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The avian dawn chorus across Great Britain: using new technology to study breeding bird song

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Declaration

The material contained within this thesis has not previously been submitted for a degree at Durham University or any other university. The research reported within this thesis has been conducted by the author unless indicated otherwise.

Stuart A. Brooker

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Abstract

The avian dawn chorus is a period of high song output performed daily around sunrise during the breeding season. Singing at dawn is of such significance to birds that they remain motivated to do so amid the noise of numerous others. Yet, we still do not fully understand why the dawn chorus exists. Technological advances in recording equipment, data storage and sound analysis tools now enable collection and scrutiny of large acoustic datasets, encouraging research on sound-producing organisms and promoting ‘the soundscape’ as an indicator of ecosystem health. Using an unrivalled dataset of dawn chorus recordings collected during this thesis, I explore the chorus throughout Great Britain with the prospect of furthering our understanding and appreciation of this daily event. I first evaluate the performance of four automated signal recognition tools (‘recognisers’) when identifying the singing events of target species during the dawn chorus, and devise a new ensemble approach that improves detection of singing events significantly over each of the recognisers in isolation. I then examine daily variation in the timing and peak of the chorus across the country in response to minimum overnight temperature. I conclude that cooler temperatures result in later chorus onset and peak the following dawn, but that the magnitude of this effect is greater at higher latitude sites with cooler and less variable overnight temperature regimes. Next, I present evidence of competition for acoustic space during the dawn chorus between migratory and resident species possessing similar song traits, and infer that this may lead either to fine-scale temporal partitioning of song, such that each competitor maintains optimal output, or to one competitor yielding. Finally, I investigate day-to-day attenuation of song during the leaf-out period from budburst through to full-leaf in woodland trees, and establish the potential for climate-driven advances in leaf-out phenology to attenuate song if seasonal singing activity in birds has not advanced to the same degree. I find that gradual attenuation of sound through the leaf-out process is dependent on the height of the receiver, and surmise that current advances in leaf-out phenology are unlikely to have undue effect on song propagation. This project illustrates the advantage of applying new technology to ecological studies of complex acoustic environments, and highlights areas in need of improvement, which is essential if we are to comprehend and preserve our natural soundscapes.

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Chapter 1

General introduction

Common nightingale *Luscinia megarhynchos*

1.1 Motivation

Currently, habitat and biodiversity losses are occurring at greater rates than at any other period in human history (IPBES, 2019), and extinction rates have risen to between 100 and 1000 times the rate during pre-human history (Lamkin and Miller, 2016). Habitat management and wildlife conservation is increasingly important in stemming declines in animal populations globally. To develop effective management strategies, there is an urgent requirement to document and monitor the occurrence and distribution of species on regional, continental and global scales, and to understand species' ecological requirements (Wilson, 2017). Traditional field methods of biodiversity monitoring and assessment are likely to be ineffective given the broad spatial extent and short time frame required to assess the current rapid biodiversity losses (Guyot et al., 2016). Recent widespread access to computational and communication technology has led to novel approaches to study the natural world (reviewed by August et al., 2015; Pimm et al., 2015). Perhaps the most familiar of these is automated collection of images and acoustic recordings for biological monitoring (August et al., 2015). Indeed, one of the most efficient means of surveying sound-producing taxa is by passive acoustic monitoring (PAM), which refers to the survey of wildlife and environments using sound recorders, or acoustic sensors, without interfering with animal behaviour (Browning et al., 2017; Sueur and Farina, 2015). PAM lends itself to rapid assessment programmes that quickly gauge the biodiversity of distinct regions (Brandes, 2008a; Riede, 1998).

With loss of habitat and biodiversity, environments lose their natural sounds (Dumyahn and Pijanowski, 2011; Pijanowski et al., 2011a), which are increasingly replaced by human-generated sounds (Schafer, 1994). While the value of the natural soundscape is recognised by humans (Davies et al., 2013), it is also of great importance to wildlife (Dumyahn and Pijanowski, 2011). The acoustic niche hypothesis (ANH) observes that sounds or vocalisations produced by species within a community are separated in frequency and time, such that there is little overlap, leading to partitioning of acoustic space (Krause, 1987). The ANH refers directly to the ecological niche concept, and, therefore, recognises that if equilibrium conditions are disrupted, for example, by the introduction of human-generated sounds, or alteration of species composition, there could be negative impacts on ecosystem functioning (Dumyahn and Pijanowski, 2011).

Birdsong is amongst the most appealing, yet complex, of sounds produced in nature, and undoubtedly makes the largest contribution to natural soundscapes in temperate regions of the world (Farina et al., 2011a). Although usually requiring trained individuals (Hobson et al., 2002), aural identification of vocalisations is the most efficient means of surveying passerine birds, especially in dense habitat, where visual detection may be compromised (Brandes, 2008a). Guidelines for traditional surveys (e.g. point counts and transects) state that surveys are optimally conducted at or around dawn, during the main breeding season, when the number of species detected per unit time is maximised (Bibby et al., 2000). Whether a researcher wishes to detect the presence of a species of interest, or to build a comprehensive list of species for biodiversity assessment, for most birds, the dawn chorus presents the optimal opportunity to achieve this efficiently. In addition, it is hypothesised that the dawn chorus differs functionally from song delivered at other times of the day, and that singing behaviour at dawn can provide insight into numerous aspects of bird ecology, including breeding stage, fitness of individuals and time and energy budgets. Yet, despite its importance to birds as a communication network, and to humans for its aesthetic value, many aspects of the dawn chorus remain a mystery. For example, few studies have assessed the influence of environmental and climatic conditions on the spatial and temporal structure of the chorus at the community level (e.g. Allard, 1930; Bruni et al., 2014; Farina et al., 2015, 2015; Leopold and Eynon, 1961; Thomas et al., 2002; Wright, 1913, 1912), and even fewer have compared singing activity in the chorus across different regions and habitats (e.g. Da Silva and Kempenaers, 2017; Mace, 1989a), or through seasons. The role of different species that take part and contribute to the chorus also remains little understood (e.g. Hasan, 2011; Keast, 1994). Indeed, we still do not fully comprehend exactly why birds sing most intensely at dawn in the first place. A greater understanding of such matters will assist in identifying and interpreting modifications to the chorus in our changing world. In turn, this can inform on the health of bird populations and communities, and on the environment as a whole.

1.2 Thesis aims and outline

The main aims of this thesis are: (1) to determine the efficacy of applying new and accessible technology in sound recording hardware and signal recognition software to the avian dawn chorus, (2) to better understand the motivation behind the dawn chorus as it builds, peaks and wanes across the country, and (3) to identify potential threats to the chorus, as we currently know it, as birds continue to adapt to changes in their environment. The specific aims of the introductory and main data chapters are outlined below:

Chapter 2 – The ecology of the dawn chorus

This chapter serves as an introduction to birdsong and the dawn chorus. I will outline seasonal singing patterns in temperate passerines, before presenting a review of current theory surrounding the existence of the dawn chorus, and of factors affecting its day-to-day timing. I will then describe the mechanisms birds may apply to counteract acoustic competition during the chorus, before ending with a review on the effects of habitat on the propagation of song at dawn.

Chapter 3 – Technological advances in the study of birdsong

Here, I will provide a report on recent technological developments in the ecological study of birdsong. I will outline novel tools currently available to ecologists, and highlight the advantages of their application. I will also point-out some areas requiring improvement.

Chapter 4 – Study sites

This brief chapter serves to introduce the study sites used for data collection in chapters 5, 6 and 7, and provides a point of reference whilst interpreting these chapters.

Chapter 5 – Automated identification and classification of birdsong: an ensemble approach

I will test an array of readily-available automated signal recognition tools (‘recognisers’), each programmed to identify several target species in a dataset of acoustic surveys of the dawn chorus. I will devise an ensemble model built upon the results returned by the recognisers, and compare the ensemble’s performance to that of each recogniser in isolation.

Chapter 6 – Tracking the avian dawn chorus across Great Britain with climate

In this chapter, I will apply an acoustic index (AI) to a large acoustic dataset of the dawn chorus, collected at multiple sites throughout Great Britain. I will use the information obtained to re-visit an assumption of the energy stochasticity hypothesis, which provides a widely-accepted explanation for the dawn chorus. I will examine the importance of variability in overnight temperature on the onset and peak of the chorus within different regions the country, and discuss the implications of my findings with respect to a changing climate.

Chapter 7 – Competition for acoustic space between resident and migratory species during the dawn chorus

Here, I will investigate interactions between pairs of species that potentially compete for acoustic space during the dawn chorus due to similarities in song parameters. I will first determine whether each species in a pair apparently avoids the other's song, before testing if the birds manage to maintain optimal song output in the presence of its competitor.

Chapter 8 – The effect of advancing leaf-out phenology on breeding bird song

Finally, I will determine the day-to-day attenuation of sounds of different frequency and transmission distance during the leaf-out process, from budburst through to full-leaf, in deciduous woodland habitat. I will then establish if climate-driven advances in leaf-out phenology have the potential to cause undue attenuation of birdsong if birds have not advanced seasonal singing activity to the same degree.

Chapter 2

The ecology of the dawn chorus

Song thrush *Turdus philomelos*

2.1 Communication by sound

Animal communication can be defined as the transmission of a signal from one individual to another, such that, in general, the signaller benefits from the response of the recipient (Slater, 1983). Communication may take place via one or a combination of sensory channels: chemical, visual, tactile, and acoustic. The most fundamental piece of information transmitted is the species identity of the signaller, which is essential when the individual is searching for a mate (Slater, 1983). In many species, one sex, typically females, may assess several sexual traits in mate choice (Bro-Jørgensen, 2010; Candolin, 2003), and the opposite sex may utilise one, two or more communicative channels to advertise these traits. The importance of visual signals to birds is obvious, as signified by the striking plumage and visual displays of many species. Some combine visual display with acoustic signals, for example, lekking black grouse *Lyrurus tetrix* (Hovi et al., 1997), a bird of moorland and early successional woodland (Cramp and Simmons, 1979). However, visual display becomes a less effective means of communication for species living in dense habitat, such as mature woodland or reedbed (Catchpole and Slater, 2008). Although male Paradisaeidae of the tropical forests of New Guinea produce, arguably, the most elaborate visual displays of all birds, vocalisation is required to attract females to display areas in the first instance (e.g. Frith and Frith, 1988). This is because acoustic signals can travel greater distances, negotiating obstructions, to reach intended receivers within densely vegetated habitat, where visual signals fail (Waser and Waser, 1977). Further advantages of acoustic communication are largely associated with the efficiency and ephemerality of sound production; unlike showy plumage, a call or song is produced only when required, but may still convey a great deal of information (Catchpole and Slater, 2008), and apparently, with little energy expenditure (Oberweger and Goller, 2001; Ward et al., 2004; but see Brackenbury, 1979; Hasselquist and Bensch, 2008). However, the distance over which an acoustic signal can be clearly heard depends on its amplitude and structure at the source, the characteristics of the medium (e.g., in terrestrial environments, wind speed, air temperature or humidity), the structure of the habitat, background noise, and the receiver's mechanism for detecting the signal (Wiley and Richards, 1978).

2.2 What is birdsong?

Bird acoustic signals are typically separated into calls and songs. In general, calls are simple vocalisations comprising one or two syllables produced by both male and female birds throughout the year, and are used over a range of contexts, including signalling alarm, assisting flock cohesion, maintaining parent-young contact, providing information about food sources, and signalling a need for food from a parent or mate (Ball and Hulse, 1998; Catchpole, 1979; Catchpole and Slater, 2008; Thorpe, 1961). Typically, the term ‘song’ is reserved for vocalisations that are generally longer, more complex, and which are produced solely by male birds of the suborder oscines (order Passeriformes) during the breeding period, when it serves two main communicative functions: declaration of territory in male-male competition, and the attraction and stimulation of females for mating (Ball and Hulse, 1998; Brenowitz et al., 1997; Catchpole, 1979; Catchpole and Slater, 2008; Kroodsma and Byers, 1991; Nowicki and Searcy, 2004; Slagsvold, 1977). However, this view of birdsong is heavily biased by the fact that most research on the topic has been carried out on species and communities in northern temperate latitudes with distinct breeding seasons, and there exist numerous exceptions (e.g. Catchpole and Slater, 2008; Morton, 1996; Price et al., 2009; Slater and Mann, 2004). For example, song is not entirely restricted to males. In the tropics and sub-tropics, where the seasons are not so strictly defined, individuals of many species remain in the same area, where males and females pair for life and co-operatively defend the same territories together for long periods (Hooker and Hooker, 1969; Morton, 1996). Within such species, both members of a pair may sing, either synchronously or alternately, to produce a duet (Farabaugh, 1982; Hall, 2004; Hooker and Hooker, 1969; Morton, 1996; Thorpe, 1963; Whittingham et al., 1997). Females of some species also regularly produce solo song (e.g. superb fairy-wren *Malurus cyaneus*: Cooney and Cockburn, 1995; stripe-headed sparrow *Peucaea ruficauda*: Illes and Yunes-Jimenez, 2009), and there is gathering evidence that female song is likely the ancestral state in some (Garamszegi et al., 2007; Price et al., 2009), or even all (Odom et al., 2014; Riebel et al., 2005), passerines. Although an increasing number of studies report female song in the northern temperate zone species (Table 2.1), it is still considered to be very rare amongst birds at these latitudes. In many of the species where it does occur, it does so only in a few individuals within a population, or at very defined periods during, or just prior to, nest building or egg-laying. The list of potential functions of female song include inter- and intra-sexual competition for nesting sites or mates, territory defence and mate attraction (Cain and Langmore, 2015; Collins, 2004), and as such, do not differ significantly from those of male song. However, in some species, its exact function remains unknown (Krieg and Getty, 2016), and the literature contains little reference to female passerine song in temperate regions at dawn (cf. Gil and Llusia, 2020). It is, therefore, unlikely that breeding bird song recorded at dawn and subjected to analyses in this thesis was produced by female birds, and female song is not considered further.

Table 2.1 A list of example publications that have reported female song in northern temperate zone birds, and the subject species. In most studies, incidences of female song were rare, and often reported for single or few individuals. Studies reporting regular song, state that song was largely delivered outside of the breeding season (Baptista et al., 1993; Hoelzel, 1996) or when accompanied by the male (McElroy and Ritchison, 1996).

Publication	Species	
Arcese et al. (1988)	Song sparrow	*Melospiza melodia*
Baptista et al. (1993)	White-crowned sparrow	*Zonotrichia leucophrys*
Beletsky (1983)	Red-winged blackbird	*Agelaius phoeniceus*
Evans Ogden et al. (2003)	Hooded warbler	*Setophaga citrina*
Hobson and Sealy (1990)	Yellow warbler	*Setophaga petechia*
Hoelzel (1986)	European robin	*Erithacus rubecula*
Kreig and Getty (2016)	House wren	*Troglodytes aedon*
Langmore and Davis (1997)	Dunnock	*Prunella modularis*
Langmore et al. (1996)	Alpine accentor	*Prunella collaris*
Mahr et al. (2016)	Blue tit	*Cyanistes caeruleus*
McElroy and Ritchison (1996)	Northern cardinal	*Cardinalis cardinalis*
Ritchison (1983)	Black-headed grosbeak	*Pheucticus melanocephalus*
Sandell and Smith (1997)	Common starling	*Sturnus vulgaris*
Taff et al. (2012)	Common yellowthroat	*Geothlypis trichas*

Song is not solely confined to the breeding season in temperate regions. Resident and migratory European robins *Erithacus rubecula* hold individual territories throughout the autumn and winter months, which they defend with song (Hoelzel, 1986; Kriner and Schwabl, 1991; Schwabl, 1992). Both sexes sing in autumn when territories are being established, although female song ceases with the onset of the breeding season (Hoelzel, 1986; Kriner and Schwabl, 1991; Schwabl, 1992). In addition, many long-distance migratory passerines that breed in the Palearctic, reportedly sing regularly whilst on their tropical African wintering grounds (Sorensen et al., 2016). In the common nightingale *Luscinia megarhynchos* (Kipper et al., 2017) and great reed warbler *Acrocephalus arundinaceous* (Sorensen et al., 2016) it is believed that this winter singing acts as practice, to improve the quality of song, rather than to function in territory defence.

Finally, song in oscines is not necessarily complex. For example, the song of the chipping sparrow *Spizella passerina* is merely a trill, comprised of repetitions of one more-or-less identical syllable (Albrecht and Oring, 1995; Marler and Isaac, 1960), and the monotonous ‘cheeping’ of a male house sparrow *Passer domesticus* appears no more complex in structure and sound than a repeated call. Nevertheless, such vocalisations fulfil the same function as more complex song in other species, and effectively, are very simple songs (Catchpole and Slater, 2008). Indeed, it is hypothesised that selection should favour simplistic song when the principal function is territory defence (Albrecht and Oring, 1995; section 2.4.3). Therefore, whether to classify a vocalisation as a call or song is also related to the perceived function of the vocalisation (Ball and Hulse, 1998). With this in mind, within the data chapters of this thesis, I consider all vocalisations that function in territory defence and mate-attraction, including those produced by males and females of the non-passerine families Strigidae, Columbidae, Picidae (including drumming) and Cuculidae. In passerines, these vocalisations (‘true song’) are presumed to be produced solely by male birds.

2.3 Seasonal rhythms in singing activity

Seasonal and diurnal changes in the intensity of singing activity are typical of temperate passerines. Photoperiod is one of the most important environmental cues regulating seasonal changes in the reproductive physiology and behaviour of northern temperate zone species (Dawson et al., 2001; Slagsvold, 1977; Smith et al., 1997b). Song activity in passerines is controlled by a network of interconnected brain regions (or nuclei), and numerous seasonally reproductive species exhibit pronounced seasonal plasticity in these regions (e.g. Brenowitz et al., 1998; Nottebohm et al., 1987, 1986;

Smith et al., 1997a; Tramontin et al., 2000), which is primarily under the control of gonadal steroid hormones, notably, testosterone (e.g. Andrew, 1969; Arnold, 1975; Brenowitz et al., 1998; Marler et al., 1988; Nottebohm et al., 1987; Poulsen, 1951; Smith et al., 1997a; Tramontin et al., 2000). Ultimately, testosterone secretion is triggered by long-day photoperiods in spring, which increase circulating concentrations during the reproductive phase (Catchpole and Slater, 2008). Photoperiod may also act independently of steroid concentrations to supplement or modulate the effects of testosterone (Smith et al., 1997b). The process culminates in a seasonal stimulating effect on song production as well as song development and crystallisation (Alward et al., 2017).

Within the seasonal cycle of physiologically-controlled song production, there are aspects under behavioural control, of which, much depends upon the function(s) of song. If song is mainly used in territorial defence, then singing should persist throughout the breeding season, even if at a reduced rate, and males should sing at increased rates when other males are singing. If the purpose of song is to protect paternity, then output should peak during the female's fertile period (*i.e.* during egg-laying; Birkhead and Møller, 1992). On the other hand, if the principal function of song is to attract and retain mates, then output should peak prior to pairing and egg-laying, and should cease upon the commencement of egg-laying; unpaired males should continue singing throughout the breeding season, and paired males should resume singing should they lose their nest or mate (Merilä and Sorjonen, 1994). Further, seasonal singing activity is likely to begin earlier in resident species than in migratory species (Fig. 2.1), as residents may have established territories prior to the arrival of spring migrants (Slagsvold, 1977). Finally, within a species, an individual may adjust his own singing activity according to his breeding stage, that of his mate, or that of neighbouring conspecifics. The result is a complex interaction of seasonal singing activity, both within and between species in a community, which is dependent on the breeding period, mating system (e.g. monogamy, polygyny or polygamy), and number of broods within a species, as well as the breeding status (paired or non-paired; e.g. Amrhein et al., 2004) and quality of individuals.

The majority of autecological studies concerning temperate-zone passerines conclude that mate attraction is the primary function of song. Indeed, for the sedge warbler *Acrocephalus schoenbaenus*, this appears to be its sole function, as males cease singing abruptly upon pairing, and they recommence singing only if their mate is lost (Catchpole, 1973). Territorial disputes between males are not settled by song, instead, intruders are actively approached by territory-holders (Catchpole, 1973). This is a pattern also recognised in the bluethroat *Luscinia svecica* (Merilä and Sorjonen, 1994), and for such species, song is confined to a short period early in the season. In other species, however, song serves a secondary function of territory announcement or territory defence (e.g. chaffinch *Fringilla coelebs* Hanski and Laurila, 1993; redwing *Turdus iliacus* Lampe and Espmark, 1987), and the seasonal period of song may persist throughout the breeding cycle. Klit (1999) confirmed that song in lesser whitethroat *Sylvia curruca* males does indeed function in territorial defence, but only until males are paired. Following this, the importance of the initial territory, and the motivation to defend it by song, decreases, and the male defends a smaller territory, surrounding the final nest site selected by the female, by actively approaching intruders.

Many passerines are polygynous, and males may continue to sing beyond attraction of a primary mate in order to attract a second mate (e.g. willow warbler *Phylloscopus trochilus*, Gil et al., 1999; great reed warbler, Hasselquist and Bensch, 1991; pied flycatcher *Ficedula hypoleuca*, Lundberg and Alatalo, 1992; common chiffchaff *Phylloscopus collybita*, Rodrigues, 1996; wood warbler *Phylloscopus sibilatrix*, Temrin, 1986), and/or to attract the mates of neighbouring males for extra-pair copulations (e.g. common reed warbler *Acrocephalus scirpaceus*, Catchpole, 1973; common stonechat *Saxicola rubicola*, Greig-Smith, 1982; great tit *Parus major*, Slagsvold et al., 1994; willow tit *Poecile montanus*, Welling et al., 1995). Conversely, Møller (1988) states that male yellowhammers *Emberiza citrinella* sing most intensely during the fertile period of their own mates in order to deter neighbouring males seeking extra-pair copulations. Poly-territorial individuals may continue singing at high intensity only when they are within a secondary territory, and song becomes reduced within the primary territory (Hasselquist and Bensch, 1991; Lundberg and Alatalo, 1992; Temrin, 1986).

In contrast to polygynous species, the Eurasian blackbird *Turdus merula* is monogamous, and sedentary pairs remain faithful from one year to the next (Snow, 1958a, 1958b). Together, they may raise up to four broods, although two or three is more typical, during a breeding season that extends between March and June (Cuthill and Macdonald, 1990; Snow, 1958a, 1958b). Snow (1958a) discovered that blackbirds in his study population in Oxford, UK were in full song by mid- to late-February, and that the vast majority of these early season singers were first-year males attempting to set-up and announce new territories. Older males did not commence singing until March, when their mates were laying their first egg clutches. Thereafter, song output from paired males varied individually, with peaks coinciding with their mate's egg-laying periods. Song ceased altogether in July, when breeding ended and moult began.

In his account of the cycle of song in the northern wren *Troglodytes troglodytes* in Cambridge, UK, Armstrong (1955) relates annual progression in song development and output with prevailing weather conditions. In a similar study on Eurasian blackbirds, Snow (1958a) observed that seasonal song onset was delayed by cold weather in February, but encouraged by mild conditions during this month. Additionally, Slagsvold (1977) found that the first seasonal peak in song activity amongst various species breeding in southern Norwegian woodlands was closely related with temperature and time of snow-melt, along with leaf-out times and invertebrate prey development.

Comprehensive studies explicitly illustrating seasonal singing activity amongst temperate woodland birds are surprisingly scant, and there has been little development upon early histograms provided by Cox (1944), which were based upon a limited dataset of counts of singing males in a British woodland (Fig. 2.1), and those of Slagsvold (1977), built upon a dataset of over 20 Norwegian woodland species. Considering the change in environmental conditions, and consequent changes to bird populations and communities during the intervening years (e.g. Burfield and van Bommel, 2004; DEFRA, 2019), these studies likely require revision.

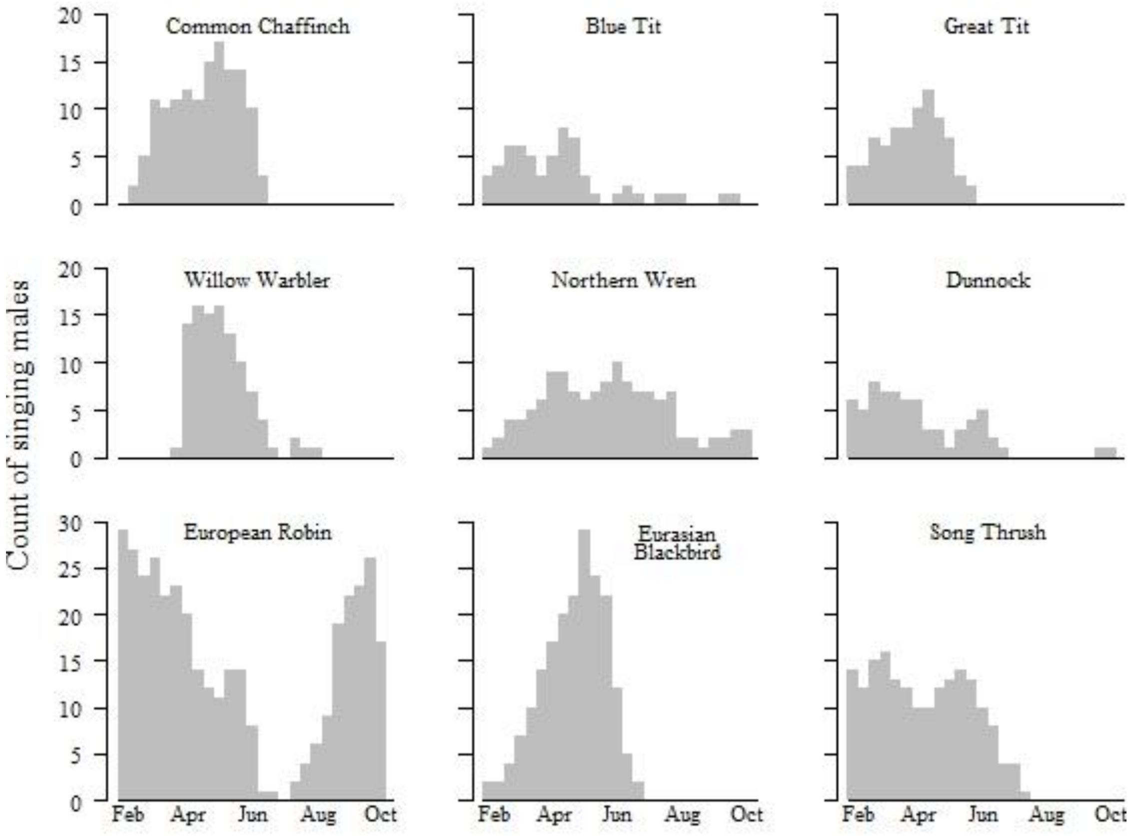


Figure 2.1 The seasonal variation in the number of males of different passerine species recorded singing during morning and evening transects in a British woodland habitat from February to October (After Cox, 1944). Peaks reflect certain stages of the breeding cycle, which may differ amongst species depending on the main function of song. Note also, the abrupt peak in the migratory willow warbler, reflecting newly-arriving male birds, compared to the gradual increase in many of the resident species.

2.4 Why do birds sing at dawn?

During the breeding season, most northern temperate zone male passerines sing most frequently and intensely during the period immediately prior to sunrise, when, together, they produce the avian dawn chorus (Armstrong, 1963). Multiple hypotheses have been proposed to explain the origin and cause of this daily phenomenon, which can be grouped into three broad categories: intrinsic factors, environmental factors and social factors (Dabelsteen and Mathevon, 2002; Farina, 2014; Stacier et al., 1996). Intrinsic factors include circadian cycles of hormone secretion and the physiological requirements of individuals. Environmental factors are represented by light levels, microclimate and habitat structure, and social factors are based upon mate attraction, territory defence and social dynamics.

2.4.1 Intrinsic factors

Circadian rhythms

In most organisms, and all birds (Cassone, 2014), many behavioural and physiological processes follow an exact rhythm, based upon an entrainable, internal biological clock (Aschoff, 1984). In the absence of external cues, the clock runs on an approximately 24 hr cycle (O'Neill et al., 2011), but is typically adjusted by variation in natural light levels (Da Silva et al., 2014). The avian pineal gland and its hormone, melatonin, play a fundamental role in entrainment and maintenance of circadian rhythms in birds (Cassone and Menaker, 1984; Gwinner et al., 1997). Darkness activates increased melatonin-release (Reiter, 1993), which, in turn, induces sleep (Ferguson et al., 2010). Pinealectomy in the house sparrow results in eradication of circadian rhythms in locomotor activity (Gaston and Menaker, 1968), and constant light conditions have the same effect on locomotor activity in intact white-throated sparrows *Zonotrichia albicollis* (McMillan, 1972). Wang et al. (2012) recognised that persistence of undirected singing in socially isolated birds (cf. Rashotte et al., 2001) reflects an endogenous motivational state that is free of regulation by external environmental and social factors. They provided evidence that melatonin not only controls diel locomotor activity in birds, but also controls rhythmicity in singing behaviour, by acting directly on the song control system in the avian forebrain.

Physiological requirements

Stochastic dynamic programming (SDP) is a computational procedure that predicts optimal behavioural routines, under specified conditions, that maximise individual fitness (Houston et al., 1988). A simple SDP model, termed the energy stochasticity hypothesis, predicts daily singing routines in birds based upon their energy reserves, and provides a general explanation for the dawn chorus (e.g. Houston and McNamara, 1987; Hutchinson, 2002; McNamara et al., 1987). The model assumes that during daytime in the breeding season, male birds must choose between two competing, but necessary, activities: foraging and singing. Foraging increases the chances of survival, but singing provides the opportunity to attract a mate, which yields a higher ultimate reward than mere survival. The birds rest overnight, when they lose mass thermoregulating. Overnight mass loss is greater on cold nights (Godfrey and Bryant, 2000; Thomas and Cuthill, 2002), and the model assumes that overnight temperatures are unpredictable. Therefore, a bird must forage throughout the day so reserves at dusk ensure survival through an almost worst-case night. At dawn, a bird may possess excess fat storage if the worst-case night did not materialise, but there are costs attributed to this, including increased metabolic expenditure, wing-loading and predation risk (Witter and Cuthill, 1993). The benefits of foraging at dawn are limited, due to low light levels (Kacelnik, 1979), but if the bird can assume foraging success later in the day, he can facilitate metabolism of excess fat by producing song at dawn, whilst also gaining the benefits of song production (Hutchinson and McNamara, 2000; Thomas, 1999).

The underlying assumptions of the energy stochasticity hypothesis have been tested directly and indirectly in the field via several food manipulation experiments. For example, Cuthill and MacDonald (1990) demonstrated that male Eurasian blackbird commenced dawn singing earlier, for a longer duration, and at a higher peak rate during periods of supplementary food provision. Similarly, supplementary-fed silvereye *Zosterops lateralis* not only achieved higher song rate than non-fed individuals, but also increased song length, and were capable of shifting song to a higher frequency band (Barnett and Briskie, 2007). Comparable responses have been observed in pied flycatcher (Gottlander, 1987), Ipswich sparrow *Passerculus sandwichensis princeps* (Reid, 1987), Carolina wren *Thyrothorus ludovicianus* (Strain and Mumme, 1988), and European robin (Thomas, 1999). A criticism of food supplementation studies, however, is that the treatment may be affecting the focal male's perception of his territory, believing it to be a more valuable resource (Barnett and Briskie, 2007), or his territory may be prone to increased intrusion from neighbouring males (Ydenberg, 1984), prompting increases in territorial song production. Perhaps the most convincing evidence supporting the energy stochasticity hypothesis has been gathered by studies evaluating the effect of day-to-day variation in temperature on singing routines. For example, Garson and Hunter (1979) showed that there exists a significant positive relationship between minimum overnight temperature and the duration of song in northern wren and great tit the following dawn. Similar responses of song rate to temperature have been found in other species (e.g. Gottlander, 1987; Reid, 1987; Strain and Mumme, 1988; Thomas, 1999). Finally, the hypothesis withstood more direct scrutiny when Thomas and Cuthill (2002) found that free-living European robins achieved greater song rate at dawn when their body mass was high. However, the authors maintain that overnight temperatures are not entirely unpredictable, as the minimum temperature of two successive nights can be correlated, and that birds may anticipate the temperature of the approaching night based upon their experience of the previous night. The authors supported a modification to the initial SDP model, when they found that birds were capable of strategically controlling mass at dusk, by increasing their daytime foraging rate if overnight temperatures were expected to be cold, and *vice versa*. Additionally, Bednekoff et al. (1994) discovered that captive great tits are capable of regulating overnight mass-loss when exposed to a variable, and hence, unpredictable, overnight temperature regime. However, the great tits consumed the same volume of food as when exposed to constant temperature regimes, and instead, regulated overnight expenditure through variation in faecal deposition, in order to match their required fat reserves at dawn. As a result, their body mass at dawn was not significantly greater on warm versus cold nights. This ability of birds to anticipate energy shortfalls, indicates that the cost of singing at dawn need not be especially great (Cuthill and Macdonald, 1990), and that all else being equal, the timing and intensity of dawn song should be the same from one day to the next, save for an exceptionally cold night.

The energy stochasticity hypothesis remains contentious, however. For example, Bruni et al. (2014) examined the dawn singing performance of six North American oscine and sub-oscine passerines following varying overnight conditions, and found that only two of these species adjusted their singing behaviour in response to overnight temperature. Additionally, the underlying theory that the dawn chorus exists largely due to a conflict between singing and foraging time has been disputed by Mace (1989a; see below section referring to light levels and inefficient foraging). Furthermore, Bruni et al. (2014) argue that locomotion would be a more efficient method of eliminating surplus energy reserves at dawn than would singing. Although, perhaps, this argument may miss the point, as birds have nothing to gain from locomotion at dawn.

2.4.2 Environmental factors

Light levels and inefficient foraging

A widely accepted explanation for the dawn chorus, and one that is incorporated into SDP models relating to the energy stochasticity hypothesis (Hutchinson, 2002), is that birds are active at dawn, but light levels are not yet sufficient for foraging. Indeed, Kacelnik (1979) states that low profitability of foraging at dawn, due to low light levels, favours application of other activities at this time, provided that birds can expect profitable foraging later in the day. At first light, singing will be at its most productive, and foraging success will begin to increase. It is, therefore, profitable to defer foraging until its success rate peaks later in the morning, and when energy reserves become low (Hutchinson, 2002). Singing then ceases as birds replenish their reserves, before resuming song bouts intermittently with foraging through the day. A second pause in singing activity just before the dusk chorus is a regular feature of models in which foraging success declines gradually at dusk (Hutchinson, 2002); if birds know that foraging success will shortly decline, they should forage intensively while success remains high. In a study complementing this theory, Avery and Krebs (1984) inferred that low temperatures at dawn also make foraging unprofitable. They found that captive great tits became increasingly successful at locating arthropod prey with increasing temperature between 2˚C and 13˚C, because prey items became more active, and hence, more visible, with increasing ambient temperature. However, it has been shown in willow warblers, that song begins each dawn within a very narrow range of light intensities, and that light intensity is always rising during song onset, but that temperature ranges are much broader, and can be either falling or rising during onset (Brown, 1963), thus, inferring that light levels play a dominant role. A related argument states that the females of some species may not leave their roosts until foraging becomes profitable later in the morning, and that the male ceases song only when the female emerges (Mace, 1986; Slagsvold et al., 1994; section 2.4.3, this thesis).

However, Mace (1989a) argued that competition with foraging time cannot explain dawn song, when she found that great tits breeding at latitudes with longer daylength went to roost at higher light levels, and had more free time in their activity budgets than conspecifics at lower latitudes, but still chose to begin singing before sunrise in the morning. Additionally, willow warblers breeding in extreme northerly regions and experiencing continuous daylight during the summer months, begin singing when either light is at a minimum or when it has just begun to increase (Brown, 1963), even though, presumably, foraging time is not limited. Nevertheless, the strong influence of light on singing activity has been emphasised by the growing interest in the effects of anthropogenic light pollution on animal behaviour. Several studies suggest that artificial light at night (ALAN) advances dawn song onset in temperate passerines (Da Silva et al., 2015, e.g. 2014; Kempenaers et al., 2010; Miller, 2006). By experimentally illuminating a dark forested habitat, Da Silva et al. (2016) found that Eurasian blackbird, great tit, blue tit *Cyanistes caeruleus* and, in particular, European robin, immediately adjusted their timing of dawn song following nights interrupted by artificial illumination.

None of these arguments, however, provide an answer as to why birds delay song onset until first light. Thomas et al. (2002) state that birds should wait until light levels are sufficient to carry out other activities relating to song, such as courtship behaviour or territorial aggression. Additionally, Krams (2001) demonstrated that vocalising crested tits *Parus cristatus* are more conspicuous and likely to be attacked by Eurasian sparrowhawk *Accipter nisus*. Thus, singing birds require clear vision in good light to detect predators.

Acoustic transmission

The acoustic transmission hypothesis (ATH; Stacier et al., 1996) states that birds sing most intensely at dawn because transmission of certain song traits is optimal under the microclimatic conditions that occur at this time of day. In particular, wind speed and atmospheric turbulence, which attenuate sound and generate background noise, are reduced at dawn. The negative effect of air turbulence on song transmission distance was demonstrated by Brenowitz (1982a) when he broadcast red-winged blackbird *Agelaius phoeniceus* song in open field habitat. His focus was on the low frequency (2.5 to 4 kHz) trill section of the song, regarded to be sufficient, in isolation, for species recognition (Brenowitz, 1982b). Ambient noise generated by wind and air turbulence was least at dawn, and rose throughout the morning to midday, when solar heat typically produces marked temperature gradients, and wind velocity and turbulence are at their greatest (Henwood and Fabrick, 1979; Richards and Wiley, 1980; Wiley and Richards, 1978). Such turbulence causes an average excess attenuation (EA; definition provided in section 2.7) of 4 to 6 dB per 100 m (Ingård, 1953), reducing the distance from the source over which signal amplitude remains at or above the threshold of detection by potential receivers. Only at dawn did broadcast red-winged blackbird song transmit sufficient distance to pass through all neighbouring conspecific territories, regardless of where the signaller was located within his own territory.

Air temperature and humidity also affect sound transmission. Increased humidity reduces attenuation and enhances transmission (Evans and Bazley, 1956), but the effect is small, and is of significance only when winds are light and the frequency of the sound is high (Griffin, 1971; Ingård, 1953). The influence of temperature is dependent on both humidity and sound frequency. Although the relationship is complex, in general, a sound with a frequency of 4 kHz, typical of many bird songs (Catchpole and Slater, 2008; Fig. 2.2, this thesis), will experience increased attenuation by air at higher temperature and lower humidity (Harris, 1966; Wiley and Richards, 1982). Conditions at dawn are typically the reverse of this (see Dabelsteen and Mathevon, 2002), and all else being equal, dawn presents optimal conditions, relative to other times of the day, for diurnal species to communicate over distance by sound (Henwood and Fabrick, 1979).

In wooded habitat, vertical temperature gradients at dawn can assist long-distance sound transmission. At this time, the air immediately above the canopy warms quicker relative to the air beneath (Geiger et al., 2003), and as long as the temperature beneath remains consistent towards the ground, the situation remains favourable for propagation of song emitted inside the woodland (Waser and Waser, 1977; Wiley and Richards, 1982, 1978). This is because the velocity of sound is greater in the warmer air above the canopy, and that the temperature gradient refracts sound that passes through it (Ingård, 1953). When temperature increases with distance above the ground, such as within a woodland at dawn, refraction deflects sound back downwards, and the sound propagates horizontally within a 'guide' aided by the consistent air temperature between the canopy and the ground (Wiley and Richards, 1982, 1978). By midday, a complex temperature gradient builds within the woodland, and the favourable conditions break down (Wiley and Richards, 1982, 1978). In open habitat, the early morning sun, unimpeded by a canopy, indirectly heats the air close to the ground, and, in contrast to the gradient within woodland habitat, the air gets progressively cooler with height. This gradient refracts sound upwards, creating a 'shadow zone' for sound propagation above the ground (Wiley and Richards, 1982, 1978). Dawn may still present the optimal time for song transmission in open habitats, but on sunny days, in particular, optimal conditions will likely break down far quicker (Brown and Handford, 2003).

Brown and Handford (2003) provided further evidence for the ATH. However, unlike prior theoretical (i.e. Henwood and Fabrick, 1979) and empirical (i.e. Brenowitz, 1982a; Waser and Waser, 1977) studies, they found no evidence that microclimatic conditions at dawn maximise sound transmission distance due to reduced attenuation. Rather, they reported a reduction in the variability of sound degradation at dawn compared to midday, and argue that the resultant consistency in signal quality reduces message ambiguity. Not all studies support the ATH, however. In a playback experiment using the song of Eurasian blackcap *Sylvia atricapilla* in the species' native deciduous temperate woodland habitat, Dabelsteen and Mathevon (2002) established that background noise, signal-to-noise ratio (SNR; definition provided in section 2.7) and EA all showed diurnal variation. As expected, background noise was lowest at dawn, immediately prior to commencement of the dawn chorus, and, accordingly, SNR at dawn was highest. However, contrary to the ATH, EA was highest at dawn and decreased gradually through the day. The authors could only speculate on why this might be, but they suggest that as the day progresses, evaporation reduces the density of leaves and their surface acoustic impedance, thus, reducing sound scatter and increasing sound 'flow'. This led the authors to conclude that dawn is not necessarily the best time of day for information transfer via song in the blackcap, and social factors must be considered to explain dawn chorusing behaviour in deciduous woodland.

2.4.3 Social factors

Mate attraction

Despite the general acceptance that male song serves to attract a female mate, direct empirical evidence from the field is surprisingly lacking (Catchpole and Slater, 2008; Eriksson and Wallin, 1986), perhaps due to difficulties in observing discreet female responses in what may amount to only a short period within the breeding cycle (Mountjoy and Lemon, 1991). Initial evidence was accumulated upon observations that the males of some species ceased singing immediately upon acquiring a mate (e.g. sedge warbler, Catchpole, 1973). Further studies experimented by removing the female in pairs of white-throated sparrow (Wasserman, 1977), great tit (Krebs et al., 1981;

Slagsvold et al., 1994) and common starling *Sturnus vulgaris* (Cuthill and Hindmarsh, 1985), and all recorded a significant increase in the singing activity of the newly ‘widowed’ male birds. Such evidence, however, is circumstantial, as it may simply be that having acquired a mate, a male is unable to devote time to singing (Wasserman, 1977). More robust evidence was provided by Eriksson and Wallin (1986), when they studied pied flycatcher and collared flycatcher *Ficedula albicollis* populations. They placed decoy dummy male birds beside entrances of several nest-boxes, modified to capture prospecting females that entered the box. Half of the male decoys were accompanied by song broadcast through a loudspeaker, and half remained ‘silent’. Nine of the ten female birds subsequently captured were found within boxes from which song was broadcast. A similar experimental set-up was used by Mountjoy and Lemon (1991) when they tested the hypothesis that male song attracts females in the common starling. They found that females were only attracted to nest-boxes that were accompanied by broadcast song. However, neither of these studies state the time of day that female birds were attracted to the broadcast song, and therefore, one cannot conclude from them that dawn song, in particular, functions in mate attraction.

Mate guarding and extra-pair paternity

Males of many bird species spend large amounts of time singing despite having already obtained a mate (Møller, 1991). Mace (1987a) observed that, although male great tits proclaimed a territory and attracted a mate with song early in the spring, they did not produce a dawn chorus until later in the season, when their mates were laying. At which time, males left their roost early in the morning and sang close to their mates’ nest cavity until she emerged. Females lay one egg each 24 hr period at dawn, and are at their most fertile one to two hours following laying (Birkhead and Møller, 1992), providing only a short ‘fertilisation window’. It is, therefore, vital to her partner that he is present at this time. As such, Mace (1987a) hypothesised that dawn song in the great tit acts as a paternity assurance, and a guard against neighbouring males seeking extra-pair paternity at this time. Once the female has emerged from her roost, the male ceases singing and actively guards her.

