumes of data. However, even where a financial cost is incurred (e.g. approx. 310 GBP for Kaleidoscope Pro, 435 GBP for the full version of Anabat Insight; January 2024 costings), auto-ID might still be more financially viable than the technician hours required for manual analysis of large datasets (Adams *et al.*, 2010). Moreover, auto-ID might also aid the accessibility and scalability of PAM for bats, especially in resource-limited settings such as in conservation organisations and for citizen science initiatives such as the BbatS (Bat Conservation Trust, 2024).

Despite the obvious theoretical benefits of automated analysis, reliable use of this approach still faces numerous challenges. Although there has been continual development of the technology and the expansion of the call libraries used as training data, significant uncertainties remain regarding variation and error rates across different auto-ID classifiers, and how these are impacted by recording quality. Sound files that contain multiple species calling simultaneously, or that are complicated by environmental noise (or internal noise from the detector itself), can make it difficult for auto-ID algorithms to reliably make classifications (Gibb *et al.*, 2019; Brinkløv *et al.*, 2023). The algorithms can also struggle to recognise variations in calls of individual bat species, attributed to factors such as habitat structure, weather conditions, and bat-specific characteristics, including age and sex (López-Baucells *et al.,* 2019). Taken together, these factors mean that risk of inaccurate classifications can be high, even if this risk remains unknown (Mac Aodha *et al.*, 2018; Barré *et al.*, 2019). Although previous studies have compared classifier performance, these have largely been undertaken using recordings from North American bat guilds (e.g. Lemen *et al.*, 2015; Nocera *et al.* 2019; Goodwin and Gillam, 2021). Rydell *et al.* (2017) compared the performance of three classifiers: SonoChiro, Kaleidoscope and BatClassify, on a European bat guild in Sweden. However, such comparisons are yet to be conducted on British bat calls, or to test contemporary classification tools, such as the BTO Acoustic Pipeline or recordings from open-source acoustic recorders, such as AudioMoth. Without a robust understanding of the error associated with automated workflows, a degree of manual auditing is still typically considered best practice when applying them to PAM data analysis, in order to validate the results (Barré *et al.*, 2019; López-Baucells *et al.,* 2019; Collins, 2023).

In this chapter, three automated classifiers are compared for the full spectrum bat data reported in **Chapter Four**, which were collected across a range of lowland habitats in the UK using Anabat Swift detectors and AudioMoth acoustic recorders (some recording at high frequency and some recording at low frequency). Data from both detector types were processed through the Bats of Europe auto-ID classifier in Kaleidoscope Pro. For comparison, auto-ID classifications were also obtained for the AudioMoth data from the BTO Acoustic Pipeline, and from BatClassify built-in to the freeware version of Anabat Insight for the Anabat Swift data. Variability in classifier-reported confidence or match ratio is assessed as a measure of self-reported classifier performance, both overall and then accounting for possible differences in performance between habitat types. The level of pairwise consensus in bat ID between classifiers is then assessed to understand when and how species are being confused, factoring in both taxonomy and habitat.

5.2 Methods

5.2.1 Acoustic data

The acoustic data used in this study were obtained from a 16-week period of passive acoustic bat monitoring, carried out across four sites, situated within a 20 km radius in the south Worcestershire/north Gloucestershire region of the United Kingdom in summer and autumn 2022 (**Chapter Four**). The four sites represented different habitat types: riparian, woodland, wood pasture, and arable. The data at each site were recorded by two types of full spectrum passive acoustic detectors: Anabat Swift (Titley Scientific, Australia) detectors and AudioMoth acoustic recorders (Open Acoustic Devices, UK).

All detectors were configured to commence recording 30 minutes prior to sunset and cease recording 30 minutes after sunrise. The on-board trigger on the Anabat Swift detectors was used to automatically activate the detector to record bats when detected. At the time of this fieldwork, the AudioMoth lacked a reliable on-board trigger for bats, therefore, these detectors were pre-configured to record all sound on a sleep:wake cycle throughout the night. The detectors were always awake for five seconds at a time; however, the frequency of these periods was determined by night lengths and memory card capacity. A total of 80 nights of acoustic data was recorded, classified and used for analysis (20 nights * 4 sites).

5.2.2 Bat species classification

Prior to any automated classification, all recordings were initially passed through a broad frequency filter (“All bats” in Anabat Insight) to assist data storage. This filtered out any recordings that did not contain sound within the range of 4-300 kHz and that were not consistent with bat calls. This removed proportionally fewer recordings for the Anabat Swift dataset (where the on-board bat trigger had been used) compared with the AudioMoth dataset (where a sleep:wake cycle was used) such that only recordings with a high feasibility of containing bat calls remained for onward automated classification. After all filter steps had been completed, all data recorded by each type of detector were processed through two automatic classifiers (Table 5.1)

Table 5.1: *Automatic classifiers used to process datasets from the two detector models*

Detector model	Automatic Classifiers
Anabat Swift	BatClassify Kaleidoscope Pro
AudioMoth	BTO Acoustic Pipeline Kaleidoscope Pro

5.2.2.1 Kaleidoscope Pro

The Bats of Europe classifier (version 5.4.0) in Kaleidoscope Pro (version 5.4.8) was applied to the acoustic data from both detector models; this is the regional reference call library appropriate to the location. The classifier gave a single species classification for each sound file or ‘call sequence’, along with a match ratio (range 0-1; higher = better), calculated from the number of calls in the sequence that match to those in the reference library for the assigned species. As per Table 5.1, all recordings were processed using Kaleidoscope Pro, regardless of the detector type by which they were recorded.

5.2.2.2 BTO Acoustic Pipeline

The AudioMoth recordings were additionally processed through the BTO Acoustic Pipeline. The pipeline’s reference library has expanded rapidly since its launch in 2021 and, at the time of this study, contained high volumes of verified reference calls recorded on AudioMoth devices (*Pers. Comm.* Stewart Newson, Developer - BTO Acoustic Pipeline). The pipeline claimed to feature significant advantages over other classifiers, including the ability to identify social calls, and unlike the classifier in Kaleidoscope Pro, also featured the ability to identify multiple species within a single recording, including those from quieter species with weaker signals. Each classification was assigned a probability value (range 0-1; higher = better).

5.2.2.3 BatClassify

The Anabat Swift recordings were additionally processed through BatClassify, a classifier developed by Scott and Altringham (2004), specifically for UK bats in woodland habitats. The classifier was integrated into the Anabat Insight call analysis software, and accessible in the freeware version of the software for full spectrum files recorded on Titley Scientific devices. BatClassify can also identify multiple species of bat calling within a single recording where applicable (*Pers. Comm.* Chris Scott, Developer – BatClassify). Moreover, as with the other classifiers, each classification was assigned a confidence value (range 0-100%; higher = better).

5.2.3 Recording selection

All potential bat call recordings were subjected to a screening process prior to any statistical analysis. Firstly, only those calls with a match ratio (Kaleidoscope Pro), probability (BTO Acoustic Pipeline), or confidence value (BatClassify) ≥ 0.5 or 50%, were carried forward, consistent with current recommendations on the analysis of classifier-assisted analysis of acoustic datasets (Barré *et al.,* 2019; British Trust for Ornithology, 2024). Henceforth, “confidence” reported as a percentage is used throughout for consistency. Secondly, the datasets were screened for recordings with multiple classifications. Whilst both BatClassify and the BTO Acoustic Pipeline can recognise calls from multiple species within a recording, Kaleidoscope Pro assigns a single overall classification. Therefore, to avoid systematic bias confounding statistical analysis, any recordings classified as containing calls from multiple species using BatClassify and the BTO Acoustic Pipeline were removed prior to analysis; these same files were also removed from the matched Kaleidoscope Pro dataset to ensure that the datasets remained balanced and symmetrical – and thus directly comparable. Finally, all recordings with a single species classification from each of the classifiers were combined and paired recordings were identified (i.e. instances where the same recording was classified ≥ 50% by *both* classifiers). These paired recordings (henceforth termed matched data) were eligible for statistical modelling. The workflow to identify recordings from the Anabat Swift and AudioMoth datasets is shown in Figure 5.1, illustrated by flow diagrams adapted from Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA) (Page *et al.*, 2021).

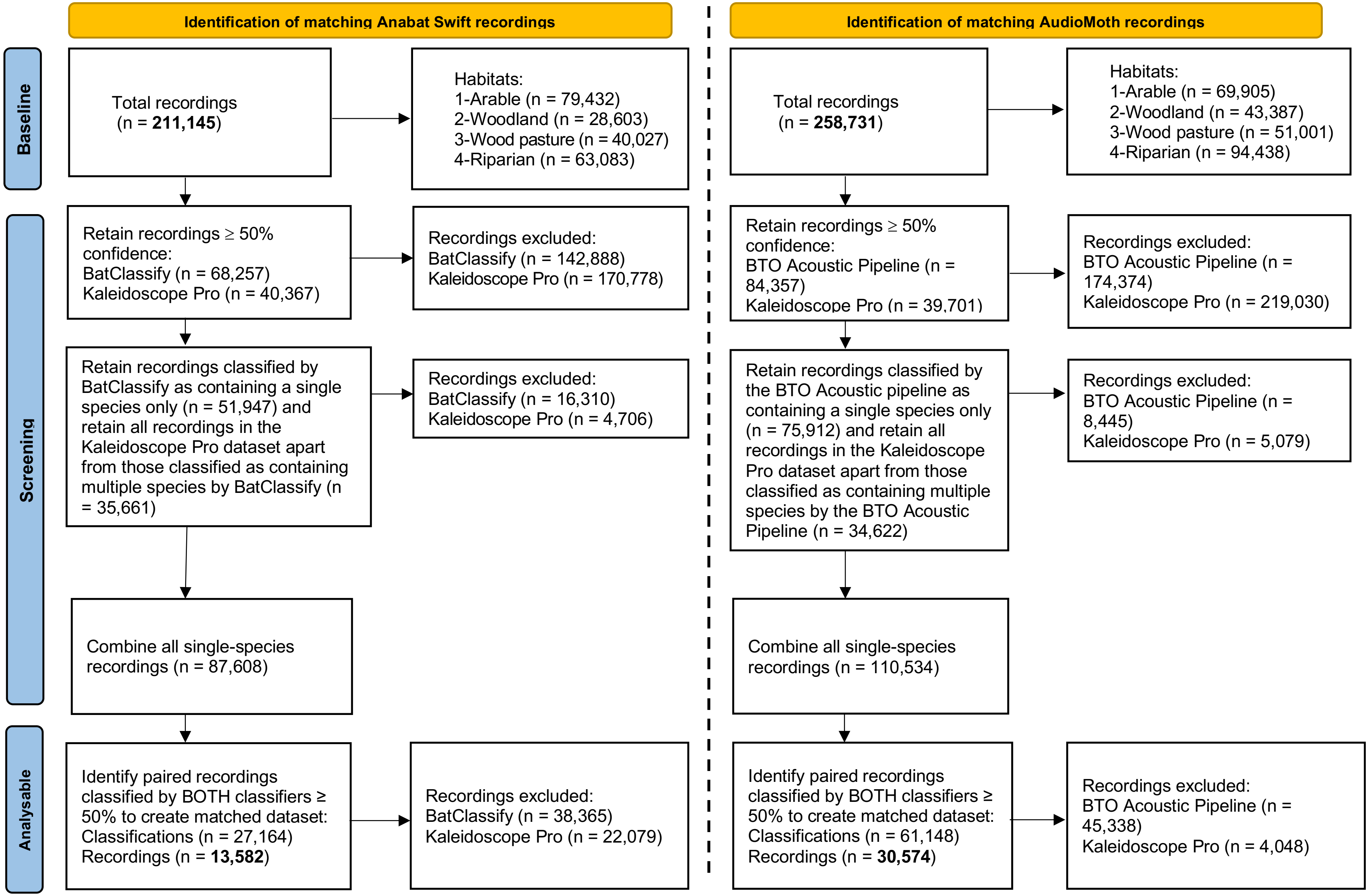


***Figure 5.1**: PRISMA workflow adapted to illustrate the identification of recordings for statistical analysis, from the two datasets*

5.2.4 Statistical analysis

Statistical analyses were carried out in R 4.2.2 (R Core Team, 2022). Initial analysis explored the percentages of recordings classified with ≥ 50% confidence, firstly for each of the four detector/classifier combinations overall and secondly when subdivided into the four habitat types. The variation in classification confidence for individual species, above the 50% threshold, was also calculated.