This hypothesis was tested by Welling et al. (1995) in the willow tit. They found that the males with fertile mates spent more time singing, and began singing earlier in the morning, than males with non-fertile mates. When the female emerged from her roost, song production decreased markedly, and almost half of all males ceased singing completely. In a follow-up study, Welling et al. (1997) prevented females from leaving their roosts, and found that males continued to sing until they were allowed to emerge. However, males were also found to sing some distance from their mate's roost (Welling et al., 1995), often at the edge of their territory. In addition, males did not necessarily copulate with their mate at dawn (Welling et al., 1995). The authors' translation of this behaviour was that dawn song in male willow tits is not produced solely to guard their own mates, but also acts to invite extra-pair copulations from neighbouring females. Likewise, Poesel et al. (2006) suggested that dawn is when female blue tits seek extrapair matings, and males singing at this time are more likely to attract these females. However, the female fertility hypothesis cannot apply to species within which unpaired males sing at dawn, unless they simply wish to attract extra-pair females.

Honest advertisement of fitness

Traits or signals that impose a cost upon the signaller can evolve under sexual selection if they are difficult to produce and honestly reflect the relative quality or resource-holding potential of the signalling individual (Zahavi, 1975). Birdsong may represent one such signal, as it is used in both male-male competition and female choice (Kroodsma and Byers, 1991; Searcy and Andersson, 1986). Singing is believed to be costly because of the energetic demands of song production. Indeed, it has been shown under both captive (Eberhardt, 1994; Ward et al., 2003) and natural (Hasselquist and Bensch, 2008) conditions, that singing significantly increases metabolic rate over basal metabolic rate. However, this direct energetic cost of singing remains contentious (cf. Oberweger and Goller, 2001; Ward et al., 2004), and, perhaps, it is more likely to be the temporal demands that singing imposes on foraging time that proves costly (Berg et al., 2005). Singing at dawn may advertise excess energy reserves at a particularly costly time of day. Indeed, Poesel et al. (2006) noted that singing activity in male blue tits peaked during the female fertile period, and that older males consistently sired more extrapair offspring than younger males, which they translated as the older males being fitter and more attractive to females. In turn, they found that male age explained a significant proportion of variance amongst individuals in the onset of dawn song, with older males singing earlier, and amongst older males, those that started to sing earlier had more mating partners. Otter et al (1997) found that age had less effect on the time that male black-capped chickadees *Poecile atricapillus* began singing in the morning, and instead, discovered that higher ranking males (which were not necessarily older), as determined by relative dominance at winter feeding stations, began singing earlier at dawn during the breeding season than lower ranking flockmates. It has also been discovered that the cost of singing could vary with the condition of the bird, as male sedge warbler with high blood parasite concentrations, invest less time in morning song flights compared to non-parasitised males (Buchanan et al., 1999). In addition, Krams (2001) provided evidence that long-distance communication is costly in terms of depredation risk, when it was found that crested tit models were prone to significantly more attacks by Eurasian sparrowhawk when accompanied by playback of calls. This argument backs-up that made earlier by Welling et al. (1997, 1995) when they noted that male willow tits remained secluded and sedentary whilst participating in the chorus, suggesting that singing at dawn is risky.

Territorial defence

The territory defence hypothesis (Slagsvold et al., 1994) assumes that song plays an important role in territory proclamation and defence. As did Mace (1987a), Slagsvold et al. (1994) recognised that male great tits sing most intensely prior to emergence of their mates at dawn during her fertile period. Contrary to Mace, however, Slagsvold hypothesised that this early morning song served to defend territory, and not directly to guard his mate. When the female has emerged during her fertile period, the resident male must guard her from extrapair mating by actively following her through his territory. During this demanding activity, he is unable to simultaneously defend his territory with song, so he must do so at a congruous time of day, and this is prior to her emergence at dawn. Temporal conflict with mate guarding, however, cannot explain why the dawn chorus extends beyond the fertile period of the female in some species. Perhaps some of the most convincing evidence that dawn song is used for territory defence is seen in migratory species, when male birds arrive earlier and establish territorial boundaries in the absence of females. For example, both paired and unpaired common nightingales exhibit high levels of dawn song from arrival through to the later stages of the breeding cycle (Amrhein et al., 2004), which is coherent with the hypothesis that dawn song is directed at rival males and functions to protect territory.

Empirical evidence that dawn song is used in territorial defence has been collected by Krebs (1977). By removing male great tits from their territories and replacing them with song broadcast through loudspeakers, he demonstrated that song alone delayed reoccupation of the vacant territories by rival males. Additionally, Amrhein and Erne (2006) experimented by simulating intrusions into the territories of male northern wrens, and discovered that the resident male increased song output during the following dawn chorus. Further, Kacelnik and Krebs (1983) posited that, due to overnight mortality of resident male birds, it may be advantageous for those seeking a territory to do so at dawn, and that this is why resident males deliver territorial song at this time. Amrhein (2003) tested this theory by radio-tagging several unpaired migratory common nightingales, and translocating them into occupied territories to imitate newly-arriving males. During the day, radio-tagged birds remained relatively stationary, outside the boundaries of occupied territories, but at dawn, they moved considerably, visiting several occupied territories. This, the authors argue, shows that these males were prospecting for territories at dawn. Furthermore, the singing activity of resident males during their study period was highest at dawn.

2.4.4 Synthesis

All of the hypotheses presented above attempting to explain the dawn chorus have been supported by researchers and refuted by others, and there is little consensus as to which, if any, is most applicable. It is widely recognised that a single hypothesis cannot account for dawn song in all species and individuals, and it is likely that several, or all, hypotheses apply at varying degrees throughout the breeding cycle (Catchpole and Slater, 2008; Hutchinson, 2002; Thomas, 1999). Some hypotheses, such as guarding mates that are most fertile at dawn (section 2.4.3), are highly species-specific (Gil and Llusia, 2020), and the inefficient foraging hypothesis (section 2.4.2), may only apply to the insectivorous feeding guild. It appears, therefore, a coincidence that all explanations should lead to dawn being the optimal singing time, and that different species are participating in the chorus for different reasons. The emerging theory behind inter-specific communication networks (see section 2.6) may hold the key as to why most species choose to sing in parallel. If dawn presents the most convenient time for gaining the benefits of song (but is not necessarily the optimal time for all), as other activities are not favoured, or it is the time of day when optimal conditions for sound propagation are met (section 2.4.2), it is not difficult to imagine how such a communication network may have evolved to persist at this time. Much more experimental work is required on individual species to gain an in-depth understanding of the dawn chorus (cf. Gil and Llusia, 2020).

2.5 The timing of the dawn chorus

Many investigations into the factors influencing the timing of the dawn chorus have concluded that specific light levels initiate singing activity in birds, and that there are characteristic times at which each species within a community engages in the chorus (e.g. Allard, 1930; Leopold and Eynon, 1961). The order of onset amongst species may be attributable to relative eye-size, especially amongst those that initiate the chorus (Berg et al., 2006; Thomas et al., 2002). This not only implicates light as the major influence on chorus timing, but also states that a perception of what constitutes 'dawn' occurs at different times during twilight for different species, depending on their visual acuity in low-light conditions. Furthermore, for a given species, the timing of 'dawn' may change with season and latitude, which have major influences on the length of both night and the twilight periods (see Table 2.2 for definitions of night, twilight and dawn used in this thesis). Latitude also influences the maximum and minimum light levels experienced at a location on a particular date (Martin, 1990). There exists, however, diel variation in song onset and output that cannot be explained by the predictable trajectory of the sun at a given location on a given date. Reproductive stage is likely to have an over-riding influence on song timing within and among species (e.g. Mace, 1987a; Welling et al., 1995), but there are also a number of extrinsic factors that may act to fine-tune song onset (Bruni et al., 2014). Weather variables are, perhaps, the most obvious, amongst which, heavy precipitation and strong wind are most likely to deter a bird from singing, not only due to their impact upon body temperature (Kennedy, 1970), but also due to the high level of masking noise produced by these conditions (Lengagne and Slater, 2002). As such, birds are expected to begin singing later, or to sing less vigorously, on wet and/or windy mornings (Bruni et al., 2014). Weather variables that reduce the amount of light perceived by birds, such as cloud cover, could also adjust chorus onset times, if the cloud delays the increase in light required for song onset. Within rural environments, where artificial light is absent, increased cloud cover has been shown to correlate positively with the time of chorus onset (Bruni et al., 2014). Finally, ambient temperature effects metabolic expenditure (Swanson, 2010), and just as the energy stochasticity hypothesis offers an explanation for the very existence of the dawn chorus, it may also provide an explanation for diel variation in chorus onset, if, as the hypothesis assumes, the timing of song onset at dawn is dependent upon overnight energy loss in birds.

Several recent analyses have revealed that ALAN modifies dawn singing behaviour in urban bird communities, such that song onset begins earlier (e.g. Kempenaers et al., 2010; Miller, 2006). Illumination by the moon may act in the same way within rural environments, by providing a light source long before light from the sun is detectable by birds (Bruni et al., 2014). Indeed, York et al., (2014) found that dawn song in male white-browed sparrow weaver *Plocepasser mahali,* varied with moon phase and its position relative to the horizon; males started singing earlier when the moon was full, compared to when it was new (see Table 2.2 for difference in illumination depending on moon phase), but only when the moon was above the horizon at dawn. The authors concluded that this observed effect of the moon on song onset was due to light intensity, rather than to other factors associated with the lunar-cycle. Likewise, Bruni et al. (2014) discovered that lunar stage affected the dawn chorus in six North American species, and that, overall, song onset was earlier during the third quarter or full moon, but, again, only when the moon was above the horizon at dawn.

Individuals may adjust song onset and output according to that of conspecifics participating in the chorus (Hodgson et al., 2018), and some might take their cue to begin singing from heterospecifics, such that choruses are the result of a multi-species communication network (Tobias et al., 2014). However, most studies have provided evidence that species limit signal interference by actively avoiding others. In response to selection, it is possible that the song of some species has shifted frequency to avoid masking by heterospecifics (Brumm and Naguib, 2009), but others may have adjusted temporal aspects of song production (section 2.6).

Table 2.2 The definitions of daylight, twilight and night as a function of the elevation of the sun (the angle between a line from the observer to the centre of the sun, and a line between the observer and the point of the horizon vertically above the sun's centre) and their natural illumination levels (after Martin, 1990). Upper and lower limits of starlight refer to variation as a function of geographical position and date. Defining night and dawn can be arbitrary, as at certain times of the year the sun does not drop below twilight zones, or does so only for short periods, yet an overnight period is still recognised. For simplicity, in this thesis, 'dawn' refers to the 90 minute period before local sunrise. This period was sufficient for sound recording equipment to capture the onset of the chorus regardless of the time of year or site location.

Condition	Limit	Sun elevation (˚)	Illumination (lux)
Daylight	upper	90	123786
	Lower (sunrise/set)	-0.8	452
Twilight:			
Civil	lower	-6	3.4
Nautical	lower	-12	0.00829
Astronomical	lower	-18	0.000646
Night:		< -18	
Moonlight	upper (full at 90˚)		0.371
	lower (0.25 at 22˚)		0.0133
Starlight	upper		0.0108
	lower		0.0003

2.6 Competition for acoustic space

Long-distance acoustic communication during the dawn chorus can be severely impaired by interference and masking from competing vocalisations emitted by multiple conspecific and heterospecific neighbours. There are several mechanisms that birds may employ to reduce acoustic interference and optimise the chances of their signal being received and correctly interpreted by intended recipients. Long-term adaptations involve evolutionary changes in song characteristics (reviewed by Brumm and Slabbekoorn, 2005), such that, for example, species occupy more-or-less distinct frequency bands (although this may be constrained by habitat; section 2.7 and Fig. 2.2), but individuals may also exhibit short-term plasticity in song structure and singing behaviour (Fig. 2.3).

Perhaps the most obvious short-term mechanism that birds can employ to counteract competition for acoustic space, is to increase the amplitude of their own song to a level above that of their competitors, as louder signals propagate further, and are more likely to be detected against a background of noise (Klump, 1996). Indeed, Brumm and Todt (2002) showed that captive common nightingales increased their vocal amplitude accordingly in response to increasing amplitude of background white noise, and that the effect was clearer if the noise was within the frequency range of nightingale song. This mechanism was also exhibited when individuals were exposed to heterospecific song within the same frequency range (Brumm and Todt, 2004). Demonstrating that the level of interference is dependent upon the overlap in frequencies between the noise and the signal (Brumm and Slabbekoorn, 2005; Dooling, 1982; Klump, 1996). With this in mind, it is conceivable that birds may regulate the spectral characteristics of their song, shifting notes into a distinct frequency space, so as to avoid overlap with others, as observed in black-capped chickadee (Goodwin and Podos, 2013). This will reduce the requirement to increase song amplitude, which may be an ineffective tactic in certain situations (Brumm, 2006). However, selection of spectral characteristics may be restricted by the effects of habitat on sound propagation as well as body size and phylogeny in birds (section 2.7), and instead, a more feasible short-term option may be to adjust temporal aspects of singing, such as shifting song production to periods, or moments, when masking noise is low.

In an early study, Cody and Brown (1969) noted the timing of morning song in sympatric common wrentit *Chamaea fuscata* and Bewick’s wren *Thyromanes bewickii* occupying dense chaparral habitat in North America. The two species organised their morning song output into cycles, such that peak output in one occurred when output of the other was low, and the times of peak activity did not overlap. Finer-scale patterns of song timing have also been observed, where birds sing at the same time in the morning, but still avoid temporal overlap with neighbouring species. Ficken et al. (1974) investigated singing interactions between red-eyed vireo *Vireo olicaceus* and least flycatcher *Empidonax minimus*, two co-occurring species with considerable overlap in song parameters. They found that the flycatcher was reluctant to begin singing when the vireo was already in song, but instead, inserted its song into the period of silence (known as a refractory period) between vireo songs. The vireo was less inclined to avoid flycatcher song in this way, indicating that one species may dominate such interactions. Popp et al. (1985) took this further when they investigated fine-scale temporal avoidance in song within an assemblage of four North American woodland species. They found that all species avoided singing during the song of another, and that overlap was rare or absent. To investigate a mechanism for overlap avoidance, the authors then broadcast a heterospecific stimulus song to free-living ovenbirds *Seiurus aurocapilla*, and noted that ovenbird song overlapped the stimulus song significantly less than predicted by chance. Instead, ovenbirds tended to begin singing immediately after a broadcast stimulus song. In a follow-up study, Popp and Ficken (1987) subsequently found that ovenbirds sang less frequently, at more irregular rates, and showed more variability in song duration during periods of stimulus song playback. This strategy of fine-scale temporal avoidance of heterospecific song was confirmed by, Brumm (2006), when he broadcast the song of six different species to captive common nightingales, and found that the nightingales showed greater variability in the temporal arrangement of their songs compared to when singing alone, which permitted them to insert their songs into the refractory periods of the other species. Brumm recognised that such flexibility is particularly suited to situations such as the dawn chorus. However, neither he, or Ficken et al. (1974), explicitly state the time of day that their observations were made, and Popp et al. (1985) conducted their experiment after sunrise, hence, their findings may or may not apply to free-living birds singing during the dawn chorus, when the motivation to sing is likely to be at its greatest (section 2.4).

The effect of heterospecific masking of song on receiving birds was investigated by Bremond (1978), with a series of playback experiments in woodland habitat. He first broadcast unmasked northern wren song with a natural refractory period of 10 s, and recorded the time taken for a neighbouring wren to respond with song. He then broadcast the same wren song, but with a background heterospecific song playing *i*) continuously over the wren song, including before and between refractory periods, and *ii*) only during the song of the wren (i.e. not during the refractory periods). On average, subjects responded quicker to the unmasked wren song. However, they also responded quicker to the masked playback where the refractory periods remained silent over the playback where they did not. This, Bremond argues, indicates that songs of sympatric species do not entirely mask wren song, as wrens eventually responded to all playbacks, but they do have a psychological effect, whereby the receiving individual becomes ‘habituated’ to the heterospecific song, and fails to immediately recognise that of its own species.

Temporal avoidance in song also occurs amongst male birds of the same species. For example, during playback of over 250 conspecific songs, Ficken et al. (1985) recorded only 10 occasions when ovenbirds actively overlapped a broadcast song, and in a prior study, Schroeder and Wiley (1983) demonstrated that male tufted titmouse *Baeolophus bicolor* seldom overlap song. However, as noted for most the above studies concerning inter-specific acoustic competition, due to the timing of the playback experiments, the results may not necessarily reflect singing behaviour during the dawn chorus. Additionally, singing interactions amongst males of the same species may reflect a more complicated behavioural pattern other than merely avoiding acoustic interference, and it is not clear from these studies whether the response of the subjects to the playback was the result of song overlap avoidance, or because individuals were replying to the broadcast song of a conspecific (Ficken et al., 1985).

A contrasting view, is that rather than partitioning acoustic space, co-occurring species may in fact show the opposite arrangement of signal clustering, culminating in extended communication networks within and between species (Tobias et al., 2014). This process might arise in bird communities when species with similar ecological requirements interact to defend common resources (e.g. Catchpole, 1978; Cody, 1978, 1969), thus, coercing the evolution of consistent territorial behaviour, such as signalling to advertise territorial ownership (Laiolo, 2012). This situation may be more evident in the complex bird communities of tropical forests, where several congeners, or other ecologically similar assemblages of birds, are likely to co-occur (e.g. Planqué and Slabbekoorn, 2008; Tobias et al., 2014), but there is indication that some temperate woodland choruses are also co-ordinated events. Malavasi and Farina (2013) performed spectral analyses of the avian dusk chorus recorded in an Italian oak woodland, and discovered that among the species singing simultaneously, many used the same frequency range. However, songs were apparently finely-timed, such that temporal overlap of heterospecific song was deliberate, but that spectral overlap was avoided. The authors acknowledge, however, that such co-ordination may be less apparent during the dawn chorus, when song may take on a different function (section 2.4).

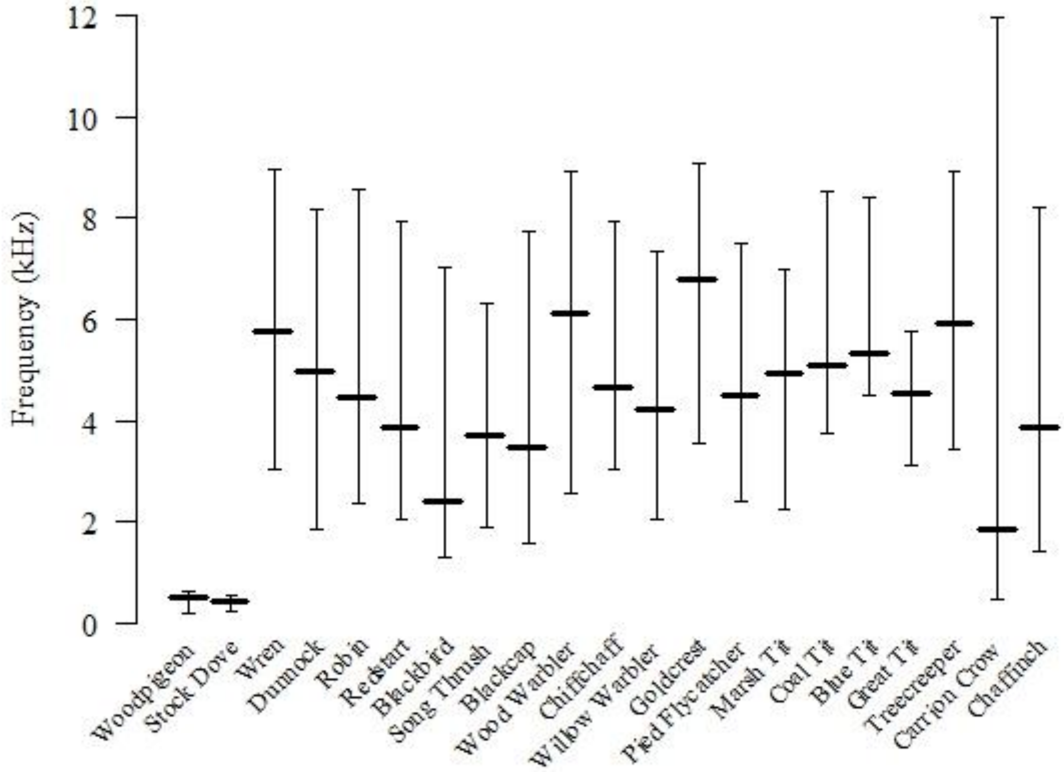


Figure 2.2 The peak frequency (thick horizontal bars) and typical frequency range of song in some common breeding British woodland birds. Mean frequency measurements (peak, minimum and maximum frequency) were obtained by spectrogram analysis of singing events within up to five high quality sample recordings per species taken from the xeno-canto repository (www.xeno-canto.org). Peak frequency refers to the frequency in the song with the greatest amplitude, which shows variation amongst species. Divergence amongst species in frequency range, however, may be constrained by body size and the acoustic properties of woodland habitat. Spectrograms and measurements were made in Raven Pro v1.4 (The Cornell Laboratory of Ornithology, Ithaca, USA). For space and clarity, species names shown are shorter common British names, rather than the international naming system used throughout the text.

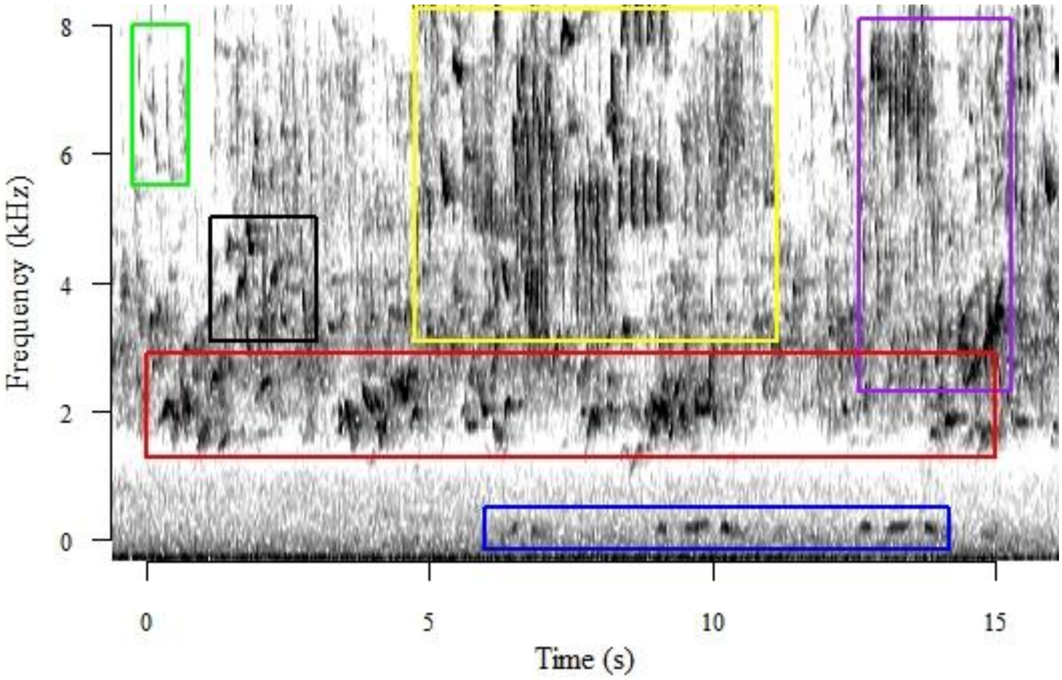


Figure 2.3 An example of acoustic niche partitioning during the dawn chorus in a British woodland bird community. Coloured boxes demarcate the songs of foreground individuals of the various vocalising species: red=Eurasian blackbird *Turdus merula*; purple=European robin *Erithacus rubecula*; green=blue tit *Cyanistes caeruleus*; yellow=northern wren *Troglodytes troglodytes*; black=Eurasian blackcap *Sylvia atricapilla*; blue=common woodpigeon *Columba palumbus*. There is available acoustic space in the frequency range below 1.5 kHz. Competition for acoustic space is greater within the 3-8 kHz frequency band, where similar physical morphology amongst species may constrain divergence. These species show apparent temporal partitioning to avoid overlap. Alternatively, they may increase song amplitude, which is reflected in the darkness of the greyscale, with black reflecting highest amplitude. However, here, this may reflect the proximity of the individual to the acoustic sensor and not necessarily the amplitude at source. Spectrogram made in Raven Pro v1.4 (The Cornell Laboratory of Ornithology, Ithaca, USA) of an acoustic survey made at RSPB Highnam Wood, Gloucestershire on 1st May 2015.

2.7 The effect of habitat

The structural properties of long-distance animal vocalisations are adapted to the acoustics of the habitat in which they live, to maximise or optimise propagation (Forrest, 1994; Wiley and Richards, 1982, 1978). In this regard, the acoustic adaptation hypothesis (AAH; Morton, 1975) proposes that shared selection pressure has led to convergence in the acoustic traits of vocalisations amongst species occupying comparable habitat-types (Slabbekoorn et al., 2002; Slabbekoorn and Smith, 2002a). The significant factors influencing convergence in birdsong are attenuation and degradation of sound (Slabbekoorn et al., 2002). Attenuation refers to a progressive decrease in a sound's amplitude (*i.e.* energy per unit surface) with increasing transmission distance (Forrest, 1994). A proportion of the total attenuation can be predicted by spherical spreading, which, in its simplest form, is the loss in a sound's amplitude as it radiates in all directions from the point source. It is proportional to the inverse-square of the transmission distance, and amounts to *c*.6 dB loss in amplitude per doubling of distance. In ideal, frictionless environments, attenuation by spherical spreading is equal to total attenuation, but in natural habitats, total attenuation is more than by spherical spreading alone. This is because of EA, caused by absorption and scattering of soundwaves by obstructions in the habitat, and absorption by the atmosphere (Forrest, 1994). Foliage increases EA (Aylor, 1972a; Martens, 1980), as does warm, dry air, although the relationship between temperature, humidity and frequency is complex (Harris, 1966). As EA increases, the operative distance of the sound is reduced. Degradation refers to changes in temporal and structural characteristics of sound, which accumulate with distance from the source (Morton, 1986). It is caused by reflections, reverberations (echoes), scattering and frequency-dependent filtering (Bradbury and Vehrencamp, 1998). The AAH considers habitat-dependent variation in attenuation and degradation to predict that long duration, low frequency syllables with narrow bandwidths, low frequency modulation and long inter-syllable gaps (e.g. whistles) should dominate in complex or densely-structured habitat (e.g. woodland). Whilst short duration, high frequency syllables, with broad bandwidths, high frequency modulations and short inter-syllable gaps (e.g. trills) should prevail in less complex or herbaceous habitat (e.g. grassland; Morton, 1975). The same selection pressures that drive inter-specific convergence in song traits can also generate intra-specific divergence when a species occupies multiple habitat types, or even similar habitats with differing background noise profiles (e.g. northern cardinal *Cardinalis cardinalis*, Anderson and Conner, 1985; grey-breasted wood-wren *Henicorhina leucophrys*, Dingle et al., 2008; blue tit, Doutrelant and Lambrechts, 2001; rufous-collared sparrow *Zonotricha capensis*, Handford and Lougheed, 1991; little greenbul *Andropadus virens*, Slabbekoorn and Smith, 2002b).

Support for the AAH was provided empirically by Brown and Handford (2000), when they transmitted artificial sounds through several habitats of varying vegetation density. Their work, however, did reveal that whistles degrade less, and, therefore, should be favoured, within both open and dense habitats. This is because whistles (or tones) concentrate energy within a narrow frequency band (as opposed to spreading the same energy over a broad range of frequencies) which can lead to an increase in signal amplitude within a given habitat, regardless of its structure. For example, Slabbekoorn et al. (2002) observed that reverberations in the whistles of green hylia *Hylia prasina*, a passerine inhabiting dense African forest, can actually benefit from degradation, as reverberations within the same narrow frequency band accumulate to produce longer, louder and more effective signals at distance. Likewise, low frequency signals should prevail regardless of habitat structure (Marten and Marler, 1977; Wiley, 1991; Wiley and Richards, 1982). The frequency range of birdsong is believed to closely match the hearing range of birds (Okanoya and Dooling, 1988), which has a maximum sensitivity of 1-5 kHz (Dooling, 1982). Within this range, lower frequencies are less affected by small obstacles in the habitat (e.g. foliage), and atmospheric absorption. Scattering and reverberations by vegetation, therefore, are greater for higher frequencies (Aylor, 1972a; Marten and Marler, 1977; Wiley, 1991; Wiley and Richards, 1982). Indeed, in deciduous woodland, Dabelsteen et al. (1993) found that the high-frequency ‘twitter’ in Eurasian blackbird song degraded more rapidly with distance than lower frequency portions of the song, and whistles projected best. During formulation of the AAH, Morton (1975) found a characteristic reduction in EA of low to mid frequencies between 1.5-2.5 kHz when transmitted at low height (<4 m) within forested habitat, a phenomenon he coined a ‘sound window’. Yet, very low frequencies (<1-2 kHz; Marten and Marler, 1977) are subject to greater EA and degradation than other frequencies when they are transmitted close to the ground (<1 m), because greater interference between the direct pathway and reflections from the ground, effectively lead to cancelation of sound in both pathways (Marten and Marler, 1977).

The validity of the AAH as an explanation for habitat-driven variation in the structure of birdsong is further disputed when it is applied to real organisms within their natural environments (Boncoraglio and Saino, 2007). Not least because the range of possible frequencies emitted by a bird is constrained by the size and shape of its body (Ryan and Brenowitz, 1985; Wallschläger, 1980) and bill (Derryberry, 2009; Podos and

Nowicki, 2004; Slabbekoorn and Smith, 2002a), regardless of the habitat it occupies. There is also concern for the theory's generality. To illustrate, Badyaev and Leaf (1997) found that temporal characteristics of *Phylloscopus* and *Hippolais* warbler songs vary with habitat structure, as predicted, but the frequency attributes of the songs remain largely unaffected, whereas Blumstein and Turner (2005) found quite the opposite when applied to the songs of Australian birds; the effect of habitat on frequency attributes of song was greater than on the temporal characteristics. Wiley and Richards (1982) point out that the AAH was formulated based upon tropical forest species, many of which sing on the ground or within 1 m of the ground, where frequencies of around 1-2 kHz are particularly favoured, whereas birds of temperate woodland generally sing at greater heights above the ground (>3 m), where a 1-2 kHz 'sound window' is not so pronounced. Therefore, the predictions of the AAH may not apply in temperate regions, as temperate woodland birds do not gain a heightened advantage from utilising lower frequencies when compared to birds in open habitat. Marten and Marler (1977) also point out that the AAH was proposed by Morton (1975) on the basis that he did not find a characteristic reduction in EA at lower frequencies (1-3 kHz) in tropical grassland habitat. Morton (1975) interpreted this as a reason why low frequencies should not be favourable in open habitats. Yet, Marten and Marler (1977) did find this effect of low frequencies in temperate grassland. Furthermore, Sorjonen (1986) argued that geographical location and the assemblage of competing species have greater influence over the song structure of selected *Luscinia* species than does habitat, and that long distance communication can be improved more efficiently by changes in singing behaviour than by changes in song structure. Such behavioural adaptations include selection of an optimal singing height and an optimal time for song production (Henwood and Fabrick, 1979). Despite the uncertainty surrounding the AAH, the vegetation characteristics of a habitat undoubtedly influence the degree of attenuation and degradation of birdsong (Aylor, 1972b, 1972a; Blumenrath and Dabelsteen, 2004; Marten and Marler, 1977; Martens, 1980; Naguib, 2003; Price et al., 1988).

Each spring, temperate woodland birds must contend with change to the acoustic properties of their environment, brought about by the emergence of new leaves and their growth through to maturation in what was previously a leafless environment (Blumenrath and Dabelsteen, 2004; Naguib, 2003). Theory suggests that the leaf-out process results in attenuation and degradation of successively lower frequencies, as the increasing leaf size and density intercepts, reflects and absorbs increasingly large soundwaves (Aylor, 1972b, 1972a; Morton, 1975; Price et al., 1988; Richards and Wiley, 1980). These physical changes to the environment are also tracked by changes to the microclimate beneath the growing canopy, such as higher temperatures, which enhance atmospheric absorption (Harris, 1966), and hence, further attenuate sound. However, at dawn, the formation of the canopy can induce temperature gradients that are favourable for sound transmission (section 2.4.2). Several playback-record experiments have been devised to measure the level of attenuation and/or degradation experienced by birds following leaf-out in deciduous woodlands. Initially, Marten and Marler (1977) broadcast artificial tones of different frequencies through several foliated and non-foliated woodland habitats, and discovered that EA increased in the foliated woodlands, when compared to the non-foliated woodlands, when sound was transmitted close to the ground (1 m), but that EA increased substantially more at greater heights (e.g. 10 m) in foliated woodlands, where soundwaves were intercepted by the canopy. In a similar experiment, Naguib (2003) measured reverberations in artificial trills of different repetition rates and frequencies broadcast in the same woodland with and without foliage, and found that, although reverberations were present within both, accumulated reverberations became stronger at shorter transmission distances in the woodland with foliage. Finally, Blumenrath and Dabelsteen (2004) broadcast great tit song elements pre- and post-leaf-out at a deciduous woodland site, and showed that the elements suffered from increased EA, reduced SNR, which is the energy in the signal relative to the energy in the background noise, as well as reduced tail-to-signal ratio (TSR), which is the energy in the reverberations relative to the energy in the preceding signal, and increased blur ratio (BR), which represents the degree of blurring of amplitude and frequency over time (Dabelsteen et al., 1993).

2.8 Artificial light at night (ALAN) and noise pollution

Climate change and associated consequences for the dawn chorus are discussed throughout the chapters of this thesis. However, additional threats to the seasonal and daily timing and magnitude of the dawn chorus come from other sources of environmental change, notably, ALAN and anthropogenic noise pollution. ALAN is touched upon in prior sections of this chapter, but warrants greater attention here. Indeed, several studies have indicated that ALAN advances the onset of dawn singing in several passerine species (Da Silva et al., 2014; Da Silva et al., 2016; Dominoni et al., 2014; Kempenaers et al., 2010; Miller 2006; Nordt and Klenke, 2013). ALAN may influence a bird's perception of dawn and daylength, altering daily and seasonal behaviour, including patterns in singing activity (Da Silva et al., 2015), and may potentially lead to physiological changes (Dominoni et al., 2013). Likewise, noise pollution from, for example, road traffic (Arroyo-Solís et al., 2013; Fuller et al., 2007; Nordt and Klenke, 2013) and airports (Dominoni et al., 2016; Gil et al., 2015) may also alter daily singing regimes, as birds adjust singing activity to avoid masking by noise. Separating the effects of ALAN and noise is difficult in some environments (Nordt and Klenke, 2013), and the relative effect of either ALAN or noise on a particular species, may differ depending on the natural singing period at dawn; ALAN tends to affect earlier-singing species (Da Silva et al., 2016), and noise appears to have greater effect on late-singing species (Dominoni et al., 2016). Interestingly, it may be that the effect of noise on song onset could be facilitated by ALAN, whereby artificial light creates an opportunity for some birds to sing earlier in the morning and avoid the masking effects of anthropogenic noise that tends to start later in the day (Da Silva et al., 2014).

As dawn song is hypothesised to function in male-male competition and female choice, modification to daily and seasonal timing of song by ALAN and noise pollution may have longer term or evolutionary fitness consequences (Da Silva et al., 2015), but these remain unknown. Singing earlier in the year or earlier in the morning might be advantageous for males, for example, increasing the likelihood of attracting a high-quality mate, or of siring extra-pair offspring (Kempenaers et al., 2010). Alternatively, earlier singing, or singing over a longer period, may come at a cost to survival, owing to increased risk of predation, or because of exhaustion or elevated stress levels (Da Silva et al., 2015).

ALAN and noise pollution are most often associated with urban environments, although they are becoming increasingly problematic within rural locations (Hölker et al., 2010). This thesis is concerned with the dawn chorus in undisturbed woodland habitat, and choices made on rural study sites reflect this (chapter 4). Although few study sites were entirely free of distant traffic noise, most were believed to be subject to relatively low levels of ALAN and noise. To include the effects of ALAN and noise in this thesis would have introduced an extra dimension of complexity that could be dealt with more comprehensively in future work (chapter 9).

Chapter 3

Technological advances in the study of birdsong

Blue tit *Cyanistes caeruleus*

3.1 Digital recording

The objective scientific study of birdsong is a relatively new field. One reason for this is that making a permanent record of song was not easy until the advent of portable tape recorders and their increased availability during the 1950s (Baker, 2001; Thorpe, 1961). Only with a permanent record, that can be slowed down, repeated and analysed in various ways, is it possible to systematically analyse the complexities of birdsong (Catchpole and Slater, 2008; Thorpe, 1961). Sound recording technology has advanced greatly in recent years, mainly due to digital audio recording methods (Brandes, 2008a), which has increased the portability of handheld recording equipment, as well as providing increased storage capacity and flexibility in recording schedules. In addition, digitised data can be efficiently stored for future use, and could potentially play an important role in future research by documenting change in acoustic populations and communities over large timescales (Sugai and Llusia, 2019), although this use could be tempered if future changes in the performance of equipment introduces bias into monitoring studies (Rempel et al., 2013).

3.2 Autonomous recording units

Acoustic monitoring of sound-producing organisms in their natural habitat has been revolutionised by the availability of autonomous recording units (ARUs). ARUs are widely used to gather ecological information on a diverse range of taxa, including insects (Hart et al., 2015; Newson et al., 2017), anurans (Acevedo and Villanueva-Rivera, 2006), fish (Gannon, 2008), cetaceans (Mellinger et al., 2007; Moore et al., 2006), bats (Newson et al., 2015), primates (Heinicke et al., 2015) and birds (reviewed by Shonfield and Bayne, 2017). ARUs are available commercially as fully programmable devices with scheduling functions (e.g. Bioacoustic Audio Recorder [BAR], Frontier Labs, Brisbane, AUS; Song Meter, Wildlife Acoustics Inc., Maynard, USA; Swift, Cornell Laboratory of Ornithology, Ithaca, USA), as low-cost programmable devices (e.g. AudioMoth, Hill et al., 2018), as open-source customisable devices (AURITA, Beason et al., 2019; Solo, Whytock and Christie, 2017), or as low-cost non-programmable USB flash drive devices (e.g. UR-09, Shenzhen HNSAT Industrial Co. Ltd, Shenzhen, China). In most cases, ARUs can be deployed in the field for extended periods without intervention. Several units can be deployed at multiple sites simultaneously, or in complex arrays (e.g. Mennill et al., 2012), providing data on spatio-temporal scales of ecological consequence, whilst negating the requirement for repeated visits to remote or hard-to-access locations. Thus, the use of ARUs leads to an objective approach with a greater degree of standardisation in data collection over human observers (Celis-Murillo et al., 2009; Heinicke et al., 2015). In addition, the innovation of omni-directional microphones with superior sound quality, equip recorders with a sensitivity similar to that of human listeners (e.g. Hobson et al., 2002; but see Hutto and Stutzman, 2009). As a result, the number of peer-reviewed studies utilising ARUs has increased dramatically in recent years. Indeed, in a literature review, Shonfield and Bayne (2017) identified 61 bird studies using ARUs between 2006 and 2017, with a notable increase in the number of articles published from 2014 to 2016. Similarly, Sugai et al., (2019) found that the number of studies using passive acoustic monitoring (PAM) have increased exponentially since the 1990s, most notably in the period 2010 to 2017. However, PAM does not necessarily require the use of programmable ARUs, and only 39% of the studies researched by Sugai et al. used such devices.

Data from acoustic survey can be used to ask fundamental questions related to ecological systems, such as species presence and habitat occupancy (e.g. Campos-Cerqueira and Aide, 2016). Challenges remain, however, when estimating abundance and density from acoustic data, although several methods have been described and tested. For example, Dawson and Efford (2009) set out multiple spatially separated acoustic recorders in the field and analysed the relative intensities in individual ovenbird *Seiurus aurocapilla* songs recorded by each recorder in the array, by applying a statistical methodology similar to that used in spatially explicit capture-recapture (SECR) studies. A major drawback of this method, however, is the cost of the equipment required. Sebastián-González et al. (2018) devised an alternative method for estimating density of Hawai'i amakihi *Chlorodrepanis virens* using a single ARU, by measuring the intensity of received signals to estimate the distance of individuals from the microphone. The method requires prior knowledge of the relative intensities of recorded signals at different distances, and, therefore, may also prove to be resource intensive (Pérez-Granados et al., 2019). A cheaper alternative is to use a vocal activity rate (VAR) index (the number of songs per unit time for a species) to infer relative abundance of a focal species (e.g. Pérez-Granados et al., 2019), although Zwart et al.

(2014) did not find this method useful in estimating the abundance of European nightjar *Caprimulgus europaeus*.

Large, long-term acoustic datasets collected by ARUs can provide new insights into the life histories of birds, their mating systems, the behavioural interactions between individuals and their ecological interactions with the environment, which were previously impractical or unattainable using traditional approaches to bird survey. By remaining in one location and monitoring continuously, or at regular intervals, use of ARUs to gather acoustic information can reveal changes in ecosystems over daily, monthly, seasonal and yearly scales. For example, following a 5-year study of Eurasian bittern *Botaurus stellaris*, Frommolt and Tauchert (2014) determined the number of calling individuals and documented changes in their spatial distribution, which was found to be connected with changes in habitat structure. Fitzsimmons et al. (2008) recorded entire 'neighbourhoods' of dawn singing black-capped chickadees *Poecile atricapillus* to quantify intricate counter-singing exchanges between competitors. Mennill and Vehrencamp (2008) provided the first detailed information on song duetting using microphone arrays to record the performance of male and female rufous-and-white wrens *Thyrothorus rufalbus*, and Kirschel et al. (2011) used recordings obtained over a 4-year period to identify individual Mexican ant-thrushes *Formicarius moniliger* by song, and determined their territorial and social dynamics.

Whilst the advantages of using ARUs are clear, it has been difficult to quantitatively assess how ARUs compare to traditional survey methods in their sampling performance of species richness (Darras et al., 2018a). Multiple studies have been designed to test the performance of ARUs against that of bird point-counts performed by human observers (reviewed by Darras et al., 2018a; Shonfield and Bayne, 2017), but there has been little consensus. Darras et al. (2018b) argued that bias is introduced by differing detection ranges between the two methods, and, thus, renders them incomparable. Therefore, Darras et al. (2018a) corrected for the detection ranges of different microphone models used in various comparison studies, and showed that both methods are statistically indistinguishable when detection range is accounted for. They concluded that high-end ARUs used 'correctly' are capable of sampling terrestrial wildlife just as well as human observers carrying out visual-aural point-counts.

3.3 Sound analysis tools

Progress in the study of birdsong was long restricted by difficulties of description and measurement (Hinde, 1969), largely due to a lack of analytical equipment. Onomatopoeic renderings of the ‘little-bit-of-bread-and-no-cheese’ variety, as used for the song of yellowhammer *Emberiza citronella*, provided very crude descriptions, and conveyed little idea of either frequency changes or the ‘quality’ of the notes (Hinde, 1969). Visual representations of birdsong was first made possible by use of oscillography (Hinde, 1969), which produces a record of amplitude as a function of time (Fig. 3.1a). However, frequency is poorly represented by oscillographic methods, and comprehensive analysis is feasible only with sounds that are maintained at fairly constant frequency and amplitude over a reasonable time period (Thorpe, 1961). Birdsong is characterised by sound patterns consisting of pulses of very short duration, large frequency range and rapid amplitude and frequency modulation, and can only be analysed by oscillographic methods at a prohibitive cost of time and effort (Thorpe, 1961). A revolution came with the invention of the sound spectrograph. This produces a spectrogram (or sonogram), which is essentially a Fourier analysis of frequency against time (Fig. 3.1b). It was initially devised for military use during World War II (Baker, 2001), and was first used to provide a visual representation of birdsong by Thorpe in 1954 (Catchpole and Slater, 2008), when his spectrograms revealed the acoustic intricacies of common chaffinch *Fringilla coelebs* song (Thorpe, 1954). Today, several commercially- or freely-available digital sound analysis software packages are available to ecologists, and include spectrographic analysis tools as standard. Some (e.g. Raven Pro, developed by The Cornell Laboratory of Ornithology, Ithaca, USA) allow the user to interact with the spectrogram using on-screen cursors, and choose from a suite of measurements of selected regions or sounds of interest.

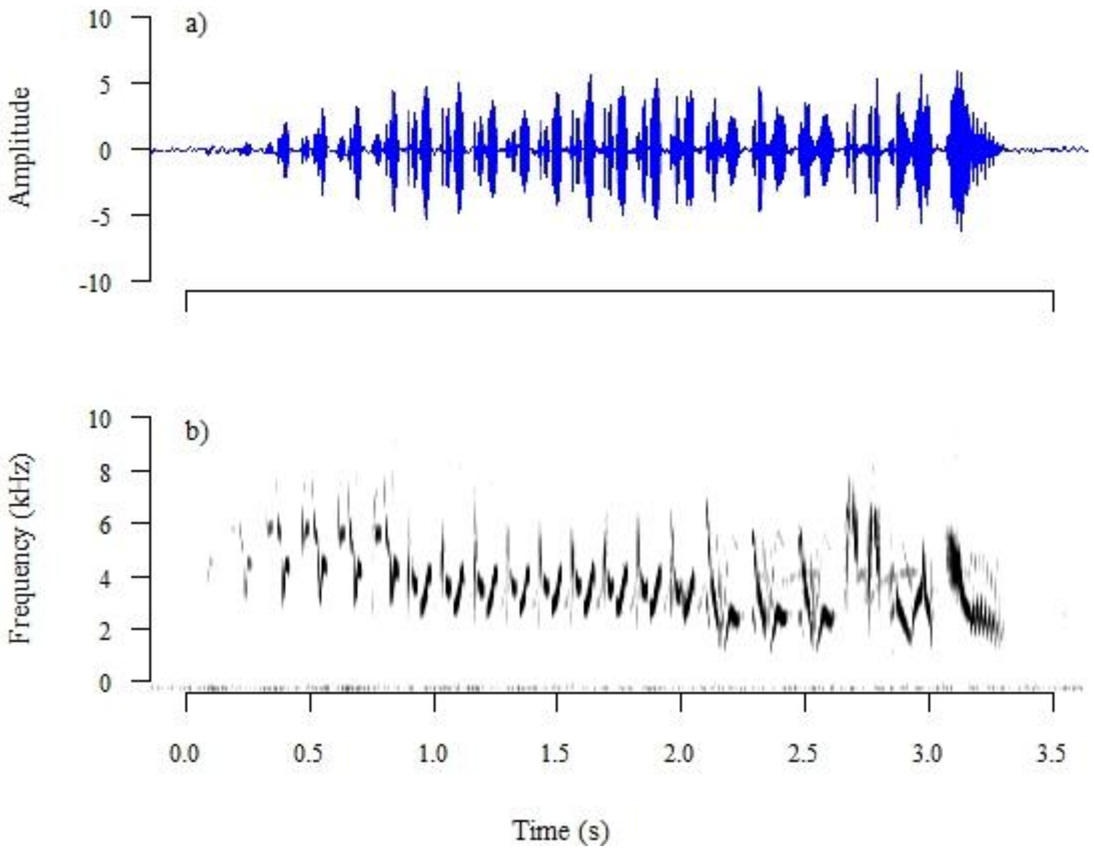


Figure 3.1 Two types of graph commonly used to visualise sound: a) the amplitude waveform (or oscillogram), where the x-axis represents the passing of time, and the fluctuating amplitude of the sound is reflected in the height of the spikes above and below zero on the y-axis, and b) the spectrogram (or sonogram), where, again, the x-axis represents the passing of time, and the y-axis represents the frequency of the sound. Information on amplitude is depicted by the darkness of the greyscale, with black reflecting the frequencies of highest amplitude. The graphs were made in Raven Pro v1.4 (The Cornell Laboratory of Ornithology, Ithaca, USA) from the same recording of common chaffinch *Fringilla coelebs* song.

3.4 Automated detection and classification of species

Despite the benefits of using ARUs for ecological data collection, there remains the difficulty of extracting meaningful and accurate information from the considerable datasets amassed. Manually browsing many hours of acoustic surveys on spectrograms can be a lengthy and prohibitive task (Sebastián-González et al., 2015), that often requires costly teams of researchers (e.g. Furnas and Callas, 2015; Sanders and Mennill, 2014). Therefore, one of the most pressing challenges in PAM, and crucial for its long-term viability (Blumstein et al., 2011), is development of reliable computer-aided automated signal recognition systems (hereafter 'recognisers') that are capable of identification to species level. The process of automatically detecting and classifying birds from sound recordings potentially presents a greater challenge than for other taxa (August et al., 2015; Brandes, 2008a; Briggs et al., 2012), as bird vocalisations are typically produced within a busy sonic environment (as opposed to the ultra- or infra-sonic environments utilised by e.g., bats and cetaceans), and are prone to masking from high background noise, and when multiple species and individuals sing simultaneously, such as during the dawn chorus, elements of song overlap in time, frequency and amplitude (Briggs et al., 2012; Luther and Wiley, 2009; Priyadarshani et al., 2018). Furthermore, the acoustic structure of song is extremely varied and complex, and may vary geographically within species (Hunter and Krebs, 1979; Slater and Ince, 1979) and seasonally within individuals (Kunc et al., 2005); signals that vary within and between individuals are particularly difficult to recognise and detect (Heinicke et al., 2015).

Many approaches to automated identification of species have been trialled in recent years (reviewed by Blumstein et al., 2011; Priyadarshani et al., 2018; Stowell and Plumbley, 2011), which have met with varying degrees of success, depending on the method used and the target species (Sebastián-González et al., 2015; Swiston and Mennill, 2009). Many approaches are built upon sophisticated machine learning methods, such as those applied to human speech recognition. For example, hidden Markov models (HMM; e.g. Brandes, 2008b; de Oliveira et al., 2015; Kogan and Margoliash, 1998; Potamitis et al., 2014; Trifa et al., 2008), Gaussian mixture models (GMM; e.g. Ganchev et al., 2015; Heinicke et al., 2015; Roch et al., 2007), support vector machines (SVM; e.g. Acevedo et al., 2009; Tachibana et al., 2014) and artificial neural networks (ANN: e.g. Chesmore and Ohya, 2004), while others use composites of these approaches (e.g. Koumura and Okanoya, 2016). Others utilise ensemble learning methods, such as random forest (e.g. Campos-Cerqueira and Aide, 2016) and decision trees (e.g. Acevedo et al., 2009; Digby et al., 2013), whilst others still, employ simpler methods, such as spectrogram cross-correlation (e.g. Frommolt and Tauchert, 2014; Mellinger and Clark, 2000; Ulloa et al., 2016). There are annual and one-off machine learning competitions, specifically aimed at driving the development of these, and other, birdsong recogniser methods (e.g. Goëau et al., 2017; Stowell et al., 2016). Very high recall (Table 3.2) of >95% has been reported for such recognisers, but this performance is often reliant on high signal strength and low background noise (Bardeli et al., 2010). Furthermore, many are custom-built for specific species or research projects, and amongst those designed to detect and identify birds, few concentrate on song produced by oscine passerines in natural unattended field recordings (Priyadarshani et al., 2018; but see Acevedo et al., 2009; Campos-Cerqueira and Aide, 2016). A further limitation of this approach is that it often requires advanced mathematics and/or programming skills to develop the algorithms, and is largely inaccessible to ecologists (Aide et al., 2013; Sebastián-González et al., 2015). As such, the wider application of these recognisers in ecological research remains untested. However, many commercially- and freely-available sound analysis software packages, such as those described above, include recogniser tools requiring little or no prior knowledge of acoustic theory, mathematics or computer programming. These recognisers are intended for widespread use, however, and their performance for a given species is unlikely to match that of custom-made recognisers. The most popular of these recognisers amongst ecologists, and their respective performances, are outlined below.

Raven Pro

Raven Pro is a sound analysis software package developed by The Cornell Laboratory of Ornithology, and has been designed for the primary function of birdsong analysis (Charif, et al., 2010; Duan et al., 2013). The programme offers two syllable-level automated signal detection methods as recognisers. The first, the 'band limited energy detector', estimates the background noise in an acoustic survey, and uses the estimate to search for sections of the survey that exceed a user-defined signal-to-noise ratio (SNR) in a specific frequency range, and during a specified time (Charif, et al., 2010; Duan et al., 2013). The second method, the 'amplitude detector', detects regions of a signal where the measure of the waveform's envelope (the area in time-amplitude space occupied by the signal; Fig 3.1a) exceeds a threshold value (Charif, et al., 2010; Duan et al., 2013). A few studies have applied these recognisers to real world data. For instance, Sebastián-González et al. (2015) used the band limited energy detector to return candidate vocalisations (detections) of Hawai'i amakihi. The recogniser achieved 93% recall, but this was at a cost of 68% false positive rate (FPR; Table 3.2). Duan et al. (2013) achieved an average of 50% recall across five Australian birds using the band limited energy detector. Precision (Table 3.2), however, was low, at 25%.

Song Scope

Song Scope is a digital signal processing programme produced by Wildlife Acoustics, Inc. Unlike Raven Pro, which includes tools for the acquisition, visualisation and measurement of signals (Charif, et al., 2010), automated recognition of acoustic signals produced by birds and other taxa is the primary function of Song Scope. The recogniser functions by clustering multiple syllables in a signal, and models them into signal structures using HMMs (Duan et al., 2013). HMMs are reported to be very sensitive to noise, and consequently, Duan et al. (2013) achieved an overall precision of just 32% when tested on the vocalisations of five Australian bird species. Additionally, Buxton et al. (2013) trained Song Scope recognisers to identify several seabird species from acoustic surveys made in the Aleutian Islands, but manual verification of the detections was necessary, as the number of false positives (FP) was high. Cragg et al. (2015) examined the reliability of Song Scope in identifying marbled murrelet *Brachyramphus marmoratus* vocalisations, and although the number of FP detections averaged just 9% in acoustic surveys with low background noise, this rose to 99% in surveys with high noise interference from non-target species' vocalisations. Wildlife Acoustics recently ceased support for Song Scope software, although it remains free of charge and available to download from their website.

Kaleidoscope Pro

Kaleidoscope Pro is produced by Wildlife Acoustics, Inc., and recently replaced Song Scope as their flagship signal processing software package. Like Song Scope, Kaleidoscope Pro utilises HMMs to detect target signals. However, it employs cluster analysis methods to group repeated signals within an acoustic survey into several clusters based on their similarity. The final recogniser is produced following manual analysis of the clusters, when the user defines which of the clusters contain the target signal, and highlights non-target signals within these clusters. The algorithms then re-compute to produce the recogniser based upon user input during the manual analysis stage. To date, Kaleidoscope has rarely been formally tested on non-chiropterans. However, Abrahams and Denny (2018) applied the programme to detect the distinctive call of capercaillie *Tetrao urogallus* in the UK, and reported relatively low recall of 35%, but achieved a FPR of just 1.3%.

monitoR

The R software (R Core Team, 2018) package monitoR contains several tools to manage an acoustic monitoring programme, but the primary focus of the package is automated detection and identification of animal vocalisations (Hafner and Katz, 2018a). The recogniser uses the relatively simple process of template matching. The process involves user creation of a template(s), consisting of example signals known to be of the target species. The template is passed through a moving window of an acoustic survey, and repeatedly scored for similarity against detected signals. monitoR offers two template types, a cross-correlation template, which uses all regions of a spectrogram defined by the user, and a binary-point template, which is based upon a map of anticipated regions of signal within a spectrogram (Katz et al., 2016a). Katz et al. (2016b) reported 83% recall using the spectrogram cross-correlation recogniser to detect black-throated green warbler *Setophaga virens* song and 66% recall for ovenbird song.

For researchers to place trust in the results returned, the recognisers outlined above must maximise true positive (TP) detections and minimise FP detections, but, at present, they do not fulfil these requirements reliably. Indeed, manual verification of the detections returned by a recogniser is a necessary process (e.g. Buxton et al., 2013; Zwart et al., 2014), and complete manual scanning of acoustic surveys remains the best option for studies requiring detailed information on, for example, temporal patterns in call frequency (Sanders and Mennill, 2014; Swiston and Mennill, 2009). In order to improve recogniser performance, Knight et al. (2017) advocated utilisation of the scoring system applied by most commercial recognisers, whereby, the recogniser assigns a score to each detection, which can be interpreted as a measure of confidence that the detection matches the target vocalisation. Users can define the score threshold, so that any detections scoring below this will be ignored. Setting a high threshold will minimise FPs, but will also result in false negatives (FN). Setting the threshold low will have the opposite effects. Given such trade-offs, and the imperfection of recogniser performance, the score thresholds set are often based upon trial-and-error and will ultimately depend upon the question being addressed and the priorities of the research (Katz et al., 2016b, 2016a). Used appropriately, however, the scoring system provides a means of controlling the output returned by recognisers to optimise the chances of arriving at the correct conclusion.

Table 3.1 An error matrix used to evaluate the predictive accuracy of automated signal detection tools (recognisers). A signal detected by the recogniser is a predicted presence, and a signal ignored by the recogniser is a predicted absence. TP=true positive; FP=false positive; FN=false negative; TN=true negative.

		Actual	
		Presence	Absence
Predicted	Presence	TP	FP
	Absence	FN	TN

Table 3.2 Common metrics used to assess the performance of automated signal detection tools (recognisers). TP=true positive; FP=false positive; FN=false negative; TN=true negative.

Metric	Formula
Recall (True Positive Rate [TPR] or sensitivity)	$\frac{\text{TP}}{\text{TP} + \text{FN}}$
False Positive Rate (FPR)	$\frac{\text{FP}}{\text{FP} + \text{TN}}$
Specificity	$\frac{\text{TN}}{\text{FP} + \text{TN}}$
Precision	$\frac{\text{TP}}{\text{TP} + \text{FP}}$

3.5 Ecoacoustics and soundscape ecology

The last decade has witnessed the emergence of ecoacoustics. Unlike traditional bioacoustics, which can broadly be defined as animal communication (Fletcher, 2007; Lomolino et al., 2015), and from which, studies typically focus on a limited set of species, ecoacoustics covers all ecological organisation levels (Sueur and Farina, 2015). The discipline of ecoacoustics includes soundscape ecology, which concentrates on macro or community acoustics, and is concerned with the composition of all sounds at a given location and time (the soundscape), considering this to be a core component of ecological processes (Guyot et al., 2016; Pijanowski et al., 2011b, 2011a). Krause

(1987) introduced the terms ‘biophony’ and ‘geophony’ to represent two of the main categories of sound within a soundscape, which are sounds produced by living organisms and geological processes (including, e.g., wind, rain and running water) respectively. Pijanowski et al. (2011b) extended the classification to include ‘anthrophony’, which is sound produced by human activity, including that of road-traffic, music and machinery, and which is commonly perceived by the listener as ‘noise’ (Dumyahn and Pijanowski, 2011). Indeed, in their seminal reviews on the subject, Pijanowski et al. (2011a, 2011a) define soundscapes as “the collection of biological, geophysical, and anthropogenic sounds that emanate from a landscape, and which vary over space and time, reflecting important ecosystem processes and human activities”.

Technological advances aimed at assisting bioacoustic research, for example, improvements made to programmable recording devices, omni-directional microphones and digital storage, also apply to ecoacoustic approaches (Sueur and Farina, 2015). However, an innovation particular to ecoacoustics is the acoustic index (AI). AIs are powerful, yet simple, metrics that return a score, or statistic, describing the distribution of acoustic energy in a soundscape and its complexity in terms of time, frequency and intensity. To date, more than 60 AIs have been developed and trialled (Bradfer-Lawrence et al., 2019). In hand with AIs, recordings made of soundscapes can be used to study the environment in multiple ways, but the initial growth of the discipline was largely due to the efficacy of linking soundscape properties to biodiversity and ecosystem health (Burivalova et al., 2019; Dumyahn and Pijanowski, 2011; Pijanowski et al., 2011b, 2011a). For instance, by applying the power spectral density AI (PSD; Gage et al., 2001), Tucker et al. (2014) showed that the soundscape reflected differences in ecological condition as a consequence of fragmentation in forest remnants in Queensland, Australia, and Fuller et al. (2015) demonstrated that the acoustic entropy index (Sueur et al., 2008), acoustic evenness index (AEI; Villanueva-Rivera et al., 2011) and normalised difference soundscape index (NDSI; Kasten et al., 2012) were associated with landscape characteristics, ecological condition and bird species richness respectively. Furthermore, although not the initial reasoning behind their formulation, AIs can offer an efficient alternative to recognisers when analysing large acoustic datasets.

The assumption underpinning the use of AIs, is that animal communities with more audible species will have greater acoustic diversity, and that acoustic diversity, in turn, correlates positively with biodiversity (Fuller et al., 2015; Gage et al., 2001; Guyot et al., 2016). However, some AIs are better suited to measuring community activity. In this respect, the acoustic complexity index (ACI; Pieretti et al., 2011) was developed based upon the observation that many biotic sounds, especially birdsong, are characterised by fluctuations in intensity, whilst geophonies and, in particular, anthrophonies, are of constant intensity (Farina et al., 2011b; Pieretti et al., 2011). Whilst filtering out human-generated background noise, the ACI has been found to correlate more closely with the number of bird vocalisations, or singing activity (Pieretti et al., 2011), than with the diversity of species in a community (Fuller et al., 2015; but see Towsey et al., 2014), and is particularly useful for emphasising change in the behaviour and composition of bird communities (Farina et al., 2011b; Pieretti et al., 2011). Indeed, the index has been successfully employed to define the arrival date of migrating songbirds onto spring breeding grounds in North America (Buxton et al., 2016), and as such, provides a useful method of monitoring climate-driven phenological shifts in songbird communities (Buxton et al., 2016). The ACI was also applied by Farina et al. (2015) to measure fine-scale temporal variation in intensity and complexity of song during the dawn chorus within several bird communities in north-western Italy. The authors demonstrated that the index is capable of defining characteristic lulls in the chorus that are hypothesised to exist around sunrise (cf. Hutchinson, 2002). Thus, based on the assumption that vocalisations provide a valid proxy for diversity within a community, ecoacoustic approaches offer a new perspective for investigating the dawn chorus, and provide an efficient bird diversity monitoring method (Guyot et al., 2016).

3.6 Synthesis

Advances made in digital audio recording equipment and data storage have opened up new and exciting possibilities for data collection in biodiversity monitoring programmes. However, for detailed acoustic studies of species, beyond presence/absence and habitat occupancy, reliable recognisers are required. These must be capable of discrimination between species' vocalisations in recordings made within realistic and noisy environments – more so than currently available software packages, such as those described in section 3.4, but whilst retaining their accessibility and easeof-use. Until recognisers possess discrimination abilities similar to human observers, they are unlikely to replace potentially costly deployment of humans in ecological studies requiring detailed information on, for example, species' densities or behaviours. AIs are encouraging for studies requiring rapid biodiversity assessment, and for gaining broad information on sound-producing animal communities, but these should be a stop-gap method for analysing large acoustic datasets. In the long-term, work should continue on developing tools that accurately obtain species-specific information from large acoustic datasets.

Chapter 4

Study sites

Goldcrest *Regulus regulus*

4.1 Location, climate, vegetation and light and noise pollution

The study sites used in chapters 5 to 7 consisted of 20 × deciduous or mixed-deciduous woodland reserves, selected to provide a geographical and climatological spread of undisturbed semi-natural wooded habitat throughout Great Britain. Site locations are shown in Fig. 4.1. One Song Meter 2+ autonomous recording unit (ARU; Wildlife Acoustics Inc, Maynard, USA) was deployed at each site to record the daily dawn chorus in multiple years (see Fig. 4.1). Environmental data loggers were deployed alongside ARUs. Two data logger models were used: Tinytag Plus 2 TGP-4500 data loggers (Gemini Data Loggers, Chichester, UK), set to log air temperature and humidity, and HOBO Pendant UA-002-64 data loggers (Onset Computer Corporation, Bourne, USA), set to log air temperature and light intensity. One data logger was placed at each site in the years 2016 and 2017 (see Fig. 4.1).

Details on the climate and vegetation characteristics of each site are provided in Table 4.1. Climate data were sourced from the Centre for Environmental Data Analysis (CEDA; https://catalogue.ceda.ac.uk/) using the dataset HadUK-Grid Gridded Climate Observations on a 1 km grid over the UK (Met Office, 2018), and the mean annual temperature and mean annual rainfall between the 10 years 2008-2017 was calculated for each site, using data for the 1 km cell in which the site was located. Vegetation data and estimated percentage canopy and understory cover were collected on one occasion at each site in spring/summer 2017, and reflect the structure and dominant species composition at that time. Vegetation data were not collected at Highnam Wood, as the site was not used in 2017.

Although predominantly located within rural landscapes, the study sites were subject to varying levels of artificial light and noise pollution. Fig. 4.2 shows the landscape (within 2.5 km) surrounding each study site, and the proximity of roads and urban (residential or industrial) areas. Durham University and Fairburn Ings, in particular, were close to urbanised areas, and only Abernethy and Minsmere did not have an A- or B-road pass within 2.5 km of the ARU (Fig. 4.2).

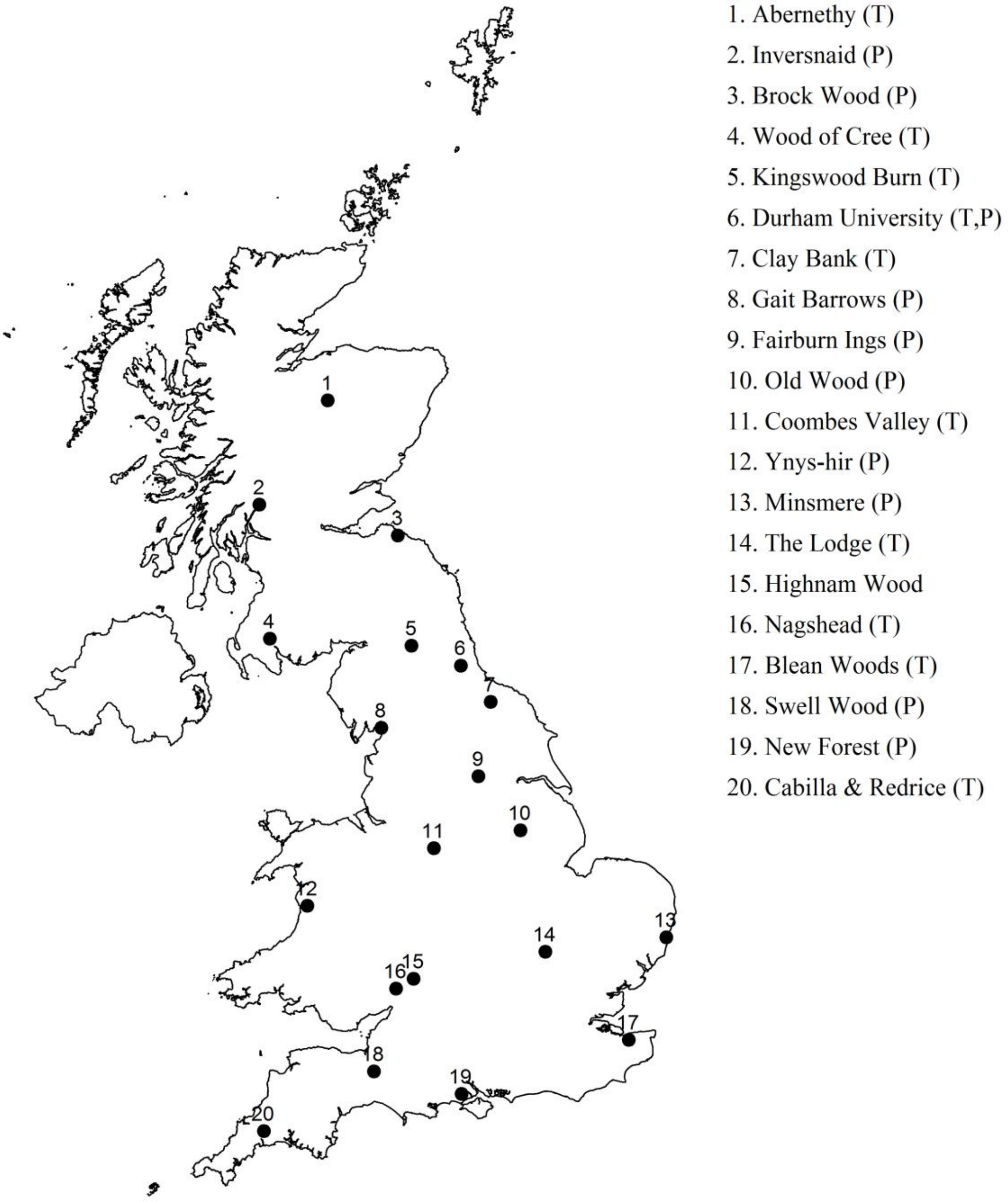


Figure 4.1 Locations and names of study sites. One autonomous recording unit (ARU) was installed at each site in multiple years (15=2014/15; 16=2015-17; 3,10,19,20=2016/17; all other sites=2014-2017). In 2016 and 2017, Tinytag Plus 2 TGP-4500 data loggers (Gemini Data Loggers, Chichester, UK) were deployed at sites where names include suffix (T), and HOBO Pendant UA-002-64 data loggers (Onset Computer Corporation, Bourne, USA) were deployed at those with suffix (P). All sites consisted of semi-natural deciduous or mixed deciduous woodland habitat.

Table 4.1 Climate, vegetation structure and dominant species of study sites. Sites listed in order of decreasing latitude.

Site name	Avg ann temp (°C)	Avg ann rain (mm)	Canopy (>5 m)		Understory (1-5 m)		Herbaceous	
			Cover (%)	Species	Cover (%)	Species	Cover (%)	Species
Abernethy	6.86	997	50	*Betula pendula*	10	*Ulex europaeus*	95	*Pteridium*, Poaceae, *Vaccinium myrtillus*, *Erica cinerea*, *Juncus* sp.
Inversnaid	9.17	3007	75	*Quercus petraea*, *B. pendula*	0	NA	85	*Pteridium*, Poaceae, *Juncus* sp.
Brock Wood	8.93	831	80	*Acer pseudoplatanus*, *Fraxinus excelsior*, *Q. robur*, *B. pendula*, *Pinus* sp.	25	*Hedera* sp., *Crataegus monogyna*, *Sambucus nigra*, *Taxas baccata*, *Abies* sp.	50	*Dryopteris* sp., *Mercuralis perennis*
Wood of Cree	9.17	1655	75	*Q. petraea*, *B. pubescens*	25	*Coryllus avellana*, *Sorbus aucuparia*	30	*Pteridium*, *Rubus fruticosus*, *Oxalis acetosella*, mosses
Kingswood Burn	8.58	957	65	*Quercus* sp., *B. pendula*, *S. aucuparia*	10	*B. pendula*, *S. aucuparia*	35	Poaceae
Durham University	9.43	742	80	*A. pseudoplatanus*, *Q. robur*, *Fagus sylvatica*	35	*Ilex aquifolium*, *S. aucuparia*	10	*Pteridium*, *Dryopteris* sp.
Clay Bank	8.71	999	50	*B. pendula*, *Alnus glutinosa*, *Abies* sp., *Salix* sp.	0	NA	80	*Pteridium*, Poaceae
Gait Barrows	9.71	1241	70	*B. pendula*	50	*C. avellana*, *I. aquifolium*	15	Mosses
Fairburn Ings	10.4	617	70	*B. pendula*, *Q. robur*, *Pinus nigra*	50	*R. fruticosus*, *C. mono*	50	Poaceae, *Impatiens glanulifera*,
Old Wood	9.99	638	70	*F. excelsior*, *Pinus* sp., *Abies* sp.	60	*C. avellana*, *C. monogyna*, *Acer campestre*, *S. nigra*, *A. pseudoplatanus*, *Lonicera* sp., *Cornus*	20	*M. perennis*, ferns
Coombes Valley	8.92	1013	75	*Q. petraea*, *Abies* sp., *Pinus* sp.	15	*I. aquifolium*	15	*Pteridium*
Ynys-hir	10.6	1408	65	*Q. petraea*	15	*A. pseudoplatanus*, *Lonicera* sp., *I. aquifolium*, *Rhododendron ponticum*, *S. aucuparia*, *C. avellana*	90	*R. fruticosus*, *Pteridium*
Minsmere	10.7	620	75	*Q. robur*, *F. sylvatica*, *C. sativa*, *B. pendula*, *A. pseudoplatanus*, *P. nigra*	0	NA	50	*Pteridium*
The Lodge	10.6	619	75	*B. pendula*, *Q. robur*, *C. sativa*, *Pinus* sp.	10	*B. pendula*	30	*Pteridium*
Highnam Wood	10.5	776	NR	*Q. robur*	NR	NR	NR	NR
Nagshead	10.1	1017	80	*Quercus* spp., *C. sativa*, *S. aucuparia*	10	*I. aquifolium*, *S. aucuparia*, *P. pendula*	50	*Pteridium*, Poaceae, mosses, ferns
Blean Woods	10.8	709	80	*Q. robur*, *F. sylvatica*, *C. sativa*	50	*F. sylvatica*, *C. sativa*, *I. aquifolium*	0	NR
Swell Wood	10.9	698	80	*Q. robur*, *A. campestre*	30	*C. avellana*, *C. monogyna*	90	*Hedera* sp., *M. perennis*, Poaceae
New Forest	10.9	878	60	*B. pendula*, *Q, robur*, *F. sylvatica*, *Populus* sp.	40	*I. aquifolium*, *C. monogyna*	65	*Pteridium*, Poaceae
Cabilla & Redrice Woods	10.8	1434	80	*Quercus* sp.	40	*I. aquifolium*, *C. avellana*	40	*Hyacinthoides non-scripta*, ferns, *Pteridium*

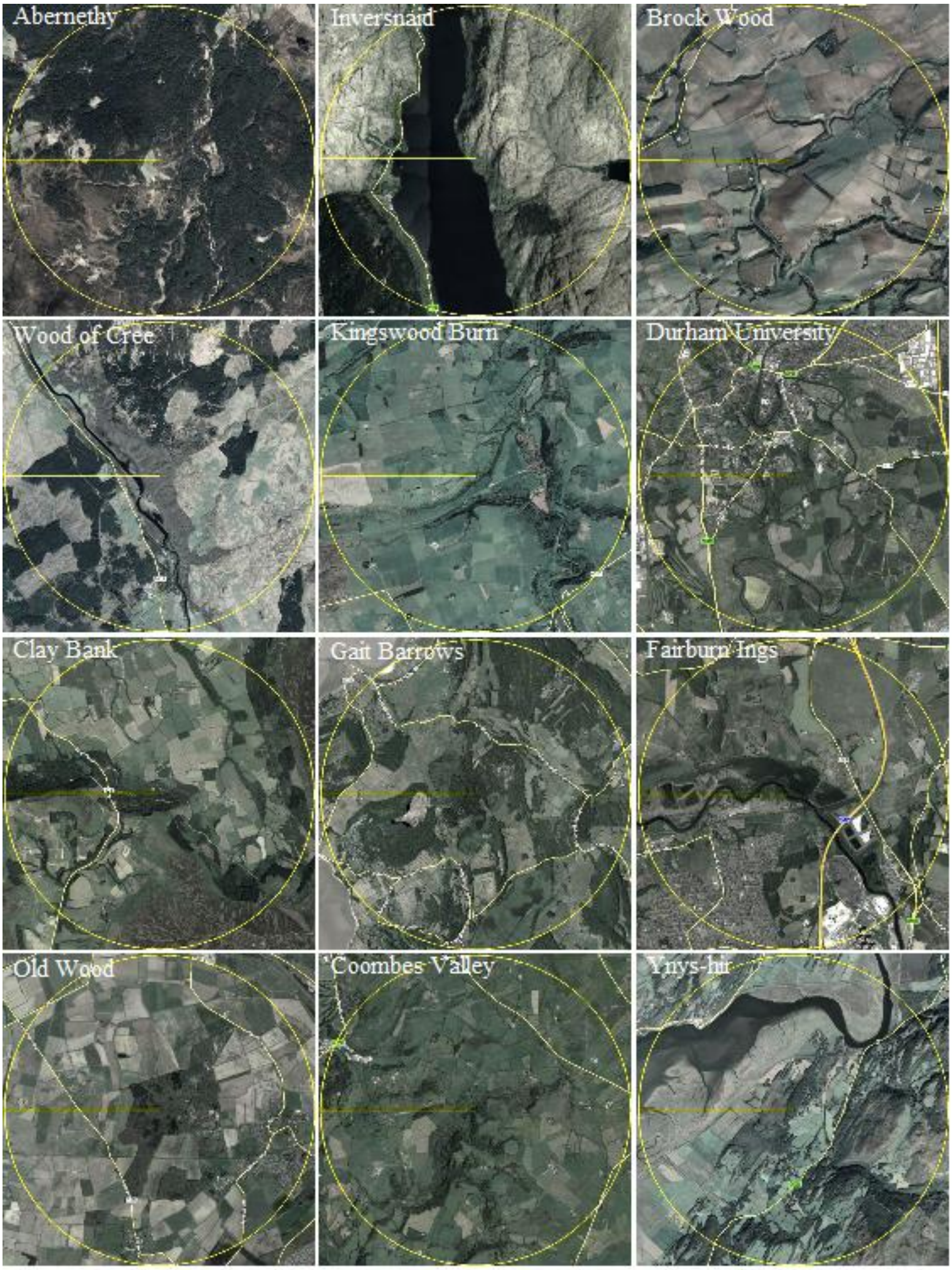

Abernethy
Inversnaid
Brock Wood
Wood of Cree
Kingswood Burn
Durham University
Clay Bank
Gait Barrows
Fairburn Ings
Old Wood
Coombes Valley
Ynys-hir

Figure 4.2 Satellite images of the 20 × study sites and their surrounding landscape. Yellow circles have 2.5 km radii extending from the co-ordinates of autonomous recording units and data loggers deployed within the sites. Pale yellow lines show A- or B-roads. Imagery taken from Google Earth Pro.

Chapter 5

Automated identification and classification of birdsong: an ensemble approach

Northern wren *Troglodytes troglodytes*

5.1 Abstract

The avian dawn chorus presents a challenging opportunity to test autonomous recording units (ARUs) and associated recogniser software in the types of complex acoustic environments frequently encountered in the natural world. To date, extracting information from acoustic surveys using readily-available signal recognition tools (‘recognisers’) for use in biodiversity surveys has met with limited success. Combining signal detection methods used by different recognisers could improve performance, but this approach remains untested. Here, I evaluate the ability of four commonly used and commercially- or freely-available individual recognisers to detect species, focusing on five woodland birds with widely-differing song-types. Using binomial generalised linear models (GLMs), I combined the scores (which reflect the perceived likelihood of a vocalisation originating from a target species) assigned to detections made by the four recognisers to devise an ensemble approach to detecting and classifying birdsong during the dawn chorus. I assess the relative performance of individual recognisers and that of the ensemble models. The ensemble models out-performed all of the individual recognisers across all five song-types. The ensemble also minimised false positive error rates for all species tested – an achievement unmatched by any recognisers in isolation. My results highlight variation in the performance of recognisers commonly used in ecology, when tested on bird species of differing song-type. Moreover, during acoustically complex dawn choruses, with many species singing in parallel, my ensemble approach resulted in detection of 74% of singing events, on average, across the five song-types, compared to 59% when averaged across the recognisers in isolation; a marked improvement. I suggest that this ensemble approach, used with suitably trained individual recognisers, has the potential to finally open up the use of ARUs as a means of automatically detecting the occurrence of target species and identifying patterns in singing activity over time in challenging acoustic environments.

5.2 Introduction

Autonomous recording units (ARUs) are increasingly used to gather ecological data for a diverse array of sound-producing animal taxa. Used appropriately, ARUs provide an efficient, standardised and unbiased data-collection procedure at lower cost than traditional site visits by skilled observers (e.g. Zwart et al., 2014). They can be deployed in situ for extended periods, recording multiple species at multiple sites simultaneously, accumulating data on spatio-temporal scales of ecological consequence, whilst limiting disturbance and reducing potentially costly visits to distant and hard-to-access locations (Blumstein et al., 2011). However, in common with other automated data collection methods in ecology (e.g. camera-traps, Norouzzadeh et al., 2018), the rate-limiting step in biodiversity studies using such data, is that of extracting information from the considerable datasets amassed. This can involve manually browsing many hours of sound recordings on spectrograms, which is a laborious task (Sebastián-González et al., 2015), potentially requiring costly teams of sound analysts (e.g. Furnas and Callas, 2015; Sanders and Mennill, 2014). Automated computer-aided signal recognition systems provide a potential solution to the problem, and reliable systems will be crucial to the viability of long-term, large-scale ecological studies using ARUs (Blumstein et al., 2011). However, despite progress in recent years, the performance of general-use signal recognition systems has failed to keep pace with advances in acoustic data collection and storage (Wimmer et al., 2013).

The process of automatically detecting and classifying birds from sound recordings potentially presents a greater challenge than for other taxa (chapter 3, section 3.4). Birdsong, in particular, is extremely varied and complex, and when multiple species and individuals sing simultaneously, such as during the dawn chorus, elements of song overlap in time, frequency and amplitude (Luther and Wiley, 2009; Priyadarshani et al., 2018). Consequently, sound recordings made during the dawn chorus often prove overwhelming for signal recognition systems, which then fail to interpret the species-specific vocalisations accurately. Indeed, many studies of automated detection systems identify target species recognition during the dawn chorus as a particularly challenging research problem (e.g. Duan et al., 2013). Yet, best practice for traditional bird surveys (e.g. point counts and transects) in many parts of the world is to survey at or around dawn during the main breeding period, to maximise the number of species detected per unit time (chapter 1, section 1.1). This also applies to surveys using ARUs, especially in long-term studies where battery life and data storage may be a limitation (Burivalova et al., 2019).

Despite the difficulties, numerous methods have been developed for automated detection and classification of birdsong (reviewed by Blumstein et al., 2011; Priyadarshani et al., 2018; Stowell and Plumbley, 2011; chapter 3, section 3.4, this thesis), drawing upon research expertise in the fields of mathematics, computer engineering, bioinformatics, acoustics and audio signal processing. As a result, several sound analysis software packages have been developed that include automated signal recognition tools (hereafter 'recognisers') aimed at facilitating the use of ARUs by ecologists with only a limited understanding of the complexities of analysing acoustic data (e.g. Charif, et al., 2010; Hafner and Katz, 2018a; chapter 3, section 3.4, this thesis). To date, recognisers appear under-utilised in the ecological literature, and studies that have used them effectively typically document habitat occupancy and rudimentary activity levels at limited spatio-temporal scales. Many of these studies also focus on detection of distinctive, diagnostic or uncomplicated vocalisations at times of day when masking from background noise is low (e.g. Abrahams and Denny, 2018; Knight et al., 2017; Swiston and Mennill, 2009; Zwart et al., 2014). Researchers attempting more ambitious usage, such as detecting and recognising passerine songs at numerous and varied locations, have been unable to create recognisers that are fit for purpose (e.g. Sidie-Slettedahl et al., 2015). Manual scanning of spectrograms remains the best option if an accurate account of singing activity, or detection of multiple species, is required (Joshi et al., 2017; Knight et al., 2017; Sanders and Mennill, 2014; Shonfield and Bayne, 2017; Swiston and Mennill, 2009). Although recognisers are designed to facilitate signal recognition by reducing the time required to analyse large datasets, they do not fully automate the process (Charif, et al., 2010; Shonfield and Bayne, 2017). The procedure therefore, invariably involves manual verification of the detections returned, which, in itself, can be a prohibitive task.

For researchers to have confidence in the output returned, recognisers must maximise the ratio of true-positive (TP) detections over false-positive (FP) errors; to assume (likely) absence, they must eliminate FP errors entirely. To assist in this, many recognisers assign a score value to each detection, which can be taken as a confidence measure of how well the detection matches the target signal (chapter 3, section 3.4). In theory, higher scoring detections are more likely to originate from the target species.

Despite their limitations, the various methods of signal detection amongst different recognisers may each have particular strengths when applied to certain situations and song-types, such that a combination of methods would produce a more robust and universal recogniser tool. Indeed, in both ecological studies and more widely, it is acknowledged that if individual predictive techniques provide some independent information, a combination of techniques will yield lower mean error than any one in isolation (Araújo and New, 2007). Here, I combine the performance of recognisers from four sound analysis software packages by using the scores assigned to detections to construct an ensemble model. The performance of my ensemble is compared to that of each of the recognisers in isolation in its ability to detect and classify birdsong correctly within noisy recordings made during the dawn chorus. I repeat this for five common British woodland bird species, which, together, exhibit a wide variation in song structure. My goal is to evaluate which approaches to automated identification perform best and to test whether combining different recognisers can enhance performance across multiple species. I evaluate methods in terms of increasing TPs and decreasing, or negating, FPs, with the aim of producing a generic approach that could be more widely applied.

5.3 Materials and Methods

5.3.1 Study Species

Stowell and Plumbley (2011) recognise five broad song-types amongst British birds. To ensure that I tested recognisers over a varied range of songs, I used an example species with song comparable to each of these five song-type groups as follows: 1) common chiffchaff (hereafter ‘chiffchaff’) *Phylloscopus collybita* (bi-syllabic), 2) northern wren (hereafter ‘wren’) *Troglodytes troglodytes* (few syllables, with a strong bigram structure), 3) European robin (hereafter ‘robin’) *Erithacus rubecula* (large vocabulary), 4) carrion crow *Corvus corone* (less-tonal), and 5) common woodpigeon (hereafter ‘woodpigeon’) *Columba palumbus* (low-pitched non-passerine).

5.3.2 Data collection

I collected acoustic data using ARUs (Song Meter 2+; Wildlife Acoustics Inc, Maynard, USA) mounted on tree trunks c.4 m from ground-level at each of 20 semi-natural mixed deciduous woodland study sites throughout Great Britain (Fig. 4.1). Each ARU was fitted with two omni-directional all-weather microphones (SMX-II; Wildlife Acoustics Inc, Maynard, USA) with a typical sensitivity of -35 to -43 dBV/pa and a frequency response of 20 Hz–20,000 Hz (Sebastián-González et al., 2015; Turgeon et al., 2017). Recordings were made in stereo, with a sample rate of 16000 Hz and 16-bit encoding. No high-pass or bandwidth filters were applied. ARUs were configured with the respective site co-ordinates and programmed to survey continuously for 135 min, commencing 90 min prior to local sunrise every day from January to August inclusive. These surveys were repeated for each of the four years 2014 to 2017. With the exception of chiffchaff, which was absent from five sites, the study species were ubiquitous throughout my study sites.

5.3.3 Test dataset

I extracted 300 samples from my dataset of acoustic surveys of the dawn chorus, considering only those made during the breeding season (March to June), using stratified random sampling, ensuring that samples were evenly distributed amongst all 20 study sites (15 per site), and across the three years 2014 to 2016 (data collection was not complete for 2017 at this time). Samples including persistent heavy rain and strong winds were excluded from the test dataset and substituted with a new, randomly-generated sample. I removed the first 30 min from each sample, as there was expected to be little or no singing activity by the study species in this early portion of the acoustic surveys. A randomly selected 300 s block of time was then extracted from each of the 300 samples. The final test dataset comprised 1500 min (300 × 300 s) of acoustic survey.

5.3.4 Manual song detection

I manually analysed the test dataset, and listened to each 300 s sample whilst simultaneously viewing its spectrogram, and recorded all the singing events by each study species in turn (definitions of singing events are provided in Appendix A.1). Behavioural Observation Research Interactive Software (BORIS; Friard and Gamba,

2016) was used to record the timing of singing events. I used the ‘live’ setting on this program whilst simultaneously viewing spectrograms on Raven Pro v1.4 sound analysis software (The Cornell laboratory of Ornithology, Ithaca, USA). If a song could not be reliably assigned to a study species (too faint/quiet, too blurred, masked by other calls, or otherwise undecipherable) it was excluded from the analysis, as were vocalisations other than song (e.g. contact and flight calls).