To explore the effects of taxonomic group and habitat on the strength of the matches between the two classifiers, Cumulative Link Models (CLMs) with logit link functions were fitted using the matched data. Two CLMs were used, one for each of the two detector types (Anabat Swift and AudioMoth). The former was calculated on the 13,582 recordings classified by *both* Kaleidoscope Pro *and* BatClassify with ≥ 50% confidence; the latter was calculated on the 30,574 recordings classified by *both* Kaleidoscope Pro *and* BTO Acoustic Pipeline with ≥ 50% confidence (Figure 5.1). In both cases, models were developed with an ordinal dependent variable whereby the matched recordings were allocated a value 1-6 determined by match strength (Table 5.2), and two predictors habitat (1=riparian, 2=woodland, 3=wood pasture, 4=arable) and one of six taxonomic groups. The taxonomic groups were: (1) ***Pipistrellus*** comprising Nathusius' pipistrelle (*Pipistrellus nathusii*), common pipistrelle (*Pipistrellus pipistrellus*) and soprano pipistrelle (*Pipistrellus pygmaeus)*; (2) ***Nyctalus/Eptesicus*** comprising Serotine (*Eptesicus seotinus*), Leisler's *(Nyctalus leisleri*) and Noctule (*Nyctalus noctula*) (3) ***Plecotus*** comprising brown long-eared (*Plecotus auritus*) and grey long-eared (*Plecotus austriacus*); (4) ***Myotis*** comprising Alcathoe (*Myotis alcathoe*), Brandt's (*Myotis brantdii*), Bechstein's (*Myotis bechsteinii*), Daubenton's (*Myotis daubentonii*), whiskered (*Myotis mystacinus*), and Natterer's (*Myotis nattereri*); (5)

Rhinolophus comprising greater horseshoe (*Rhinolophus ferrumequinum*) and lesser horseshoe (*Rhinolophus hipposideros*); and (6) ***Barbastella*** comprising barbastelle (*Barbastella barbastellus)*. These groups were determined by genus, with the exception of the combined *Nyctalus/Eptesicus* grouping. This was partially necessitated because BatClassify does not attempt to separate the three species, owing to similar call types. The CLM models were used to calculate predicted probability values for recordings falling within each of the six categories after allowing for habitat and taxonomic group. Finally, occurrences of lack of consensus between classifiers were explored to identify the combinations of species classifications most commonly encountered.

Table 5.2: *"Match strength" criteria used to score the degree of consensus for each recording using any two classifiers for statistical analysis.*

"Match strength" score	**Criteria**	**Anabat Swift data (n)**	**AudioMoth data (n)**
1	Species do not match	692	2,919
2	Species match, both classifiers 50-74% confident	70	114
3	Species match, one classifier 50-74% confident and the other classifier ≥75% confident	1,702	2,941
4	Species match, both classifiers 75%-98% confident	3,784	5,624
5	Species match, one classifier 75%-98% confident and the other classifier ≥99% confident	6,588	12,640
6	Species match, both classifiers ≥99% confident	746	6,336

5.3 Results

From a total of 211,145 Anabat Swift recordings, 40,367 (19.12%) were classified by Kaleidoscope Pro, and 68,258 (32.33%) were classified by BatClassify as containing bat calls with a confidence value ≥ 50%. Habitat specific details are shown in Table 5.3.

Table 5.3: *Numbers of Anabat Swift recordings and percentages of recordings classified with a ≥ 50% match ratio/confidence value, by each of the classifiers, in each habitat.*

		Kaleidoscope Pro		**BatClassify**	
	Total recordings	≥ 50% confidence	%	≥ 50% confidence	%
Riparian	63,083	20,402	32.34	26,060	41.31
Woodland	28,603	6,477	22.65	15,966	55.82
Wood Pasture	40,027	10,779	26.93	17,224	43.03
Arable	79,432	2,709	3.41	9,007	11.34

From a total of 258,731 AudioMoth recordings, 39,701 (15.35%) were classified by Kaleidoscope Pro, and 84,357 (32.61%) were classified by the BTO Acoustic Pipeline as containing bat calls, with confidence value ≥ 50%. Habitat specific details are shown in Table 5.4.

Table 5.4: *Numbers of AudioMoth recordings and percentages of recordings classified with a ≥50% match ratio/confidence value, by each of the classifiers, in each habitat.*

		Kaleidoscope Pro		**BTO Acoustic Pipeline**	
	Total recordings	≥ 50% confidence	%	≥ 50% confidence	%
Riparian	94,438	24,759	26.22	50,142	53.10
Woodland	43,387	4,625	10.66	14,199	32.73
Wood Pasture	51,001	7,521	14.75	14,279	28.00
Arable	69,905	2,796	4.00	5,737	8.21

At this initial screening stage it was evident that both the BTO Acoustic Pipeline and BatClassify classified higher percentages of the recordings in their respective datasets with a confidence value ≥ 50%, than did Kaleidoscope Pro. This trend was evident across all habitats.

5.3.1 Classifier identification confidence

The mean confidence values (≥ 50%) for each species/species group, for each classifier, are plotted in Figure 5.2. Species in the genus *Rhinolophus* were the most confidently classified species (lesser horseshoe for Kaleidoscope Pro and BatClassify, greater horseshoe for the BTO Acoustic Pipeline). Conversely, species in the genus *Myotis* tended to be classified with the least confidence, with the BTO Acoustic pipeline not classifying any recordings with ≥ 50% confidence for Alcathoe bat and Bechstein’s bat.

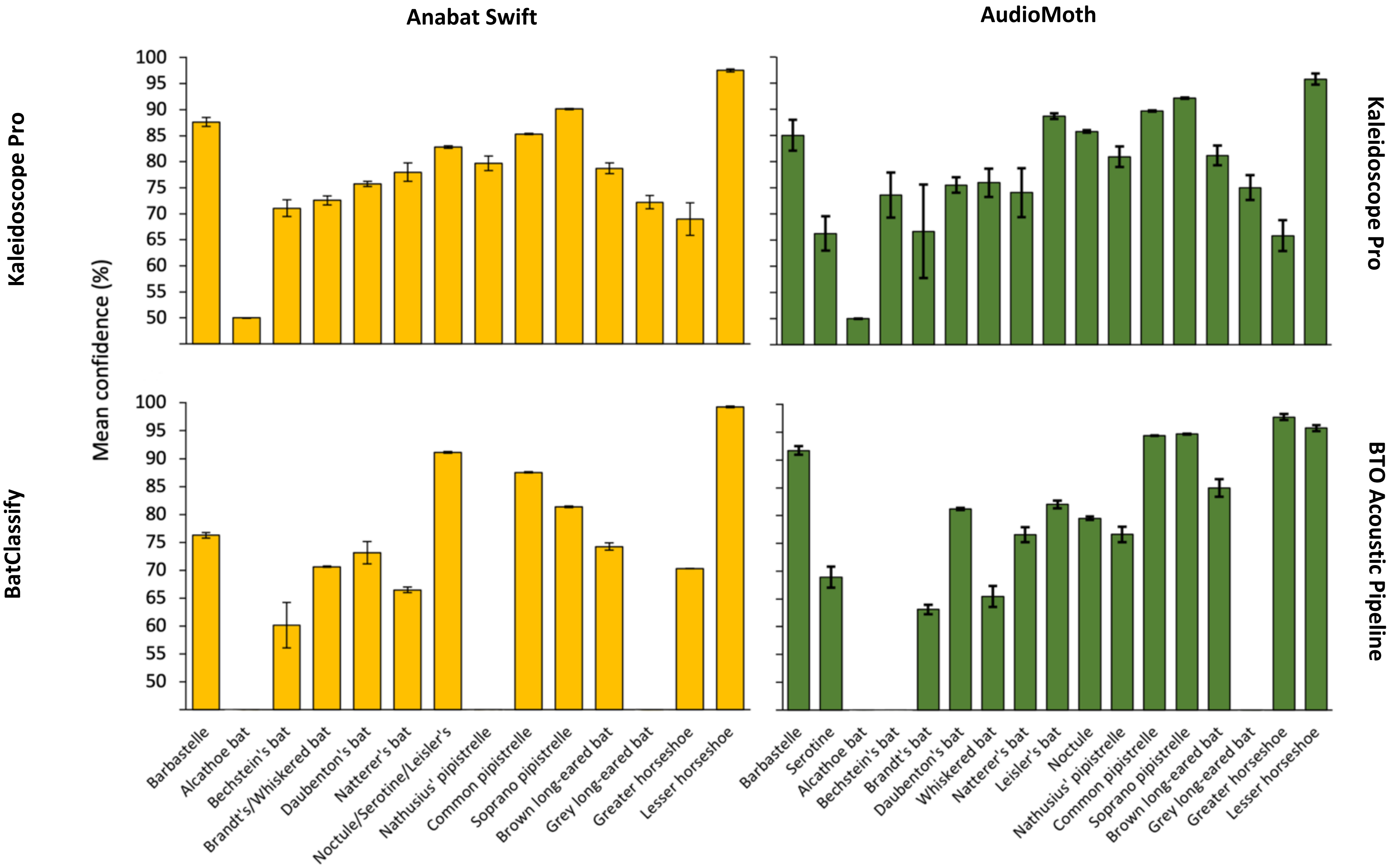


Figure 5.2*: Mean confidence values ≥50% for each species/species group by each classifier, on each of the datasets. Error bars show SEM (±1se).*

5.3.2 Consensus between classifiers

5.3.2.1 Anabat Swift

A total of 13,547 Anabat Swift recordings was classified as containing bat calls with a confidence value ≥ 50% by both classifiers (matched data). The percentages of recordings that were classified with ≥50% confidence using Kaleidoscope Pro that were also classified as a single species recording with ≥50% confidence using BatClassify, and *vice versa* are shown in Table 5.5.

Table 5.5: *The percentages of classifications made ≥ 50% confidence by each classifier used on the Anabat Swift data, that were present in the dataset for both classifiers*

	Total recordings (≥ 50% confidence)	**No. recordings present in both datasets**	**%**
BatClassify	51,947	13,582	26.15
Kaleidoscope Pro	35,661	13,582	38.09

The optimal CLM (χ^2=6465.3, df=23, P<0.001) included both factors of habitat and taxonomic group, and the interaction term between habitat and taxonomic group, all of which were statistically significant (P<0.001 in all cases). The model was a substantially better fit (AIC=64,513) than the null model (AIC=70,933) (Burnham and Anderson, 2002). The mean predicted probabilities of match strength between the two classifiers, calculated by the model for each habitat are shown in Figure 5.3, and for each taxonomic group in Figure 5.4. The predicted probabilities calculated for each interaction between the factors are shown in Figure 5.5.

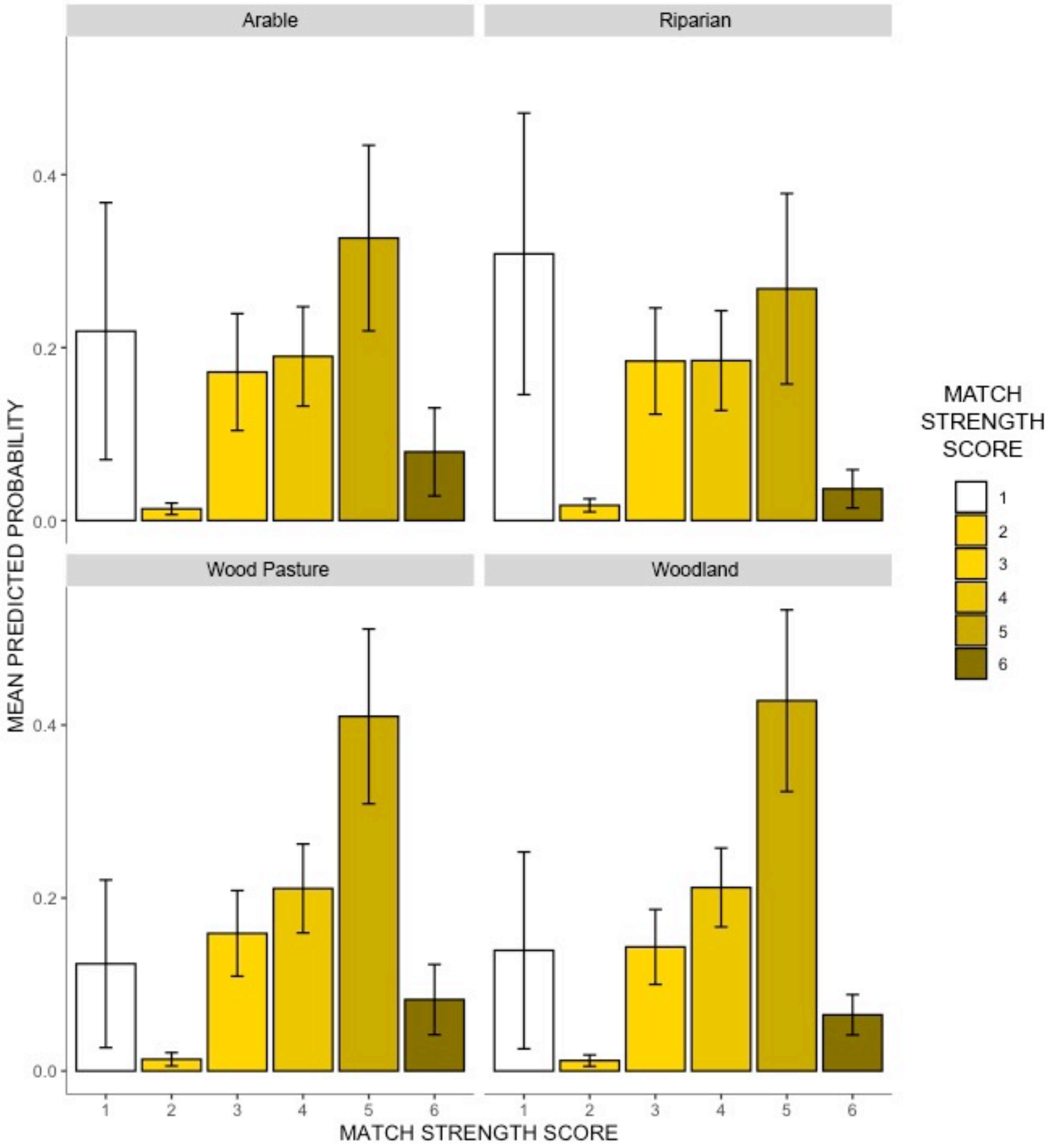


Figure 5.3: *Mean probabilities predicted by the model of obtaining each match strength score (with a higher score indicating a stronger match), within each habitat using the Anabat Swift dataset (see Table 5.3 for definitions of match strength scores). Error bars show SEM (±1se).*