5.3.5 Automated song detection

Training dataset

I created individual recognisers for each study species from each of four sound analysis software packages, using singing events taken from a standardised training dataset. The full training dataset consisted of one manually-selected 105 min acoustic survey (i.e. a 135 min survey less the first 30 min) of the dawn chorus from each of my 20 study sites, or, in the case of chiffchaff, from each study site that the species was present. This ensured that the song of each study species was represented with examples of varying structure and quality; thus, creating recognisers designed for general use across multiple study sites. Acoustic surveys included within the test dataset (section 5.3.3) were exempt from selection for the training dataset. Here, I provide the necessary information on the detection method used (where applicable) and ‘score’ settings chosen from each of four sound analysis software packages and associated recogniser tools. More detail on each recogniser is provided in chapter 3 (section 3.4). A detailed methodology for recogniser construction is provided in Appendix A.2.

monitoR

I used the cross-correlation template-matching for my analyses, as this method performed better than the binary-point method in preliminary tests with my dataset. Monitor provides a score based upon Pearson’s correlation coefficient (Pearson’s R), representing a detected signal’s similarity to the template. I built recognisers following instructions in the demonstration vignette (Hafner and Katz, 2018b) and the suggested workflow in Katz et al. (2016a).

Raven Pro

I used the band-limited energy detector for my analyses, as preliminary tests showed that this performed better than the amplitude detector with my dataset. Raven assigns an 'Occupancy' measurement to detections, which represents the percentage of samples within a selection that must exceed the background noise signal-to-noise ratio (SNR) threshold in order for the signal to be considered a positive detection. I used this measurement as a score. Raven offers a large repertoire of additional measurements applicable to detections; I selected the 'Average Power (dB)' measurement, as I surmised that this value could also predict the probability that detections are correct. I built recognisers following instructions available within the Raven v1.4 User's Manual (Charif, et al., 2010).

Song Scope

Song Scope assigns both a 'Score' and 'Quality' value to detections. Score represents the statistical fit of the detection to the recogniser's model, and Quality indicates a signal quality confidence. Detections must reach both a user-defined minimum Score and minimum Quality to count. Song Scope also returns a 'Level (dB)' value, which is the peak signal level of the vocalisation in detections. I built recognisers following instructions available within the Song Scope v4.0 documentation (Wildlife Acoustics, Inc., 2011), whilst also consulting Agranat (2009) for additional advice on settings.

Kaleidoscope Pro

Kaleidoscope assigns a score to detections, based upon their distance from the centre of the cluster. In this case, lower scores indicate better matches to the training data. I constructed recognisers using the cluster analysis function, following a tutorial video available from the software developer (Wildlife Acoustics, Inc., 2018a) and instructions within the Kaleidoscope v5 documentation (Wildlife Acoustics, Inc., 2018b).

5.3.6 Ensemble model

I used the scores assigned to the detections made by the four recognisers, plus additional measurements provided by Raven (Power) and Song Scope (Quality and Level), to construct an ensemble model for each study species. I used generalised linear models (GLMs) with binomial errors, implemented using the glm function in the *stats* package in R (v3.5.2; R Core Team, 2018), to predict whether the study species was singing or not within each acoustic survey segment of 1 s duration (hereafter ‘segment’), with the recogniser scores and additional measurements, and their interaction terms, as explanatory variables. I used the R package *MuMIn* (v1.42.1; Barton, 2018) to rank candidate models by Akaike information criterion (AIC), and selected the highest ranking model. This process was repeated using cloglog, logit and probit links; the link that produced the highest ranking model with the lowest AIC was retained (Burnham and Anderson, 2002). To assess the performance of individual recognisers in isolation, binomial GLMs were used to model the probability of obtaining positive detections but only including the recogniser scores from an individual recogniser in three cases (monitoR, Raven and Kaleidoscope), or, for Song Scope, with both Score and Quality as covariates. Again, all GLMs were repeated using cloglog, logit and probit links, and the links that produced the models with the lowest AIC were chosen. Further details on the modelling process, and model specifications, are provided in Appendix A.3.

5.3.7 Recogniser performance analysis

To assess the respective performances of each recogniser and the ensemble, I used area under the receiver operating characteristic curve (AUC-ROC). An ROC curve essentially describes the compromise between sensitivity and false positive rate (FPR; Table 3.2). If the area under the curve (AUC) is equal to 1, the classifier achieves perfect accuracy. AUC-ROC was calculated for each species using the R package *ROCR* (v1.0-7; Sing et al., 2005), and curves were drawn using the *PRROC* package (v1.3.1; Grau et al., 2015). I then calculated *i*) the minimum distance between the ROC curves and x=0, y=1 (roc01), i.e., the point in the ROC curve that is closest to the top-left corner of the plot; lower distances are optimal, as they represent greater sensitivity relative to the corresponding false positive rate (see Metz, 1978), and *ii*) the minimum modelled probability of obtaining a positive detection at which the false positive rate (FPR) remained at zero (i.e. the probability threshold that negated FP errors but which returned TP detections), for each recogniser and the ensemble, using the R package *cutpointr* (v0.7.4; Thiele, 2018). Further detail on this process is provided in Appendix A.4.

I tested for statistical difference amongst the recognisers and the ensemble in *i*) AUC-ROC, and *ii*) roc01 using linear mixed-effects models (LMMs) implemented in the R package *lme4* (v1.1.20; Bates et al., 2015) with model fit by maximum likelihood. AUC-ROC and roc01 performance varied amongst the study species; hence, species was included as a random intercept term in both models. I performed Tukey post-hoc pairwise tests of recognisers using the R package *emmeans* (v1.3.1; Length et al., 2019). I confirmed that normality and homoscedasticity assumptions were met by plotting the model residuals as Q-Q plots and against fitted values respectively.

To test the ensemble's ability to recognise broad-scale patterns in singing activity over time, I applied the ensemble models to the 60 × 300 s acoustic surveys selected to be the model test data (Appendix A.3), omitting samples from which the study species was absent (chiffchaff was excluded from this analysis due to the low number of datapoints following these omissions), and including all 300 segments of those that remained. I used the roc01 probabilities (as defined above) as cutpoints, and correlated the number of segments within each sample survey identified as positive detections by the ensemble against the corresponding numbers identified by manual analysis. Pearson's r was calculated as a measure of similarity. To demonstrate the ensemble's potential to recognise fine-scale patterns in singing activity, I manually selected a sample survey for each species, and aggregated the segments into 30 × 10 s blocks. I then correlated the number of segments within each 10 s block identified as positive detections by the ensemble with the corresponding numbers identified by manual analysis, and calculated Pearson's r.

5.4 Results

The ensemble model produced higher AUC-ROC values than all four component recognisers in isolation for all study species (Fig. 5.2; Table 5.1). The ensemble also attained lower roc01 values than all component recognisers in isolation for all study species, with the exception of chiffchaff, where Song Scope attained a lower roc01 value (Fig. 5.2; Table 5.1). No one recogniser in isolation performed consistently better, in terms of AUC-ROC or roc01, than any other across all study species (Fig. 5.2; Table 5.1). The sensitivity (i.e. the proportion of study species' 1 s singing events correctly identified as such) of the ensemble model at the optimal (lowest) roc01 cutpoint value for each study species averaged 74% amongst the species (chiffchaff=70%, wren=74%, robin=63%, carrion crow=81% and woodpigeon=82%; Fig. 4.2), whilst sensitivity averaged across all component recognisers and study species at their respective optimal roc01 cutpoint values was 59% (chiffchaff=50%, wren=70%, robin=53%, carrion crow=62% and woodpigeon=58%). These sensitivity values, however, were achieved at a cost of varying FPRs (Appendix A.4, Table A.6). The ensemble returned a minimum probability of obtaining a positive detection, whilst suppressing FPR to zero, for all study species. At this probability, FP errors were negated whilst TP detections remained. No recogniser in isolation achieved this for all study species, and Raven did not achieve this for any (Appendix A.4, Table A.7).

Table 5.1 The area under the receiver operating characteristic curve (AUC-ROC) and the minimum distance from the ROC curve and the point x=0, y=1 (roc01) for an ensemble model and the four component recognisers when detecting and classifying the song of five bird species within acoustic surveys made during the dawn chorus. Lower roc01 values are optimal as they represent greater sensitivity (the proportion of species' 1 s singing events correctly identified as such) relative to the corresponding false positive rate (the proportion of species' 1 s non-singing events incorrectly identified as 1 s singing events). The ensemble attained the lowest roc01 values for all species, with the exception of chiffchaff, where Song Scope roc01 was lowest.

Species	Ensemble		monitoR		Raven		Song Scope		Kaleidoscope	
	AUC-ROC	roc01	AUC-ROC	roc01	AUC-ROC	roc01	AUC-ROC	roc01	AUC-ROC	roc01
Chiffchaff	0.658	0.528	0.606	0.616	0.502	0.689	0.640	0.496	0.548	0.829
Wren	0.756	0.412	0.661	0.472	0.696	0.442	0.647	0.479	0.641	0.523
Robin	0.699	0.476	0.604	0.633	0.591	0.588	0.570	0.608	0.653	0.525
Carrion crow	0.836	0.268	0.669	0.512	0.782	0.337	0.738	0.393	0.739	0.433
Woodpigeon	0.832	0.291	0.779	0.334	0.676	0.437	0.753	0.385	0.626	0.733

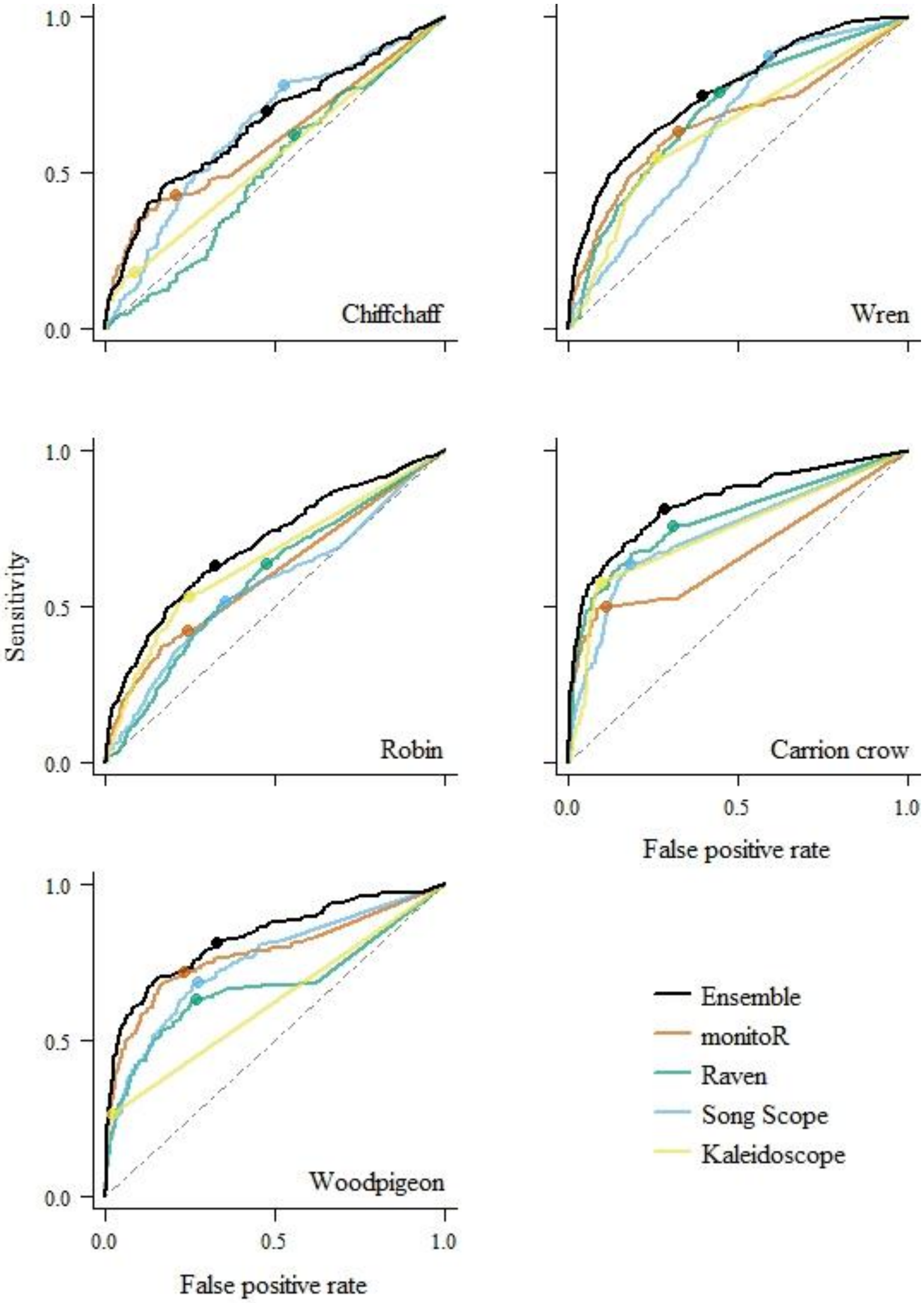


Figure 5.2 The performance of an ensemble model and the four component recognisers when detecting and classifying the song of five bird species within acoustic surveys made during the dawn chorus. Filled circles show the minimum distance between the curves and the point x=0, y=1 (roc01). Dashed lines show random performance.

AUC-ROC was significantly different amongst the recognisers and the ensemble ($\chi^2(4)=57.63$, $p<0.001$). Tukey post-hoc tests showed that the ensemble attained significantly higher AUC-ROC than did all recognisers in isolation (monitoR, $p=0.020$; Raven, $p<0.001$; Song Scope, $p<0.001$; Kaleidoscope, $p<0.001$). Additionally, both monitoR ($p<0.001$) and Raven ($p=0.030$) attained significantly greater AUC-ROC than Kaleidoscope (Fig. 5.3a). Likewise, the roc01 statistic was significantly different amongst the recognisers and the ensemble ($\chi^2(4)=112.63$, $p<0.001$). Tukey post-hoc tests again showed that the performance of the ensemble was significantly better, with roc01 less than that of all other recognisers in isolation (monitoR, $p<0.001$; Raven, $p=0.036$; Song Scope, $p<0.001$; Kaleidoscope, $p<0.001$). Additionally, the roc01 of monitoR ($p<0.001$), Raven ($p<0.001$) and Song Scope ($p<0.001$) were all significantly lower than that of Kaleidoscope (Fig. 5.3b).

The number of segments within sample surveys identified by the ensemble as positive singing events correlated positively with the numbers identified by manual analysis for all species tested (Fig. 5.4). Pearson’s r was moderate for three study species, and strong for carrion crow (Fig. 5.4). Likewise, the number of segments within 10 s blocks of chosen sample surveys identified by the ensemble as positive singing events, correlated positively with the numbers identified by manual analysis for all study species. Pearson’s r ranged from weak (chiffchaff) to very strong (robin; Fig. 5.5)

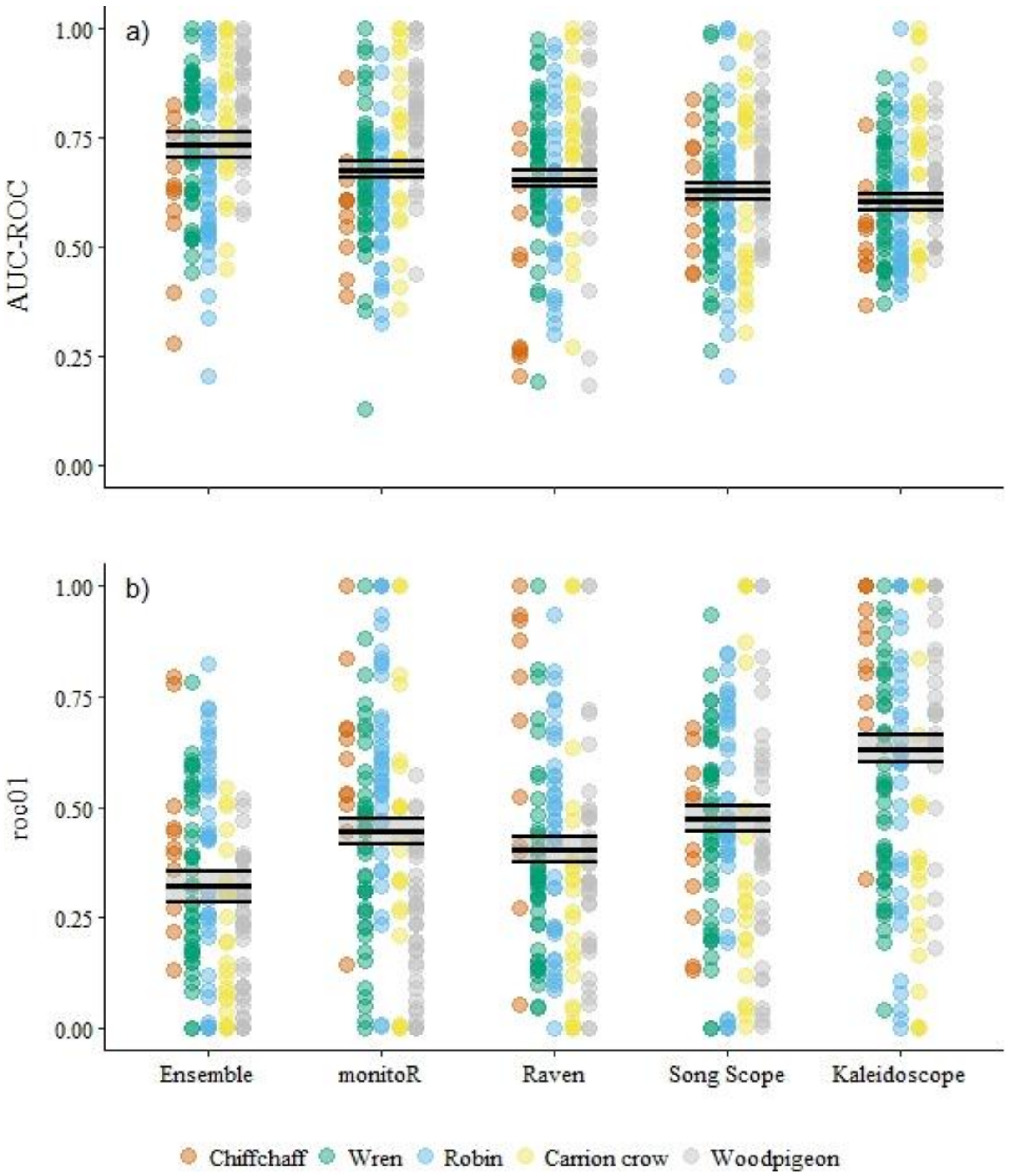


Figure 5.3 Results of linear mixed-effects models (LMMs) testing for difference in a) the area under the reciever operating characteristic curve (AUC-ROC), and b) the minimum distance between the ROC curve and x=0, y=1 (roc01) of an ensemble model and the four component recognisers when detecting and classifying the song of five bird species within acoustic surveys made during the dawn chorus. Lower roc01 values are optimal as they represent greater sensitivity relative to the corresponding false positive rate. Thick horizontal bars represent mean values, and thin bars represent ±1SE, having accounted for the random intercept effect of species. Data points of species are plotted; n=155 for each recogniser.

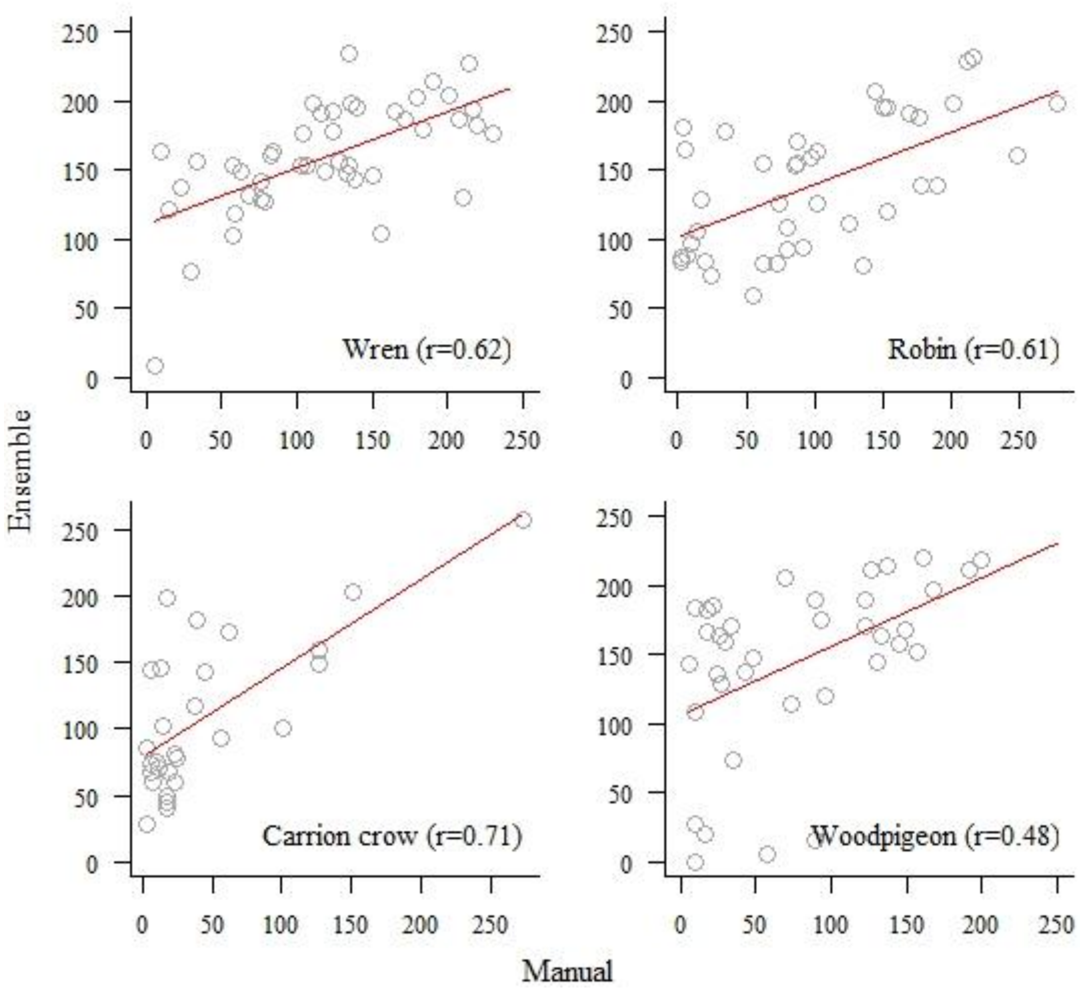


Figure 5.4 The number of 1 s segments within each of n × 300 s acoustic surveys of the dawn chorus identified as positive singing events by manual analyses versus the number predicted by automated analyses using an ensemble recogniser model, and the Pearson’s correlation coefficient, for four bird species with differing song-types. Wren, n=45; robin, n=40; carrion crow, n=28; woodpigeon, n=37.

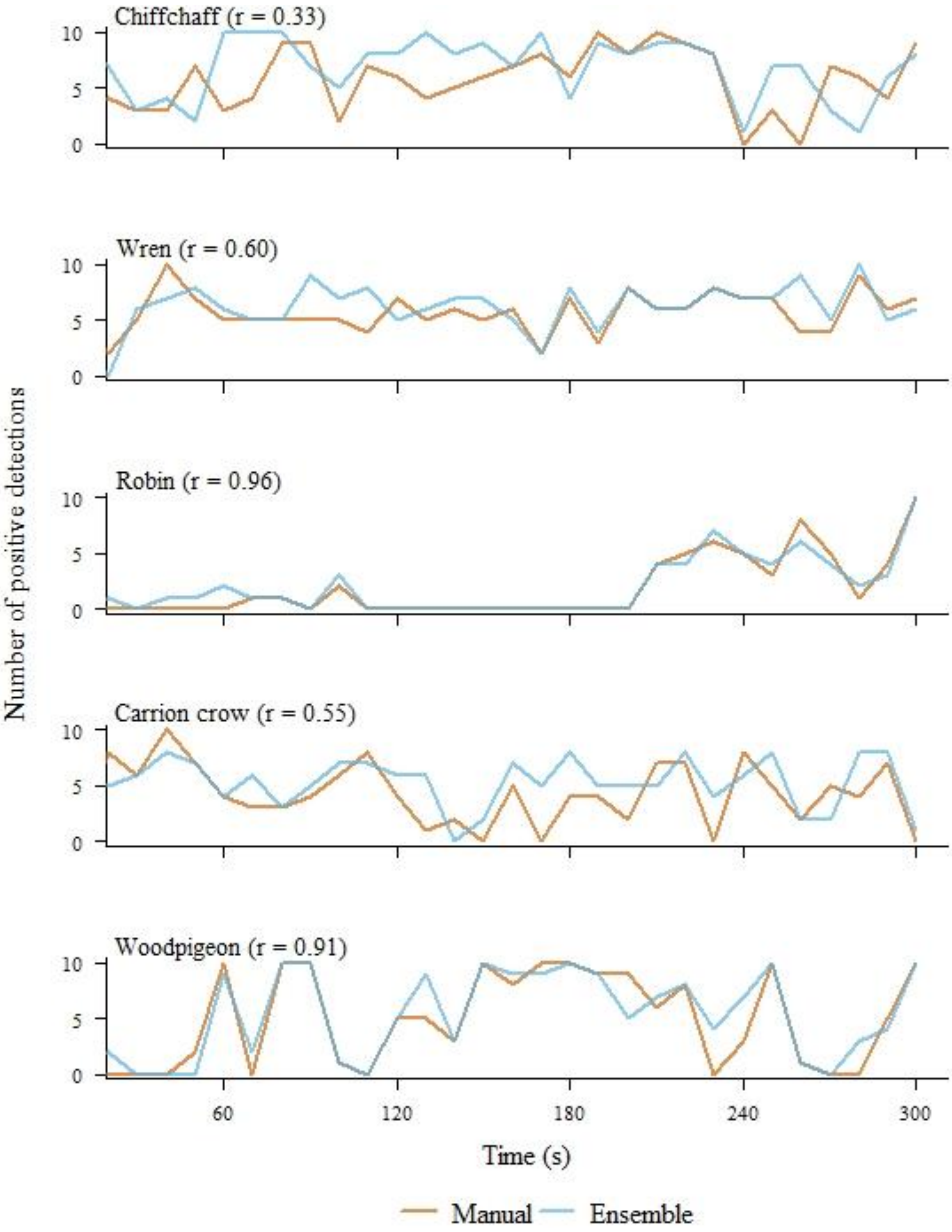


Figure 5.5 The number of seconds per 10 s interval that the songs of five bird species were detected by manual analyses of sample 300 s acoustic surveys of the dawn chorus (one survey selected for each species), and the corresponding number returned by automated analyses using ensemble recogniser models. The ensemble models were capable of identifying fine-scale patterns in song output over time for the range of species. Pearson's correlation coefficients, assessing the relationship between the two methods, are shown in parentheses.

5.5 Discussion

If automated acoustic recognisers are to be more widely adopted in ecological studies, there is a need for improved recogniser performance in detecting and classifying vocalisations within noisy acoustic surveys. I assessed the individual performance of four readily-available recognisers and found that their ability to detect the singing events of bird species with contrasting vocalisations was highly variable. In parallel, I developed an ensemble approach, whereby scores assigned to detections made by the four recognisers were combined to model probabilities of singing events by individual species. My ensemble model performed significantly better than all component recognisers in isolation when tested on the song of five species in acoustic surveys made during the dawn chorus at 20 woodland sites throughout Great Britain. The mean probability of the ensemble correctly identifying individual singing events across my five study species was 74%, compared to 59% probability when the respective performances of the component recognisers were averaged across the study species. The ensemble worked by 'weighting' the scores of the component recognisers, improving classification of the 'true signal', and reducing both the error and unreliability of the recognisers when operated in isolation (Araújo and New, 2007). Hence, the ensemble takes the particular strengths from each recogniser's detection method, resulting in a favourable performance across all species tested. Considering that my study species represent the five broad song-types recognised amongst British birds (cf. Stowell and Plumbley, 2011), and are likely to be representative of song-types more broadly, it is reasonable to postulate that my ensemble method would perform favourably across other bird communities and also across other taxa and regions.

The performance of the individual recognisers was inconsistent across my five study species, reflecting the suitability of their respective signal detection methods to particular song structures, frequency ranges, and background noise; no individual recogniser was comprehensive in its ability (cf. Brandes, 2008a). For example, Raven concentrates on detecting the energy within a specified frequency band, and does not consider the internal structure of a song (Duan et al., 2013). It is, therefore, prone to a high FPR. This was especially apparent with chiffchaff song, where Raven's performance was barely better than random (Fig. 5.2; Table 5.1). Despite chiffchaff song being of a relatively simple structure, Raven was unable to discriminate between the target signal and background noise in the 3.5-7 kHz frequency band in the period around sunrise, when most species participate in the chorus. Song Scope performed considerably better in this situation, despite its method of detecting song structure using HMMs also being sensitive to noise (Briggs et al., 2012; Duan et al., 2013). By contrast, Song Scope performed poorly for wren, despite wren song being delivered at the same time as chiffchaff, and in a broadly overlapping frequency band. This may be due to the high amplitude of wren song increasing the SNR, allowing Raven to detect it more easily, whereas there was sufficient variability in wren song structure across all dates and sites in the test dataset to limit discrimination by Song Scope. Wren typically sing at lower elevations (c.3 m Holland et al., 1998) than chiffchaff (which sings high in the canopy; Rodrigues, 1996). Wren song would, thus, be closer to the ARU microphones, which were set at c.4 m. The resultant difference in amplitude might explain the difference in their detection by Raven. In a prior comparison of recogniser performance, detecting the distinctive call of common nighthawk *Chordeiles minor* in less complex acoustic conditions at twilight, Knight et al. (2017) found that Song Scope performed best (as measured using AUC-ROC), followed by monitoR, then Raven, then Kaleidoscope. From my study species, carrion crow most closely resembles common nighthawk in terms of the structure of its vocalisation, but I obtained a very different order in AUC-ROC performance, i.e. Raven then Kaleidoscope/Song Scope, then monitoR (Fig. 5.2; Table 5.1), highlighting the potential problems of relying on only one recogniser for detection. It is apparent, therefore, that relative performances of individual recognisers are variable, and dependent upon the species and the situation within which acoustic surveys are made, and, no doubt, in the methods applied by the user during their construction. By comparison, the relative performance of my ensemble model remained consistently high across all species tested.

In many applications of ARUs, the minimum requirement is detecting the occurrence, or occupancy probability, of a species of interest at a given location (e.g. Furnas and Callas, 2015). Unfortunately, recognisers invariably return FP errors from acoustic surveys, which are particularly problematic when the species of interest is absent from the location, and which contravene a major assumption of many occupancy models (MacKenzie et al., 2006). This error can be reduced, or resolved, if there is a minimum probability of obtaining a positive detection at which the FPR remains at zero. I showed that none of the recognisers tested in isolation could achieve this probability cutpoint across all five of my study species (no individual recogniser enabled the detection of more than three species), but that this was achievable using my ensemble model (Appendix A.4, Table A.7). This means that to determine occurrence for each of my study species, I need only consider the detections made at or above the minimum threshold probability. Within this reduced dataset, I should be confident that the detections are of the target species only. If no detections are returned at or above the minimum probability, and the target species is otherwise a reliable contributor to the dawn chorus, I could infer that the species is absent. The more TP detections that exceed the minimum probability (Appendix A.4, Table A.7), the more confident this assumption should be. Importantly, an ensemble approach might, thus, enable the use of ARUs to determine apparent species presence-absence data for sites, if recognisers are available for all candidate species.

When accurate accounts of daily or seasonal patterns in song frequency or singing behaviour is important, a large majority of the singing events within acoustic surveys must be detected (Shonfield and Bayne, 2017), whilst FP errors remain negligible. In this regard, a good recogniser will minimise the distance from the ROC curve to the point x=0, y=1 (where the distance is denoted roc01). This was beyond the capabilities of all individual recognisers tested for most of my study species singing during the dawn chorus, and the ensemble also fell short for some species in its performance here (Fig. 5.2; Table 5.1). This was particularly true for chiffchaff, where sensitivity at the optimal roc01 was 70%, which was attained at the cost of a 48% FPR (Fig. 5.2; Appendix A.4, Table A.6). The best performing ensemble model was for carrion crow, where sensitivity at the optimal roc01 was 81% at a cost of a 28% FPR (Fig. 5.2; Appendix A.4, Table A.6). Nevertheless, the roc01 for the ensemble across the five study species was significantly less than for all component recognisers in isolation (Fig. 5.3b), and, for all study species except Song Scope's chiffchaff recogniser, the ensemble model had a lower or equal FPR for any given sensitivity value (Fig. 5.2).

An ensemble approach based on the best available current recognisers is still only partly capable of correctly detecting and classifying all individual singing events of species. In particular, when the singing activity of my study species' in acoustic surveys was low, the ensemble had high FP rates (note high y-intercepts in Fig. 5.4). When the singing activity of the species was greater, the ensemble correlated well with the observed number of singing events over broad timescales (i.e. 300 s; Fig. 5.4). The ensemble also demonstrated potential for very high performance in recognising singing activity patterns over fine timescales (i.e. 10 s) for most species tested (Fig. 5.5), and although the ensemble model for chiffchaff largely failed to identify the nuances in timing of singing events, it still correctly estimated the mean number of events across the sample (Fig 5.5). However, further development of individual recognisers and the ensemble approach will be required for reliable application to studies on song output and singing behaviour.

Building ensemble recogniser models can be a lengthy process, as they require familiarity with the controls and construction of each component recogniser. Nonetheless, if they are used to examine large acoustic datasets, the enhanced performance of ensembles over the use of the component recognisers in isolation will likely out-weigh the initial time invested and, once constructed, they can be applied to a wide range of species, study sites and datasets. An alternative to investing in building an ensemble recogniser would be to allocate effort to training an individual recogniser. However, diminishing returns, together with the relatively narrow domain of performance of each individual recogniser, suggest that the outcome would be unlikely to match an ensemble approach in its breadth. Mine and previous studies suggest that major improvements can still be made to available recognisers. Future improvements to any one recogniser are also likely to improve the performance of an ensemble modelling approach, enabling a much wider utility of ARUs for ecological studies.

With both diversity and abundance of species declining at greater rates than ever before in human history (IPBES, 2019), there is a pressing need to monitor the state of our wildlife. I present a method based on five species with different vocal characteristics that improves acoustic signal recognition performance significantly. My ensemble method offers the potential for inexpensive, robust monitoring of species. Clearly, the method needs to be tested on a wider range of species, but the potential use of ARUs for widespread use is now within our grasp. My ensemble approach could be used for a range of purposes, including to provide evidence for: policy makers (e.g. the presence of qualifying species in protected areas), those wishing to provide evidence of the presence of species on sites notified for developments (e.g. Environmental Impact Assessments), and scientists exploring ecological and behavioural research questions.

Chapter 6

Tracking the avian dawn chorus across Great Britain with climate

Common chaffinch *Fringilla coelebs*

6.1 Abstract

Despite its significance in the life-cycles of birds, the avian dawn chorus remains little understood. Several hypotheses have attempted to explain the motivation for the chorus, but none apply to all birds all of the time. The energy stochasticity hypothesis offers a general explanation, and states that birds sing more at dawn if they possess excess energy reserves at this time. A key assumption of the hypothesis is that overnight temperature dictates energy-loss, such that cooler temperatures lead to reductions in singing activity the following dawn, culminating in later dawn choruses and lower chorus peaks. Prior empirical evidence supporting this assumption is largely based on studies of single species at single sites. Here, I test the assumption on entire bird communities at multiple geographically and climatologically distinct sites, whilst accounting for the effect of other environmental variables, including light, which is often implicated as the most influential factor determining chorus timing. I used autonomous recording units (ARUs) to make acoustic surveys of the daily dawn chorus at 19 woodland sites throughout Great Britain during the main breeding season (April to June) in two years. I applied the acoustic complexity index (ACI) to the surveys, and used the scores obtained to calculate *i*) chorus onset time, *ii*) time of chorus peak, and *iii*) the magnitude of the peak in the chorus (chorus intensity) for each day at all sites. I conclude that the respective effects of overnight temperature and light on the timing of chorus onset and peak differed with latitude. Light was the over-arching factor at all sites, but it had relatively greater effect at lower latitudes, whereas overnight temperature became more important at higher latitudes, where temperature regimes are more likely to limit overnight energy retention in birds. Contrary to the assumptions of the energy stochsticity hypothesis, the magnitude of the chorus peak was not influenced by variation in minimum overnight temperature, but instead, responded negatively to the minimum temperature of the previous night. This effect was more pronounced at lower latitudes, where variance within overnight temperature regimes was greater, suggesting, perhaps, that birds utilise the minimum temperature of the previous night to predict that of the forthcoming night, but make errors in judgement leading to lower chorus peaks, especially where overnight temperatures are more variable. However, my interpretation of the data is offered tentatively, as I was unable to reliably isolate the respective effects of light and temperature in my analyses. Further work should aim to

achieve this. The implications of my results in the context of a changing climate are discussed.

6.2 Introduction

Each day in spring, during a period preceding sunrise, many male northern temperate zone passerines deliver their most intense song bout of the day, when together, they produce a phenomenon known as the avian dawn chorus. Several hypotheses have been proposed to explain the chorus (chapter 2, section 2.4), but no single one can account for all species and individuals. In fact, the assemblage of current hypotheses are not mutually exclusive, and any one, or combination thereof, may apply to some species at least some of the time (Hutchinson, 2002; Thomas, 1999). One broad explanation for the chorus that gained momentum towards the turn of the century, and one that incorporates some of the assertions made by other hypotheses, is the energy stochasticity hypothesis (chapter 2, section 2.4.1). This hypothesis is based upon stochastic dynamic programming (SDP) models, which determine optimal behavioural regimes under specified conditions that maximise individual fitness (Houston et al., 1988). In all SDP models of daily singing regimes, overnight energy loss in birds is dependent upon minimum overnight temperature (Thomas and Cuthill, 2002), which was varied stochastically in initial models (Hutchinson et al., 1993; McNamara et al., 1987). However, Hutchinson and McNamara (2000) extended these models to reflect the possibility that birds possess the ability to predict the forthcoming overnight temperature due to its correlation with that of the previous day (see e.g. Bednekoff et al., 1994). If stochasticity in overnight energy loss is removed from models, which could be achieved by minimising variability in overnight temperature (Hutchinson et al., 1993; McNamara et al., 1987), they predict that the dawn chorus will be diminished, or lost altogether, and replaced with a lower, constant intensity of song production through the morning (Hutchinson, 2002).

The underlying assumptions of the energy stochasticity hypothesis have been tested directly and indirectly in previous research involving free-living temperate birds (chapter 2, section 2.4.1), although few studies have focused on the relationship between minimum overnight temperature and the onset of the chorus (Bruni et al., 2014). The hypothesis remains contentious, however, as only two of six North

American oscine and sub-oscine passerines studied by Bruni et al. (2014) altered their singing behaviour in direct response to temperatures at dawn. Furthermore, behavioural analysis of captive great tits *Parus major* has revealed that fully-satiated birds may choose to rest rather than sing during daylight hours (Mace, 1989b), and free-living conspecifics living at high latitudes, with longer day-length and foraging time, go to roost at higher light levels than those at lower latitudes (Mace, 1989a), yet, all still chose to sing most intensely at dawn despite having the opportunity to sing at other times of the day. Hutchinson (2002) addressed the latter point by extending the SDP model further, to incorporate a time-of-day dependence on the probability of gaining benefits from singing (i.e. the probability of pairing success). The most recent published SDP models concerning the dawn chorus (Hutchinson, 2002) predict that cloud cover and associated light level determine chorus onset, and that overnight temperature has greater relative effect on chorus duration and intensity.

As is the case with many hypotheses used to explain the dawn chorus, support for (and opposition to) the energy stochasticity hypothesis has been gathered largely based on the behaviour of single species at single sites, and often involving a small number of individuals over a limited timescale. However, Gil and Llusia (2020) state that the most relevant test of the model should focus on different populations experiencing contrasting environmental conditions, or on different species that differ in their sensitivity to weather, to offer a comparative perspective. Recent advances in acoustic recording hardware and sound analysis tools now allow researchers, equipped with large acoustic datasets accumulated over several sites simultaneously for extended periods of time, to reconsider the hypothesis in this way. However, difficulty in extracting meaningful species-specific information from large acoustic datasets remains a limiting factor (Shonfield and Bayne, 2017). Acoustic indices (AIs) have been implemented as a means to overcome this difficulty, by providing broad analyses of sound-producing animal communities, using numerical depictions (a score or statistic) of the distribution of energy in acoustic surveys (Depraetere et al., 2012; Towsey et al., 2014; chapter 3, section 3.5, this thesis). Numerous AIs have been developed and trialled, and many have been shown to reflect species diversity and community structure (reviewed by Buxton et al., 2018). Further, some may be applied to recognise variation in daily animal activity. Indeed, Farina et al. (2015) used AIs to characterise dawn chorus singing behaviour in Mediterranean bird communities.

Here, I apply one such index, the Acoustic Complexity Index (ACI; Pieretti et al., 2011), to a large dataset of acoustic surveys taken of the dawn chorus at multiple woodland sites located at varying latitudes throughout Great Britain, and each facing different environmental conditions. The ACI has been shown to be a very effective metric in describing the acoustic signature of community activities, and is one of the best indicators of changes to the behaviour and composition of avian communities amongst currently available AIs (Farina et al., 2015; Pieretti et al., 2015, 2011; Towsey et al., 2014). I determine the emergence and peak of the dawn chorus across the country each day during the main breeding season, and use the information obtained to revisit the energy stochasticity hypothesis, and the assumption that variation in overnight temperature influences the timing and peak of the chorus. More specifically, I test the theory that cooler overnight temperatures act to suppress or delay the chorus. I also consider the effect of light, as light is often regarded as the most influential factor in the determination of chorus timing (e.g. Hutchinson, 2002; Kacelnik, 1979, Kacelnik and Krebs, 1983). If an effect of temperature exists, it might differ amongst sites, or regions, depending upon local temperature regimes. I discuss my results with reference to the prior theory, and consider their implications amid a rapidly changing climate. This study represents the first comprehensive investigation into the timing of the avian dawn chorus throughout Great Britain.

6.3 Methods and materials

6.3.1 Field methods

I recorded the dawn chorus at 20 semi-natural mixed deciduous woodland sites throughout Great Britain (Chapter 4) during the months January to August inclusive in the years 2014 to 2017 using the equipment and methodology described in chapter 5 (section 5.3.2). For this particular study, I considered only the acoustic surveys made during the core breeding season (April to June) in the years 2016 and 2017, as data loggers accompanied the ARUs only in these two years. The study also did not include Highnam Wood, as acoustic surveys were not made at this site in 2016 and 2017. It was necessary to correct for drift in the ARU clocks, and, therefore, upon deployment in the field, I set the ARU clock to GMT as per the website https://greenwichmeantime.com. Then, during routine maintenance visits, for battery and flash card renewal, and upon collection of the ARU, I compared the time on the ARU clock with GMT and noted the time lost/gained by the ARU clock since deployment. All times were then subsequently corrected to true GMT, assuming a linear drift in time deviation in ARU clocks. I recorded environmental data at each site using one of two data logger models: Tinytag Plus 2 TGP-4500 (Gemini Data Logger Ltd, Chichester, UK), programmed to record ambient temperature (°C) and relative humidity (%), and HOBO Pendant UA-002-64 (Onset Computer Corporation, Bourne, Maine, USA), programmed to record ambient temperature (°C) and light levels (lux), at 10-minute intervals throughout the entire study period. Each logger model was geographically evenly distributed amongst the sites (Fig. 4.1), and fixed alongside the ARU. The exception was Durham University, where one of each model was deployed. This permitted a comparison of temperature readings returned by the two different models. ARUs and microphones were exchanged amongst sites between years, so that no site received the same recording equipment in both years, but data loggers were assigned to the same site throughout.