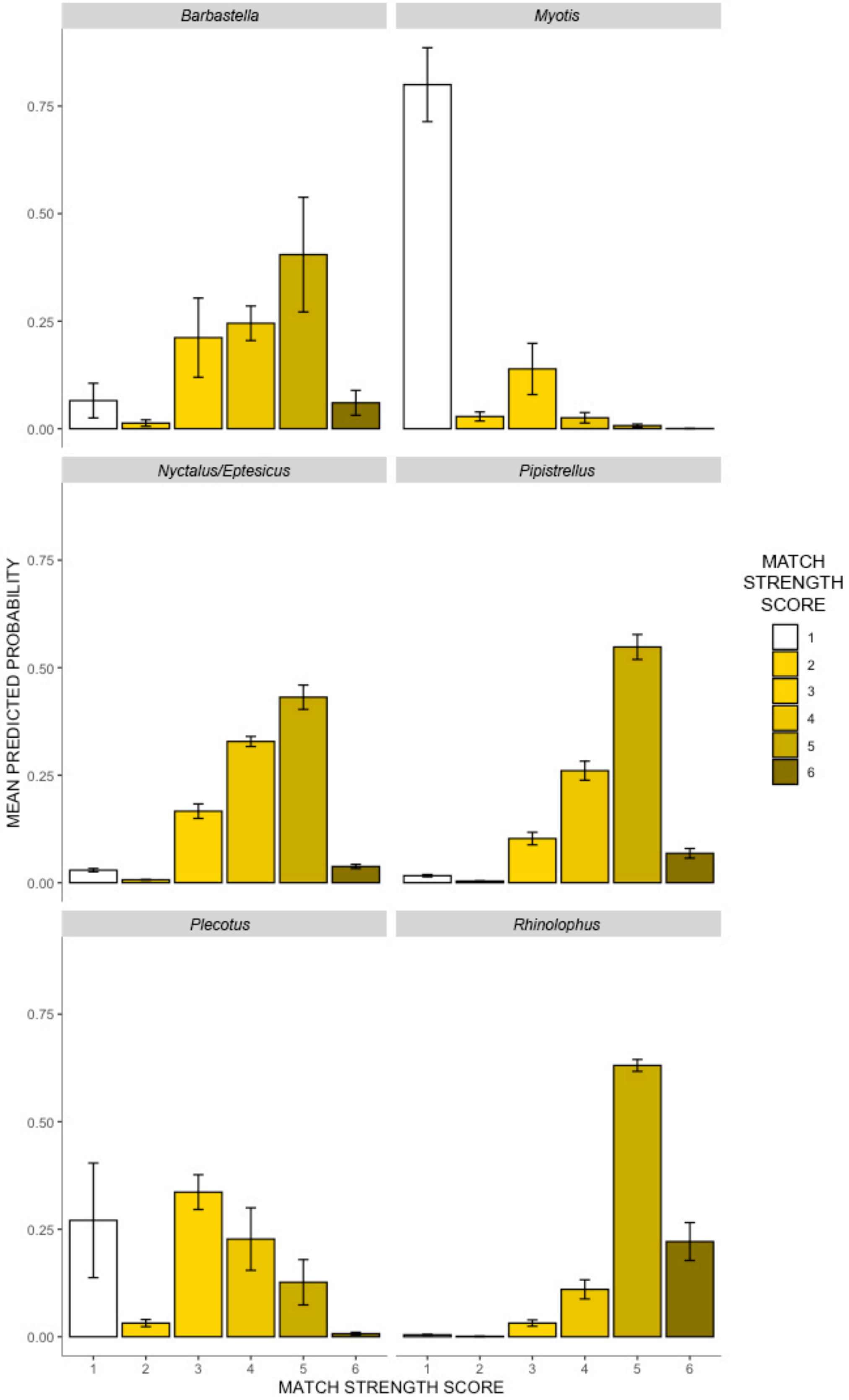


Figure 5.4: *Mean probabilities predicted by the model of obtaining each match strength score (with a higher score indicating a stronger match), for each taxonomic group using the Anabat Swift dataset (see Table 5.3 for definitions of match strength scores). Error bars show SEM (±1se).*

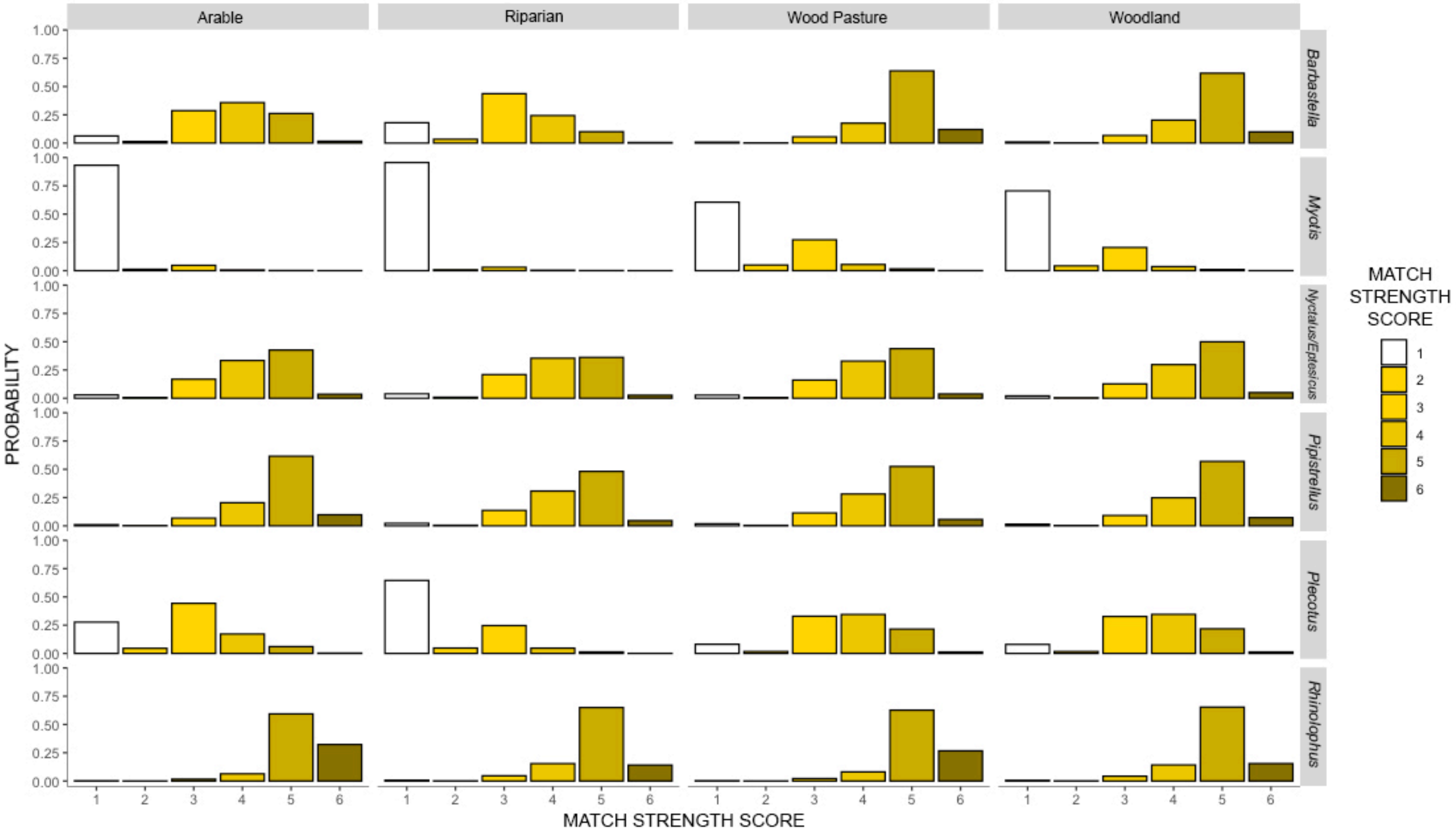


Figure 5.5: *Probabilities predicted by the model of obtaining each match strength score (with a higher score indicating a stronger match), for each interaction between habitat and taxonomic group, using the Anabat Swift dataset (see Table 5.3 for definitions of match strength scores).*

The significance of the factor of habitat (Figure 5.3), appeared to be driven by differences in the match strength scores most likely to be obtained in the arable and riparian habitats, as opposed to the wood pasture and woodland habitats. In the latter two habitats, a strong match score of 5 was predicted to be most likely, with a mean probability in wood pasture of 0.49 (±0.10 SEM), and a mean probability in woodland of 0.43 (±0.11 SEM). On the other hand, in the arable and riparian habitats no single score was predicted to be most likely obtained. Moreover, obtaining a score of 1, indicating disagreement between the classifiers was predicated to be comparatively more likely than in the woodland and wood pasture habitats, particularly in the riparian habitat (0.31 ± 0.16 SEM).

The classifiers were much less likely to agree on recordings involving *Myotis* classifications, compared to the other five taxonomic groups (Figure 5.4). A score of 1, indicating no match, was predicted to be the most likely score obtained for *Myotis* classifications, with a mean probability of 0.80 (±0.08 SEM). For the other taxonomic groups, with the exception of *Plecotus*, a strong match score of 5 was predicted as being the most likely to be obtained.

When considering the interaction between the factors (Figure 5.5), the predicted probability of obtaining the lowest match strength score of 1 (no agreement), was high for *Myotis* recordings in all habitats (ranging from 0.61 in woodland to 0.96 in riparian). Conversely, the highest match strength score of 6 was predicted to be most likely to occur between classifiers on recordings involving classifications in the *Rhinolophus* taxonomic group in arable habitat (0.32), with this interaction having highest probability of both classifiers agreeing with ≥99% confidence.

5.3.2.2 AudioMoth

A total of 30,574 AudioMoth recordings was classified as containing bat calls with a confidence value ≥ 50% by both of the classifiers (the matched data). The percentage of recordings that were classified with ≥50% confidence using Kaleidoscope Pro that were also classified as a single species recording with ≥50% confidence using the BTO Acoustic Pipeline, and *vice versa* are shown in Table 5.7.

Table 5.6: The percentages of classifications made ≥ 50% confidence by each classifier used on the AudioMoth data, that were present in the dataset for both classifiers

	Total recordings (≥ 50% confidence)	**No. recordings present in both datasets**	**%**
BTO Acoustic Pipeline	75,912	30,574	40.28
Kaleidoscope Pro	34,622	30,574	88.31

The optimal CLM (χ^2=3877.1, df=15, P<0.001) included both factors of habitat and taxonomic group, and the interaction term between these two factors. Both factors and the interaction term were statistically significant (P<0.001 in all cases). In this dataset, recordings involving *Barbastella* or *Plecotus* classifications were found to occur too infrequently for meaningful statistical analysis, so were therefore omitted. The model was a better fit (AIC=175,626) than the null model (AIC=179,473) (Burnham and Anderson, 2002). The mean predicted probabilities of match strength between the two classifiers calculated by the model for each habitat are shown in Figure 5.6, and for each taxonomic group in Figure 5.7. The predicted probabilities calculated for each interaction between the factors are shown in Figure 5.8.

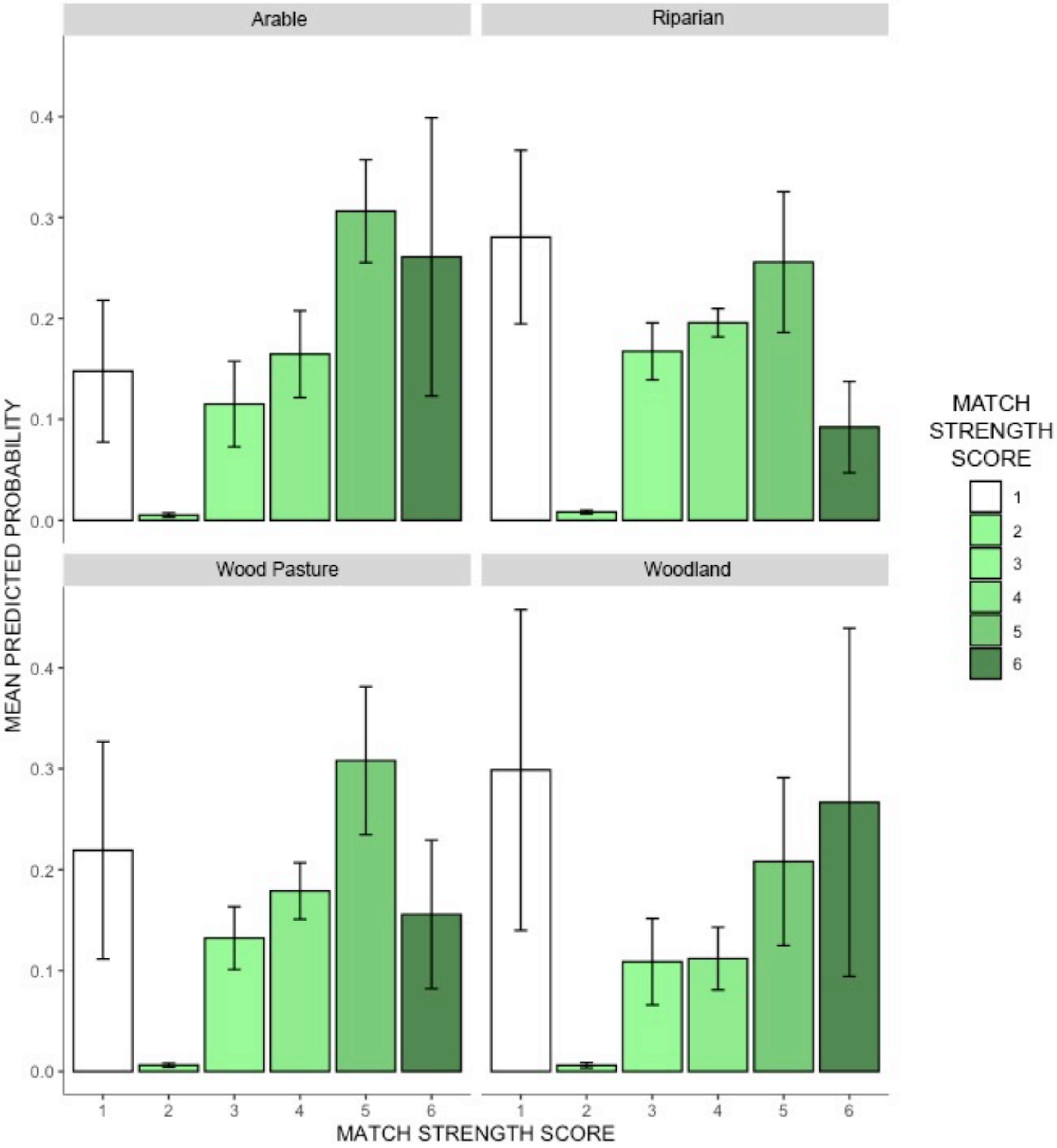


Figure 5.6: *Mean probabilities predicted by the model of obtaining each match strength score (with a higher score indicating a stronger match), within each habitat using the AudioMoth dataset (see Table 5.3 for definitions of match strength scores). Error bars show SEM (±1se).*

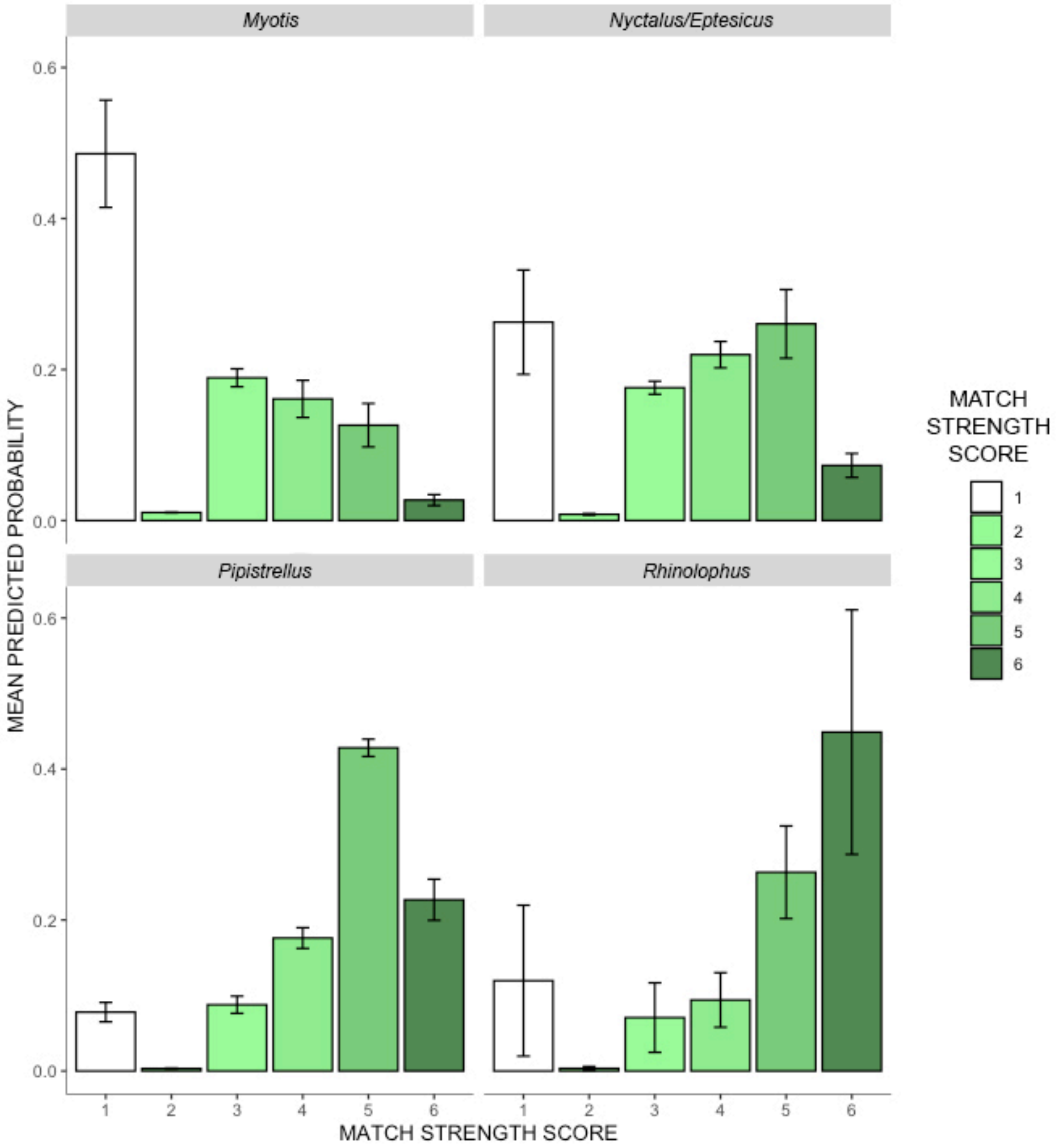


Figure 5.7: *Mean probabilities predicted by the model of obtaining each match strength score (with a higher score indicating a stronger match), for each taxonomic group, using the AudioMoth dataset (see Table 5.3 for definitions of match strength scores). Error bars show SEM (±1se).*

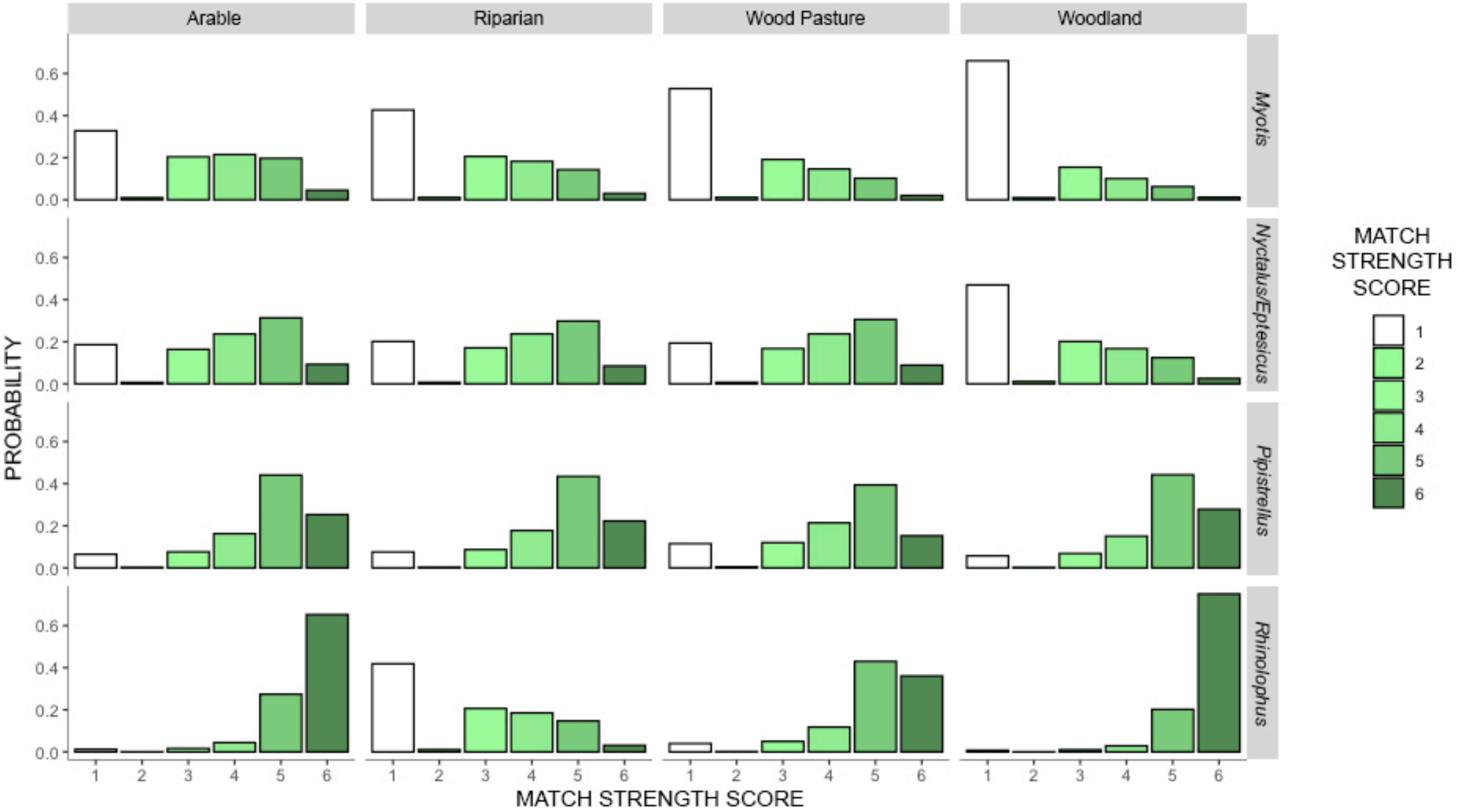


***Figure 5.8**: Probabilities predicted by the model of obtaining each match strength score (with a higher score indicating a stronger match), for each interaction between habitat and taxonomic group, using the AudioMoth dataset (see Table 5.3 for definitions of match strength scores).*

In contrast to the Anabat Swift dataset, no single match strength score was predicted to be considerably more likely to be obtained, in any of the habitats (Figure 5.6). However, a lack of agreement (match strength score 1) was seen to be the most likely outcome in the riparian (0.28 ± 0.09 SEM) and woodland habitats (0.30 ± 0.16 SEM), whereas in the arable habitat a strong match, scoring 5 or 6, was predicted to be the most likely outcome (5 = 0.31 ± 0.05 SEM, 6 = 0.26 ± 0.14 SEM).

Classifiers generally did not agree on recordings involving classifications in the *Myotis* taxonomic group (Figure 5.7), where obtaining the lowest match strength score of 1 (species do not match), was predicted to be the most likely outcome, with a mean probability of 0.49 (± 0.07 SEM). Conversely, the maximum match score of 6 (both classifiers agree with ≥99% confidence), was seen to be the most likely outcome (0.45 ± 0.16 SEM) where *Rhinolophus* classifications were concerned.

Finally, when considering the interactions between factors (Figure 5.8), disagreement between classifiers was predicted to be the most likely outcome for *Myotis* classifications, particularly in woodland habitat (0.66). Classifier disagreement was also predicted to be the most likely outcome for the *Nyctalus/Eptesicus* group in woodland (0.47), and for the *Rhinolophus* group in the riparian habitat (0.42). In contrast, the maximum match strength score of 6 was predicted to be the most likely outcome for recordings involving *Rhinolophus* species in the arable (0.65) and woodland (0.75) habitats.