6.3.2 Data collection

Acoustic Complexity Index scores

Prior to calculation of ACI scores, I removed all acoustic surveys that included heavy rain or strong winds, as these weather conditions not only deter birds from singing (e.g. Bruni et al., 2014; O'Connor and Hicks, 1980), but also strongly influence ACI scores (Towsey et al., 2014). Each of the remaining surveys was split into 135 × 1 min .wav soundfiles using Audacity audio software (http://www.audacityteam.org/). ACI scores were determined using R software (v3.5.2; R Core Team, 2018) and the *soundecology* package (v1.3.3; Villanueva-Rivera and Pijanowski, 2016). An ACI score was computed for both channels of each 1 min soundfile using the acoustic_complexity() function, configured with a cluster size (j) of 5 sec, and a fast-fourier transformation (FFT) window (fft_w) of 512 points. Output consisted of a dataframe of ACI scores for each 1 min segment of each acoustic survey arranged in order of time, in minutes, relative to sunrise (i.e. -90 to 44). By default, the ACI score calculated for the left channel was chosen for further analyses, except for cases where the right channel produced consistently higher ACI scores (due to, for example, the left microphone being partially obscured by growing vegetation in the field). ACI scores were calculated for the frequency range 200 to 8000 Hz, which represented the full range of frequencies in the acoustic surveys, but with a high-pass filter set at 200 Hz to remove low-frequency anthropogenic background noise (e.g. distant road traffic). A detailed description and formula for the ACI is provided by Pieretti et al. (2011).

Dawn chorus peak

To calculate standardised times of peak and onset of the dawn chorus, I first corrected for ARU clock drift in the times assigned to the 1 min soundfiles at each site, assuming drift was consistent between the ARU and GMT. The peak in the dawn chorus for each acoustic survey at each site was then calculated as the peak rolling 5-min mean in ACI scores for the 1 min segments. As this definition of the peak is based upon ACI score, it actually refers to the maximum ‘complexity’ in the chorus, which is typically acheived when the range of frequencies represented within a recording is both broad and variable through time. As such, it provides indication of the number of different species and individuals singing, or the song rate of individuals.

Dawn chorus onset time

Defining dawn chorus onset time is subjective. I explored three methods for its calculation, and checked for agreement amongst them. I further validated the onset times by correlating them with a dataset of manually-observed first song times in four prominent species common to all study sites, selecting the most parsimonious of the three methods for further analyses. The first method (onset.1) used a smoothed function to characterise variation in ACI scores over time in a given acoustic survey (Mason et al., 2014 provides a detailed description of the function, where it is used to estimate onset of spring green-up using NDVI score). First, the ACI scores within each acoustic survey were scaled according to the following formula:

$$\frac{ACI\ score - minimum\ ACI\ score}{maximum\ ACI\ score - minimum\ ACI\ score}$$

Curves were then fit to the scaled values. The chorus onset time was calculated as the maximum second derivative of the curve, i.e. when the rate of increase in ACI score was at its maximum (Appendix B.1, Fig. B.1a). The second and third methods utilised previously calculated peak ACI scores. The first of these methods (onset.2) took the minute in an acoustic survey at which the ACI score equalled, or surpassed, a threshold equal to 20% of the corresponding peak ACI score for that survey (Appendix B.1,

Fig. B.1b). The third method (onset.3) was similar, but instead, used a 20% threshold based upon the mean minimum and mean maximum peak ACI scores amongst all acoustic surveys taken at a site during the survey period April to June (Appendix B.1, Fig. B.1b). A separate threshold was calculated and applied depending on the year in which an acoustic survey was taken, as changes to the exact location, positioning or performance of the ARUs at a site between years may have resulted in bias towards greater ACI scores within one of the years. The threshold was calculated as:

$$\text{onset.3} = \sum_{k}^{n} \frac{(peak_{max} - peak_{min} \times 0.2) + peak_{min}}{N}$$

where, k and n are the first and final acoustic surveys for a site within the study period in a year, $peak_{max}$ and $peak_{min}$ are the maximum and minimum peak 5-min rolling mean in ACI scores respectively in an acoustic survey, and N is the total number of acoustic surveys for a site within a year.

Correlation between the onset times of the three methods, calculated using Pearson’s correlation coefficient, was moderate (r=0.450 to r=0.680), and onset.2 had greater correlation with both of the other methods (Appendix B.1, Fig. B.2). To validate onset times by correlating with manually-observed times of first song in selected species, I first selected a subset of acoustic surveys, comprising one survey per site per week in 2016 and 2017. If the acoustic survey for the selected day had previously been removed from the dataset due to heavy rain or strong wind, I selected the acoustic survey from the following or the next available day. I then viewed spectrograms of the surveys using Raven Pro v1.4 sound analysis software (The Cornell Laboratory of Ornithology, Ithaca, NY, USA), configured with the FFT window set at 256 points, and contrast and brightness set at 62%. I scrolled through each spectrogram and recorded the time of the first song of European robin *Erithacus rubecula*, song thrush *Turdus philomelos*, Eurasian blackbird *T. merula* and northern wren *Troglodytes troglodytes*. The song needed to be discernible both visually in the spectrogram (given the settings above) and audible through headphones in order to count, and it needed to lead into a prolonged or continuous bout of song (a single, errant strophe of song did not count). I then calculated Pearson’s correlation coefficients to measure the relationship between first song times of each species in turn and the chorus onset times calculated by the three different methods. This showed that onset times returned by onset.2 had strongest correlation with the first song times of three of the four species (European robin, Eurasian blackbird and northern wren; Appendix B.1, Fig. B.3), and hence, provided a more likely representation of the ‘true’ variation in chorus onset times across the entire dataset. For this reason, combined with onset.2’s greater congruence with the other two methods (see above), I chose to use onset.2 onset times in statistical analyses.

Minimum overnight temperature

I calculated minimum overnight temperature as the lowest temperature recorded by a data logger in the period between midnight and the time of commencement of an acoustic survey each day. Differences in temperatures recorded by the two logger types (Pendant and Hobo loggers) deployed together at Durham were minimal at cooler temperatures, such as those experienced overnight (mean=0.35°C ±SD 1.00°C between midnight and 0800 hrs). Nevertheless, I applied a correction factor to temperatures returned by the Pendant loggers in the full dataset. Calibration was performed using the lm() function in the *stats* package of base R to model the temperature values returned by the Tinytag logger at Durham University as a function of those returned by the Pendant logger. Following removal of outlying datapoints using the outliers() function in the *sjstats* package (v0.17.3; Lüdecke, 2019), the model resulted in the following correction factor, applied using the predict() function in the *stats* package, to all minimum overnight temperature values returned by Pendant data loggers:

$$Revised\ minimum\ overnight\ temperature \\ = -0.001140 + 0.975375\ \times minimum\ overnight\ temperature$$

I then calculated the mean minimum overnight temperature throughout the study period (April to June in both years) for each site, and subtracted the mean from the recorded minimum overnight temperatures to obtain deviations from the mean. This accounted for potential acclimatisation by local bird communities to the different mean temperatures amongst the sites in my analyses. As birds may possess some ability to predict the forthcoming overnight temperature based upon that of the previous day or night (Bednekoff et al., 1994; Hutchinson and McNamara, 2000; Thomas and Cuthill, 2002), I included a variable in statistical analyses that accounted for the previous night’s minimum temperature. For this, I calculated deviations from the mean as detailed above, but using the minimum temperature of the previous night.

To account for other factors influencing the timing and peak of the dawn chorus in my analyses, I gathered information on date, light level, moon phase, prevailing climate and avian community composition.

Sun elevation

I calculated sun elevation (the angle between a line from the observer to the centre of the sun, and a line between the observer and the point of the horizon vertically above the sun's centre) at *i*) the time of chorus onset, and *ii*) the time of chorus peak for each day at each site using the solarpos() function of the R package *maptools* (v.1.0-1; Bivand et al., 2020). Measured under standard conditions, illumination (light level) is entirely dependent on sun elevation, and any difference between the observed illumination and that predicted, is caused by local influences, for example, cloud cover (Nielsen, 1963). I did not use light level measurements returned by Pendant data loggers, as these loggers were only deployed at half of the study sites (chapter 4, Fig. 4.1).

Moon phase

I used two measurements to account for the potential effects of moon phase on the dawn chorus. First, I established if the moon was above the horizon at any point between the commencement of an acoustic survey and the time of civil twilight during the survey (assuming that the effect of moon illumination would be largely negated by civil twilight), and recorded moon presence as a binomial variable [1,0]. The second measure was the moon phase (%) at midnight preceding the acoustic survey. Moonrise times and illumination for each site were taken from https://aa.usno.navy.mil/.

January to March temperature and precipitation

To allow for the possibility of climate during the months leading into the breeding season having effect on dawn chorus onset during the study period, I sourced climate data from the Centre for Environmental Data Analysis (CEDA; https://catalogue.ceda.ac.uk/) using the dataset HadUK-Grid Gridded Climate Observations on a 1 km grid over the UK (Met Office, 2018), and calculated the mean temperature and the total rainfall for the months January to March for the years 2016 and 2017 for each site, using data for the 1 km cell in which a site was located.

Community composition

The timing and peak of the dawn chorus may be dependent on the community of species present at a site and their relative abundance. I used the test dataset described in chapter 5 (section 5.3.3), and the information on singing events obtained from the process described in chapter 5 (section 5.3.4) to sum the durations of the singing events for each species across all 15 × 300 s samples per site to obtain a total singing duration for each species at each site. From this, I established that 13 species were responsible for 91% of all dawn song produced amongst the sites. I applied principal component analysis (PCA), using the prcomp() function in the *stats* package of base R, to determine the relationships amongst sites in the composition of dawn song, using the unscaled total singing durations of the 13 dominant singing species as variables (Appendix B.2). I extracted the co-ordinates for the first two PCs (which explained 48% of the total variation in the data) for each site using the R package *factoextra* (v1.0.5; Kassambara and Mundt, 2017), and included the values in statistical analyses as two measures of variation in community composition amongst the sites (community 1 and community 2 respectively).

6.3.3 Statistical analysis

I tested for the effect of minimum overnight temperature on *i*) dawn chorus onset time *ii*) the time of dawn chorus peak, and *iii*) the magnitude of dawn chorus peak using linear mixed-effects models (LMMs), implemented in the R package *nlme* (v3.1-137; Pinheiro and Bates, 2019). I included the following co-variates in the initial model: previous night minimum temperature, Julian date, sun elevation, moonrise, moon illumination, January to March mean temperature, January to March total rainfall, community measure 1, community measure 2, latitude, longitude and year. I also included the following relevant interaction terms: minimum overnight temperature × previous night minimum temperature, minimum overnight temperature × light level, minimum overnight temperature × moonrise, minimum overnight temperature × moon illumination, light level × moonrise, light level × moon illumination, moonrise × moon illumination, January to March mean temperature × January to March total precipitation, community 1 × community 2 and latitude × longitude. As I was interested in the varying effects of minimum overnight temperature on the response variables at the different sites, I included a random intercept and slope that permitted minimum overnight temperature to vary by site. Following data exploration, I removed Julian date and January to March mean temperature from models, as they were highly co-linear with sun elevation and latitude respectively. I then used the dredge() function in the R package *MuMIN* (v1.42.1; Barton, 2018) to fit all possible models, and compared models using AIC (Burnham and Anderson, 2002). I performed model averaging using the mod.avg() function in the *MuMIN* package, considering all models simpler than the top model with ΔAIC <6, and took the significant effects ($p \leq 0.05$) in the full average model to be my final model variables. I kept the main effects of a variable if it was included in a significant interaction term. I then refitted the final model using restricted maximum likelihood (REML; Zuur et al., 2009). I confirmed that assumptions of normality and homoscedasticity were not violated by plotting the residuals as Q-Q plots and against fitted values respectively.

6.4 Results

The sun elevation at the time of chorus onset decreased with decreasing latitude (Fig. 6.1B). Likewise, sun elevation was lower at the time of chorus peak at lower latitudes (Fig. 6.1C). LMMs accounting for the effect of sun elevation on chorus onset time showed that increasing positive deviations from the mean minimum overnight temperature led to later chorus onset at sites located at all latitudes (Table 1, Fig. 6.1D), and that this delaying effect of increasing overnight temperature became greater with decreasing latitude (Fig. 6.1D). The time of chorus peak also became later with increasing positive deviations from the mean minimum overnight temperature at all latitudes (Table 1, Fig. 6.1E), and although the effect of minimum overnight temperature on the time of the chorus peak was not as great as its effect on chorus onset, the effect was, in general, greater at lower latitudes (Fig. 6.1E). Minimum overnight temperature was not retained as a significant variable following the model selection process for predicting the maginitude of the chorus peak (Table 1). However, increasing positive deviations from the mean minimum overnight temperature of the previous night led to decreased chorus magnitude (Table 1). This effect was greater at higher latitudes (Fig. 6.2).

Table 1 Coefficients of the fixed effects of the most parsimonious linear mixed effects models (LMMs), as guided by AIC, for factors influencing *i*) dawn chorus onset time, *ii*) time of dawn chorus peak, and *iii*) magnitude of dawn chorus peak within acoustic surveys taken at 19 mixed deciduous woodland sites throughout Great Britain from April to June 2016 and 2017.

Variable	Value	SE	t
Dawn chorus onset time			
Min. overnight temp.	5.69	0.402	14.17
Min. overnight temp. previous night	-0.85	0.067	-12.72
Moonrise	-1.47	0.345	-4.27
Sun elevation	4.03	0.119	34.02
Year: 2017	4.20	0.348	12.06
Min. overnight temp. × Min. overnight temp. prev. night	-0.13	0.012	-11.18
Min overnight temp. × Sun elevation	0.52	0.028	18.58
Dawn chorus peak time			
Latitude	-1.94	0.162	-12.02
Min. overnight temp.	1.16	0.134	8.69
Min. overnight temp. previous night	-0.80	0.048	-16.46
Moon illumination	-0.03	0.005	-6.03
Sun elevation	8.80	0.053	165.21
Year: 2017	2.71	0.262	10.34
Min. overnight temp. × Min. overnight temp. prev. night	-0.07	0.008	-8.58
Min. overnight temp. × Moon illumination	-0.01	0.001	-4.82
Min overnight temp. × Sun elevation	0.25	0.013	19.28
Dawn chorus peak magnitude			
Community 2	0.11	0.043	2.56
Jan-Mar rainfall	-0.82	0.154	-5.33
Min. overnight temp. previous night	-4.87	0.946	-5.15
Sun elevation	-8.45	1.728	-4.89

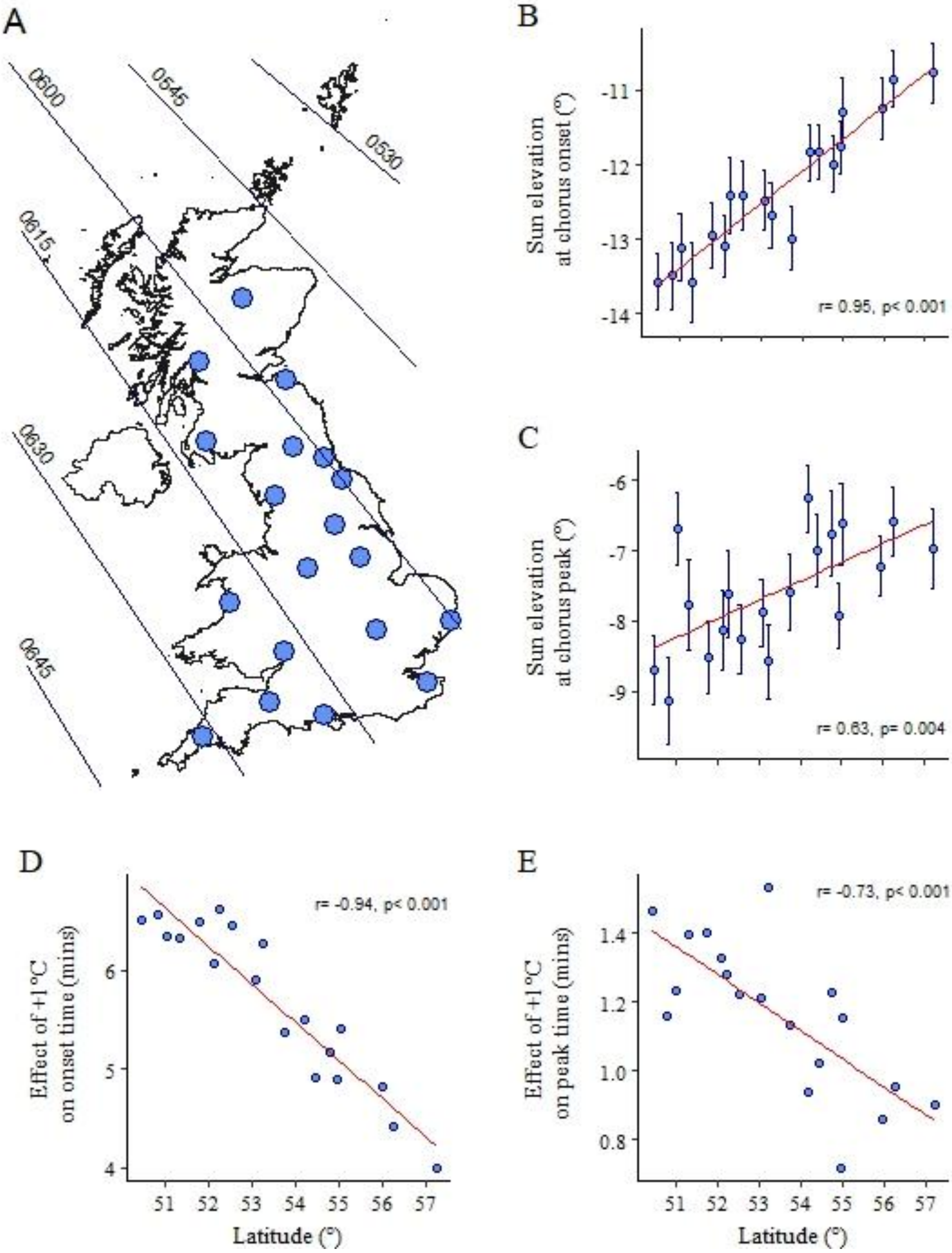


Figure 6.1 The difference in the timing of the avian dawn chorus with variation in sun elevation and minimum overnight temperature at woodland study sites located at various latitudes across Great Britain during the core breeding season (Apr-Jun). (A) The locations of woodland study sites. Isochrones show the time (GMT) of sunrise across the United Kingdom in mid-May (the mid-point in the study period). If light levels were the sole determining factor, the chorus would be expected to advance in an approximately south-westerly direction across the country. (B) The mean sun elevation at chorus onset time at sites with increasing latitude. Error bars ±1SE. (C) The mean sun elevation at the time of chorus peak at sites with increasing latitude. Error bars ±1SE. (D) The effect of 1°C increase in minimum overnight temperature on chorus onset time

at sites with increasing latitude. (E) The effect of 1°C increase in minimum overnight temperature on the time of chorus peak at sites with increasing latitude. In D and E, Y-axis values are from linear mixed-effects models (LMMs), and are the coefficients for the random effect of minimum overnight temperature on chorus onset and peak time respectively when varied by site. r = Pearson's correlation coefficient (B-E).

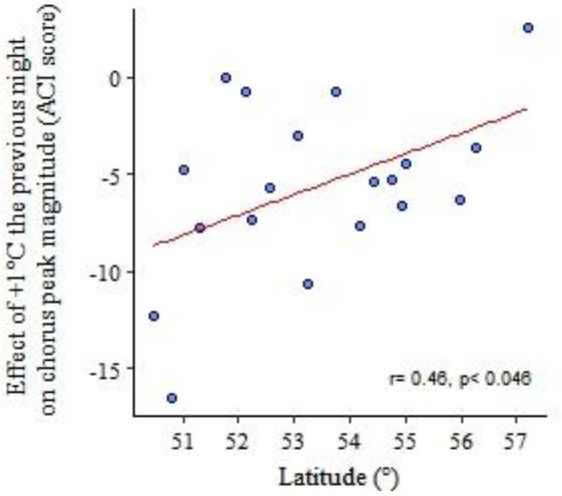


Figure 6.2 The effect of 1°C increase in the minimum overnight temperature of the previous night on the magnitude of the dawn chorus, as measured by the acoustic complexity index (ACI), at sites with increasing latitude.

6.5 Discussion

The avian dawn chorus is of clear significance in the life cycles of birds. Yet, despite robust literature based upon observations of dawn singing behaviour in individual species (Mace, 1987b; Stacier et al., 1996; chapter 2, this thesis), research has yet to firmly establish exactly why birds sing collectively as dawn. The energy stochasticity hypothesis provides a general, but contentious, explanation, and has been formed on the assumption that birds possess lower energy reserves at dawn following cooler nights, leading to reduced song output, later chorus onset and lower chorus peak. I tested this assumption by applying the ACI to a large dataset of acoustic surveys made of the dawn chorus at 19 woodland sites located at varying latitudes throughout Great Britain during the core bird breeding season. I modelled daily chorus onset and peak in response to minimum overnight temperatures and light levels (sun elevation), amongst other environmental variables that may have influence on the chorus.

The onset of the dawn chorus occurred at lower sun elevation at lower latitudes, ranging from a mean angle of -13.6˚ (astronomical twilight; Table 2.2) at the lowest latitude (50˚ 27') to -10.8˚ (nautical twilight) at the highest latitude (57˚ 12'; Fig. 6.1B). That is to say, birds began singing at lower light levels at lower latitudes. In theory, such systematic latitudinal variation in response to sun elevation is unexpected if the chorus responds to a common light threshold at all latitudes. It is possible, therefore, that chorus onset responds to the rate of change in light level during twilight, rather than responding to the actual light level produced at a particular stage. Due to latitudinal differences in the trajectory of the sun relative to the local horizon, the sun rises more rapidly at lower latitudes, with steeper transitions from dark to light, whilst at higher latitudes, the sun moves at a shallower angle relative to the horizon, and remains within twilight zones for longer periods prior to sunrise (Daan and Aschoff, 1975). At the very highest latitude study site towards the end of the study period in late June, the sun would not have moved below the nautical twilight zone prior to dawn, whereas at late June at the lowest latitude study site, the sun would enter astronomical twilight (see Table 2.2 for sun elevation and illumination relating to these different periods of twilight) overnight. The vision of birds at lower latitudes may achieve greater dark adaptation due to experiencing darker nights (cf. Martin, 1990, pp8-10). This might allow for increased perception of subtle changes in light level and result in earlier chorus onset relative to sun elevation. Alternatively, because the transition from low-light conditions to the light threshold at which alternative activities become profitable (e.g. foraging) is reached more rapidly, and in order to gain the benefits from singing, or for song bouts to be a length that is effective, birds at lower latitudes may have become entrained to begin singing at lower light levels. Similar results were obtained for the time of dawn chorus peak, which was reached at lower mean sun elevation at lower latitudes (Fig. 6.1C). The latitudinal relationship was not quite as regimented as for chorus onset, however. This might be expected, as more species and individuals will sing at the time of the chorus peak than at chorus onset, thus, introducing the potential for a greater number of factors, other than light, that may be site-specific, to act upon singing behaviour. For example, social factors, such as the density of individuals within the community, and the number of neighbours may determine when or whether an individual sings during the peak on a given morning (e.g. Hodgson et al., 2018; Liu, 2004).

Mean minimum overnight temperature (the mean of the absolute temperature recorded) also exhibited a strong latitudinal cline, decreasing with increasing latitude (Appendix B.3, Fig. B.5A). According to the energy stochasticity hypothesis, this may also explain, at least in part, why chorus onset occurred at lower light levels at lower latitudes, as birds, on average, may have possessed greater energy reserves at dawn at lower latitudes due to warmer overnight temperature regimes. If this were the case, one might also expect warmer overnight temperatures to lead to earlier choruses within sites. However, results from LMMs revealed the opposite; increasing positive deviations from the mean minimum overnight temperature (i.e. warmer temperatures) led to later chorus onset and peak at all study sites, and the effect was greater at lower latitudes (Fig. 6.1). This appears counter to the assumptions of the energy stochasticity hypothesis. It is possible, however, that the observed delaying effect of increasing minimum overnight temperature on the timing of chorus onset and peak was in fact an effect of cloud cover on light levels, rather than one of temperature. Overcast nights tend to be warmer, but they are also darker at dawn, as the clouds conceal illumination from the rising sun. This view is supported by the positive coefficients for sun elevation in LMMs for chorus onset and time of chorus peak (Table 6.1); under overcast (but warmer) conditions, sun elevation was greater at onset and peak. Viewed in this way, my results support the conclusion reached by Hutchinson (2002) that variation in light level, rather than in overnight temperature, is the most important factor influencing the timing of the dawn chorus.

Bruni et al. (2014) concluded that cloud cover alone was not the major influence on the timing of the dawn chorus within their study region (located at 46˚ 29' N, -84˚ 04' E), and that it may only effect species that commence song at certain stages of the chorus (i.e. chorus onset), as only two of their six study species showed significantly delayed singing activity when the sky was cloudy. Indeed, they found that more of their focal species were significantly influenced by moonlight during the night than by cloud cover and light from the sun at dawn – a set of results which is not entirely at odds with those from my study, but I report a relatively small effect of moonlight (Table 6.1). In theory, cloud cover should have relatively greater effect on the timing of the chorus at higher latitudes, where the mean rate of change in light levels is lower, as it will take longer for a given light intensity threshold to be reached under cloud cover (Daan and Aschoff, 1975). On this basis, and if it is assumed that the observed positive effect of minimum overnight temperature on onset times is actually an effect of cloud cover on light level, one should expect a greater effect size at higher latitudes, but the opposite trend was observed; chorus onset and peak were delayed longer by warmer temperatures at lower latitudes (Fig. 6.1D and E). This might indicate that an effect of minimum overnight temperature does exist on the timing of the dawn chorus after all, but in my analysis, it is concealed within the effect of cloud cover. It might be assumed that deviations from the mean minimum overnight temperature have greater effect on chorus timing at higher latitudes because these regions have lower overnight temperature regimes (Appendix B.3, Fig. B.5A) and overnight temperature is more likely to be a limiting factor in overnight energy retention and subsequent dawn singing activity. If so, positive deviations from the mean temperature at higher latitudes may act to off-set some, but not all, of the delay in chorus timing generated by increased cloud cover. At lower latitudes, mean temperatures may not limit overnight energy retention to the same degree, and consequently, deviations from the mean minimum overnight temperature may not have such an effect. The delaying effect of minimum overnight temperature observed in the models for lower latitudes, is therefore, almost entirely due to cloud cover, and there is potentially little or no off-set of warmer temperature concealed within the observed effect sizes. So, whether there is an effect or not of overnight temperature on the timing of the chorus, could be dependent upon the regional temperature regime. Prior studies have demonstrated a strong positive correlation between minimum overnight temperature and duration of dawn song bouts in great tit, northern wren *Troglodytes troglodytes* and European robin *Erithacus rubecula* (Garson and Hunter, 1979; Thomas 1999), but the relationship between temperature and the timing of the chorus is less clear. For example, Bruni et al. (2014) found that only two of six species were influenced by temperature alone, and Brown (1962) found that willow warbler *Phylloscopus trochilus* in Oxford, UK commenced singing over a broad temperature range (-1˚C to 11˚C), whilst the range of light levels remained very narrow.

Minimum overnight temperature was not retained by model selection when identifying significant variables that influenced the magnitude of the dawn chorus peak (Table 6.1). This is counter to the conclusion of Hutchinson (2002), who’s SDP models predicted that overnight temperature has a significant effect on chorus duration and intensity (although Hutchinson’s definition and measure of chorus ‘intensity’ is not clear). However, the minimum overnight temperature of the previous night was retained in models (Table 6.1), and at all latitudes, warmer temperatures on the previous night decreased the chorus peak. This result is challenging to interpret, but it may relate to overnight energy reserves if birds utilise the temperature of the previous night to attempt to predict the temperature, and hence, energy-loss, of the forthcoming night (cf. Hutchinson and McNamara, 2000). Reductions in the magnitude of the chorus peak (i.e. lower maximum ACI scores) could have been caused by (*i*) fewer individuals participating in the chorus, (*ii*) participating individuals singing less intensely, or (*iii*) fewer individuals singing at any one time. If the minimum overnight temperature of the previous night was warm, birds, expecting the temperature of the forthcoming night to be similar, may have foraged less during daylight hours in preparation for the forthcoming night. If the forthcoming night was not as warm as the previous night, birds may have possessed depleted energy reserves at dawn, resulting in either of (*i*) to (*iii*) above. Such an effect might be more pronounced in regions where variance in minimum overnight temperature is greater, as the forthcoming overnight temperature may be more difficult to predict. Data show that the effect was greater at lower latitudes (Fig. 6.2), and the trend was for lower latitudes to have greater variance in minimum overnight temperature (Appendix B3, Fig. B.5B). This explanation, however, is not consistent with that I provide for the observed delaying effect of minimum overnight temperature on the timing of the chorus at higher latitudes. As, if birds are better able to predict the forthcoming overnight temperature at higher latitudes, leading to lower reduction in the magnitude of the chorus compared to that at lower latitudes, why should they not be capable of doing the same in terms of the timing of the chorus? Furthermore, the energy stochsticity hypothesis and associated SDP models predict that lower variation in overnight temperatures will result in less intense choruses (Hutchinson, 2002).

Rises in mean overnight temperature (Stone and Weaver, 2005; Vose et al., 2005) and day-to-day variability in temperature (i.e. sudden fluctuations in temperature and changes in temperature extremes, Pendlebury et al., 2004) are distinct characteristics of recent climate change, and the response of the dawn chorus to overnight temperatures currently observed at lower latitudes may magnify and become typical across much of Britain in future years. That is, less influence of overnight temperature on the timing of the chorus, due to warmer mean temperatures, and lower peaks in the chorus (or less intense choruses) due to unpredictability in overnight temperature regimes. It is uncertain how population and community dynamics will respond to these conditions in the long-term, particularly if dawn song acts as an honest advertisement of fitness, where singing at cooler temperatures, or success in competitive interactions, act to increase population fitness (e.g. Poesel et al., 2004). It has been demonstrated previously that temperature variability, as well as mean temperature, is important in regulating metabolism in birds (Pendlebury et al., 2004), leading to alterations in physical activity and foraging behaviour. Climate matching analysis indicates that coastal regions of western France currently experience a climate similar to that predicted for southern England by 2050 (Broadmeadow et al., 2005), and dawn choruses with similar community compositions in this area of continental Europe, may provide indication of future choruses in Britain, if British bird communities can adapt in the long-term.

My results show that the dawn chorus, like many other biological rhythms, is sensitive to climatic parameters and their variability. In this study, I have tested, for the first time at multiple sites with contrasting environmental conditions, the assumptions of the energy stochsticity hypothesis that variation in overnight temperature influences the timing and intensity of dawn singing activity in birds. The results of my study are challenging to interpret, however. Overall, data are consistent with the theory that day-to-day variation in light level is the major influence on the timing of the dawn chorus. However, variation in overnight temperature may also influence the timing of the chorus, but only noticeably so at higher latitudes, where temperature regimes are cooler and likely to place a limitation on overnight energy retention. My study did not support the conclusion of Hutchinson (2002), that variation in overnight temperature influences the intensity of the chorus. This may be because birds use their experience of the previous night's temperature to anticipate their energy reserves at dawn. Lower chorus peaks may be due to errors in judgement – which are more likely to occur in regions with greater variation in overnight tempertures. A major limitation to my study, however, is that information on cloud cover was not available for the fine spatial and temporal resolution required for my study design. Therefore, it was not possible to reliably disentangle the respective effects of overnight temperature and cloud cover on the timing and peak of the dawn chorus. My interpretations of the data, therefore, are offered tentatively. There is clearly more work to do, and a next step should focus on acquiring a suitable measure of cloud cover, and also perhaps of overnight wind speed (cf. Hutchinson, 2002), so that firmer conclusions may be drawn in our understanding of the dawn chorus.

Chapter 7

Competition for acoustic space between resident and migratory species during the dawn chorus

Common chiffchaff *Phylloscopus collybita*

7.1 Abstract

In many terrestrial habitats, the avian dawn chorus is the primary example of animal communication amid a background of vocalisations produced by different species competing for acoustic space. Individuals may establish a routine, whereby they avoid singing when a species with similar song traits is vocalising. Migratory species may arrive after routines have been established amongst individuals of resident species, thus, disturbing singing behaviour and song rate in residents. Migrants may also have difficulty in establishing their own acoustic niche. I used passive acoustic monitoring (PAM) methods to survey the dawn chorus at multiple woodland sites throughout Great Britain. Using information extracted from the acoustic surveys, I tested for association in the timing of singing events made by two closely-related migratory species, wood warbler *Phylloscopus sibilatrix*, a long-distance migrant declining throughout much of its European breeding range, and common chiffchaff *P. collybita*, an increasing short-distance migrant currently expanding its European breeding range, with resident species displaying similar song traits to each. I then tested whether the song rate (the total time singing within 60 s periods of acoustic survey) of each migratory species was affected by that of the paired resident, and *vice versa*. There was a significant association between the timing of singing events by wood warbler and northern wren *Troglodytes troglodytes*, with temporal overlap in singing events less than expected by chance. However, the song rate of each species was not significantly affected by that of the other, inferring that the two species may have established a mutually beneficial singing routine. Conversely, there was no association in the timing of singing events of the chiffchaff and great tit *Parus major*, indicating that the two species sang indiscriminately with respect to one another, despite close spectral and temporal similarities in their respective songs. However, the song rate of great tit was negatively affected by increasing song rate in the chiffchaff. Finally, there was significantly less temporal overlap in chiffchaff and wren singing events than expected by chance. The wren seemingly dominated this interaction, as its song rate remained unaffected by increasing chiffchaff song rate, but chiffchaff song rate was negatively affected by that of the wren. This study provides evidence that free-living migrant-resident species pairs with similar song traits avoid temporal overlap of song during the dawn chorus, a period when most birds are committed to song production, and that deferential species may be pressured into singing at sub-optimal rates. The productivity of both migratory and

resident woodland birds depends on their ability to communicate effectively with conspecifics. With woodland bird community composition currently experiencing unprecedented change due to anthropogenic disturbances, there may be consequences for some species if competition for acoustic space changes as a result.

7.2 Introduction

In animal communication, it is essential that signals are detected by the intended recipients and that they convey a clear message amid interference from background noise (Bradbury and Vehrencamp, 1998; Brumm and Slabbekoorn, 2005; Endler, 1992). Failure in these requirements may lead to receiver error, and ultimately result in loss of fitness for the individuals involved, for example, due to increased risk of aggressive encounters or missed mating opportunities (Wiley, 2006). In acoustic communication, background noise takes two general forms. The first is abiotic noise, which consists of geophonies (e.g. wind, rain and running water) and anthrophonies (e.g. road-traffic noise). The second is biotic noise, or biophony, which is noise produced by other organisms within the environment, be they intra- or inter-specific to the signaller and receiver. Biotic noise is a particular concern for those animals engaging in multi-species choruses, and for whom it is especially difficult to discriminate between conspecific and heterospecific signals (Brumm and Slabbekoorn, 2005; Wollerman and Wiley, 2002). In many parts of the world, the avian dawn chorus presents the most challenging example of acoustic communication amongst high levels of background noise produced by other species.

The conventional view of the avian dawn chorus is that species have evolved spectrally distinct songs, so as they avoid overlap with heterospecifics (Miller, 1982). However, restrictions are imposed on song divergence by habitat structure (Morton, 1975), such that species occupying the same habitat may actually show convergence in signal properties (Cardoso and Price, 2010). Additionally, body size, trachea length and the structure of the bill, as well as phylogeny, will constrain spectral and temporal limits of songs (Derryberry, 2009; Ryan and Brenowitz, 1985; Slabbekoorn and Smith, 2000). Furthermore, ecologically similar species living in sympatry may acquire similar signals to facilitate interspecific territoriality (Cody, 1969; Laiolo, 2012; Tobias and Seddon, 2009). Songs with similar features have a greater chance of interfering with each other, and consequently, birds have developed an array of short-term behavioural strategies to avoid acoustic masking, such as increasing song amplitude, shifting frequency, and making broad- and fine-scale modifications to the timing of song (chapter 2, section 2.6). Flexibility in temporal arrangement of song permits birds to insert their songs into periods of silence (known as refractory periods) of varying length between the songs of other species. However, avoiding temporal overlap with heterospecific song in this way, may constrain individuals to sing at lower than optimal rates (Popp et al., 1985).

Acoustic competition during the breeding period potentially presents a greater problem for arriving migratory species. Residents are present in a habitat year round and initiate breeding, and therefore, seasonal singing activity, prior to the arrival of most migrants (cf. Both and Visser, 2001). During this time, neighbouring residents may learn to recognise each other and establish relationships, from which, individuals may benefit by mutual interest in preventing settlement by intruders (Temeles, 1994). These neighbours may become accustomed to each other's song (Lambrechts and Dhondt, 1995), leading to alternate singing routines and even co-ordinated multi-species communication networks within communities (Malavasi and Farina, 2013; Naguib, 2005; Tobias et al., 2014). The arrival of migrants may initially create biophonic disturbances, in much the same way as introduction of an invasive species (e.g. Pijanowski et al., 2011b), thus, altering the existing acoustic partitioning.

Here, I investigate the reciprocal effect of song output in two migratory European-breeding *Phylloscopus* warbler species on the singing behaviour of resident species with similar song traits. Wood warbler *P. sibilatrix* is a small (c.12 g; Dunning, Jr, 2008) long-distance migrant, wintering in sub-Saharan Africa. The species is declining throughout much of its northern and western breeding range in Europe (Burfield and van Bommel, 2004), including in the UK, where the population has fallen by an estimated 63% between 1970 and 2017 (DEFRA, 2019), and is now associated primarily with mature upland oak woods in northern and western regions of the country (Mallord et al., 2012). The nominate race common chiffchaff (hereafter 'chiffchaff') *P. c. collybita*, that breeds in central and western Europe (incl. UK; Catry et al., 2005), is a smaller (8-9 g; Dunning, Jr, 2008), short-distance migrant, wintering in south-western Europe, the Mediterranean and west Africa (Catry et al., 2005). Its population trend contrasts with that of wood warbler, having increased by 110% in recent decades (DEFRA, 2019). Both species are insectivorous and forage by leaf gleaning, but despite their close relationship and ecological similarity, the acoustic structure of their respective songs differ markedly.

Prior studies experimentally testing interspecific acoustic competition have either taken place after sunrise (e.g. Popp et al., 1985), or have failed to explicitly state the timing of experiments (e.g. Ficken et al., 1974), so it is unknown whether the outcomes apply during the dawn chorus, when the motivation to sing is at its daily peak for most birds (Mace, 1987b; Stacier et al., 1996). Some studies also applied playback methods to illicit responses from focal species (e.g. Popp et al., 1985), and/or used captive subjects (e.g. Brumm, 2006). This study, using daily dawn chorus data across 20 woodland sites throughout Great Britain, represents the first investigation into competitive singing interactions between resident and migrant species during the dawn chorus within entirely natural settings.

7.3 Methods and materials

7.3.1 Acoustic data collection

I recorded the dawn chorus at 20 semi-natural mixed deciduous woodland sites throughout Great Britain (Fig. 4.1) during the months January to August inclusive in the years 2014 to 2017 using the equipment and methodology described in chapter 5 (section 5.3.2.).

7.3.2 Acoustic analysis

I used the 1500 min test dataset described in chapter 5 (section 5.3.3), and the information on singing events obtained from the process described in chapter 5 (section 5.3.4) as my dataset for this study.

7.3.3 Selection of species pairs

I selected resident species most likely to compete for acoustic space with the two chosen migratory species based upon similarities in core temporal and spectral song parameters. To do this, I downloaded high quality (24100 Hz, 16-bit encoding) sample recordings of song for every species within the 1500 min dataset (up to five recordings per species) from the xeno-canto repository (www.xeno-canto.org). Preference was given to recordings made in the UK, but if high quality UK recordings were unavailable or not suitable, then recordings made in France, Belgium or Netherlands were chosen. Preference was also given to recordings made during the main northern temperate zone breeding period (March to June), at dawn or in the early morning. I used Raven Pro v1.4 (The Cornell Laboratory of Ornithology, Ithaca, USA) to generate spectrograms. Up to five songs per recording (the number selected reflected the complexity and/or variation in a species' song) were described quantitatively using on-screen cursors to measure temporal and spectral traits. Temporal features were measured from spectrograms configured with broadband filter settings (window=Hann, Fast Fourier Transform [FFT] =512, overlap=93.8%, brightness=55%, contrast=55%) to maximise temporal resolution. Spectral features were measured from spectrograms configured with narrowband filter settings (window=Hann, FFT=1024, overlap=96.9%, brightness=55%, contrast=55%) to maximise spectral resolution. The following song parameters were measured: *i*) maximum frequency (Hz), *ii*) minimum frequency (Hz), *iii*) frequency range (Hz; maximum frequency minus minimum frequency), *iv*) peak frequency (Hz; the frequency in the song with the greatest amplitude), *v*) duration (s), *vi*) syllable rate (number of syllables s^{-1}). When it was clearly decipherable, only the first harmonic was included in spectral measurements. I then calculated the mean value for each parameter across all songs for each species. I scaled and centred the dataset of mean song parameters and made a dendrogram using the pheatmap package (v1.0.12; Kolde, 2019) in R software (v3.5.2; R Core Team, 2018), with Euclidean distance clustering and Ward.D2 agglomeration methods. I determined the optimal number of clusters using the fviz_nbclust() function, set to k-means clustering methods, in the R package *factoextra* (v1.0.5; Kassambara and Mundt, 2017). I then selected paired resident-migrant species from the dendrogram on the basis of 3-4 very similar song parameters (Fig. 7.1). For wood warbler, this was northern wren (hereafter 'wren') *Troglodytes troglodytes*, and for chiffchaff, this was great tit *Parus major* (Fig. 7.1). To provide a comparison with a second species' song, that was not so well-matched as the first, I also paired chiffchaff with wren, and wood warbler with great tit, to form additional resident-migrant species pairs. However, following preliminary analysis, I found I was unable to match wood warbler with great tit, as my dataset contained too few interactions between the two species to meet the assumptions of statistical analyses. I then recorded whether each of the four selected species was singing or not within each 1 s interval of each 300 s acoustic survey sample using binary [1,0] coding.

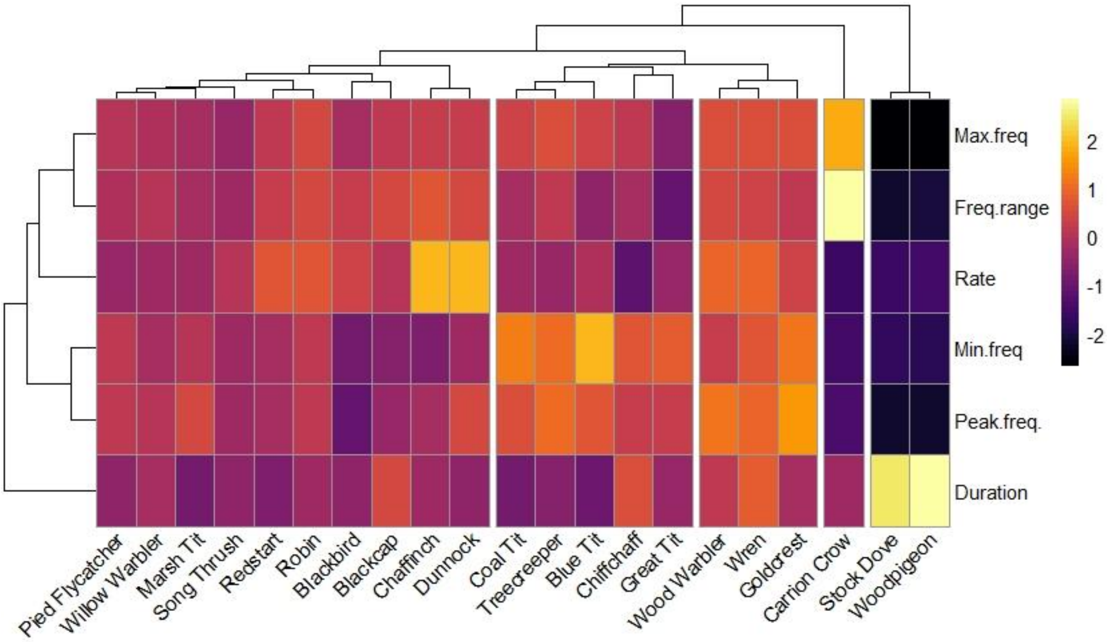


Figure 7.1 Results of Euclidean distance hierarchal cluster analysis showing relationships between the songs of 21 bird species recorded 'singing' in acoustic surveys of the dawn chorus at 20 mixed deciduous woodland sites throughout Great Britain during the months March to June 2014-2016, based upon six song parameters. The colour scale represents an index of divergence from the mean scaled value, across all species, for a song parameter, whereby, zero represents the mean value across all species, dark shades represent values lower than the mean (negative) and light shades represent values higher than the mean (positive). The optimal number of clusters for the dataset, as determined by the k-means clustering method, is five. The dendrogram shows wood warbler *Phylloscopus sibilatrix* paired with wren *Troglodytes troglodytes*, and chiffchaff *P. collybita* paired with great tit *Parus major*. For space and clarity, species names shown are shorter common British names, rather than the international naming system used throughout the text.