5.3.3 Species confusion

5.3.3.1 Anabat Swift

Analysis of the lack of consensus between BatClassify and Kaleidoscope Pro found species in the genus *Myotis* to be the most common cause of disagreement. Instances where recordings were classified as Brandt's/Whiskered bat by BatClassify, but as Daubenton's bat by Kaleidoscope Pro, accounted for 49.93% of all instances of confusion (Figure 5.5).

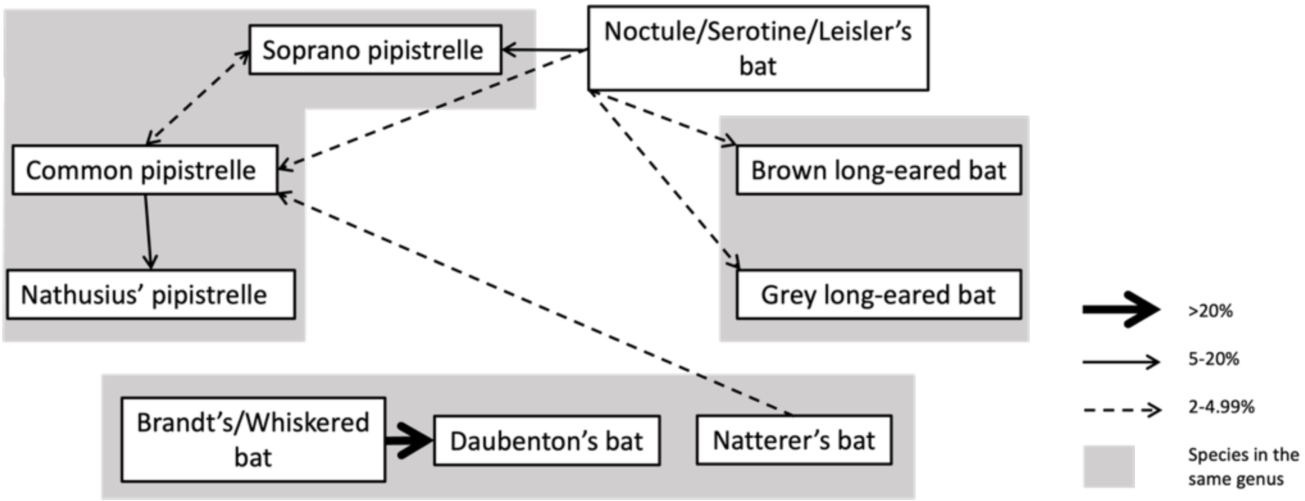


Figure 5.9*: Species classifications most commonly involved in a lack of consensus between classifiers in analysing Anabat Swift recordings (origin of arrow = BatClassify classification, tip of arrow = Kaleidoscope Pro classification).*

5.3.3.2 AudioMoth

Analysis of species most commonly confused when a lack of consensus was observed between classifiers was predominantly driven by instances where a recording was classified as common pipistrelle by the BTO Acoustic Pipeline, but as a soprano pipistrelle by Kaleidoscope Pro (53.1% of the recordings for which confusion was observed). Additionally, there were cross-genus confusions, most prominently where recordings were classified as either common or soprano pipistrelle by the BTO Acoustic Pipeline, but as noctule by

Kaleidoscope Pro (12.09% and 16.86% of the recordings for which confusion was observed, respectively). All other species confusions were minor (<5% of recordings for which confusion was observed) (Figure 5.6).

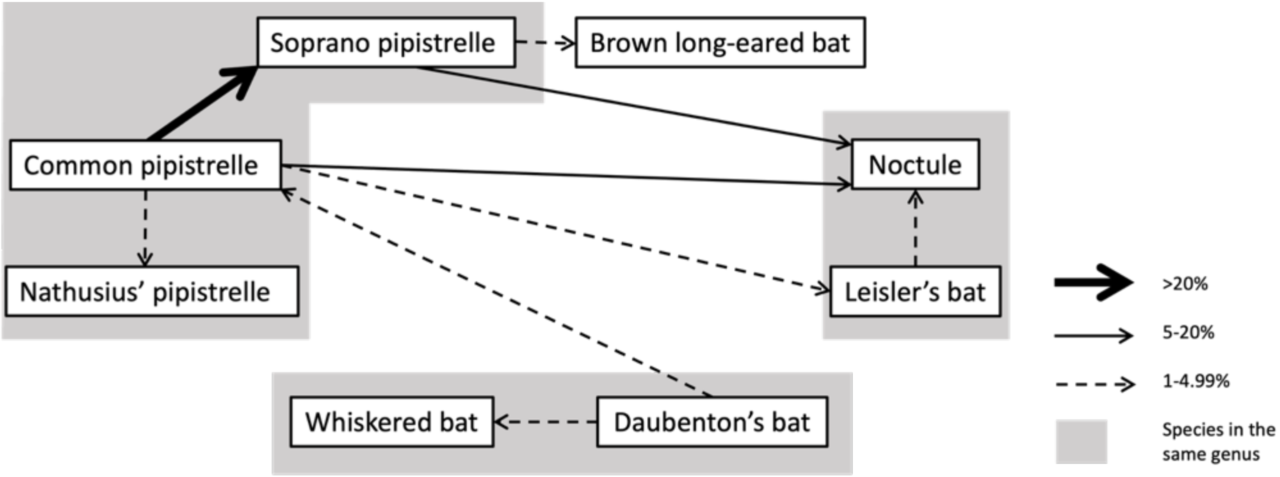


Figure 5.10: *Species classifications most commonly involved in a lack of consensus between classifiers in analysing AudioMoth recordings (origin of arrow = BTO Acoustic Pipeline classification, tip of arrow = Kaleidoscope Pro classification).*

5.4 Discussion

Notable differences were observed in the overall performance of the different classifiers. In both datasets, Kaleidoscope Pro classified fewer recordings above the confidence threshold than either BatClassify (Anabat Swift), or the BTO Acoustic Pipeline (AudioMoth). There were similarities in the habitat and taxonomic group effects in both datasets, with a lack of consensus predicted to be most likely to occur in riparian habitat, and for recordings potentially containing calls from the genus *Myotis*. The classifications most frequently confused when there was a lack of consensus were predominately species within the same genus, for both the Anabat Swift (*Myotis*) and AudioMoth (*Pipistrellus*) datasets.

5.4.1 Classifier confidence

In order to minimize false positives in automated classification workflows Barré *et al.* (2019) recommend discarding any recordings that do not exceed a confidence threshold of ≥ 50%. This approach is adopted in the recommendations for auditing results from the BTO Acoustic Pipeline (British Trust for Ornithology, 2024). However, in this study, the proportion of recordings not meeting this threshold was seen to vary widely, depending on the classifier used. Overall, Kaleidoscope Pro classified fewer of the recordings above the threshold (19.12% in the Anabat Swift dataset, 15.35% in the AudioMoth dataset) than either BatClassify (32.33%) or the BTO Acoustic Pipeline (32.60%). The metrics used to define confidence varies between classifiers (Lemen *et al.,* 2015). The value assigned by Kaleidoscope Pro is calculated based on the number of calls (which Kaleidoscope terms 'pulses') within the recording that match the classification, and is thus technically a match ratio. However, because a single species classification is assigned for each recording, the match ratio has the potential to be impacted by the presence of calls from multiple species. For example, all calls of the classified species may be considered a match for one specific species, but these may account for <50% of the calls in the recording, such that the match ratio would also be <50%.

The mean confidence values for each species classification made by Kaleidoscope Pro were similar in both the AudioMoth and Anabat Swift datasets, with lesser horseshoe, barbastelle and soprano pipistrelle classifications being associated with the highest mean confidence values. On the AudioMoth dataset, the BTO Acoustic Pipeline was most confident on these same species, as well as greater horseshoe. However, further manual auditing conducted in **Chapter Four** found all greater horseshoe classifications to be false positives. The affected recordings typically contained noise around 80 kHz, within the peak frequency range of greater horseshoe echolocation calls. Greater horseshoe classifications were made by all classifiers, in both datasets, reaffirming the importance of a degree of manual auditing in analysis workflows, irrespective of detector type, classifier type, or reported confidence values. Species in the genus *Myotis* were among the least confidently classified in both datasets by all classifiers, likely driven by similarities in call parameters, and peak frequency overlaps with other genera, such as *Pipistrellus* (Gibb *et al.,* 2019).

5.4.2 Habitat and taxonomic effects

Within the Anabat Swift dataset the significance of habitat in determining the resulting predicted classifier match strength would appear to be driven by an increased chance of strong agreement in woodland and wood pasture habitats compared to the arable and riparian habitats. The principal drawback of conducting pairwise analysis on unverified field recordings is that it is impossible to determine if one classifier is performing more accurately than the other (Lemen *et al.*, 2015). However, BatClassify was originally developed for UK bats in woodland (Titley Scientific, 2024), and therefore may more confidently classify recordings in these types of habitats, resulting in the higher probability of obtaining a stronger classifier match score.

The significant effect of habitat in both datasets was seen to be subtle, particularly for the AudioMoth dataset. Here, no single match strength score was predicted to be much more likely to be obtained, in any of the habitats. In woodland for example, a score of 1 indicating no match, and a score of 6 indicating the strongest possible match, were equally likely outcomes. However, the arable habitat was seen to be where strongest matches were most likely, and disagreement least likely. This habitat was the most homogeneous and open of the four habitats surveyed. This lack of habitat complexity and clutter is likely to increase detectability and improve the overall quality of the recordings produced by the AudioMoth MEMS microphone (MacAodha *et al.,* 2018), resulting in better classifier performance, and an increased likelihood of consensus.

In terms of the effect of taxonomic group on predicted classifier match strength, there were notable differences between the datasets and respective pairs of classifiers. Calls attributed to the genus *Myotis* are notoriously challenging to classify to species level, even by skilled practitioners (Vaughan *et al.*, 1997; Russ, 2012). The findings presented indicate that this is also the case for automated analysis, with the classifiers found to be highly likely to disagree on recordings involving *Myotis* species classifications in both datasets. In the Anabat Swift dataset this was largely driven by recordings classified as Brandt’s/Whiskered bat by BatClassify being classified as Daubenton’s bat by Kaleidoscope Pro, likely as a result of interspecific overlap in call parameters (Rydell *et al.*, 2017). Moreover, Kaleidoscope Pro classified some recordings in the dataset as Alcathoe bat, a nationally rare *Myotis* species, which was not classified by BatClassify. Given that all study sites were well outside the known distribution for this species in the UK, it is highly unlikely that Kaleidoscope Pro was performing accurately in this instance. Recordings classified in the *Rhinolophus* and *Pipistrellus* taxonomic groups were predicted to produce the strongest matches between classifiers in both datasets. *Rhinolophus* calls have distinctive call shapes and high frequencies, and were, therefore, largely agreed upon by the classifiers, despite being short range and prone to attenuation. *Pipistrellus* calls are also distinctive and unlikely to overlap with other taxonomic groups in terms of call parameters (Russ, 2012).

5.4.3 Species involved in a lack of classifier consensus

Within both datasets the pairs of species involved most frequently in cases of disagreement, were in the same genus. Within the Anabat Swift dataset, confusion between Brandt's/Whiskered bat and Daubenton's bat, both in the genus *Myotis,* accounted for almost half of the occurrences of confusion between BatClassify and Kaleidoscope Pro. These findings are consistent with those of previous studies (Rydell *et al.*, 2017; Thomas and Davison, 2022) which found Kaleidoscope Pro and/or BatClassify were unreliable in identifying *Myotis* calls to species level. Similarly, within the AudioMoth dataset, confusion between common pipistrelle and soprano pipistrelle, both in the genus *Pipistrellus*, accounted for over half (53.1%) of all occurrences of confusion. Although calls from the two species are typically distinguished by differences in peak frequency, plasticity of *Pipistrellus* calls can vary substantially, depending on environmental or behavioural factors (Montauban *et al.*, 2021). This can create considerable overlap in characteristic call frequencies for the two species, which can lead to classifier confusion.

5.4.4 Implications and recommendations

These findings support the recommendations of previous work; automated classifiers should still be used with caution, and if possible, in conjunction with manual auditing by skilled technicians (Russo and Voigt, 2016; Rydell *et al.*, 2017; Brabant *et al.*, 2022; Solick *et al.*, 2024). Although adopting a confidence threshold into analysis workflows can aid in reducing false positives, they will not be eliminated altogether. For applications intolerant to error, manual auditing will still be required, for example in establishing the presence/absence of particular species for impact assessments (Barré *et al.*, 2019). Despite improvements in classifier accuracy in recent years with the expansion of reference call libraries, the pairwise disagreement between widely used classifiers on the same recordings shown here highlights that there remains the potential for misidentification. With the increasingly wider use of open-source acoustic recorders such as AudioMoth, consideration also needs to be given to the relative quality of recordings obtained by different devices. The call libraries used to train classifiers typically contain example calls of known species, and there may be a tendency to select high quality calls for inclusion in the library (Lemen *et al.*, 2015). These may not relate well to recordings from complex habitats or lower quality microphones, resulting in misidentification. However, the BTO Acoustic Pipeline was seen here to classify more recordings over the confidence threshold than Kaleidoscope Pro on AudioMoth recordings, perhaps indicating how training data that relate well to the recordings being classified can yield more reliable results. Moreover, with the capacity to apply PAM techniques to a range of taxa, including terrestrial mammals, birds, and insects, establishing comprehensive reference libraries for these taxonomic groups will be vital, as PAM is largely focused on bats in temperate regions (Sugai *et al.*, 2019).

As the technology available to conduct PAM for bats continues to evolve, producing increasingly large datasets from extended periods of recording and multiple detector networks, ensuring that the analysis of these acoustic data remains reliable is key. As discussed in **Chapter Four**, the requirement to undertake PAM for bats is becoming increasingly more extensive. For example, in the UK, the latest edition of the Bat Conservation Trust's Bat Survey Guidelines (Collins, 2023), increased the required level of PAM effort considered sufficient to assess the baseline conditions for bats in ecological impact assessments. Automated classification of bat calls has the potential to improve the efficiency of analysis workflows, saving substantial resources. However, standardising these workflows remains a major challenge. Complexities include the continually expanding array of classifiers that are available, and variation in the quality of the recordings produced by different types of acoustic recorders (Brinkløv *et al.*, 2023). Therefore, further work to estimate classifier error rates across different detector/classifier combinations would be beneficial, particularly for practitioners when deciding which classifiers to use, based on their sites, target species, and PAM devices.

5.5 Chapter summary

1. *Kaleidoscope Pro classified fewer recordings above the confidence threshold than either BatClassify (in the Anabat Swift dataset) or the BTO Acoustic Pipeline (in the AudioMoth dataset.*
2. *The effects of habitat and taxonomy on classifier consensus were similar for both datasets, with the most disagreement between classifiers predicted to occur in riparian habitats, and/or where recordings contain potential Myotis calls.*
3. *The species classifications involved in cases of classifier disagreement differed between datasets but were most frequently between species belonging to the same genus.*

CHAPTER SIX: Conclusions

At home on the family smallholding, Hinton-on-the-Green, Worcs. – an invaluable field site for testing equipment and data collection

This chapter synthesises the common themes and summarises the scope of the research from each of the preceding chapters. The key findings, original contributions to knowledge, and implications for applied ecological practice are outlined and discussed, along with potential avenues for future research.

6.1 Summary of research

The research contained within this thesis aimed to evaluate the effectiveness of applying digital technology to passive ecological surveying and monitoring techniques for bats. The chapters have built upon one another conceptually. The introduction (Chapter One) considered the requirements and needs for ecological surveying and monitoring, in light of the threats currently faced by biodiversity globally, and in the United Kingdom, specifically. Traditional and novel survey and monitoring techniques currently used in the region were outlined, initially for mammals more generally, and for bats in additional detail. The current gaps in knowledge regarding their efficacy were identified, to provide context for the thesis aims and objectives. In the first data chapter, Chapter Two, the impact of spatiotemporal and abiotic factors on PAM data was investigated. The strengths and caveats of PAM were then investigated further, by comparing the effectiveness of PAM in relation to active transect surveys (Chapter Three). These findings were built upon in Chapter Four to further explore optimal survey protocols for PAM, using a large dataset analysed using a predominantly automated workflow. Finally, the reliability of automated workflows to analyse the large datasets produced by PAM, was investigated further (Chapter Five).

Chapters Two and Three primarily used secondary data, collected at 14 sites across southern England between 2015 and 2017. Chapter Two used 3,242 hours of Passive Acoustic Monitoring (PAM) data while Chapter Three used 2,349 hours of PAM data; in both cases these were supplemented by data from active walked transect surveys. Chapters Four and Five used primary PAM data, collected from four sites across south Worcestershire and north Gloucestershire over 112 nights between June and October 2022 (Figure 1.12).

6.2 Synopsis of research findings

Continual advances in digital technology, and the development of devices to passively monitor wildlife, have rapidly expanded the range of techniques that can be used in ecological surveying and monitoring (Besson *et al.*, 2022). For bats, these include an expanding selection of open-source and commercial PAM devices, which as their capabilities improve and costs reduce, are (1) accessible to a wider range of practitioners (Browning *et al.*, 2017), (2) able to be used in greater numbers if required to maximise efficacy (Hill *et al.*, 2017), and (3) capable of being applied to an increasing range of taxa to record wider ecological soundscapes (Middleton *et al.*, 2023). Consequently, understanding the strengths and caveats of novel PAM equipment and field protocols, and how they compare to more traditional and established means of surveying and monitoring, are priority research areas, particularly for cryptic, crepuscular, or nocturnal taxa such as bats.

The overarching aims of the research contained in this thesis were to empirically test, critique and evaluate: (1) the relative benefits and caveats of methods used in the field for collecting optimal monitoring data; (2) how different survey methods can contribute to furthering knowledge of species ecology and behaviour; and (3) how survey methods can be effectively applied in ecological research and conservation practice. In the following sections, for each chapter, the background is outlined and the main findings presented diagrammatically to illustrate the associations between findings within each chapter and how these link to the next chapter where appropriate. The methodological considerations for each chapter are summarised, the key results are evaluated in relation to the research aims and, original contributions to knowledge are highlighted.

6.2.1 Chapter Two

Chapter Two tested the effects of spatiotemporal and abiotic factors on the bat activity recorded by passive, fixed-point detectors. This chapter aimed to investigate knowledge gaps pertaining to factors which potentially influence local foraging and commuting activity. Temporal activity patterns for overall bat activity, and that of individual species and genera were examined, along with the effect of moonlight (Adams *et al.*, 1994; Negraeff and Brigham, 1995), and the influence of other weather-related abiotic factors (Erickson and West, 2002). The key findings from this chapter are summarised in Figure 6.1.

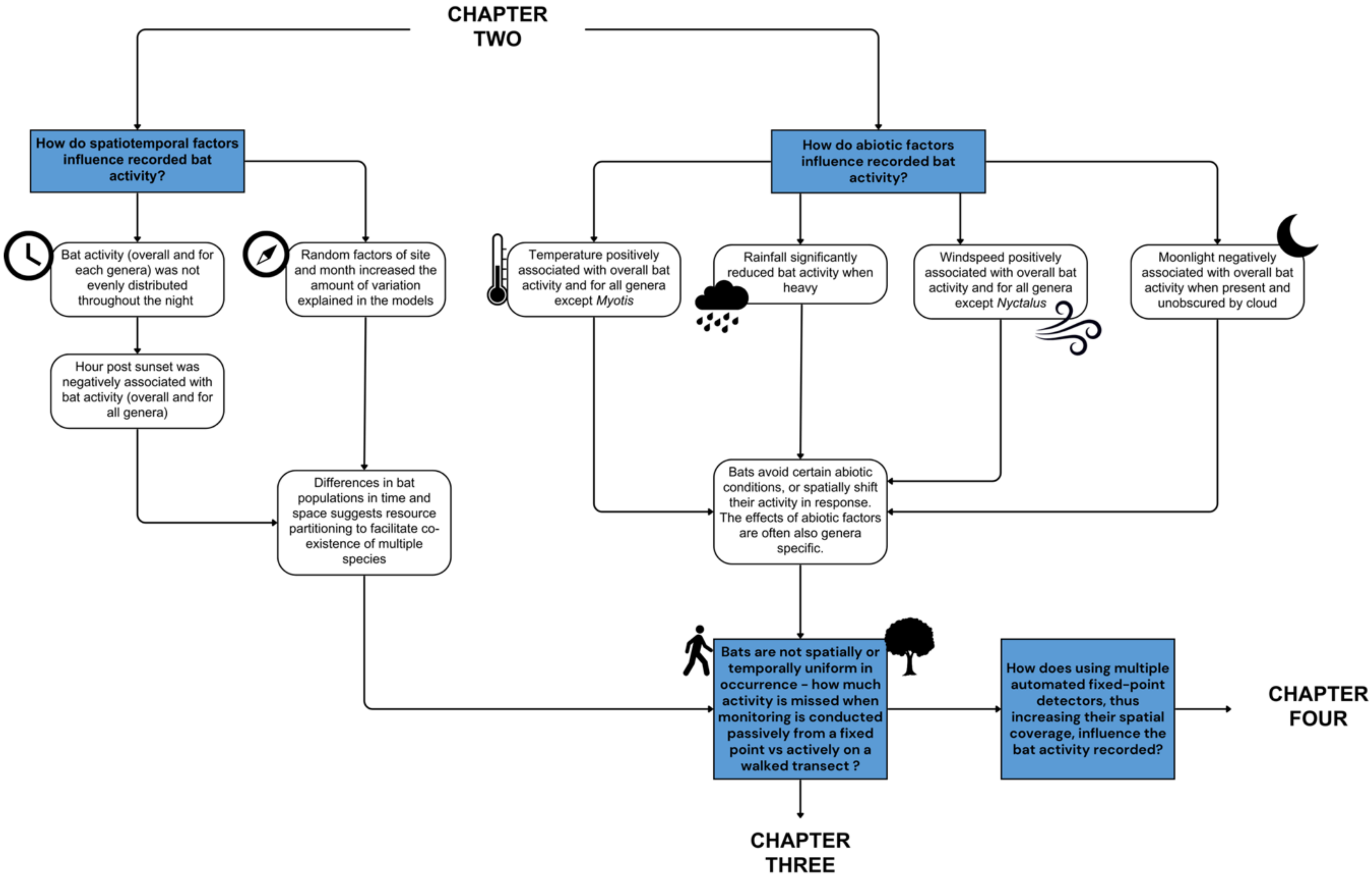


Figure 6.6.1: *A summary of the main results from Chapter Two*

This chapter drew primarily on secondary data to examine how abiotic factors can influence the data collected. The findings from this chapter demonstrated a number of potential limitations of passive bat surveying, demonstrating how the spatiotemporal distribution of bat activity, and therefore detectability, can be influenced by light (in this case moonlight), rainfall, and windspeed. On the other hand, the temporal variation in activity, both overall and for individual genera, highlighted the benefit of being able to record activity on an automated basis for full, and consecutive nights. The original contributions from this chapter are outlined in Box 6.1.

Box 6.1: Original contributions to knowledge - Chapter Two

The activity levels of British bats are negatively impacted by moonlight when unobscured by cloud cover

The publication arising from this chapter (Perks and Goodenough, 2020) has received 19 citations as of August 2024.

The phenomenon of "lunar phobia" in bats was largely considered to affect only frugivorous species in tropical regions (Saldana-Vazquez and Munguia-Rosas, 2013), however, it had additionally been observed in temperate bats in North America (Adams et al., 1994). Despite previous work on mainland Europe finding no evidence of aversion to moonlight by bats (Negraeff and Brigham, 1995; Hecker and Brigham, 1999), moonlit nights were seen here, in the first study undertaken in the UK, to be associated with lower levels of bat activity. The extent of cloud cover was also seen to be a contributing factor, with activity levels being lowest when the moon was unobscured by cloud.

6.2.1.1 Methodological considerations

Weather data sourced retrospectively from records: the weather data used in this study were sourced as hourly records from the nearest available weather station to each site, rather than being collected directly from each field site in real time.

Call analysis conducted manually from zero crossing data: manual auditing and classification of bat calls remains a subjective process. At the time of publication, recording in zero crossing format was widely undertaken in practice, and remains a popular option, although higher quality full spectrum recordings arguably facilitate more robust analysis.

6.2.2 Chapter Three

Chapter Three built upon the findings of Chapter Two relating to the non-uniform occurrence of bats in time and space. The chapter compared the efficacy of two acoustic bat survey types: automated fixed-point surveys, which cover large temporal periods but are limited spatially, and walked transect surveys, which are more restricted temporally but cover a greater spatial extent. Two datasets were examined, one comprising concurrent data collected via the two methods within the same two-hour window at the same site, and one comprising these same data, and additional fixed-point data from an extended time period (akin to the survey frameworks and sample effort in many commercial bat surveys, for example at development sites). At the time of publication, previous published work comparing acoustic bat survey methods had focused on comparing automated fixed-point detection with driven transects in North America (Tonos *et al.,* 2014; Braun de Torrez *et al.,* 2017a). The key findings from this chapter are summarised in Figure 6.2.