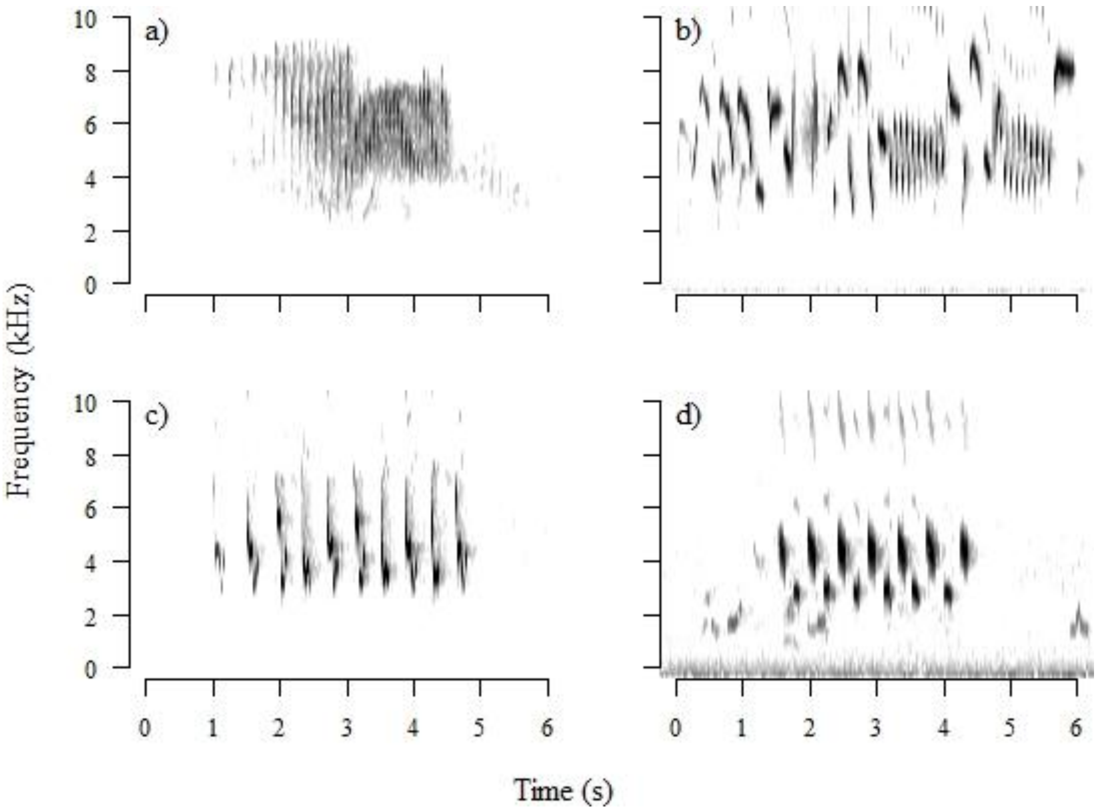


Figure 7.2 Spectrograms of example songs from the four study species, a) wood warbler *Phylloscopus sibilatrix*, b) northern wren *Troglodytes troglodytes*, c) common chiffchaff *P. collybita*, and d) great tit *Parus major*, demonstrating the spectral and temporal similarities between the songs of species pairs (a-b and c-d). Of the six parameters chosen to distinguish species' song, Euclidean distance hierarchal cluster analysis matched wood warbler and the wren most closely by maximum frequency, frequency range (maximum frequency – minimum frequency) and syllable rate (number of syllables s^{-1}), and matched the chiffchaff and great tit most closely by minimum frequency and peak frequency (the frequency in the song with the highest amplitude), as denoted by similarity in colour shading in Fig. 7.1. Spectrograms were made in Raven Pro v1.4 (The Cornell Laboratory of Ornithology, Ithaca, USA) configured with a Hann window and a FFT of 256 points.

7.3.4 Statistical analysis

I applied Pearson's χ^2 tests to detect associations in the timing of singing events in each resident-migrant pair. The binary data obtained from the acoustic analysis for each 300 s acoustic sample was divided into five 60 s segments. Only segments where both species of a resident-migrant pair were singing for ≥10 s and ≤50 s were retained for the analysis. This increased the likelihood that counts of all possible outcomes were ≥5 for all 60 s segments of acoustic survey. As a singing event typically lasts for a few seconds or more, when a study species was singing within a given 1 s interval of acoustic survey, there was increased likelihood that the species was also singing in an adjacent 1 s interval. Thus, each 1 s observation in a singing [1] or non-singing [0] event, within a 60 s segment of acoustic survey, was not independent of the other 1 s observations within the same event. To reduce the effect of non-independence of data on the statistical analysis, I randomly selected one 1 s interval from each singing and non-singing event for the migratory species, along with the corresponding binary value for the resident species. I then compiled all the randomly-selected 1 s observations into a single dataframe, and performed χ^2 tests using the chisq.test() function in the *stats* package of base R. Yates' continuity correction was not applied, as the expected counts for any given outcome were ≥5. The direction of significant associations was determined by drawing up contingency tables of observed and expected counts.

I used linear models (LMs), applied using the lm() function in the *stats* package of base R, to test for an effect of the song rate (total time spent singing per 60 s segment of acoustic survey) of wren on the song rate of wood warbler and *vice versa*. These two species co-occurred at just one site (Inversnaid; Fig. 4.1). Song rate interactions between chiffchaff and great tit, and chiffchaff and wren, were tested with linear mixed-effects models (LMMs) implemented in the R package *nlme* (v3.1.137; Pinheiro and Bates, 2019) with model fit by maximum likelihood. These species pairs co-occurred at multiple sites, and the effect of each species on the other potentially varied amongst them, hence, site was included as random intercept and slope terms in all LMMs. To prepare the datasets for the analyses, I returned to the binary data obtained for the 300 s segments of acoustic survey, and once again, divided each into five 60 s segments. First, I retained only the 60 s segments within which the migratory species was singing ≥1 s, and summed the total time singing by the migratory species within each. I then summed the corresponding total time singing by the paired resident species within each of the 60 s segments. To prepare dataframes for testing the effect of song rate in the migratory species on that of the resident, I repeated this process, but retained only the 60 s segments where the resident species was singing ≥1 s. I excluded from this dataset, any acoustic surveys taken prior to the expected arrival of the migratory species across the UK. For the wood warbler, I took this to be day 120 (April 30), and for the chiffchaff, day 90 (March 31; both based upon Mason, 1995). I included the covariates Julian date, time of day (expressed as the time, in minutes, relative to local sunrise) and year in all

LMs and LMMs (as fixed effects) to account for the effect of these parameters on the song output of the focal species. I checked that normality and homoscedasticity assumptions were met by plotting the model residuals as Q-Q plots and against fitted values respectively, and used the weights =varPower() command in the *nlme* package to incorporate heteroscedasticity in the LMMs when required.

7.4 Results

There was a significant negative association between the timing of singing events by wood warbler and wren within 60 s segments of acoustic survey ($\chi^2_{(N=152)}$ =6.90, p=0.009), with less temporal overlap in singing events than expected by chance. However, the song rate of wood warbler (the total time singing within 60 s segments) was not significantly affected by the song rate of wren (Fig. 7.3a) and *vice versa* (Fig. 7.3b). There was no association between the timing of singing events in chiffchaff and great tit ($\chi^2_{(N=293)}$ =0.29, p=0.590), but the song rate in chiffchaff negatively affected the song rate of great tit (Fig. 7.3d). By contrast, the song rate of chiffchaff was unaffected by that of great tit (Fig. 7.3c). This effect of chiffchaff on great tit song rate was very similar amongst all sites where the species co-occurred (Fig. 7.3d). There was also a significant negative association between the timing of singing events in wren and those of chiffchaff ($\chi^2_{(N=1382)}$ = 33.29, p<0.001), and the song rate of chiffchaff was negatively affected by that of wren (Fig. 7.3e). This affect was negative at all sites where the two species co-occurred and sang together, although the magnitude of the effect differed amongst sites (Fig. 7.3e). There was no effect, however, of song rate in chiffchaff on the song rate of wren (Fig. 7.3f).

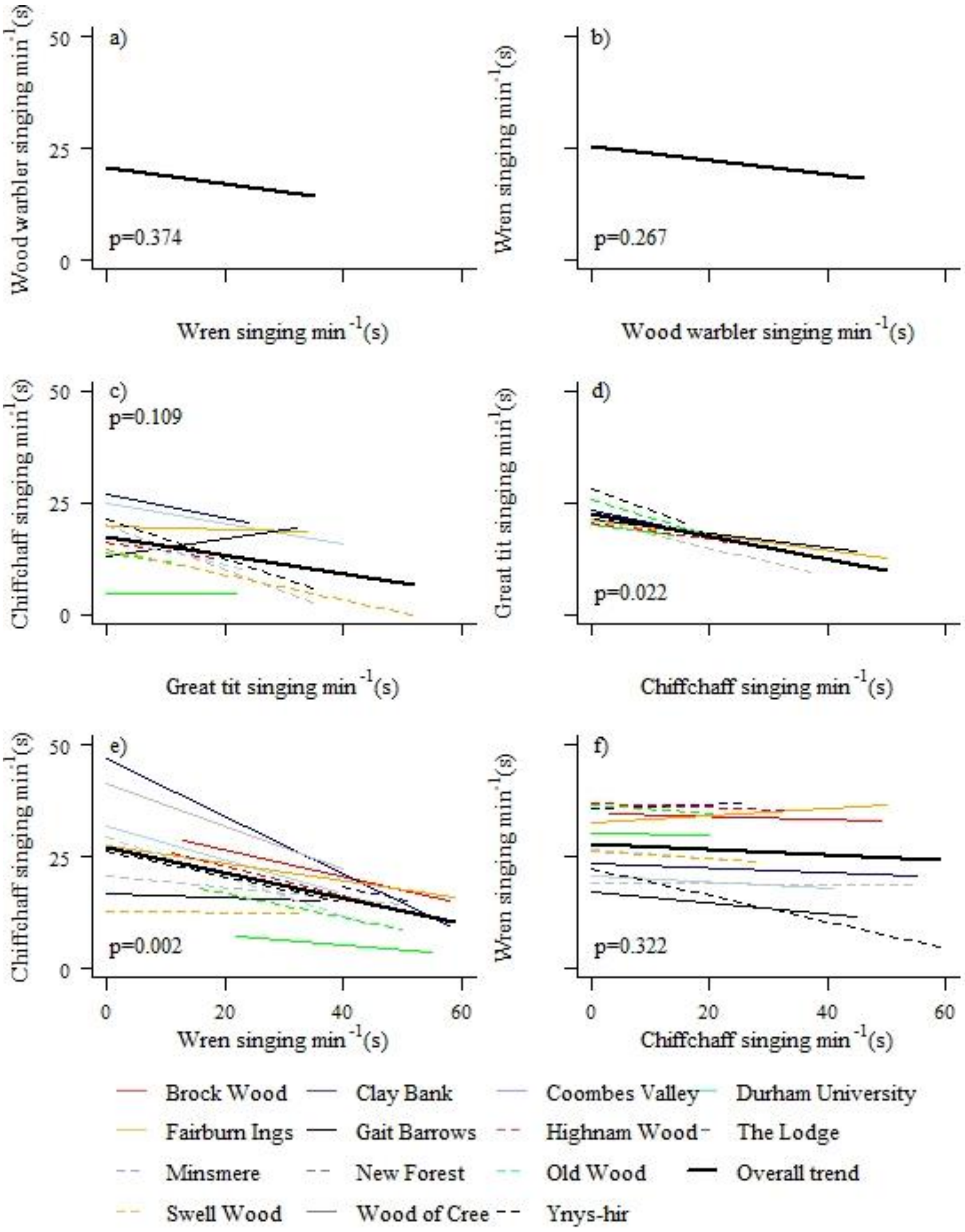


Figure 7.3 The effect of song rate (total time singing) of a species in a resident-migrant pair on the song rate of the other species in the pair per 60 s segment of acoustic survey made during the dawn chorus at a total of 20 mixed deciduous woodland sites throughout Great Britain. Trend lines show the effect of each species whilst accounting for the effects of date, time relative to sunrise and year, as modelled by linear models (LMs; a-b), or, where the paired species co-occurred at multiple sites, by linear mixed effects models (LMMs; c-f). In c-f, the trend for each site is also shown. P values relate to the significance of the overall trend in respective models.

7.5 Discussion

The avian dawn chorus is the best known example of animal acoustic communication undertaken amid a background of communications from heterospecifics. Birds participating in the chorus must compete for acoustic space to maximise the chances of their signal being received and correctly interpreted by the intended recipients. Competition for acoustic space may be particularly problematic for migratory species arriving after residents have settled onto territories and have established relationships with existing neighbours, especially if the properties of the migrant's song closely match that of a competing resident. Using PAM, I investigated the effect of song produced by two closely-related migratory species, wood warbler and chiffchaff, on the singing behaviour of resident species with similar song traits, and *vice versa*, during the dawn chorus at woodland sites throughout Great Britain. I found evidence of competitive interactions between all three resident-migrant species pairs tested.

My results indicated a reciprocated temporal avoidance of song in wood warbler and wren. Temporal overlap in the song of the two species was significantly less than if they were singing indiscriminately with respect to one another. However, each species' song rate (the total time singing per 60 s of acoustic survey) was not significantly affected by the song rate of the other species, although the trend in both cases was negative (Fig. 7a-b). This might indicate that the two species were capable of alternating their songs in an efficient manner, so as they both inserted their song into the refractory periods of the other, with neither species dominating proceedings. Additional work, applying my methods to a larger sample size, may be required to confirm this relationship. Co-ordinated choruses amongst heterospecific birds are not unrealistic, however. Indeed, multi-species avian choruses have been described within species-rich tropical systems (e.g. Planqué and Slabbekoorn, 2008; Tobias et al., 2014). The phenomenon has also been tentatively suggested in a temperate system by Malavasi and Farina (2013), who hypothesised that species competing for acoustic space during the dusk chorus in an Italian oak wood, intentionally fine-tune the timing of song, such that temporal overlap occurred with heterospecific song, but frequency overlap and spectral masking was avoided. The two species here, however, co-occurred and regularly sang at just one study site (Inversnaid), where a relatively low number of resident species was recorded.

Early experimental work on temporal avoidance of song, likely failed to account for the non-independence of singing events (e.g. Ficken et al., 1974). The length of refractory periods, the gaps between singing events, can be relatively constant in some species (e.g. Lemon and Chatfield, 1971), and, therefore, if an individual begins a singing event within the refractory period of another, this could explain the pattern of alternating song throughout the rest of the song bout (Planck et al., 1975). However, despite this criticism, such alternating song is regularly cited as a reliable example of temporal acoustic partitioning in birds.

Unlike the relationship reported for the wood warbler and wren, chiffchaff and great tit apparently sang indiscriminately with respect to one another, despite their spectral and temporal similarities (Fig. 7.1; Fig. 7.2). However, great tit song rate was significantly negatively affected by chiffchaff song rate (Fig. 7.3d), and the magnitude of this relationship was constant amongst all sites where the species co-occurred (Fig. 7.3d). By contrast, the song rate of chiffchaff remained unaffected by that of great tit, although the relationship was negative at most study sites (Fig. 7.3c). This combination of outcomes is challenging to interpret. Great tit certainly appeared to sing less when chiffchaff was singing, but did not avoid temporal overlap. It may be that chiffchaff often sang indiscriminately in respect of great tit, and the length of its singing events and refractory periods varied (perhaps in response to a third competitor), thus, making it difficult for the great tit to predict when to begin singing and avoid acoustic masking.

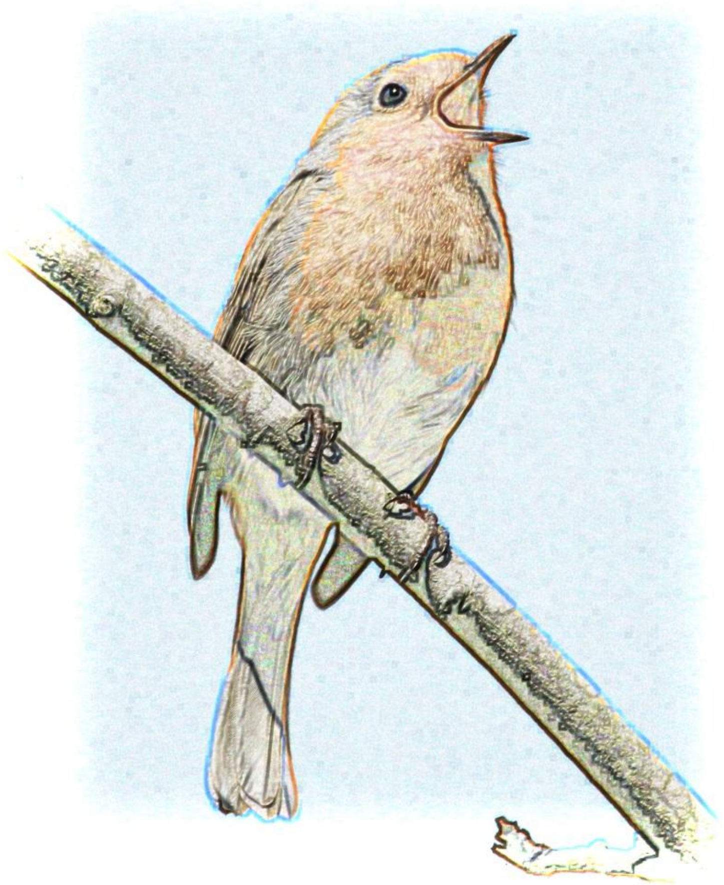
Temporal overlap in the songs of chiffchaff and wren was significantly less than expected by chance. Chiffchaff song rate was significantly negatively affected by wren song rate, but the reverse was not true, perhaps suggestive of vocal dominance by wren. These respective trends were evident at most study sites (Fig. 7.3e-f). At sites where they co-occurred, wren was likely singing closer to optimal rate (unless it was also competing with a third species), and chiffchaff at sub-optimal rate. Therefore, chiffchaff song rate was more adversely affected by competing wren song than by that of great tit, although chiffchaff song is better matched spectrally and temporally to the latter (Fig. 7.1; Fig. 7.2). However, from a distance of 1 m, the sound pressure level of wren song is around 10 dB higher than chiffchaff (Brackenbury, 1979). This, coupled with considerable spectral overlap in the two species' songs (Fig. 7.2), may explain these results, and highlights that song amplitude also needs to be considered in singing interactions amongst heterospecifics. The relationship found here between chiffchaff and wren is comparable to that reported by Ficken et al. (1974), where red-eyed vireo dominated singing interactions with least flycatcher, in one of the only prior studies that have tested competition for acoustic space in entirely free-living birds.

When analysing acoustic surveys, the distance of a bird from a potential competitor could not be gauged, and individuals of the same species were not discriminated. This might impose some limits on interpreting my results. Nevertheless, my use of PAM ensured that birds were singing openly, and that they produced a natural response to interference from competitors. These circumstances may not be possible to recreate using playback of a stimulus song, as prior studies (e.g. Brumm, 2006; Popp et al., 1985).

To conclude, the arrival of migratory birds back to their breeding grounds appears to cause resident species with similar song traits to adjust their singing behaviour and song output. In return, migrants may also be compelled to sing at sub-optimal rates when competing for acoustic space with certain resident species. Woodland bird community composition in the UK and Europe is currently experiencing unprecedented change, partly due to contrasting responses amongst species to climate change, habitat-loss and other anthropogenic disturbances, not least, the opposing breeding population trends observed for long- and short-distance migrants (e.g. Both et al., 2010; Hewson et al., 2007; Leech and Crick, 2007; Sanderson et al., 2006) and earlier summer migrant arrival dates (e.g. Cotton, 2003; Jonzén et al., 2006). Such community changes could, via acoustic competition, lead to unexpected consequences for species, which may not be intuitive, based upon more usual competitive interactions, resulting in altered fitness.

Chapter 8

The effect of advancing leaf-out phenology on breeding bird song



European robin *Erithacus rubecula*

8.1 Abstract

Temperate woodland birds exhibit extreme flexibility in delivery and perception of song, permitting long-distance communication amidst changes to the acoustic environment. One such annual change in temperate woodlands is with leaf-out of foliage each spring. These changes coincide with the core breeding period and consequent seasonal peak in singing activity. Recent climate-driven advances in leaf-out phenology may have introduced an additional impediment to long-distance communication, leading to information-loss between the signaller and intended recipients at critical stages in the reproductive cycle, with potential fitness consequences for the individuals involved. To estimate aural attenuation, I broadcast artificial test sounds (of frequencies commonly utilised by birds in temperate woodland habitat) and the song of three European woodland bird species (northern wren *Troglodytes troglodytes*, European robin *Erithacus rubecula* and common chiffchaff *Phylloscopus collybita*) each day from budburst through to leaf maturation. The attenuated sounds were recorded by microphones situated at different heights and increasing distances from the loudspeaker. However, because of time constraints, I analysed attenuation in the recorded artificial test sounds only. I modelled the day-to-day attenuation during leaf-out using linear models (LM). I then determined the level of attenuation eight days into the leaf-out period, as this is the average advance of leaf-out phenology in Europe since 1971, and attenuation at this point represented the level experienced by birds if they have not advanced their seasonal singing activity to the same degree. Although statistically significant linear changes in sound attenuation were recorded with leaf-out, the effect size was small, amounting to a mean of 1.13 dB loss of energy when microphones were situated at a height of 1.5 m, and 0.46 dB gain in energy when microphones were situated at 5 m, across all frequencies and distances from budburst through to leaf maturation. Consequently, the level of attenuation eight days into the leaf-out period was also low. The rate of attenuation during the leaf-out process was similar amongst frequencies and distances, although there was an indication that higher frequency (8000 Hz) test sounds attenuated at a greater rate at far distance (60 m). Attenuation of sound changed linearly with leaf size and density during the leaf-out period in deciduous woodland. The effect was dependent on the height of the receiver, however, and results indicate that birds may counteract the negative effect of increasing foliage on sound transmission during leaf-out by adjusting their position in the canopy.

Current advances in leaf-out phenology are unlikely to cause undue attenuation of song in the early stages of the breeding season in European birds for most species. However, there could be greater effect on other measures of sound degradation that require further investigation, as increasing foliage may negatively affect long-distance communication in birds, not by a reduction in amplitude, but through temporal adjustments in sound, whereby syllables in song become indistinct through increased reverberation of sound (i.e. ‘blurring’). This chapter presents preliminary findings, and further work will measure attenuation in the recorded playback of the three bird songs, and will analyse the effect of leaf-out on additional measures of sound degradation.

8.2 Introduction

Birdsong is a highly elaborate form of acoustic signal transmitted within and between species (Becker, 1982), and is critical in the reproductive period of passerine birds, when its intricacies encode information concerning the location, identity, social status, fitness and reproductive state of the signaller (Holland et al., 1998; Naguib et al., 2019, 2011). In order for the benefits of song to be fulfilled, song must be audible and interpretable to the intended recipient. Song structure, however, is modified by the environment during transmission between signaller and receiver, and if this leads to information-loss, there may be fitness consequences for the individuals involved (Badyaev and Leaf, 1997). Information-loss could be accentuated by habitat-change, land degradation and climatic change if these processes alter the environmental conditions from those within which signals have evolved (Farina and Pieretti, 2014). For example, if birds have not adjusted seasonal peaks in song production to match climate-driven advances in leaf-out phenology of woodland trees, song could suffer from increased attenuation at crucial stages in the reproductive cycle, potentially affecting breeding demography.

The effect of habitat structure on the structure and transmission of birdsong is well documented (reviewed in chapter 2, section 2.7), where one of the most significant factors is sound attenuation. In natural habitats, attenuation is expected to increase with the presence and density of foliage (Bradbury and Vehrencamp, 1998; Wiley, 1991; Wiley and Richards, 1982, 1978), although the precise relationship is dependent upon the sound’s frequency, as, somewhat paradoxically, foliage may exert an amplifying rather than an attenuating effect on low to mid frequency sounds under certain conditions (Martens, 1980). As such, temperate woodland birds are potentially exposed to erratic changes in the acoustic properties of their environment within the breeding period, as the leaf-out process in trees and seasonal growth of herbaceous vegetation often coincides with the seasonal peak in singing activity. Indeed, Apol et al. (2018) propose that species living within habitats with seasonal variation in structure have evolved diverse call repertoires in order to counter these changes. Several experiments have demonstrated that sound transmission is compromised following leaf-out in wooded habitat (reviewed in chapter 2, section 2.7). Increases in attenuation post leaf-out serve to reduce the operative distance of a signal (Blumenrath and Dabelsteen, 2004). A potential solution for the signaller and/or receiver is to adjust perch height in the understory or canopy (Blumenrath and Dabelsteen, 2004; Henwood and Fabrick, 1979; Mathevon et al., 1996), as the formation of an 'acoustic channel' between the canopy and understorey vegetation at this time can counteract the negative effect of attenuation, and may even amplify signal energy (Morton, 1975; Wiley and Richards, 1982, 1978). However, these prior studies have compared attenuation only pre-budburst and post- leaf-out, with no study having examined the fine-scale and day-to-day change in attenuation as leaf-out progresses, or of potential non-linearity in attenuation related to the constantly changing size, shape, density and orientation of leaves.

Advances in leaf-out dates of temperate deciduous trees and earlier growing seasons in plants are amongst the most striking consequences of climatic warming on ecological systems (Hoegh-Guldberg et al., 2018; Menzel et al., 2006; Post et al., 2001). Indeed, trends in leaf-out and flowering in Europe show an evident advance of 2.5 d decade^{-1} (0.25 d yr^{-1}) during the period 1971-2000 (Menzel et al., 2006). It is widely acknowledged, however, that advances in phenology have been greater in some taxonomic groups than in others, and that advances in higher trophic levels have lagged behind those made by primary producers over comparative time-scales (Both et al., 2009; Visser et al., 2012). This disparity has caused mismatch in the lifecycles of organisms and their food supply (Visser et al., 2012, 1998). A particularly well-documented example is advancing leaf-out in deciduous trees, the timing of peak caterpillar emergence, and the reproductive phenology of insectivorous woodland passerines, where emphasis is placed on egg-laying dates of the birds (e.g. Visser et al., 1998). The effect of phenological changes on other reproductive behaviour in birds, however, is little known. Here, I aim to explore the potential impact of advancing leaf phenology on the acoustic environment experienced by breeding birds.

Sequences in peak singing activity are intricately linked to the reproductive cycle of passerines (Naguib et al., 2019; Slagsvold, 1977), and males of many species sing most intensely at dawn during the strategic periods of territory establishment and mate attraction, as well as immediately prior to the egg-laying stage of their mate (Møller, 1991). Mismatch in leaf-out phenology and peaks in song production may force signallers and receivers to adjust their respective strategies in order to maintain long-range communication, potentially at a cost to individual fitness (Blumenrath and Dabelsteen, 2004), and may even lead to more physical encounters with individuals encroaching into apparently unoccupied territorial peripheries. As the recent advances in temperate leaf-out phenology are on a scale of 1-2 weeks, it is important to understand what effect, if any, these changes have on song attenuation and degradation if birds are not advancing breeding, and thus singing behaviour, to the same degree.

I devised a dawn playback experiment to measure day-to-day attenuation in artificial pure-tone test sounds of five different frequencies typical of songs of temperate woodland birds. I recorded attenuation across the period of budburst through to leaf maturation in canopy trees. I estimate the day-to-day attenuation in the sounds according to frequency and propagation distance in the woodland as the leaf-out process progresses, and test whether the position of the sound's source and receiver during this process affected sound attenuation. Finally, I demonstrate how, in cases where avian breeding phenology has not kept pace with leaf-out, dawn song may already be subject to changes in attenuation at critical stages in the reproductive cycle.

8.3 Methods and materials

8.3.1 Study site

The experiment was conducted at Blaid's Wood, Durham, UK (54° 45' 21" N, -1° 34' 4" E), in a 120 m × 60 m block of semi-natural mixed deciduous woodland habitat. The dominant canopy species were sycamore *Acer pseudoplatanus* (60% cover), beech *Fagus sylvatica* (8%), wych elm *Ulmus glabra* (8%), ash *Fraxinus excelsior*, sessile oak *Quercus petraea* and grey alder *Alnus incana* (all 6%). The height of the canopy averaged 22 m, and started 8-10 m above ground level. The mean trunk circumference of the canopy trees at breast height (1.5 m) was 141 cm (range: 42-320 cm), and the inter-tree spacing at ground level averaged 3.8 m (range: 2-6.5 m; detail provided in Appendix C.1). The understory consisted of hazel *Corylus avellana*, holly *Ilex aquifolium* and hawthorn *Crataegus monogyna*, along with saplings and young individuals of the canopy species. The herbaceous layer was dominated early in the study period by wood anemone *Anemone nemorosa* and, to a lesser extent, lesser celandine *Ficaria verna*. These species increasingly gave way to abundant bluebell *Hyacinthoides non-scripta*, dog's mercury *Mercurialis perennis* and bracken *Pteridium aquilinum* growth as the study period progressed.

8.3.2 Microphone and recorder calibration and set-up

To record playback of test sounds at the study site, I used 18 × Song Meter 2+ (Wildlife Acoustics, Inc, Maynard, USA) autonomous acoustic recorders (ARUs), each fitted with a single omni-directional all-weather microphone (SMX-II; Wildlife Acoustics, Inc, Maynard, USA) with a typical sensitivity of -35 to -43 dBV/pa and a frequency response of 20 Hz–20,000 Hz (Sebastián-González et al., 2015; Turgeon et al., 2017). I calibrated all ARUs and microphones prior to deployment using a Nor1251 acoustic calibrator (Norsonic AS, Tranby, Norway) modified to emit a 65 dB tone; all microphones used in the playback experiment returned a gain value of between -15 dB and -18 dB, which was a measure of the microphones' responsiveness, with higher values reflecting a greater response to sound. To measure the recording ability of the ARUs, a microphone that returned a gain value of -15 dB was plugged in to each channel of each ARU in turn, and the test tone played via the calibrator. Readings were taken from the root-mean-square voltage (V_{rms}) signal level shown on the LCD screen of the ARUs. ARUs that returned lower V_{rms} were paired with microphones that returned higher gain readings, and *vice versa*, so that the overall performance of the ARU/microphone pairs were comparable. ARUs were configured to record in mono, with a sample rate of 16000 Hz and 16-bit encoding. No high-pass or band-width filters were applied. ARUs were arranged into three linear transects (six ARUs per transect) emanating from a common 'base-point' within the study site, and leading in different directions through the woodland (Fig.8.1). Within each transect, ARUs were placed as close as possible to 15 m, 30 m and 60 m from the base-point, which I refer to as 'near', ‘mid’ and ‘far’ localities from hereon (Appendix C.2 provides distances to nearest 1 m). These distance bands were chosen to reflect typical territory diameters, and fractions thereof, of many small woodland passerines (e.g. Blumenrath and Dabelsteen, 2004; Brenowitz, 1982a; Dabelsteen et al., 1993; Holland et al., 1998). For example, mean core territory size of blue tits *Cyanistes caeruleus* and great tits *Parus major* (two of the most frequent woodland passerines) have been estimated at *ca.* 5000 m^2 and 6700 m^2 respectively (equating to circular ranges of radii 40 m and 50 m (Krebs, 1971). At each distance, two ARUs were deployed, one being set at 5 m, and another at 1.5 m above ground level within each transect, representing typical signaller and receiver positions of many woodland bird species (e.g. Blumenrath and Dabelsteen, 2004; Holland et al., 1998, 1998; Polak, 2014). ARUs were positioned so that microphones were facing towards the base-point, and all remained in their respective positions throughout the study period.

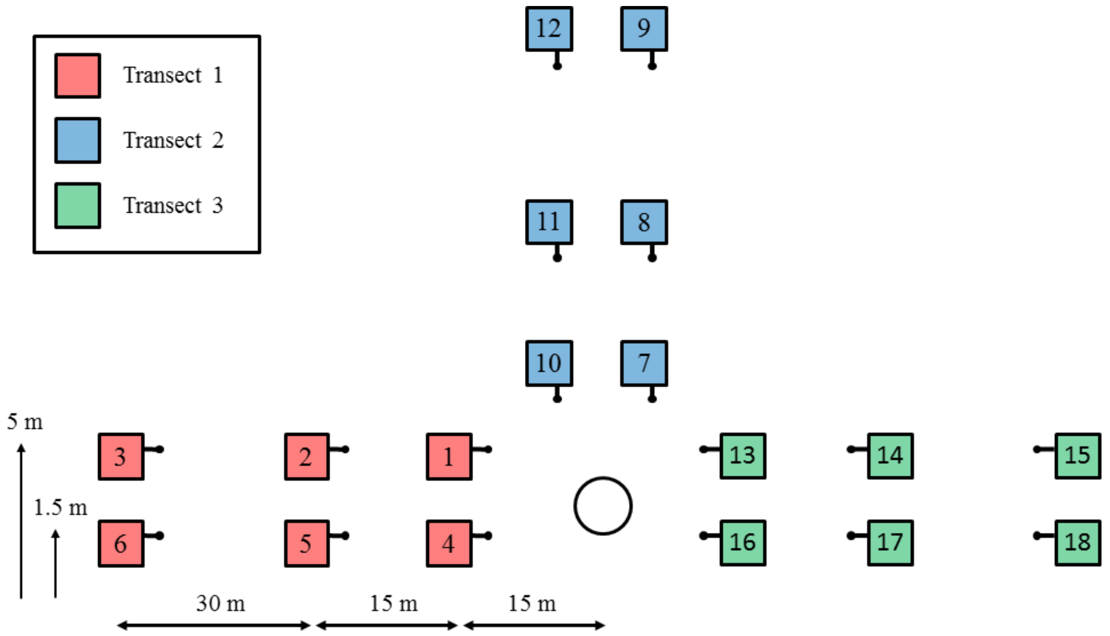


Figure 8.1 Positioning and numbering of autonomous acoustic recorders (ARUs) attached to trees within the study site. Three transects of six ARUs radiated from a common 'base-point' (open circle), where the loudspeaker was located. Within transects, three ARUs were placed at 5 m, and three at 1.5 m, above ground level. Distances shown between ARUs and base-point are approximate and not to scale, and were similar for all transects (Appendix C.2).

8.3.3 Test sounds and playback

I generated five × 3 s sine wave pure-tones of frequencies 500 Hz, 1000 Hz, 1500 Hz, 4000 Hz and 8000 Hz as .wav files from www.audiocheck.net, and converted them to mp3 format for use as test sounds in the playback experiment. The five tones represented the dominant frequency bands of song in European temperate woodland passerines (chapter 2, Fig. 2.2 and Fig. 2.3). I also downloaded from the xeno-canto online repository (https://www.xeno-canto.org/) a high-quality example of song by three common European woodland bird species for use as test sounds in the playback experiment: northern wren *Troglodytes troglodytes*, European robin *Erithacus rubecula* and common chiffchaff *Phylloscopus collybita*. Playback of the test sounds was performed using an M-Audio AV30 speaker with built in pre-amp (M-Audio, Cumberland, Rhode Island, USA) attached to an Edirol R-05 mp3 player (Roland Corporation, Osaka, Japan). The peak sound pressure level of song in European woodland passerines has been shown to vary between approximately 75 dB at 1 m for goldcrest *Regulus regulus* to 100 dB in song thrush *Turdus philomelos* (Brackenbury, 1979). In order to replicate this, test sounds were played-back at amplitudes ranging from 85 dB for the 500 Hz tone to 100 dB for the 1500 Hz tone, as measured at 1 m prior to playbacks using a Decibel X Pro v6.2.3 sound pressure level meter (Skypaw Co., Ltd, Hanoi, Vietnam) for iphone, with A-weighting frequency filter.

Playback of the test sounds took place from 16th April to 21st May 2018, which captured all stages of leaf growth from budburst through to leaf maturation in the dominant tree and understory species within the study site. It also covered the period of growth and flowering of the dominant herbaceous understorey vegetation. A reference playback of unattenuated test sounds, to which attenuated test sounds were compared in subsequent sound analysis, was made at the beginning of the study period (16th April), 1 m from an ARU, and with the speaker at the same height as the reference microphone (1.5 m). Playback was then carried-out with the speaker facing towards each transect in turn, once with the speaker at 1.5 m height, and again with the speaker at 5 m height. Playback was initiated and completed within the 1 hr period following sunrise each day. This meant that environmental conditions were similar to those of the dawn chorus whilst avoiding the main dawn chorus itself (which diminished markedly at sunrise during this period), which may have unduly masked the test sounds. The test sounds were played-back in the same order each day, and the order of transects was kept constant throughout the study. The primary abiotic factors known to attenuate sound are temperature, wind and humidity (Henwood and Fabrick, 1979), though wind effects tend to dominate when present (Attenborough, 2014). To minimise the effect of wind, therefore, playback was limited to mornings when wind-speeds were $\leq$ 5 kmph, as measured using a handheld anemometer (Technoline EA-3010, TechnoTrade Import-Export GmbH, Berlin). Playback was also avoided during precipitation, as rain imposes considerable constraints on sound transmission (Lengagne and Slater, 2002). I measured temperature and humidity at 5 min intervals throughout the study period using a Tinytag Plus 2 TGP-4500 data logger (Gemini Data Logger Ltd, Chichester, UK) placed 5 m above ground level.

8.3.4 Sound analysis

Due to time constraints, I analysed attenuation only in the five artificial pure-tone test sounds. I analysed the playback recordings of attenuated test sounds made by the ARUs, and the unattenuated reference playback by viewing spectrograms on Raven Pro v1.4 software (The Cornell Laboratory of Ornithology, Ithaca, USA). Spectrograms were configured with a Hann window and a Fast Fourier Transform (FFT) size of 256 samples, corresponding to a frequency resolution of 62.5 Hz with a sampling rate at 16 kHz. Brightness and contrast controls were set to 65%. Selections (*i.e.* time-frequency rectangles) were made around individual test sounds on the spectrograms, spanning the full 3 s duration of the sound along the time axis, and +/-25 Hz either side of the sound's peak energy frequency on the frequency axis (e.g. 475 Hz to 525 Hz for a 500 Hz test sound). The average power (dB) within the selection was recorded, which was the sum of the selection's power spectral density divided by the number of time-frequency bins in the selection (Charif, et al., 2010). The average power recorded in the attenuated test sounds was subtracted from the average power in their respective unattenuated reference sounds to obtain measurements of total attenuation. Unlike some studies, I did not subtract the predicted attenuation by spherical spread to obtain EA values (e.g. Blumenrath and Dabelsteen, 2004; Marten and Marler, 1977; Naguib, 2003). This was because calculations of spherical spread assume that sound is radiating equally in all directions (Attenborough, 2014), and ignore ground effects, which are the result of interference between sound travelling directly from the source to the receiver, and sound reflected from the ground, when both source and receiver are close to the ground (Attenborough, 2014), as in my study design. Furthermore, calculated values of spherical spread are constant for a given distance from the source, and change in day-to-day attenuation at a particular receiver (which was the focus of my study) would have been unaffected by the subtraction of attenuation by spherical spread. I did, however, calculate estimates of attenuation of the test sounds due to air absorption at each microphone distance from the speaker, as this would have differed on a daily basis. I used air temperature and relative humidity measurements, collected on each day of the experiment, to calculate air absorption using http://www.sengpielaudio.com/calculator-air.htm (as ISO 9613-1:1993), and subtracted the resultant value from the total attenuation figures. In addition to measuring the power within the test sounds, I measured the stationary background noise underlying each test sound by making additional 3 s time-frequency selections of the spectrogram immediately prior to, or immediately following (whichever best matched the background noise underlying the test sound), the respective test sound, and which matched the frequency range of the test sound.

8.3.5 Statistical analysis

All statistical analyses were carried-out in R (v3.5.2; R Core Team, 2018). Initially, to identify any potential non-linearity in the relationship between the number of days since budburst (hereafter ‘day’) and attenuation of the test sounds, I applied generalised additive models (GAMs) to the dataset using the gam() function in the *mgcv* package (v1.8-28; Wood, 2019). I constructed two models, one that varied the effect of day on attenuation by distance category (hereafter ‘distance’), and another that varied the effect of day by the frequency of the test sound (hereafter ‘frequency’). Background noise was included as an additional smoothed term in both models, and the categorical variables distance, frequency, microphone height and loudspeaker height were included as linear terms. Automatic smoothing in the GAMs, however, forced linear fits to the effect of day on attenuation for all distance categories (Appendix C.3, Fig. C.1), and likewise for most frequencies (the effect of day on the 4000 Hz frequency test sound showed non-linearity, but was not significant at the 5% level, and, thus, there was no certainty as to the shape or direction of the effect; Appendix C.3, Fig. C.2). I therefore, applied linear models (LM) to the dataset using the lm() function in the *stats* package of base R. LMs offer increased flexibility over GAMs when adding multiple and higher-order interaction terms, and are less prone to over-fitting. The initial LM consisted of the main effects of day, distance, frequency, microphone height, loudspeaker height and background noise, along with all second-order interactions. I then used the dredge() function in the *MuMIN* package (v1.42.1; Barton, 2018) to fit all possible models, and compared models using AIC (Burnham and Anderson, 2002). I performed model averaging using the mod.avg() function in the *MuMIN* package, considering all models simpler than the top model with ΔAIC <6, and took the significant effects ($p \leq 0.05$) in the full average model to be my final model variables. I kept the main effect of a variable if it was included in a significant interaction term. I confirmed that normality and homoscedasticity assumptions were met by plotting the model residuals as Q-Q plots and against fitted values respectively.

8.4 Results

The variables included in the final averaged model testing for the effect of the number of days since budburst on attenuation of the test sounds are listed in Table 8.1

(coefficients are provided in Appendix C.4). Distance and tone frequency, and their interaction terms, had most influence on attenuation of the sounds, as would be expected following acoustic theory. Days since budburst had a significant effect on the level of attenuation in the sounds (Table 8.1). However, the effect differed depending on microphone height; attenuation increased with day when microphones were placed at 1.5 m, but decreased (i.e. sound became progressively amplified) when microphones were placed at 5 m (Table 8.1, Fig. 8.2). Across all frequencies and transmission distances, these opposing responses amounted to a mean change in attenuation of 1.13 dB and -0.46 dB during the entire leaf-out period, and 0.24 dB and -0.10 dB during the first 8 days of leaf-out, for microphones situated at 1.5 m and 5 m respectively (Fig. 8.2). The model selection process did not retain the second-order interaction terms day × frequency or day × distance (Table 8.1), as the effect of increasing day on attenuation was similar amongst the three distance categories (Fig. 8.3a), and amongst the different frequencies (Fig. 8.3b). However, there was a general trend of increasing attenuation with day detectable at far distance, where there was a mean difference in attenuation of 2.6 dB between the first and last day of the leaf-out process (Fig. 8.3a). This trend was similar for the 8000 Hz frequency, for which attenuation increased by a mean of 2.3 dB from budburst to full-leaf (Fig. 8.3b). The difference in attenuation at budburst versus that at full-leaf for each of the frequencies at each distance (not accounting for loudspeaker or microphone height) is shown in Fig. 8.4. The trend amongst frequencies was similar at all distances, although less pronounced at near distance. All trends amongst distances suggested that a ‘sound window’ existed between 1500 Hz to 4000 Hz in the study site at full-leaf, whereby sounds within this frequency range attenuated less than sounds outside of this range (Morton, 1975).

Table 8.1 The explanatory variables in a linear model (LM), following a model selection process guided by AIC, testing for the effects on attenuation of test sounds of five different frequencies broadcast through a loudspeaker at two heights (1.5 m and 5 m) and received by microphones located at three distance categories from the loudspeaker, and at two heights (1.5 m and 5 m), in a mixed deciduous woodland in Durham, UK, whilst accounting for the effect of background noise. *N*=4274.

Source of variation	df	Sums of squares	Mean squares	F
Days since budburst (Day)	1	191	191	7.611
Distance category (Distance)	2	232589	116294	4629.221
Frequency of test sound (Frequency)	4	24902	6226	247.814
Microphone height	1	34	34	1.359
Loudspeaker height	1	2	2	0.060
Background noise	1	189	189	7.540
Day × Microphone height	1	174	174	6.944
Backgound noise × Distance	2	72	36	1.430
Distance × Frequency	8	6285	786	31.274
Frequency × Microphone height	4	2839	710	28.256
Frequency × Loudspeaker height	4	1115	279	11.096
Microphone height × Loudspeaker height	1	194	194	7.7165

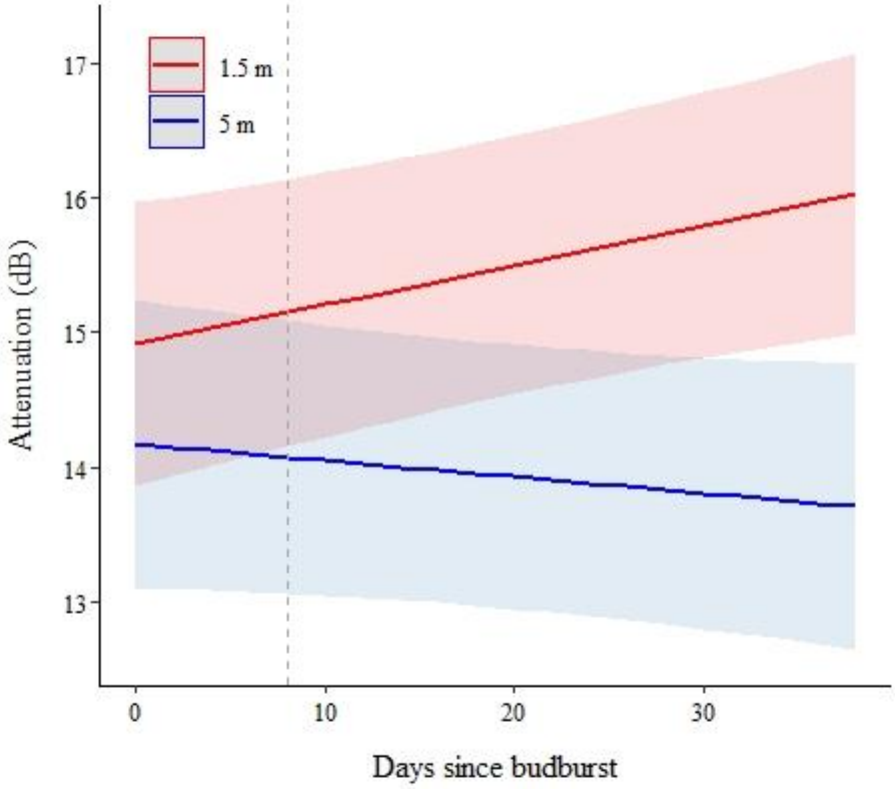


Figure 8.2 The attenuation of acoustic energy according to the height of receiving microphones amongst five pure-tone test sounds of frequency 500 Hz, 1000 Hz, 1500 Hz, 4000 Hz and 8000 Hz broadcast through a loudspeaker in a mixed deciduous woodland in Durham, UK during the leaf-out period in the trees, from budburst to full-leaf. Microphones were placed in three distance categories from the loudspeaker. Dashed vertical line at day 8 denotes the estimated advance in leaf-out phenology in European deciduous trees during the period 1971-2000 (as Menzel et al., 2006), and highlights the maximum change in attenuation of birdsong, should birds not have advanced their reproductive cycle, and hence, singing activity, to the same degree.

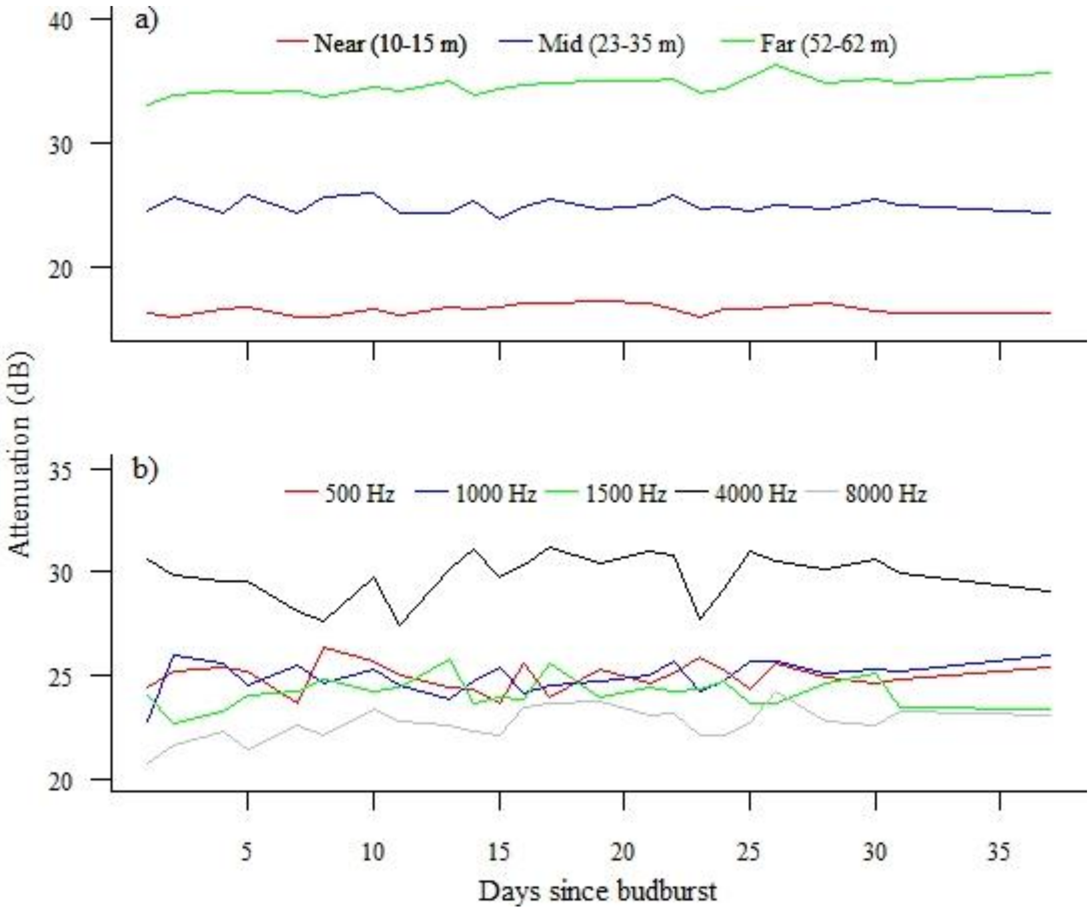


Figure 8.3 The attenuation in five pure-tone test sounds broadcast through a loudspeaker and recorded by receiving microphones located at three distance categories from the loudspeaker during the leaf-out period from budburst to full-leaf in the trees of a mixed deciduous woodland habitat in Durham, UK, according to a) microphone distance category, and b) frequency of the test sound.

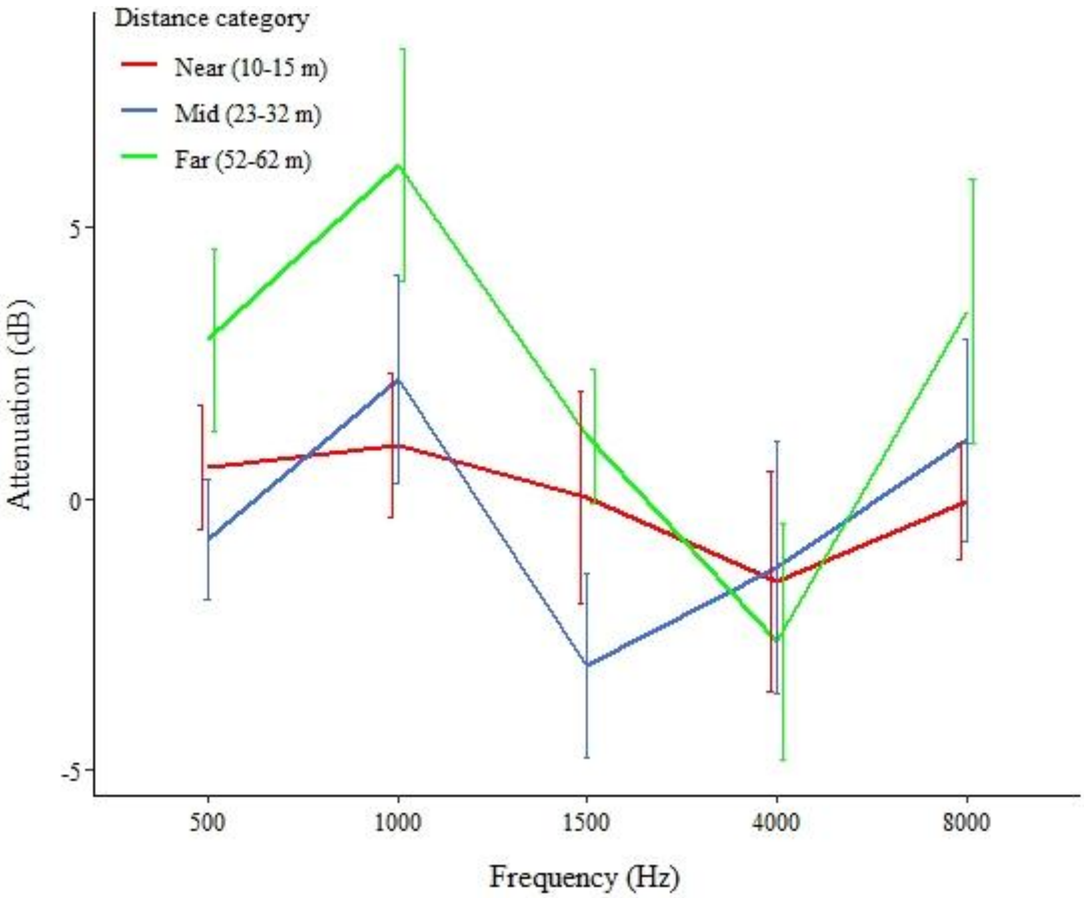


Figure 8.4 The difference between the attenuation of acoustic energy at budburst and the attenuation of acoustic energy at full-leaf in five pure-tone test sounds of different frequency broadcast through a loudspeaker (once at 1.5 m and once at 5 m) and recorded by six receiving microphones (three situated at 1.5 m height and three at 5 m) located at each of three distance categories from the loudspeaker in a mixed deciduous woodland habitat in Durham, UK. N=12 for each distance category. Error bars=±1SE. To avoid overlap, some error bars are shown off-centre from datapoints.

8.5 Discussion

Temperate woodland birds are exposed to significant changes to their acoustic environment as leaves unfurl and reach maturation in the spring. Climate-driven advances and alterations in leaf-out phenology may introduce additional attenuation of song at crucial stages in the reproductive cycle. By measuring day-to-day attenuation of energy in sounds of different frequency each dawn from budburst through to full-leaf, I show the progressive attenuation of sound during the full leaf-out process, and the potential effect of current advances in leaf-out phenology on the attenuation of song in temperate woodland birds.

The attenuation of broadcast pure-tone sounds was significantly affected by the number of days since budburst (Table 8.1; Appendix C.3). However, attenuation increased by a mean of just 1.13 dB across all frequencies and transmission distances during the leaf-out period , and only when the receiving microphone was situated at a height of 1.5 m (Fig. 8.2). When the microphone was situated higher, at 5 m above the ground, attenuation decreased by 0.46 dB as the leaf-out process progressed (Fig. 8.2). These values of attenuation induced by leaf-out in trees are comparable with those obtained previously for EA in great tit song (Blumenrath and Dabelsteen, 2004), where an increase in sound energy was also found following leaf-out at short transmission distances (*i.e.* 15 m).

The location of both signaller and receiver, with respect to the ground, temperature gradients, and other obstacles within the habitat, can affect the transmission of signals between them (Wiley and Richards, 1982, 1978). My results are congruent with prior studies that identify receiver height (e.g. Balsby et al., 2003; Dabelsteen et al., 1993; Marten and Marler, 1977), and/or source height (e.g. Mathevon et al., 1996) as factors affecting sound attenuation. In the context of my study, this means that as leaf-out progresses, it becomes increasingly advantageous for receivers to be located at 5 m above the ground, rather than at 1.5 m. As leaf-out proceeds in deciduous woodland, an ‘acoustic channel’ or ‘wave-guide’ (Wiley and Richards, 1982, 1978) may form between the canopy trees and understory shrubs, where sound attenuates less than at other heights (Morton, 1975). Under certain conditions, sound may even become amplified due to the accumulation of the direct signal, reflections from foliage and deflections from favourable temperature gradients (Wiley and Richards, 1982, 1978), such as those that persist at dawn (Wiley and Richards, 1982, 1978) and, as my results may infer, when trees are in full-leaf. Signaller and receiver may both take advantage of acoustic channels by adjusting their respective positions. Mathevon et al. (1996) stated that, ideally, both should be above the understory (e.g. 5 m) for horizontal rather than diagonal (e.g. either signaller or receiver at 1.5 m) sound transmission, when determining the optimal woodland singing height for northern wren *Troglodytes troglodytes*. However, this may not have been applicable at my study site, as results show that attenuation was greater when the loudspeaker was situated at 5 m height, and that this increased further if both the loudspeaker and microphone were at 5 m (Appendix C.3). This stresses that caution is advised when generalising on the sound properties of different woodland sites, which may differ with tree species composition, canopy and understory density, and topography.

Despite relatively minor losses (or gains) in acoustic energy across all distances and frequencies, there was a general trend for increasing attenuation with day at the far distance (Fig. 8.3a), and the 8000 Hz frequency sound (Fig. 8.3b). The effect of increasing distance on attenuation was greatest for the 8000 Hz sound (Appendix C.4), and although not tested statistically, the strength of this interaction may have increased as the leaf-out process progressed. The scale of energy-loss in the 8000 Hz frequency sound at far distance could have negative implications for fitness of signalling birds that regularly utilise this frequency (e.g. goldcrest, wood warbler *Phylloscopus sibilatrix* and some elements of northern wren and European robin *Erithacus rubecula* song; chapter 2, Fig. 2.2 and 2.3), if the operative distance of the signal is unduly reduced, potentially leading to missed mating opportunities or expenditure of energy actively chasing intruders or pursuing potential mates. Fitness of receivers, on the other hand, may be compromised if they are actively chased and attacked by signallers, or if they remain unaware of potential mating opportunities. However, extrapolation of data to produce accurate estimates of attenuation at operative distances beyond those for which measurements are made is difficult, as not only is attenuation by spherical spread non-linear, so is EA within heterogenous habitat (Aylor, 1972b).

Prior studies in fully-foliated wooded habitat have detected a characteristic dip in attenuation of frequencies between 1000 Hz and 2000 Hz when transmitted close to the ground (the ‘sound window’). Above this frequency range, attenuation essentially increases linearly with frequency (Embleton, 1963; Marten and Marler, 1977; Morton, 1975; Price et al., 1988), as higher frequencies are increasingly prone to interception and subsequent absorption by foliage and the atmosphere (Aylor, 1972b; Price et al., 1988). Indeed, I found that the 1500 Hz sound attenuated less at full-leaf than at budburst at mid distance (Fig. 8.4). At near and far distances, this phenomenon occurred most markedly in the 4000 Hz frequency. However, Marten and Marler (1977) state that the window may vary from site to site, occurring at greater frequency with transmission height above ground level, and that it may disappear altogether at greater heights. The labile nature of the window may explain this discrepancy.

My analyses did not detect any significant non-linearity in day-to-day attenuation during the leaf-out process (Appendix C.3), despite the complexity of the relationship between attenuation, frequency and distance (e.g. Blumenrath and Dabelsteen, 2004; Naguib, 2003), and the infinite number of potential modifications to sound and its transmission that might occur due to the changing size, shape and orientation of woodland foliage in the spring. Instead, the test sounds attenuated (or amplified) in a linear manner, and there was not, for example, an initial large effect immediately following budburst that subsequently subsided as leaves matured, or *vice versa*, for any sound frequency or at any transmission distance.

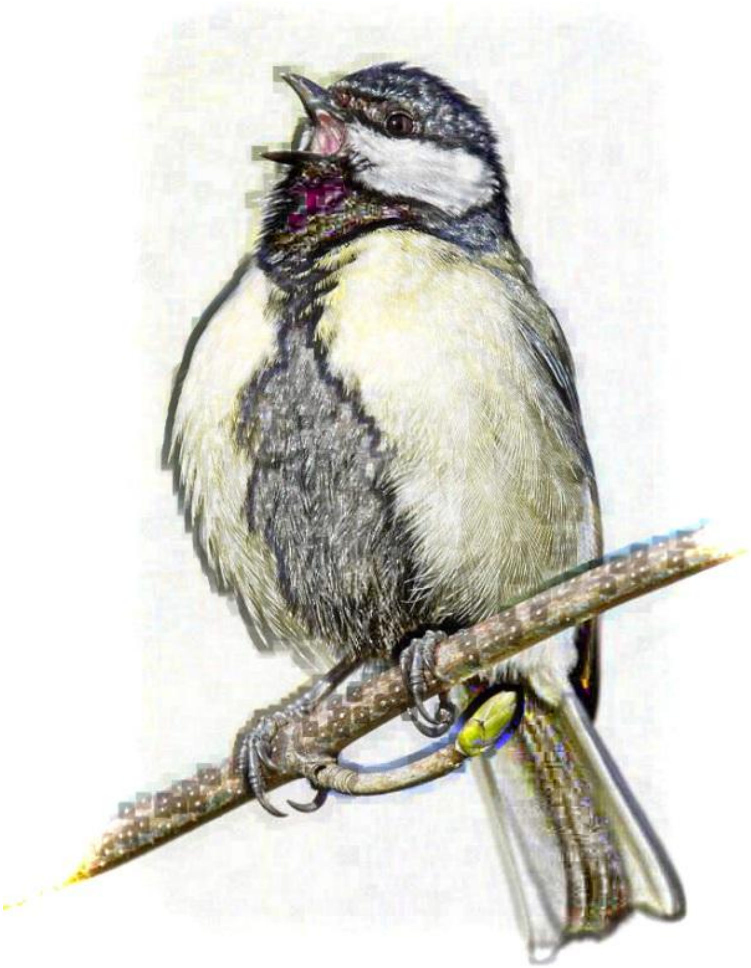
The predominantly shallow and linear increases/decreases in attenuation across the entire leaf-out process evidently translated into very small changes in attenuation of energy during the initial eight days of the process; the increase in attenuation during the initial eight days for receivers situated at 1.5 m was 0.24 dB, and 0.10 dB decrease in attenuation when at 5 m height (Fig. 8.2). Such small changes in energy are unlikely to translate into significant loss or gain in transmission distance. Each year, signalling birds must exhibit plasticity in singing behaviour, and receivers in song perception, in order for effective long-range communication to be maintained during the leaf-out period. This may include adjustment of perch height (Balsby et al., 2003; Dabelsteen et al., 1993; Mathevon et al., 1996; this study), increasing song amplitude (Brumm and Todt, 2002), or altering the frequency (Goodwin and Podos, 2013) or temporal aspects (Slabbekoorn and den Boer-Visser, 2006) of song. Assuming such plasticity exists in all birds, current advances in leaf-out phenology of 2.5 d decade^{-1} (Menzel et al., 2006) are unlikely to increase attenuation of song to a magnitude that unduly reduces the ability of birds to maintain long-range transmission during the breeding period. Furthermore, future advances in leaf-out phenology may not force greater attenuation of song, as current research suggests that advance in leaf-out of European trees has declined from 4 days °C^{-1} warming during the period 1980-1994, to 2.3 days during 1999-2013, and that further advance will become limited by warming-related reduction in winter chilling, and low light levels in early spring (Fu et al., 2015), although future responses may be species-specific (Flynn and Wolkovich, 2018).

It is important to stress that this chapter presents preliminary findings, and further work is required to measure attenuation during the leaf-out period in the recordings made of my three example bird songs (section 8.3.3). Use of pure-tones in my analyses demonstrated how frequencies regularly utilised by temperate woodland birds attenuated during the leaf-out period, but, whereas the tones are similar in structure to some whistle-like syllables in song (e.g. those of Eurasian blackbird *Turdus merula* and common nightingale *Luscinia megarhynchos*), they do not necessarily reflect the broad song structure of most species, which may consist of broad-band syllables (e.g. common chiffchaff *Phylloscopus collybita*), trills (e.g. northern wren) or large frequency shifts (e.g. common nightingale, European robin and song thrush). By focusing energy within a narrow frequency band, tonal sounds may attenuate more slowly compared to broad-band sounds. Indeed, Dabelsteen et al. (1993) found that the high-frequency ‘twitters’ in Eurasian blackbird song suffered greater attenuation than the low-frequency whistles. Analyses of authentic birdsong may show different trends in attenuation during the leaf-out period, or reinforce my results using tones. Further, some species sing from perches at higher elevations than those replicated in my study (e.g. common chiffchaff; Rodrigues, 1996). Martens and Marler (1977) found that artificial tones attenuate more substantially at a height of 10 m within in the canopy compared to lower heights in a woodland, so there might be a greater effect of advancing leaf-out phenology at these heights than was found in my study. Also, attenuation of energy is only one measure of degradation in birdsong. Foliage also causes reflections, reverberations scattering and frequency-dependent filtering, which accumulate with distance from the source (Bradbury and Vehrencamp, 1998), and manifest as changes to temporal and structural properties of sound (Morton, 1986). Calculation of day-to-day change in further measures of sound degradation may reveal consequences for birdsong under advancing leaf-out phenology not highlighted by attenuation alone. Finally, higher vegetation density at full-leaf would cause greater background noise from rustling leaves during wind. I purposely carried out playback on mornings with little discernible wind, but there could be an effect of earlier leaf-out on the degradation of birdsong due to the additional background noise in windier conditions.

In conclusion, my study found a significant, but weak, linear effect of day-to-day leaf-out on the attenuation of energy in tests sounds. The magnitude and direction of the effect was dependent on the height of the receiver, confirming that birds may, to some degree, counteract any negative effect of leaf-out on attenuation of song by adjusting perch height. Attenuation during the leaf-out process did not differ significantly depending on the sound’s frequency or the distance of the receiver from the sound’s source, although there was a signal that the effect was greater for the highest frequency at the furthest distance. Current advances in leaf-out phenology of 2.5 d decade^{-1} are unlikely to have had undue negative effect on the transmission of birdsong should birds not have advanced seasonal peaks in singing behaviour to the same degree. Further work using playback of authentic birdsong and/or playback at greater height in the canopy may, however, reveal a greater effect of advancing leaf-out phenology.

Chapter 9

General Discussion



Great Tit *Parus major*

9.1 Synthesis

In this thesis, I have applied state-of-the-art acoustic recording technology to further our knowledge of bird behaviour during the avian dawn chorus and to confront prior theory relating to the existence of the chorus. The dawn chorus presents the optimal challenge for automated computer-assisted signal recognition systems (‘recognisers’), and this work has served to underline that advances made in this field have failed to keep pace with those made in acoustic data collection, but that ecologists can improve performance by applying readily-available recognisers in novel ways. Using acoustic technology to build upon prior research, this project has identified, or emphasised, physical and behavioural adaptations made by birds, and constraints put upon them, as they endeavour to be heard and correctly interpreted amid the high background noise of the dawn chorus. Here, I briefly discuss the findings of this project in the context of three broad categories, two of which were introduced in chapters 2 and 3 – the ecology of the dawn chorus, and technological advances in the study of birdsong. The third category is one which underlies much of the thought and discussion throughout the thesis, and is the influence of environmental change on future dawn choruses and, in turn, the impact this may have on bird populations.

9.1.1 The ecology of the dawn chorus

Advances in acoustic technology now permit researchers, equipped with ‘big data’, to reaffirm, revise, refute or build-upon prior theory attempting to explain the avian dawn chorus. In chapter 6, I called upon an extensive dataset of acoustic surveys to re-visit the energy stochasticity hypothesis, and, specifically, to question the assumption that cooler overnight temperatures lead to delayed and reduced dawn singing activity (e.g. Hutchinson, 2002; Thomas and Cuthill, 2002). My interpretation of my results largely reinforced this assumption. Importantly, however, by applying the theory across multiple geographically and climatologically distinct sites simultaneously, I concluded that the magnitude of the effect of overnight temperature varied with latitude, and that variation may be linked to means and day-to-day variability in regional temperature regimes. This finding not only serves to illustrate that birds and their singing routines at dawn are very sensitive to fluctuation in climate, but also questions whether the assumption concerning overnight temperatures will still apply to future choruses when considering climate change (section 9.1.3), or whether the assumption currently applies at latitudes beyond those of Great Britain. Indeed, much of the theory surrounding the energy stochasticity hypothesis has been built upon observations made of bird communities in temperate regions (largely in the UK), and many empirical tests supporting the hypothesis (or assumptions thereof) have been carried-out on birds living at temperate latitudes (e.g. Barnett and Briskie, 2007; Gottlander, 1987; Reid, 1987; Thomas, 1999). At higher latitudes, where temperatures are cooler, but where overnight periods of darkness are very short or absent, and light cues to begin singing are not distinct, day-to-day variation in temperature and light levels may interact differently (cf. Brown, 1963; Da Silva and Kempenaers, 2017), and the latitudinal gradient in the response of the chorus to variation in overnight temperature, as observed in my results, may no longer apply. Whilst further south, for example, in Mediterranean regions, where the dawn chorus remains a prominent feature (e.g. Farina et al., 2011b), but where the lowest overnight temperatures may not limit dawn song output, variation in minimum overnight temperature may cease to affect chorus onset and peak.

Signalling and receiving birds possess strategies to help them maintain effective long-distance communication following changes to their environment. For example, by exhibiting plasticity in their physiology (e.g. Bednekoff et al., 1994) and behaviour (e.g. Brumm, 2006, 2004; Da Silva et al., 2016; Ficken et al., 1974; Mathevon et al., 1996). In chapter 7, I confirmed that acoustic competition amongst species is a common occurrence during the dawn chorus, as two from three migrant-resident species pairs exhibited some apparent negative effect of song in one species on the singing behaviour of the other. Some species may demonstrate fine-scale temporal partitioning of song (e.g. Brumm, 2006), a behaviour that I propose amongst free-living wood warbler *Phylloscopus sibilatrix* and northern wren *Troglodytes troglodytes* (chapter 7). Such behaviour, however, is typically more pronounced in tropical regions, where the number of species and individuals are greater and acoustic niches are narrower (e.g. Planqué and Slabbekoorn, 2008; Tobias et al., 2014), and has not previously been reliably recorded in free-living birds during the dawn chorus in temperate regions. I inferred a second example of behavioural plasticity in chapter 8, when I suggested that birds might adjust song perch height to take advantage of ‘acoustic channels’ or ‘wave-guides’ that form at certain heights in woodland as leaf-out in the canopy and understory progresses (Wiley and Richards, 1982, 1978).

Overall, this study emphasises a requirement to continue monitoring and asking questions of the dawn chorus, as alterations to its timing, magnitude and performance can serve as an indicator of bird population and community fitness, and act as a warning system for general ecosystem health. Furthermore, knowledge gained of the dawn chorus in birds can shed light on less-familiar choruses performed by other taxa, for example, primates (Schel and Zuberbühler, 2012), anurans (Narins et al., 2006), fish (Parsons et al., 2017) and insects (Young, 1981).

9.1.2 Technological advances in the study of bird song

The use of autonomous recording units (ARUs) in this study permitted collection of an unrivalled dataset of acoustic surveys of the avian dawn chorus collected simultaneously at multiple woodland sites throughout Great Britain. It was not an original intention of this project to devise novel methods for extraction of detailed species-specific information from these surveys, but instead, to use existing commercially- or freely-available recognisers. However, this proved to be an obstacle for the project, as, although current readily-available recognisers provide accessibility, they lack reliability, and return a large number of false positive detections, especially when applied to high noise environments, such as the avian dawn chorus. The ensemble approach to automated species identification and classification described in chapter 5, offers a simple, yet effective, solution. A central focus of this chapter was to propose the application of ensemble modelling methods (e.g. Araújo and New, 2007) to automated acoustic signal identification, and it should be stressed, that the ensemble need not include the same combination of recognisers as used in my study. Indeed, the ensemble approach can be extended beyond the dawn chorus and birds, to provide improved recognition accuracy for other sound-producing taxa. For example, the method may also be tested on bats. Current readily-available recognisers have particular difficulty in distinguishing uncharacteristic bat vocalisations, most notably, the echolocation calls of the various *Myotis* species (Rydell et al., 2017). However, the complication in automated classification of *Myotis* species lies not in masking background noise, as is often the case with birds, but in the high degree of variation and overlap in spectral parameters amongst the species' vocalisations, which may render identification impossible using acoustic methods alone (Rydell et al., 2017). Acoustic indices (AIs), introduced via the field of ecoacoustics, provide an alternative approach to the use of recognisers and species-specific identification. My use of the acoustic complexity index (ACI) in chapter 6 verified the efficacy of using this particular AI in studies of the dawn chorus (cf. Farina et al., 2011b), and potentially, of sound-producing animal communities more widely. I found that the ACI was capable of successfully identifying gradation and peaks in the complex soundscape of temperate woodland at dawn. In turn, the ACI can be a valuable tool in long-term monitoring programmes documenting changes to the composition and behaviour of bird communities (Farina et al., 2011b; Pieretti et al., 2011).

9.1.3 The influence of climate change on the dawn chorus

There is convincing evidence that birds are already being affected by climate change (reviewed by Crick, 2004; Møller et al., 2010; Pearce-Higgins and Green, 2014). Changes in population dynamics (Sæther and Engen, 2010), and to the distribution ranges of species (Brommer and Møller, 2010), will alter the composition of communities (Brotons and Jiguet, 2010), with indirect effects on the performance, timing and magnitude of the dawn chorus (Sueur et al., 2019). This project has highlighted some of these effects, as well as some more direct influences on bird physiology, influencing behaviour and decision-making during the dawn chorus. In chapter 6, I found evidence that the timing and peak of the chorus in Great Britain is controlled, in part, by overnight temperatures, and that this effect varied with geographical location. I concluded that higher temperatures led to earlier onset and peak, especially at higher latitudes, potentially prolonging chorus duration (although chorus duration was not recorded). I suggested that these effects may continue into the future until they no longer respond to variation in overnight temperature under the predicted temperature increases (Easterling et al., 1997; Stone and Weaver, 2002). This, in turn, might imply that dawn choruses could be less intense in future, whereby competition for acoustic space is reduced, with, perhaps, implications for the fitness of bird populations, as intense competition between species and individuals tends to select for fitter individuals. These ‘relaxed’ choruses need not be entirely negative, however. In chapter 7, I suggested that acoustic competition between species during the dawn chorus can lead to sub-optimal song rates in deferential species. Less intense choruses might allow these species to sing at greater rates, albeit, perhaps, not at the optimal time (e.g. if dawn song functions in mate guarding, and hence, timing is dictated by the behaviour of the female). That said, I also refer to the distinctive responses to climate change reported for short- versus long-distance migratory species (e.g. Both et al., 2010), and the effect this may have on community composition and acoustic competition amongst species; those species that benefit from climate change may extend their distribution range, and dominate acoustic space (Sueur et al., 2019). For example, the UK population of common chiffchaff *Phylloscopus collybita* has increased dramatically in recent decades (DEFRA, 2019), potentially in response to reduced winter severity in Europe (Tellería et al., 2016), and consequent reductions in migratory distances endured by individuals (Newson et al., 2016). An increase in chiffchaff density and range, and an apparent negative effect of this species' song rate on that of the resident great tit *Parus major* (chapter 7), may counteract any advantage associated with less intense choruses at dawn for the great tit. I also concluded that potential increases in day-to-day variability, or greater extremes, in minimum overnight temperature with climate change (Pendlebury et al., 2004), could lead to changes in the timing of the dawn chorus, if birds have difficulty in judging forthcoming overnight temperatures, and consequently fail to budget energy reserves accordingly. Finally, in chapter 8, I implied that recent levels of climate-driven advance in leaf-out phenology of 2.5 d decade^{-1} (Menzel et al., 2006), attenuate higher frequency elements of birdsong (e.g. those ≥8000 Hz) to a degree that may unduly affect long-distance communication. This, along with the potential attenuation associated with climate-driven changes to woodland vegetation composition and structure (Fuller et al., 2007), could, in the long-term, reduce the fitness of some bird populations.

9.1.4 Further anthropogenic challenges for the dawn chorus

This thesis is, to a great extent, concerned with the effects of climate change on the dawn chorus. However, anthropogenic noise pollution and artificial light at night (ALAN) also pose serious threats to the chorus, and the fitness of the individuals, populations and communities that participate (chapter 2, section 2.8). For example, the important influence of illumination from the sun on the timing of the chorus, as reported in chapter 6, highlights the potential effect that ALAN may have as it encroaches further into rural areas (Hölker et al., 2010), by confusing birds' perception of what constitutes 'dawn'. The effect of ALAN might be more intense at lower latitude sites, where overnight periods are darker, and where I found that chorus onset responded to lower light levels (chapter 6). Indeed, Kempenaers et al. (2010) found that there were no artificial light effects on onset of singing at a very high latitude site (65˚N) compared to lower latitude sites (48˚N and 37˚N), which they attributed to decreased contribution of artificial light at high latitudes. In some locations, the potential effects of competing species (chapter 7) and earlier leaf-out phenology (chapter 8) on dawn birdsong may be insignificant compared to the masking effect of anthropogenic noise pollution, as urban areas and transport networks continue to expand and encroach upon rural areas (Seto et al., 2012). Considering the importance of dawn singing in the lifecycles of birds, it is imperative that the effects of noise and ALAN on bird singing behaviour in urban and rural locations are fully understood.

9.2 Future work

The ACI provided a valid holistic depiction of the dawn chorus from my acoustic surveys (chapter 6), but future work should strive to understand dawn singing behaviour in individual species. For bioacoustics methods to be truly viable in such large-scale studies, reliable recognisers that are capable of species identification and classification must be accessible to researchers (Blumstein et al., 2011). Further collaboration with mathematicians, computer scientists and acousticians is required to drive the development of new algorithms and computer-aided approaches to automated species identification, and to improve upon the performance of current recognisers. In the meantime, future research should consider alternative approaches to extracting meaningful information from large acoustic datasets. For example, additional work on my ensemble approach to automated identification can create optimal combinations of recognisers for a particular species or song-type. When established, combinations can be relayed to and implemented by fellow researchers. Thus, reducing their time spent on constructing ensemble recognisers. Crowd-sourcing has been employed to identify species from large datasets of camera-trap images (e.g. MammalWeb, Hsing et al., 2018; Snapshot Serengeti, Swanson et al., 2015), whereby members of the general public are recruited to classify images via dedicated website platforms. This novel approach could be utilised to classify bird species by their vocalisations within large acoustic datasets. The detailed species-specific information obtained within my dataset can be used to address multiple questions and issues concerning the ecology of the dawn chorus and bird behaviour during this event, expanding greatly upon the findings presented in this thesis.

Knowledge of seasonal and daily song patterns in individual species would provide a truly intricate view of the dawn chorus. For example, the pairwise competitive interactions addressed in chapter 7, which were limited to just a few species-pairs in this thesis due to time constraints, can be extended to encompass entire communities. At its simplest level, the order of song in species can be discerned, but the potential for multi-species interplay and co-ordination in singing events, previously unknown in temperate dawn choruses, can also be investigated with knowledge of fine-scale temporal patterns in species' singing events. Additionally, those species most likely to be affected by advances in leaf-out phenology and other seasonal changes to vegetation structure (chapter 8) can be determined if precise seasonal and daily singing routines can be established. Seasonal song output can also be related to breeding stage in birds, which, apart from its general use in understanding the function of the dawn chorus, may be of particular use for repeat-nesting species, such as Eurasian blackbird *Turdus merula* and song thrush *T. philomelos*, for which little is known on the timing of nesting attempts later in the season (D. Leech, pers. comm., March 3, 2016). The information already obtained within my dataset can address these questions for different regions of the country, but the dataset can be extended further by making acoustic surveys in alternative habitat-types (e.g. grassland, scrub or wetlands), where different sets of environmental conditions may drive the onset and peak of the chorus. This may be especially important in urban areas, where the effects of ALAN and anthropogenic noise on the timing and intensity of bird song are considerable.

9.3 Conclusion

Singing at dawn is so critical to male temperate-zone birds, that they are compelled to do so amid the noise of countless others. The resultant cacophony is of considerable cultural and aesthetic value to people, yet we still do not fully comprehend the motivation behind this daily event. Recent advances in recording and sound analysis technology now allow practitioners to investigate birdsong and the chorus as never before. By using this technology, this study has illustrated the sensitivity of birds to changes in their environment, and how this may manifest in the response of their singing behaviour at dawn. The information presented in this thesis is extremely valuable, but with an increasing urgency to mitigate environmental change and biodiversity-loss, it is vital that sound recording and analysis methods continue to develop, particularly within the field of automated signal recognition, if we are to fully understand the health of populations and communities, and to preserve their requirements during the dawn chorus as well as more widely.

Appendix A

Supporting information for chapter 5

A.1 Definitions of singing events

For common chiffchaff *Phylloscopus collybita* and carrion crow *Corvus corone*, with mono- or bi-syllabic songs, a singing event was considered to be complete when a non-vocalising gap exceeded the regular gap between syllables. For example, a single *caw* was considered a complete song of a carrion crow, when gaps between *caws* exceeded the typical inter-syllable duration (Fig. A.1a and A.1d). For northern wren *Troglodytes troglodytes* song, with a series of syllable blocks, or phrases, that follow in dependable succession, the entire series of phrases were included in a single singing event (Fig. A.1b). By contrast, for the European robin *Erithacus rubecula*, which produces continuous song with extended inter-phrase gaps, I recorded each phrase as a singing event (Fig. A.1c). Results from manual analyses were used as the benchmark for assessing the performance of the recognisers.

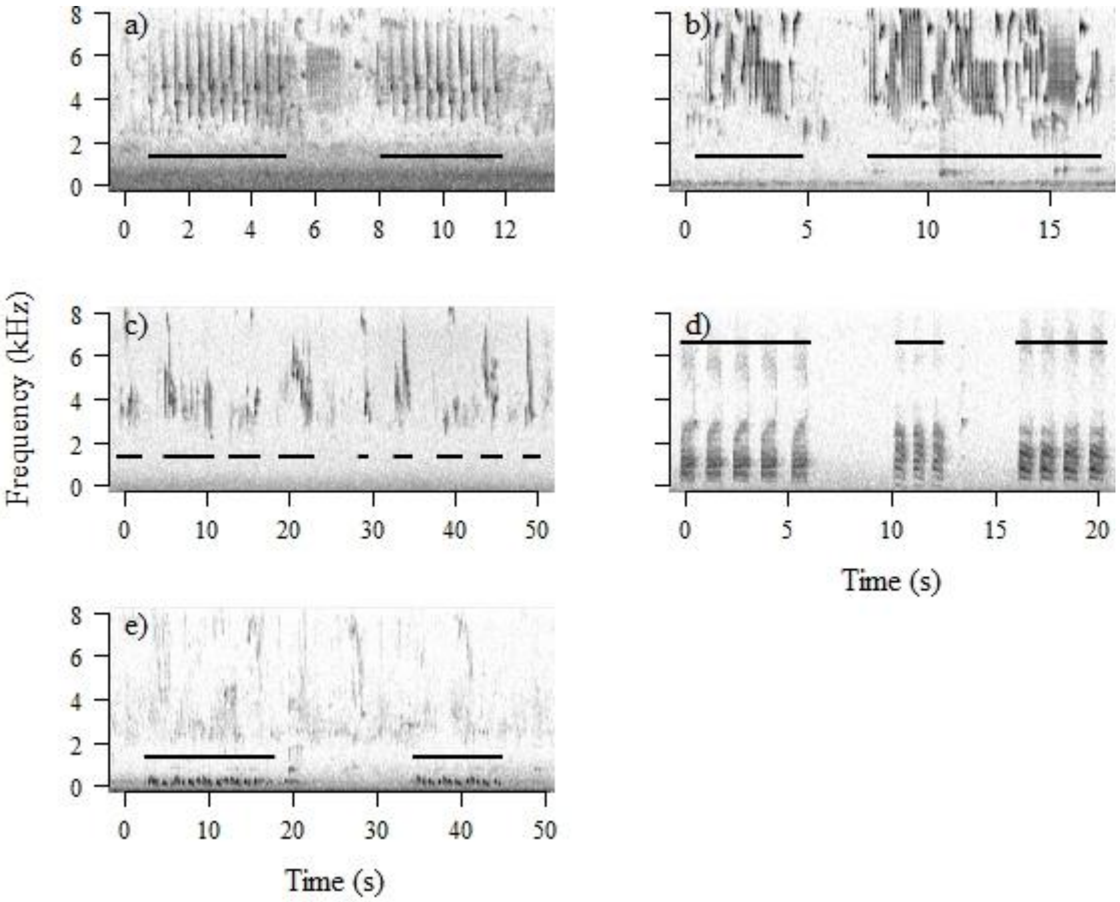


Figure A.1 Example spectrograms of the study species, a) common chiffchaff *Phylloscopus collybita*, b) northern wren *Troglodytes troglodytes*, c) European robin *Erithacus rubecula*, d) carrion crow *Corvus corone*, and e) common woodpigeon *Columba palumbus*, made on Raven Pro v1.4 (The Cornell Laboratory of Ornithology, Ithaca, USA) from my own acoustic surveys using Song Meter 2+ autonomous recording units (Wildlife Acoustics Inc, Maynard, USA). Thick black dashes show individual singing events as they were recorded in manual song detection. Note that time scale varies amongst a-e.

A.2 Building recognisers

A.2.1 monitoR

I extracted sound clips containing examples of the study species' song from the training dataset using the viewSpec function. I then generated templates from the sound clips using the makeCorTemplate function. The final number of templates extracted differed according to the study species, and reflected the level of complexity and variation in the song (Table A.1). The templates were then integrated to create a recogniser using the combinCorTemplates function. The more templates within a recogniser, the longer it takes to complete the scanning process. To reduce the duration of the scanning process, templates that did not return detections within preliminary tests on a subset of acoustic surveys from my dataset, where I knew the study species was present, were removed from the recogniser, until the best possible performance, in terms of scanning duration and the number of correct detections, was found. Prior to scanning the test dataset with the final recogniser, I set the score threshold to zero using the score.cutoff command, so that all detections, regardless of their score, were included in the results output. The recogniser then scanned the test dataset of 300 × 300 s sample surveys using the corMatch function. Multiple templates within a recogniser may register detections with the same singing event. Therefore, I used the findPeaks function to return the detections with the highest scores. I then used the timeAlign function to order the detections by their occurrence within sample surveys. In order to avoid overlapping or duplicate detections, I set the tolerance command to equal the duration of the longest template in the recogniser. MonitoR assigns times to detections, which represent the position of the centre-point of the matching template within the acoustic survey. It does not return start times or durations of detections, and as my subsequent analyses required these measurements, I calculated them using the time at the centre-point and duration of the matching template.

Table A.1 Parameter settings used for study species' recognisers built using the R package monitoR (Hafner & Katz, 2018a).