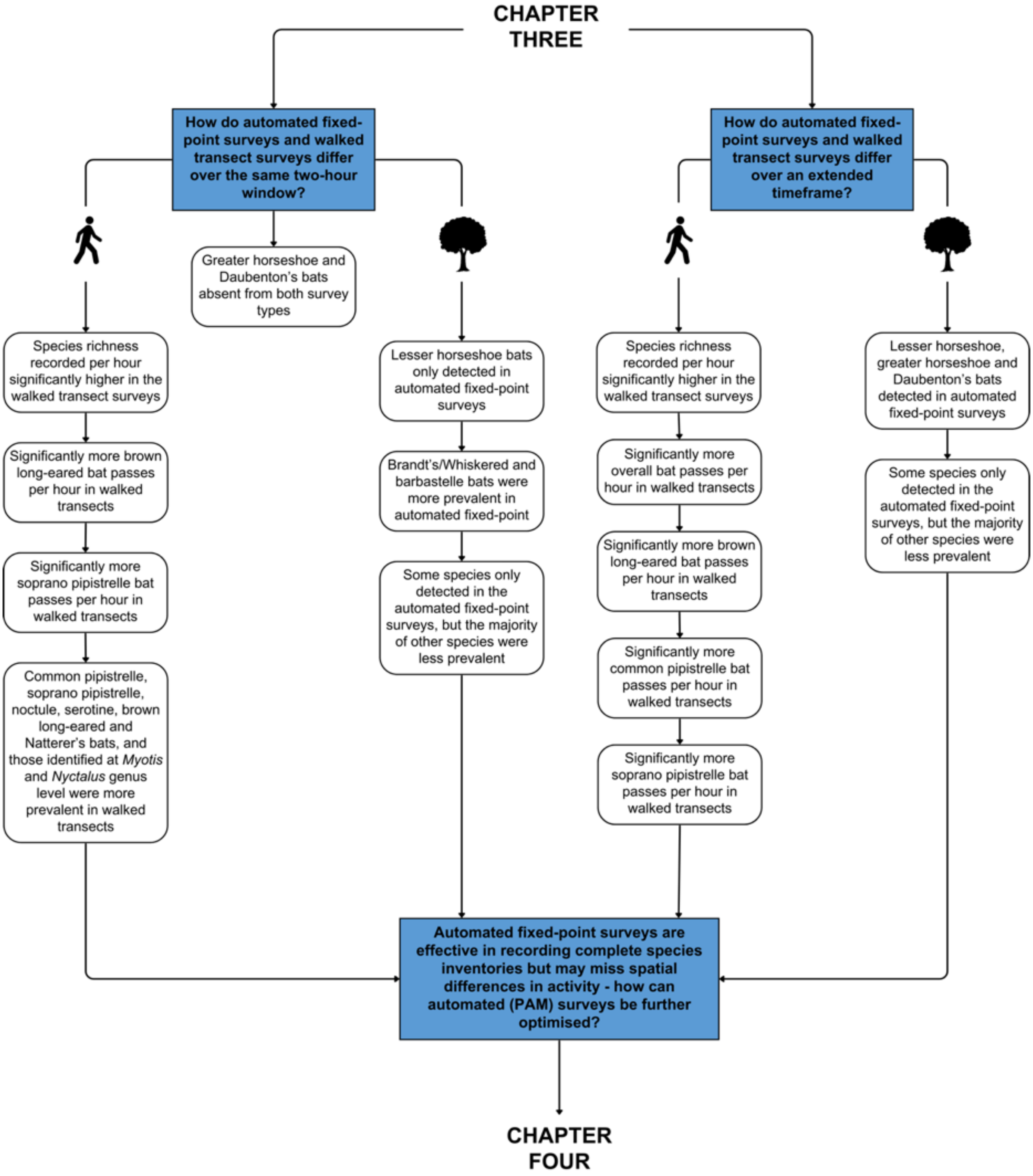


Figure 6.6.2: *A summary of the main results from Chapter Three*

Chapter Three drew primarily on secondary data, to examine the spatiotemporal strengths and limitations of the two most extensively used acoustic bat survey methods undertaken in the UK and in other regions globally. The findings of the method comparison in this chapter highlighted the strengths of automated fixed-point surveys, finding that some species (lesser horseshoe, Daubenton's bat) would not have been recorded if only transect surveys were used. However, each of the methods tested had different strengths and caveats, with the results of the walked transect surveys demonstrating how much activity is missed per hour by only recording from a fixed location. This was seen to be particularly important for brown long-eared bats, which echolocate sparingly with low energy calls, and were seen to be recorded significantly more frequently in the transect surveys. Taken together, these findings reinforce the importance of using a combination of acoustic survey methods, to determine reliable baseline assessments for bats. The original contributions from this chapter are outlined in Box 6.2.

Box 6.2: Original contributions to knowledge - Chapter Three

Walked transect and automated fixed-point surveys should be used together to establish baseline ecological conditions for bats.

At the time of publication, previous work comparing active and passive methods for conducting bat surveys was confined to North America and the comparison of driven transects over large areas, and passive surveys (Tonos et al., 2014; Braun de Torrez et al., 2017a). This chapter demonstrated that, for a European bat guild, a combination of active and passive surveys is optimal: although passive surveys record more species overall, active walked transect surveys record more species per hour, including some (e.g. brown long-eared) which were infrequently detected in the passive surveys. The publication arising from this chapter was cited in the latest edition of the Bat Conservation Trust's Good Practice Guidelines (Collins, 2023) in support of continuing a requirement for active surveys in assessing baseline conditions for bats as part of ecological impact assessments.

6.2.2.1 Methodological considerations

Length of walked transects not standardised: The transects walked at each site varied in length. They were always walked by two surveyors, but this could be each walking a separate transect within a larger site, or both walking the same transect in opposite directions. This is typical of industry standard methodology (transects are not standardised), and these data were collected in this context. However, precision could have been improved by ensuring transects were as consistent as possible across the different sites.

Call analysis conducted manually from zero crossing data: see section **6.2.1.1** above.

6.2.3 Chapter Four

Chapter Four extended the work on the efficacy of PAM techniques for bats, undertaken in Chapters Two and Three, by examining a range of PAM protocols in four distinct habitats. With the expanding range of PAM technology currently available, three types of devices were empirically compared: commercial full spectrum detectors (Anabat Swift), commercial zero crossing detectors (Anabat Express), and open-source acoustic loggers (AudioMoth). The development of open-source acoustic loggers, such as AudioMoth (Hill *et al.*, 2017), in recent years, which are available to purchase at a fraction of the cost of commercial equipment, has created opportunities for a wider range of users to undertake PAM, along with making protocols which utilise multiple devices, more financially viable. However, knowledge gaps around usability, configuration, and recording quality compared to commercial equipment remain (Browning *et al*, 2017; Gibb *et al.*, 2019). The key findings from this chapter are summarised in Figure 6.3.

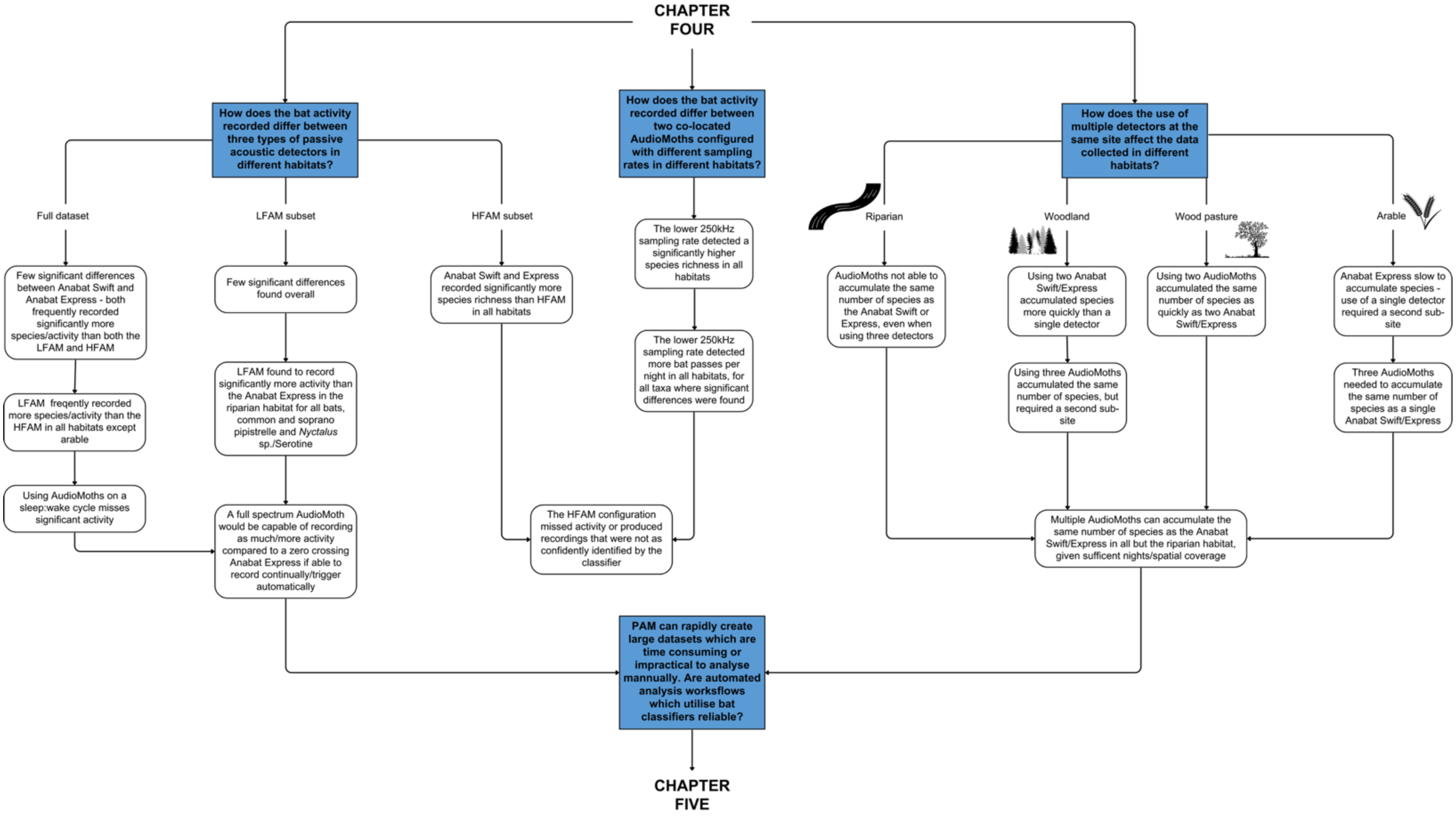


Figure 6.6.3: *A summary of the main results from Chapter Four*

Chapter Four built on the preceding two chapters via the collection of new primary data, to look specifically at passive bat monitoring protocols in practice. The findings from this chapter demonstrated how equipment choice and protocol design can impact the data collected by PAM. Using commercial detectors with automatic bat triggers, particularly in full spectrum, was seen to have a number of benefits. They recorded more activity and accumulated species inventories efficiently, yet their principal caveat lies in their purchase price. However, the intriguing findings from with the AudioMoth recording periods, suggest that using an open-source full spectrum device, could perform as well, if not better than a commercial zero crossing detector, if they were configured to record continually or to trigger reliably. Similarly, where the aim of PAM is to establish species presence, using multiple AudioMoths across the area of interest, was seen here to be effective. Arguably, the most important drawback to all the protocols evaluated was the large amounts of data produced. Manually analysing such datasets can be impractical, particularly when PAM has been undertaken for extended time periods and often with multiple devices. In these instances, analysis is commonly conducted at least partially, with the use of a classifier (Chapter Five). The original contributions from this chapter are outlined in Box 6.3.

Box 6.3: Original contributions to knowledge - Chapter Four

AudioMoth acoustic recorders are capable of performing similarly or better than commercial zero crossing bat detectors for species that call at lower frequencies.

It has been speculated that the lower quality micro-electromechanical systems (MEMS) microphones used in AudioMoth devices (Gibb et al., 2019) may result in fewer bat detections compared to commercial equipment. To the author's knowledge, this was the first comparison of AudioMoth with both full spectrum and zero crossing Anabat detectors. When recording at the same time, few differences were found in the recorded activity between the AudioMoth and zero crossing detector. Moreover, the AudioMoth recorded significantly more bat passes per hour for all bats, and for common pipistrelle, soprano pipistrelle and Nyctalus/Eptesicus in riparian habitat.

Using multiple AudioMoth devices can serve as a viable alternative for assembling species inventories in woodland, wood pasture and arable habitats

The substantially lower purchase cost of AudioMoths over commercial equipment makes the use of multiple devices across a site a viable option for many practitioners (Hill et al., 2017). This research found that in doing so, even without continuous or triggered recording, multiple (3) AudioMoths were able to record the same species inventory as commercial equipment in three of the four habitats tested (the exception being riparian).

6.2.3.1 Methodological considerations

Analysis of recordings was conducted using a workflow that incorporated an automated bat classifier: PAM using multiple detectors over extensive time periods, inherently produces large datasets. Here, a threshold of self-reported classifier confidence was set at

50% to minimise false positives. Classifications of notable or less abundant species were manually audited, along with a random sample of recordings classified as more common/abundant species, to verify classification feasibility. Although classifiers should not be solely relied upon, manual auditing datasets of this size is typically impractical, and remains a subjective process.

6.2.4 Chapter Five

Chapter Five investigated the key methodological consideration raised in Chapter Four, regarding the reliability of PAM analysis workflows which include automated classification of bat calls. Gaps in knowledge concerning error rates of classifiers have previously resulted in calls for caution in their use (Russo and Voigt, 2016; Rydell *et al.*, 2017). Despite expansions in call libraries and subsequent improvements in classifier accuracy, uncertainty remains, especially with the recent necessity to apply them to lower quality recordings from open-source acoustic loggers, such as AudioMoth (Gibb *et al.*, 2019; Brinkløv *et al.*, 2023). In this chapter, the two full spectrum datasets from Chapter Four, one recorded by Anabat Swifts, and the other by AudioMoths were used to test pairwise classifier agreement. All data had been classified by Kaleidoscope Pro for analysis in the previous chapter. Additionally, the Anabat Swift data were classified by BatClassify, the classifier included in the Anabat Insight analysis software. The AudioMoth data were additionally classified by the BTO Acoustic Pipeline, a contemporary classifier, with a proportion of its training data recorded on AudioMoth devices. The key findings from this chapter are summarised in Figure 6.4.

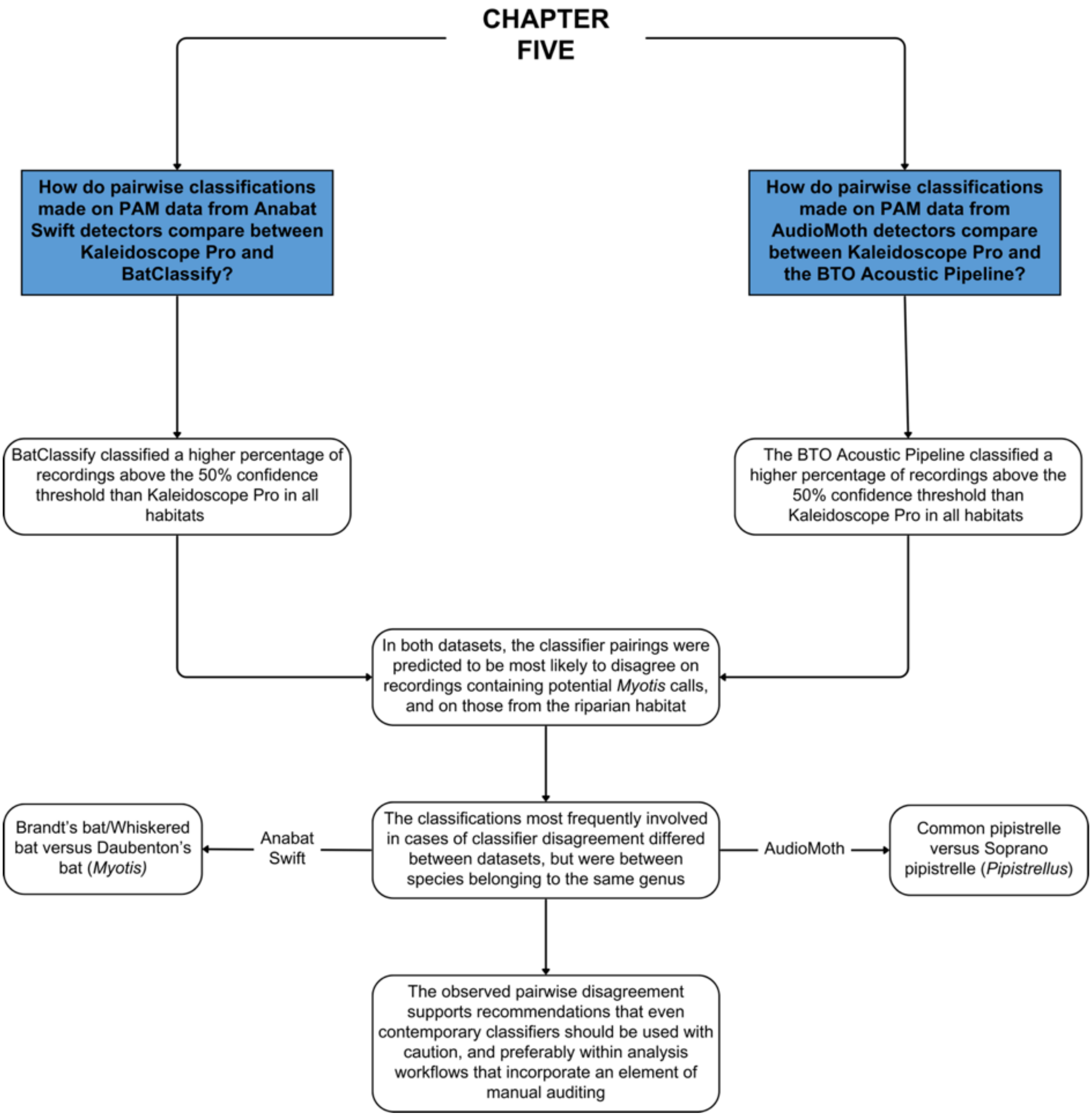


Figure 6.6.4: *A summary of the main results from Chapter Five*

Chapter Five, built on the preceding chapter to consider the analysis of the large acoustic datasets generated in the field. This chapter found pairwise disagreement between commonly used classifiers, regardless of the device on which the recordings were produced. Therefore, although their use can potentially streamline analysis workflows, they still cannot be relied on exclusively. The original contributions from this chapter are outlined in Box 6.4.

Box 6.4: Original contributions to knowledge - Chapter Five

Pairwise disagreement occurs between contemporary bat classifiers, but is largely restricted to classifications belonging to the same genus.

Consistent with previous work (Lemen et al., 2015), pairwise disagreement was observed between commonly used classifiers, on recordings of European bats, produced by both commercial and open-source equipment. However, in both cases, the pairs of classifications most frequently involved in instances of disagreement were from within the same genus and had similar call types.

6.2.4.1 Methodological considerations

The true species identities of the recordings were not known: the recordings used in this chapter were collected passively in field conditions, therefore, the species of bat calling in each recording could not be known with complete certainty. The pairwise analysis between classifiers was useful in identifying instances where the classifiers were most likely to be inaccurate, however it remains possible that one classifier could have always performed perfectly, with the disagreement being caused by the other.

6.4 Implications and recommendations for ecological research, policy and practice

It has been widely acknowledged that solutions to the current biodiversity crisis need to be based on robust and accessible evidence (Pullin *et al.*, 2004; Field *et al.*, 2005; Mihoub *et al.*, 2017). The collection of field data to support Evidence-based Conservation (EBC) can be difficult for some taxa (e.g. nocturnal bats), as a result of their life history and behavioural traits. As introduced in Chapter One, technological approaches to ecological surveying and monitoring have the potential to scale up mammal recording at local and national scales. The implications and recommendations for policy, practice and future research from the key findings of the research presented in this thesis, are set out in Table 6.1.

Table 6.1: *Implications and recommendations for policy, practice, and future research.*

Thematic area	Finding	Implications for policy and practice	Recommendations for policy and practice	Future research
Bat behaviour and detectability	Bats are not spatially or temporally uniform in occurrence owing to niche partitioning between species, and avoidance of certain abiotic conditions, or spatial shifts in activity in response.	Reiterated the importance of conducting whole night surveys to capture temporal variations in activity. Moreover, these findings demonstrated the importance of additionally conducting surveys over multiple nights, such that any nights with sub-optimal abiotic conditions, and therefore reduced activity, can be accounted for.	Passive acoustic surveys should be undertaken across full nights where possible to ensure peak activity times for all species are covered (Perks and Goodenough, 2020; Chapter Two).	Further investigate the effects of moonlight on temperate bat activity by concurrently recording light levels and bat activity in the field to build upon Chapter Two. The potential for spatial shifts in activity could also be explored by comparing recordings in sheltered and exposed areas.
Acoustic bat survey techniques	Automated surveys are an efficient means of recording species inventories but may miss spatial differences in activity.	With the increasing capabilities of passive acoustic technology, some research has suggested that more labour-intensive, active transect surveys are now inferior (Teets *et al.*, 2019). However, spatial trends in activity may be missed by only recording activity at a fixed location (Perks and Goodenough, 2021; Chapter Three).	A combination of passive and active acoustic surveys should continue to be used when establishing baseline conditions for bats in ecological impact assessment contexts, as detailed in the latest edition of the Bat Conservation Trust's Good Practice Guidelines (Collins, 2023).	See below recommendations for investigation into using AudioMoths as multi-detector networks to increase the spatial coverage of passive surveys.
Passive Acoustic Monitoring (PAM) of bats	Multiple AudioMoths can accumulate the same number of species as commercial equipment in certain habitats, but often require longer periods of deployment to do so.	Although a viable alternative for certain applications, AudioMoth recording quality is inherently lower, meaning their use must be carefully considered. Commercial equipment is currently likely to be the most robust option where feasible, particularly in complex/species rich habitats.	Commercial bat detectors should be used where possible for passive acoustic bat surveys in high quality habitat, or where less abundant species are the target of the survey (Chapter Four). This supports the findings of Kunberger and Long (2023) and Starbuck *et al.* (2024).	Further consider the use of the latest configurable frequency triggers for AudioMoth, and build on Chapter Four to evaluate how using the devices in this way compares to commercial equipment.

Passive Acoustic Monitoring (PAM) of bats	A full spectrum AudioMoth would be capable of recording as much or more activity than a zero-crossing detector, if able to record continually or trigger automatically.	Increased capacity for more practitioners to undertake PAM, in the absence of prohibitive equipment costs. Additionally, lower costs increase the feasibility of deploying multiple devices within an area of interest, increasing spatial coverage (see above), and perhaps mitigating some of the drawbacks compared to active transect surveys.	AudioMoths should be considered for applications where the cost of commercial equipment is prohibitive (Chapter Four). Current examples include the national British Bat Survey (BBatS) which was launched as a beta version in 2023. AudioMoth devices are loaned to volunteers to collect data in pursuit of monitoring long-term population trends (Bat Conservation Trust, 2024).	
Passive Acoustic Monitoring (PAM) of bats	The HFAM configuration missed activity or produced recordings that were not as confidently identified by the classifier.	Configuring AudioMoth with the highest possible sampling rate of 384 kHz (Hill *et al.*, 2019) is not necessarily best practice, depending on the aims of the survey and the microSD cards (brand and speed) that are available.	AudioMoths should be configured with a 250 kHz sampling rate when targeting bats, unless higher frequency bats (e.g. lesser horseshoe) are the specific target of the survey as this resulted in better data (potentially due to reducing self-noise generated by SD card writes) (Chapter Four).	Further test the varying levels of self-noise generated by different microSD cards in AudioMoths using differing sampling rates, and how this impacts classification to extend Chapters Four and Five.
Automated classification of bat calls	Pairwise disagreement was found between the classifiers regardless of detector type, with both pairings most likely to disagree on potential *Myotis* calls.	Pairwise disagreement highlights how no classifier is perfect. The findings from Chapter Five, support previous recommendations that analysis should still not yet be fully automated.	Even contemporary classifiers should not be used as a stand-alone means of conducting bat call analysis (Chapter Five). Consistent with the earlier recommendations of Russo and Voigt (2016) and Rydell *et al.* (2017), an element of manual auditing of recordings by suitably experienced technicians, should still be integrated into analysis workflows.	Additional work to further understanding of classifier error by testing classifiers on verified recordings, and whether different classifiers are better suited to analysing recordings from particular devices, species, or habitats to extend Chapter Five.

Taken together, the research presented in this thesis contributes to the development of best practice, through refining and evaluating the comparative effectiveness of PAM approaches to bat surveying and subsequent data analysis. As discussed, these approaches have a number of key advantages, in particular through enabling robust assessment, and the potential to increase capacity for bat monitoring nationally, which is of particular importance in the UK (as outlined in Chapter One).

Techniques that can be undertaken passively, without the need for specialist training or handling licenses, and minimal surveyor input, vastly improves their usability, and subsequently the scalability of surveying and monitoring initiatives to which they are applied. Scalability is of particular importance to the national scale monitoring schemes, which provide data to assess and monitor the status of species populations. Such schemes have faced criticism from within the scientific community, primarily because they are considered to lack specific scientific research questions. However, monitoring schemes can be classified into three distinct categories: passive, question-driven, and mandated (Lindenmayer and Likens, 2010), with the majority of national schemes falling into the latter category, acting as surveillance, rather than providing sufficient data to address specific questions at site level. In the UK, national mandated monitoring data are essential in providing evidence of progress towards the current target of halting biodiversity decline by 2030, and it is therefore imperative to address instances of data deficiency. Ultimately, reliable surveying and monitoring data are vital, both at local scales for legislation compliance and informing conservation action, and at national scale for surveillance of species populations and to monitor progress towards national and international biodiversity targets.

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