Parameter	Species				
	Chiffchaff	Wren	Robin	Carrion crow	Woodpigeon
No. of templates	6	14	14	8	5
FFT size	256	256	256	256	256
FFT transformation	Hanning	Hanning	Hanning	Hanning	Hanning
FFT overlap	None	None	None	None	None
Minimum frequency (Hz)	0	0	0	0	0
Maximum frequency (Hz)	8000	8000	8000	8000	8000
Density of points	1	1	1	1	1
Score threshold	0.0	0.0	0.0	0.0	0.0
Plot frame ratio	1	1	1	1	1
Tolerance (s)	7	2.9	3.5	5	12.5

A.2.2 Raven Pro

I extracted examples of study species' singing events from the training dataset. The number of examples varied amongst species, and reflected the level of complexity and variation in the song (Table A.2). I then measured the song parameters required to construct the recogniser from the set of example songs (Table A.2). Using the same subset of test surveys as used for preliminary tests of all other recognisers during their construction, adjustments were made iteratively to the parameters until the best possible recogniser performance was found. Prior to scanning the test dataset with the final recogniser, I set Occupancy to the minimum allowable value of 1.0. Raven does not provide the facility to merge two channels in stereo surveys, and returns two sets of detections – one for each channel. To eliminate duplicate detections, I matched the two sets by values returned in the Begin Time and End Time measurements, using the foverlaps function in the R package *data.table* (Dowle et al., 2019). All detections made in the left channel were retained, and detections made in the right channel that overlapped in time with those in the left, were removed. Detections made in the right channel that did not overlap with those in the left were added to the list of left channel detections to produce a single set.

Table A.2 Parameter settings used for study species' recognisers built using Raven Pro software (The Cornell Laboratory of Ornithology, Ithaca, NY).

Parameter	Species				
	Chiffchaff	Wren	Robin	Carrion crow	Woodpigeon
Minimum frequency (Hz)	3500	3100	2300	700	270
Maximum frequency (Hz)	7000	7900	7900	1800	645
Minimum duration (s)	1.064	0.6	0.72	0.6	2
Maximum duration (s)	13	7	7.112	12	16
Minimum separation (s)	0.192	0.032	0.104	0.4	0.12
SNR threshold (dB)	3	2	3	5	2.5
Block size (s)	40	21	21	30	45
Hop size (s)	15	9	9	10	20
Percentile	25	25	25	30	30

A.2.3 Song Scope

I extracted example singing events (called ‘annotations’ in Song Scope) from my training dataset. The number of annotations required to build recognisers varied amongst species, and reflected the level of complexity and variation in the song (Table A.3). A well-balanced set of annotations were chosen, encompassing the breadth of variation in song structure and quality, as well as the breadth of noise profiles present amongst the training dataset (cf. Priyadarshani et al., 2018). All, however, clearly showed the syllable structure of a single individual and were not unduly masked by non-study species or other background noise. Annotations were loaded into the Song Scope recogniser builder as a single class. The configuration of additional settings available on the Song Scope interface was specific to each study species (Table A.3). Settings were adjusted iteratively, and annotations added and removed, by testing the recognisers on the same subset of my acoustic surveys as used in preliminary testing of all other recognisers, until the best possible performance was found. Some researchers have iteratively tested recogniser performance against the set of annotations used to build them (e.g. Knight et al., 2017; MacLaren et al., 2018), ensuring that recognisers, at minimum, could recognise all the signals from which they were built. However, such a high level of self-training may create recognisers too specific for the level of inter-site and intra-species variation within my broad test dataset. The final recogniser cross-training (a measure of how well the model fits the training data) varied amongst study species, ranging from 61.48±3.11 for woodpigeon to 72.45±4.91 for robin (Table A.3). Prior to scanning the test dataset with the final recognisers, I set the Quality and Score thresholds to zero, and merged the signals from each channel, to return a single set of detections without duplicates.

Table A.3 Parameter settings used and cross-training values for study species' recognisers built using Song Scope software (Wildlife Acoustics Inc., Maynard, USA).

Parameter	Species				
	Chiffchaff	Wren	Robin	Carrion crow	Woodpigeon
Number of annotations	90	203	268	150	40
Sample rate	16000	16000	16000	16000	16000
Max sample delay	64	64	64	64	64
FFT	256	256	512	256	512
FFT overlap	1/2	1/2	1/2	1/2	1/2
Band Pass Filter:					
Min	50 (3.1 kHz)	55 (3.4 kHz)	74 (2.3 kHz)	10 (625 Hz)	10 (312 Hz)
Max	70 (7.5 kHz)	67 (7.6 kHz)	256 (8 kHz)	22 (2 kHz)	14 (750 Hz)
Amplitude gain	0	0	0	0	0
Background filter (s)	1	1	1	1	1
Max syllable (ms)	1500	1500	701	1496	1500
Max syllable gap (ms)	271	401	341	800	701
Max song (ms)	10001	10001	7401	12000	30001
Dynamic range (dB)	20	17	18	12	23
Algorithm	2.0	2.0	2.0	2.0	2.0
Max complexity	25	48	48	25	25
Max resolution	8	13	18	8	10
Cross training (%)	69.38 ± 5.25	69.05 ± 3.09	72.45 ± 4.91	65.48 ± 6.04	61.48 ± 3.11
Total training (%)	69.13 ± 4.80	68.96 ± 4.06	72.55 ± 5.11	66.16 ± 5.18	61.24 ± 3.18

A.2.4 Kaleidoscope Pro

I used the full training dataset as input into the classifying process, and, using a configuration of settings specific to each study species (Table A.4), Kaleidoscope grouped all the signals it could detect into clusters. I then examined the output for clusters containing the study species' song, and detections within the cluster were labelled 'True' or 'False' depending on whether they were the study species song or not. Detections containing poor examples of the study species song, or those masked by non-study species, were left unlabelled. This process trained Kaleidoscope to recognise only the verified signals in the next step. Kaleidoscope then re-scanned the training dataset and re-clustered the detections, according to their labels, to produce the final recogniser. I set the distance from cluster centre to the maximum allowable value of 2.0 to simulate a zero score threshold. The recogniser then scanned all samples within the test dataset in a single pass. Only detections classified as ‘true’ were retained from the output. Duplicate detections made in both left and right channels were detected using the foverlaps function in the R package *data.table*. The best scoring duplicate (i.e. that with the lowest distance from the cluster centre) was retained. To make the scores of the final list of detections comparable to those of other recognisers in the study (i.e. on a scale of zero to one, with ‘one’ signifying top score), I halved their value and then subtracted it from one.

Table A.4 Parameter settings used for study species’ recognisers built using Kaleidoscope Pro software (Wildlife Acoustics Inc, Maynard, USA).

Parameter	Species				
	Chiffchaff	Wren	Robin	Carrion crow	Woodpigeon
FFT window	256	256	256	256	256
Max dist. from cluster centre:					
outputs in cluster.csv	1.0	1.0	1.0	1.0	1.0
for building clusters	0.5	0.5	0.5	0.5	0.5
Max states	12	12	14	12	10
Max clusters	500	500	500	500	500
Minimum frequency (kHz)	3125	2500	2312	600	312
Maximum frequency (kHz)	7500	8000	8000	2000	750
Minimum length (ms)	0.1	0.1	0.1	0.1	0.1
Maximum length (ms)	10	8	7.4	10	20
Maximum inter-syllable (ms)	0.27	0.35	0.34	0.5	0.7

A.3 Building ensemble models

I matched the singing events of each study species identified by manual song detection against all 300 segments of 1 s duration (hereafter ‘segments’) of each 300 s sample in the test dataset, resulting in a binomial outcome of either ‘1’ (study species singing) or ‘0’ (study species not singing) for every segment of the sample. I then matched the detections returned by each recogniser in turn to the segments of each sample survey using the start time and duration measurements returned by the recogniser (Raven, Song Scope and Kaleidoscope) or otherwise calculated (monitoR, see A.2.1). The respective recogniser scores and additional measurements assigned to detections were placed alongside the matching segments. If, for any given segment, a recogniser did not make a detection, a score of zero was assigned. To reduce pseudo-replication during the modelling process due to non-independence of data-points, 50 × segments were randomly selected from each 300 s sample in the test dataset. From this reduced dataset of 15000 segments, I selected all segments from three sample surveys randomly-selected from each of the 20 study sites (3000 segments = 20% of data) to be my model test data. The Power measurement returned by Raven and the Level measurement returned by Song Scope were found to be collinear with Raven Occupancy and Song Scope Score respectively, and, consequently, were removed from the modelling process. Generalised linear models (GLM) with binomial errors were built using the remaining 12000 segments (80% of data), and final models were tested using the model test data. GLMs for individual recognisers were built using the same dataset of 12000 segments, and all were tested on the same 3000 segment model test data.

Table A.5 Coefficients of binomial generalised linear models (GLMs) predicting the probability of obtaining a positive detection from scores assigned to detections made by the recognisers of the four signal recognition software programs and the ensemble model. m.score=monitoR Score; r.score=Raven Occupancy; s.score=Song Scope Score; s.qual=Song Scope Quality; k.score=Kaleidoscope distance from centre of cluster.

a) Common chiffchaff *Phylloscopus collybita*

Variables/Interactions	Estimate	SE	z value	p
Ensemble (link=cloglog)				
Intercept	-4.772	0.218	-21.927	2.0E-16
k.score	2.205	1.033	2.134	3.3E-02
m.score	4.730	0.570	8.300	2.0E-16
r.score	1.450	0.364	4.023	5.7E-05
s.qual	-1.674	1.717	-0.975	3.3E-01
s.score	2.792	0.356	7.835	4.7E-15
k.score × r.score	3.255	0.975	3.339	8.4E-04
k.score × s.qual	-18.647	8.492	-2.196	2.8E-02
k.score × s.score	-0.399	1.315	-0.304	7.6E-01
m.score × r.score	-2.222	0.813	-2.734	6.3E-03
r.score × s.qual	-1.170	0.526	-2.225	2.6E-02
r.score × s.score	-1.975	0.560	-3.526	4.2E-04
s.qual × s.score	3.215	2.547	1.262	2.1E-01

k.score × r.score × s.qual	-8.277	2.579	-3.209	1.3E-03
k.score × s.qual × s.score	34.751	12.485	2.783	5.4E-03
monitoR (link=cloglog)				
Intercept	-2.924	0.047	-62.200	2.0E-16
m.score	4.135	0.260	15.880	2.0E-16
Raven (link=probit)				
Intercept	-1.555	0.033	-47.690	2.0E-16
r.score	0.233	0.048	4.840	1.3E-06
Song Scope (link=probit)				
Intercept	-20.236	0.054	-37.162	2.0E-16
s.score	0.154	0.093	12.408	2.0E-16
s.qual	-3.019	0.713	-4.233	2.3E-05
s.score × s.qual	4.285	1.082	3.961	7.5E-05
Kaleidoscope (link=cloglog)				
Intercept	-2.844	0.041	-69.610	2.0E-16
k.score	4.195	0.190	22.090	2.0E-16

b) Northern wren *Troglodytes troglodytes*

Variables/Interactions	Estimate	SE	z value	p
Ensemble (link=cloglog)				
Intercept	-3.375	0.130	-25.958	2.0E-16
k.score	1.736	0.255	6.821	9.1E-12
m.score	4.234	0.579	7.311	2.7E-13
r.score	1.179	0.209	5.644	1.7E-08
s.qual	-4.843	1.619	-2.991	2.8E-03
s.score	2.249	0.248	9.065	2.0E-16
k.score × r.score	-0.795	0.382	-2.081	3.7E-02
k.score × s.qual	-13.874	2.893	-4.796	1.6E-06
k.score × s.score	-1.582	0.443	-3.575	3.5E-04
m.score × r.score	0.087	0.842	0.103	9.2E-01
m.score × s.qual	-10.884	6.248	-1.742	8.1E-02
m.score × s.score	-2.408	1.075	-2.240	2.5E-02
r.score × s.qual	0.120	0.342	0.350	7.3E-01
r.score × s.score	-1.340	0.367	-3.650	2.6E-04
s.qual × s.score	7.095	2.366	2.998	2.7E-03
k.score × r.score × s.score	1.574	0.613	2.566	1.0E-02
k.score × s.qual × s.score	22.202	4.253	5.220	1.8E-07
m.score × r.score × s.qual	-2.662	1.378	-1.932	5.3E-02
m.score × r.score × s.score	2.590	1.477	1.754	7.9E-02
m.score × s.qual × s.score	15.414	9.000	1.713	8.7E-02
monitoR (link=cloglog)				
Intercept	-1.859	0.033	-55.770	2.0E-16
m.score	4.508	0.127	35.530	2.0E-16
Raven (link=cloglog)				
Intercept	-1.734	0.035	-49.760	2.0E-16

r.score	0.137	0.041	27.500	2.0E-16
Song Scope (link=probit)				
Intercept	-1.184	0.029	-41.120	2.0E-16
s.score	1.155	0.056	20.720	2.0E-16
s.qual	-8.552	0.548	-15.590	2.0E-16
s.score × s.qual	13.116	0.816	16.070	2.0E-16
Kaleidoscope (link=logit)				
Intercept	-1.316	0.028	-47.770	2.0E-16
k.score	2.201	0.074	29.770	2.0E-16

c) European robin *Erithacus rubecula*

Variables/Interactions	Estimate	SE	z value	p
Ensemble (link=logit)				
Intercept	-2.043	0.071	-28.797	2.0E-16
k.score	0.957	0.206	4.644	3.4E-06
m.score	2.557	0.371	6.894	5.4E-12
r.score	0.243	0.113	2.156	3.1E-02
s.qual	-3.003	0.970	-3.097	2.0E-03
s.score	-0.183	0.148	-1.230	2.2E-01
k.score × r.score	0.938	0.310	3.026	2.5E-03
k.score × s.qual	-5.964	2.483	-2.402	1.6E-02
k.score × s.score	0.535	0.373	1.435	1.5E-01
m.score × s.qual	-15.403	4.488	-3.432	6.0E-04
m.score × s.score	-0.891	0.652	-1.367	1.7E-01
r.score × s.qual	0.772	0.402	1.922	5.5E-02
s.qual × s.score	4.766	1.395	3.417	6.3E-04
k.score × r.score × s.qual	-1.995	1.024	-1.948	5.1E-02
k.score × s.qual × s.score	10.729	3.514	3.054	2.3E-03
m.score × s.qual × s.score	23.542	6.452	3.649	2.6E-04
monitoR (link=cloglog)				
Intercept	-1.605	0.025	-63.750	2.0E-16
m.score	2.641	0.120	22.070	2.0E-16
Raven (link=cloglog)				
Intercept	-1.782	0.038	-46.420	2.0E-16
r.score	0.785	0.052	15.210	2.0E-16
Song Scope (link=probit)				
Intercept	-0.948	0.026	-36.821	2.0E-16
s.score	0.142	0.049	2.903	3.7E-03
s.qual	-3.974	0.349	-11.387	2.0E-16
s.score × s.qual	6.909	0.505	13.677	2.0E-16
Kaleidoscope (logit)				
Intercept	-1.695	0.031	-54.830	2.0E-16
k.score	2.233	0.080	27.830	2.0E-16

d) Carrion crow *Corvus corone*

Variables/Interactions	Estimate	SE	z value	p
Ensemble (link=cloglog)				
Intercept	-4.655	0.114	-40.928	2.0E-16
k.score	2.647	0.525	5.037	4.7E-07
m.score	7.400	0.683	10.835	2.0E-16
r.score	2.794	0.383	7.297	3.0E-13
s.qual	0.214	3.071	0.070	9.4E-01
s.score	0.970	0.385	2.521	1.2E-02
k.score × m.score	-3.172	1.853	-1.712	8.7E-02
k.score × r.score	1.867	0.795	2.348	1.9E-02
k.score × s.score	-1.385	0.847	-1.636	1.0E-01
m.score × r.score	-5.352	1.366	-3.918	8.9E-05
m.score × s.qual	-6.672	1.876	-3.557	3.8E-04
m.score × s.score	5.613	1.590	3.531	4.1E-04
r.score × s.qual	-21.791	6.280	-3.470	5.2E-04
r.score × s.score	-2.555	0.792	-3.225	1.3E-03
s.qual × s.score	0.911	5.067	0.180	8.6E-01
r.score × s.qual × s.score	36.838	9.897	3.722	2.0E-04
monitoR (link=cloglog)				
Intercept	-3.910	0.066	-59.620	2.0E-16
m.score	9.279	0.304	30.570	2.0E-16
Raven (link=cloglog)				
Intercept	-3.874	0.066	-58.970	2.0E-16
r.score	3.844	0.134	28.670	2.0E-16
Song Scope (link=logit)				
Intercept	-3.716	0.072	-51.613	2.0E-16
s.score	2.183	0.202	10.828	2.0E-16
s.qual	-13.908	1.785	-7.791	6.6E-15
s.score × s.qual	25.734	2.824	9.111	2.0E-16
Kaleidoscope (link=probit)				
Intercept	-1.917	0.025	-77.920	2.0E-16
k.score	2.727	0.103	26.490	2.0E-16

e) Common woodpigeon *Columba palumbus*

Variables/Interactions	Estimate	SE	z value	p
Ensemble (link=logit)				
Intercept	-4.567	0.159	-28.822	2.0E-16
k.score	-19.411	5.038	-3.853	1.2E-04
m.score	7.524	0.583	12.908	2.0E-16
r.score	2.295	0.316	7.263	3.8E-16
s.qual	-18.700	4.072	-4.593	4.4E-06
s.score	2.214	0.344	6.436	1.2E-10
k.score × m.score	79.473	17.336	4.584	4.6E-06
k.score × r.score	10.753	3.923	2.741	6.1E-03
k.score × s.qual	-27.737	10.916	-2.541	1.1E-02

k.score × s.score	42.382	8.750	4.844	1.3E-06
m.score × s.qual	22.699	15.934	1.425	1.5E-01
m.score × s.score	-2.824	1.222	-2.311	2.1E-02
r.score × s.score	-0.575	0.644	-0.892	3.7E-01
s.qual × s.score	36.513	7.357	4.963	6.9E-07
k.score × m.score × s.score	137.779	29.617	-4.652	3.3E-06
k.score × r.score × s.score	-21.991	6.814	-3.227	1.3E-03
k.score × s.qual × s.score	43.279	18.752	2.308	2.1E-02
m.score × s.qual × s.score	-45.849	28.083	-1.633	1.0E-01
monitoR (link=cloglog)				
Intercept	-3.390	0.055	-61.400	2.0E-16
m.score	8.066	0.185	43.570	2.0E-16
Raven (link=cloglog)				
Intercept	-2.813	0.047	-59.290	2.0E-16
r.score	3.257	0.100	32.540	2.0E-16
Song Scope (link=logit)				
Intercept	-2.758	0.061	-45.310	2.0E-16
s.score	2.627	0.131	20.090	2.0E-16
s.qual	-28.140	1.940	-14.510	2.0E-16
s.score × s.qual	53.001	3.475	15.250	2.0E-16
Kaleidoscope (link=cloglog)				
Intercept	-2.023	0.027	-76.140	2.0E-16
k.score	4.042	0.092	44.050	2.0E-16

A.4 Recogniser performance analysis

To calculate the area under the receiver operating characteristic curve (AUC-ROC), and statistics based upon the ROC curve, I split the 3000 segment model test data for each species, along with the modelled probabilities of obtaining positive detections for each recogniser, by the constituent sample surveys, thus creating 60 × samples of 50 × observations per study species. It was not possible to calculate statistics based upon the ROC curve for sample surveys within which the study species was absent, as sensitivity, which constitutes the y-axis of the ROC curve, cannot be calculated when true positive (TP) and false negative (FN) detections are both equal to zero; such samples were excluded from the analyses. I then calculated AUC-ROC and roc01 values for all remaining sample surveys and all study species using the R packages *ROCR* (Sing, Sander, Beerenwinkel, & Lengauer, 2005) and *cutpointr* (Thiele, 2018).

Table A.6 Sensitivity (Sens) and false positive rate (FPR) at the minimum distance from the ROC curve to the point x=0, y=1 (roc01) for each recogniser and study species, and the mean across all study species for each recogniser.

Species	Recogniser									
	Ensemble		monitoR		Raven		Song Scope		Kaleidoscope	
	Sens	FPR	Sens	FPR	Sens	FPR	Sens	FPR	Sens	FPR
Chiffchaff	0.698	0.475	0.426	0.205	0.621	0.557	0.781	0.526	0.178	0.083
Wren	0.744	0.394	0.631	0.321	0.755	0.444	0.870	0.591	0.546	0.264
Robin	0.629	0.325	0.424	0.239	0.637	0.474	0.517	0.353	0.535	0.245
Carrion Crow	0.811	0.282	0.500	0.109	0.758	0.308	0.640	0.180	0.575	0.093
Woodpigeon	0.817	0.330	0.720	0.231	0.635	0.268	0.688	0.270	0.268	0.017
Mean	0.7398	0.3612	0.5402	0.2210	0.6812	0.4102	0.6992	0.3840	0.4204	0.1404

Table A.7 The minimum probability (Prob) of obtaining a positive detection at which the false positive rate (FPR) remains at zero for an ensemble model and the four component recognisers when detecting and classifying the song of five bird species within acoustic surveys made during the dawn chorus, and the corresponding number of true positive (TP) detections. By reducing the FPR to zero, this means that using the cutpoint values for Prob presented will produce no false positive (FP) errors (this is of key importance when these methods are used to detect species occurrence, which is an aim common to many surveys). Only the ensemble model enabled detection with no FP errors for all five study species.

Species	Ensemble		monitoR		Raven		Song Scope		Kaleidoscope	
	Prob	TP	Prob	TP	Prob	TP	Prob	TP	Prob	TP
Chiffchaff	0.765	4	NA	0	NA	0	NA	0	NA	0
Wren	0.928	16	0.676	13	NA	0	NA	0	NA	0
Robin	0.911	3	0.550	3	NA	0	0.681	3	NA	0
Carrion crow	0.883	8	NA	0	NA	0	0.546	3	NA	0
Woodpigeon	0.979	6	0.742	22	NA	0	0.926	13	0.983	11

Appendix B

Supporting information for chapter 6

B.1 Calculation of dawn chorus onset times

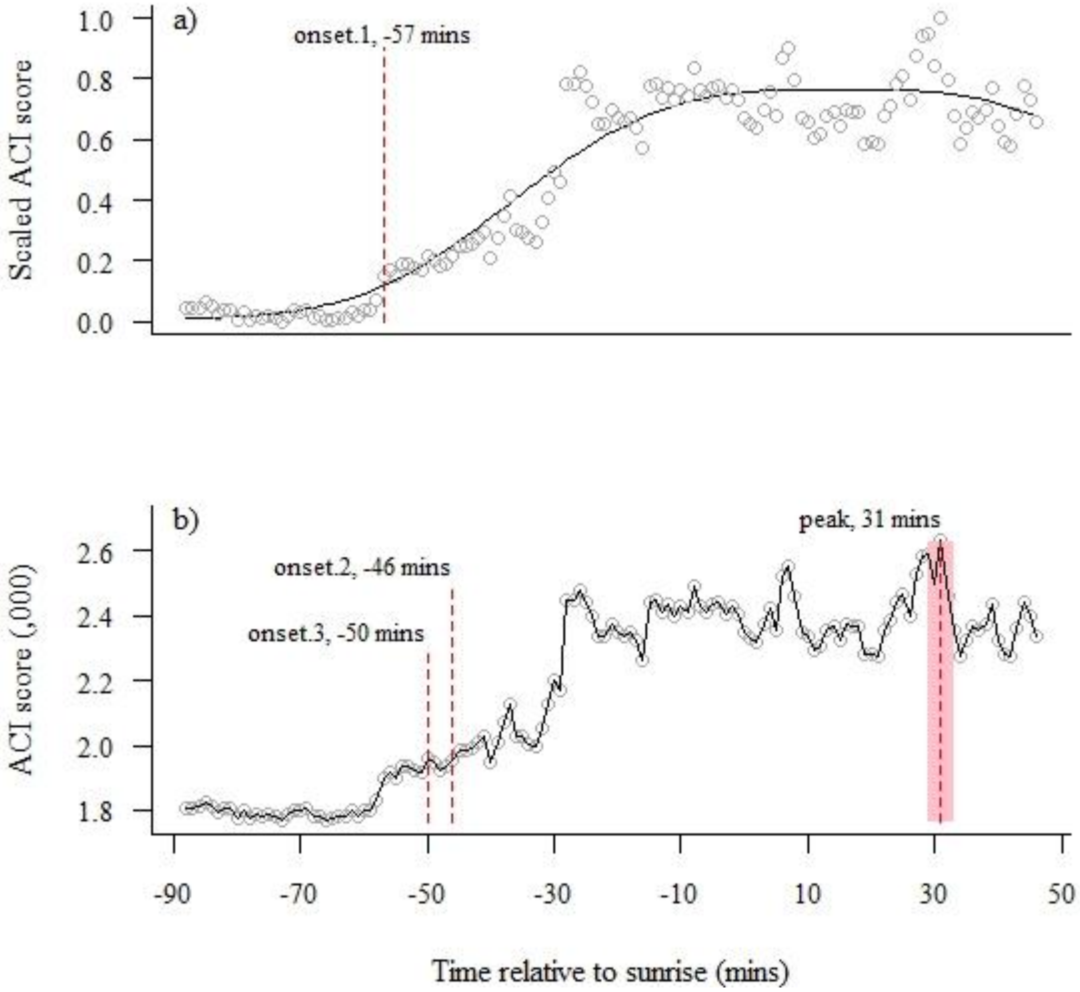


Figure B.1 Comparison of dawn chorus onset times calculated by three different methods in an example acoustic survey taken at Abernethy on 18th May 2016. Data points show the Acoustic Complexity Index (ACI) scores for each minute of the survey. a) Method 1 (onset.1): the curve is the fitted relationship, and the vertical line shows the maximum second derivative of the curve, which is taken to be the chorus onset time. Note that this method used scaled ACI scores; b) method 2 (onset.2): the chorus onset time is the minute that the ACI score reaches, or surpasses, 20% of the peak rolling 5-min mean in ACI scores for the survey (pink bar). The time of the peak is the central minute of the peak rolling 5-min mean. In method 3 (onset.3), the time of onset is the minute when the ACI score reaches, or surpasses, a predefined ACI score threshold based upon the mean peak scores during the study period (April to June) at each site in each year. The threshold for Abernethy in 2016 was 1886.5, which, in the example, was reached at 50 mins prior to sunrise.

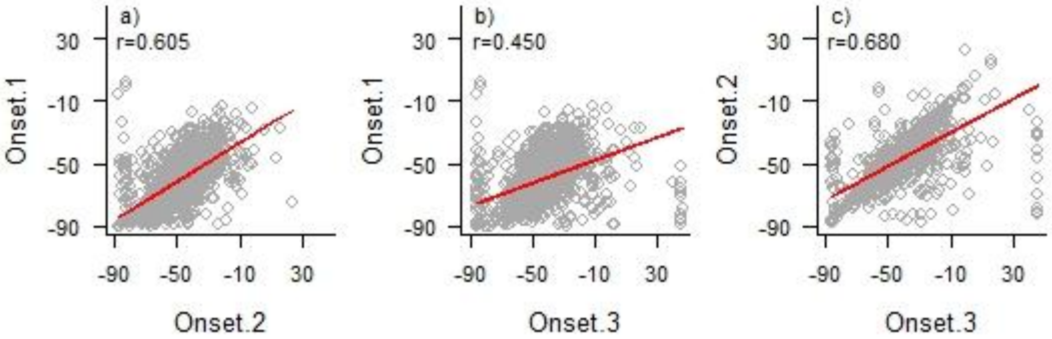


Figure B.2 The relationships amongst dawn chorus onset times calculated by three different methods along with the corresponding Pearson's correlation coefficient (r).

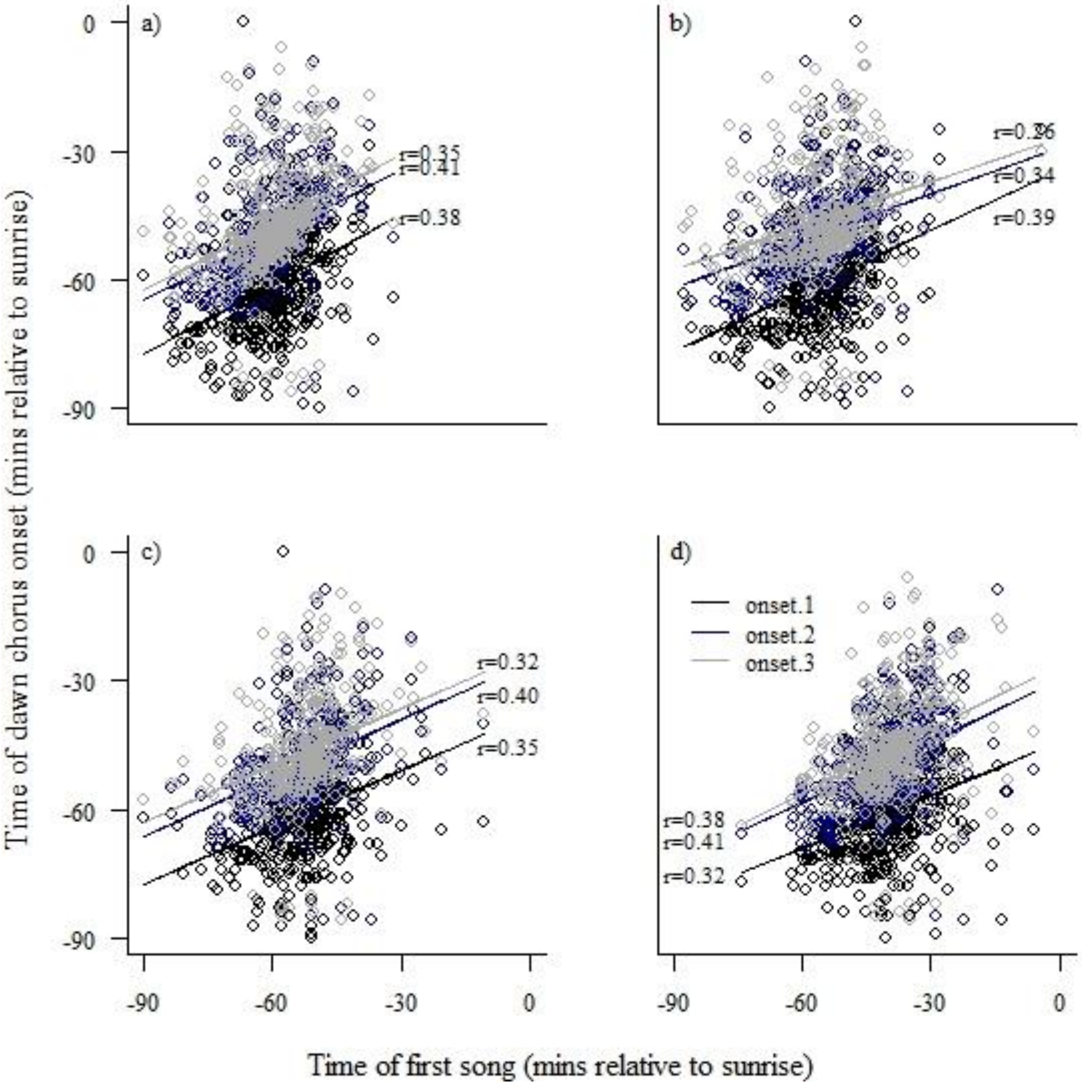


Figure B.3 The relationship between the observed time of first song in a) European robin *Erithacus rubecula*, b) song thrush *Turdus philomelos,* c) Eurasian blackbird *T. merula*, and d) northern wren *Troglodytes troglodytes* and the time of dawn chorus onset as calculated by three different methods along with the corresponding Pearson's correlation coefficients (r).

B.2 Determination of community composition

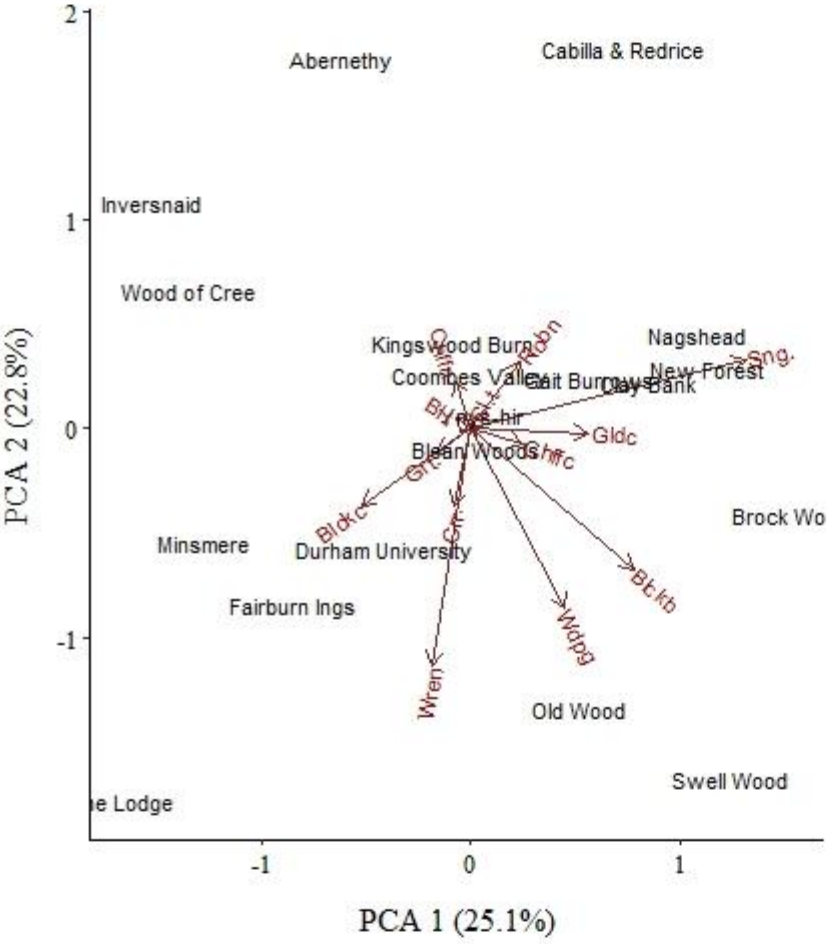


Figure B.4 Principal component analysis (PCA) showing the relationship amongst study sites according to the total time spent singing by 13 species, that accounted for 91% of all song production amongst the sites, in 15 × 300 s acoustic surveys made during the dawn chorus at each site. Species names are abbreviated: Bl.t=blue tit; Blckb=blackbird; Blckc=blackcap; Chffn=chaffinch; Chiffc=chiffchaff; Cl.t=coal tit; Crr=carrion crow; Gldc=goldcrest; Grt.=Great tit; Robin=robin; Sng.=song thrush; Wdpg=woodpigeon.

B.3 Mean and variance in minimum overnight temperature

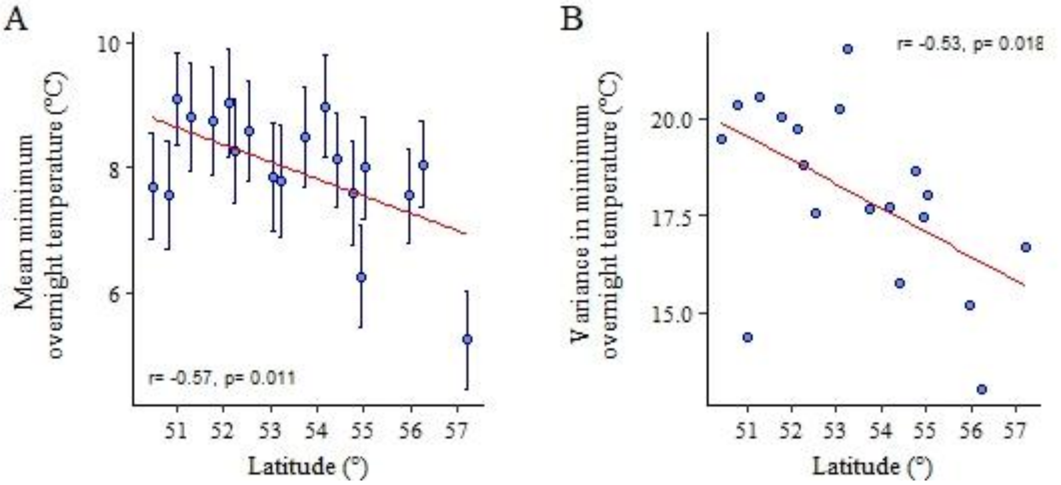


Figure B.5 The (A) mean minimum overnight temperature (±SE), and (B) variance in minimum overnight temperature recorded by data loggers at 19 mixed deciduous woodland study sites between April and June (incl.) in the years 2016 and 2017 plotted against latitude. Pearson's correlation coefficients (r) are shown along with the corresponding p value.

Appendix C

Supporting information for chapter 8

C.1 Tree measurements

Table C.1 The canopy trees of the study site and measurements. 52 × canopy trees were selected within the bounds of the study area in the study site. cbh= circumference of trunk at breast height (1.5 m); inter-tree spacing= the distance of the tree to its nearest neighbouring canopy tree; * trees to which ARUs were fixed.

Species	Common name	Approx. height (m)	cbh (cm)	Inter-tree spacing (cm)
Acer pseudoplatanus	Sycamore	22	132	2.6
Acer pseudoplatanus	Sycamore	22	133	4.4
Acer pseudoplatanus	Sycamore	22	111	3.4
Acer pseudoplatanus	Sycamore*	25	165	5.5
Acer pseudoplatanus	Sycamore	25	197	3.7
Acer pseudoplatanus	Sycamore	22	95	3.7
Acer pseudoplatanus	Sycamore	20	88	2.6
Acer pseudoplatanus	Sycamore	25	140	2.6
Acer pseudoplatanus	Sycamore	20	60	3.9
Acer pseudoplatanus	Sycamore*	20	90	5.0
Acer pseudoplatanus	Sycamore	25	170	5.1
Acer pseudoplatanus	Sycamore	20	95	5.2
Acer pseudoplatanus	Sycamore*	20	130	5.2
Acer pseudoplatanus	Sycamore	25	105	5.2
Acer pseudoplatanus	Sycamore*	25	149	2.2
Acer pseudoplatanus	Sycamore	20	128	2.2
Acer pseudoplatanus	Sycamore	25	140	2.0
Acer pseudoplatanus	Sycamore	25	180	2.0
Acer pseudoplatanus	Sycamore	22	87	4.8
Acer pseudoplatanus	Sycamore	22	130	4.4
Acer pseudoplatanus	Sycamore	22	97	4.0
Acer pseudoplatanus	Sycamore*	22	125	4.0
Acer pseudoplatanus	Sycamore	25	166	2.5
Acer pseudoplatanus	Sycamore	25	150	2.0
Acer pseudoplatanus	Sycamore*	25	200	3.2
Acer pseudoplatanus	Sycamore	25	200	3.1
Acer pseudoplatanus	Sycamore	25	155	2.5
Acer pseudoplatanus	Sycamore	15	70	2.5
Acer pseudoplatanus	Sycamore	25	193	6.5

Acer pseudoplatanus	Sycamore	25	230	6.5
Acer pseudoplatanus	Sycamore	25	150	4.4
Fagus sylvatica	Beech*	25	177	4.0
Fagus sylvatica	Beech	25	192	NR
Fagus sylvatica	Beech	30	320	2.2
Fagus sylvatica	Beech	25	240	6.0
Ulmus glabra	Wych Elm	5.5	42	NR
Ulmus glabra	Wych Elm	20	85	3.9
Ulmus glabra	Wych Elm	10	55	2.5
Ulmus glabra	Wych Elm	20	80	2.0
Fraxinus excelsior	Ash	25	175	2.7
Fraxinus excelsior	Ash*	25	130	5.8
Fraxinus excelsior	Ash	25	190	4.5
Quercus petraea	Sessile Oak	25	194	2.2
Quercus petraea	Sessile Oak	20	44	2.0
Quercus petraea	Sessile Oak	25	200	3.1
Alnus incana	Grey Alder	15	48	2.7
Alnus incana	Grey Alder	10	50	3.1
Alnus incana	Grey Alder	25	105	5.5
Populus × canadensis	Black Poplar	30	240	5.8
Populus × canadensis	Black Poplar*	25	133	4.4
Aesculus hippocastanum	Horse Chestnut	20	130	5.2
Aesculus hippocastanum	Horse Chestnut	25	240	5.0
Mean		22.4	141.0	3.8

C.2 Set-up of autonomous recording units

Table C.2 Height of autonomous recording units (ARUs) and distance from ‘base-point’.

Transect No.	ARU no.	Height (m)	Distance (m)
1	1	5	10
	2	5	29
	3	5	62
	4	1.5	10
	5	1.5	29
	6	1.5	62
2	7	5	10
	8	5	23
	9	5	52
	10	1.5	10
	11	1.5	23
	12	1.5	52
3	13	5	15
	14	5	32
	15	5	57
	16	1.5	15
	17	1.5	32
	18	1.5	57

C.3 Results of generalised additive models

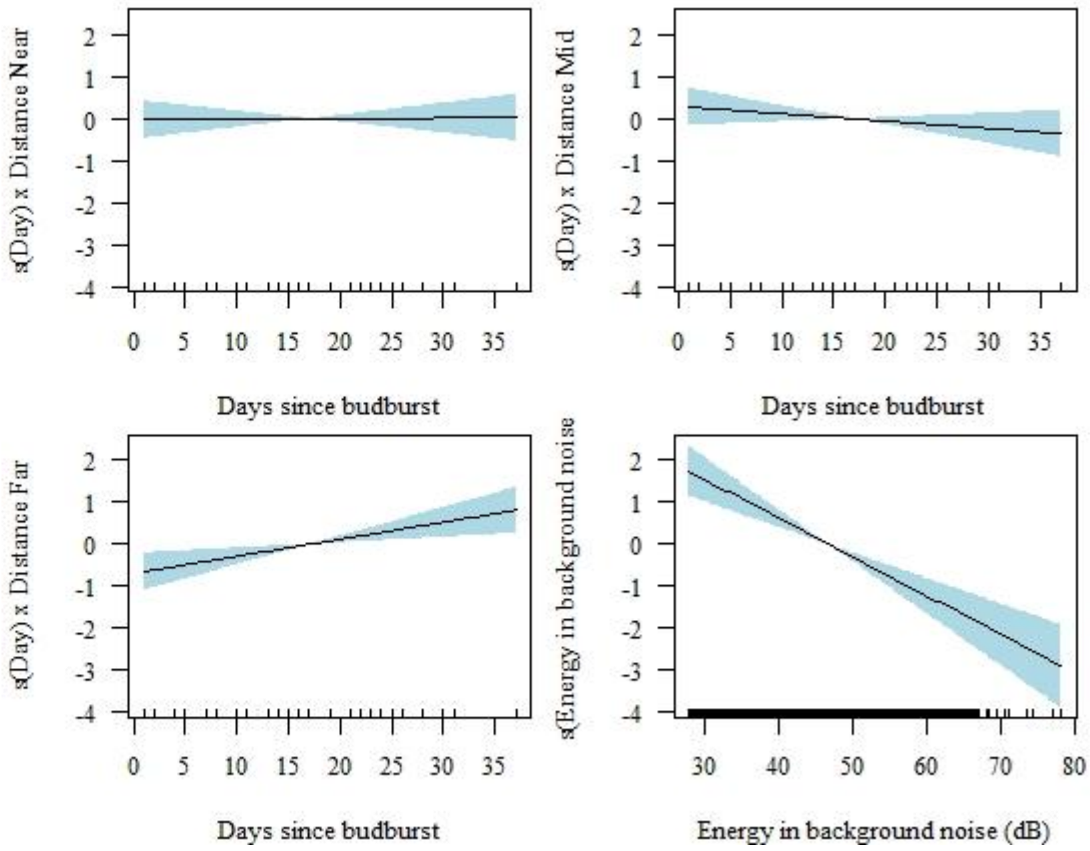


Figure C.1 Results of generalised additive models (GAMs) for the effect of the number of days since budburst (day) on the attenuation of five test sounds of different frequency (500 Hz, 1000 Hz, 1500 Hz, 4000 Hz and 8000 Hz) played-back through a loudspeaker at two heights (1.5 m and 5 m) and received by microphones at two heights (1.5 m and 5 m) within three distance categories in a mixed deciduous woodland in Durham, UK. The smoothed effect of day was varied by distance category. The automatic smoothing applied by the *mgcv* package in R (Wood, 2019) forced linear relationships to the data for each distance category. The smoothed effect of background noise is also shown.

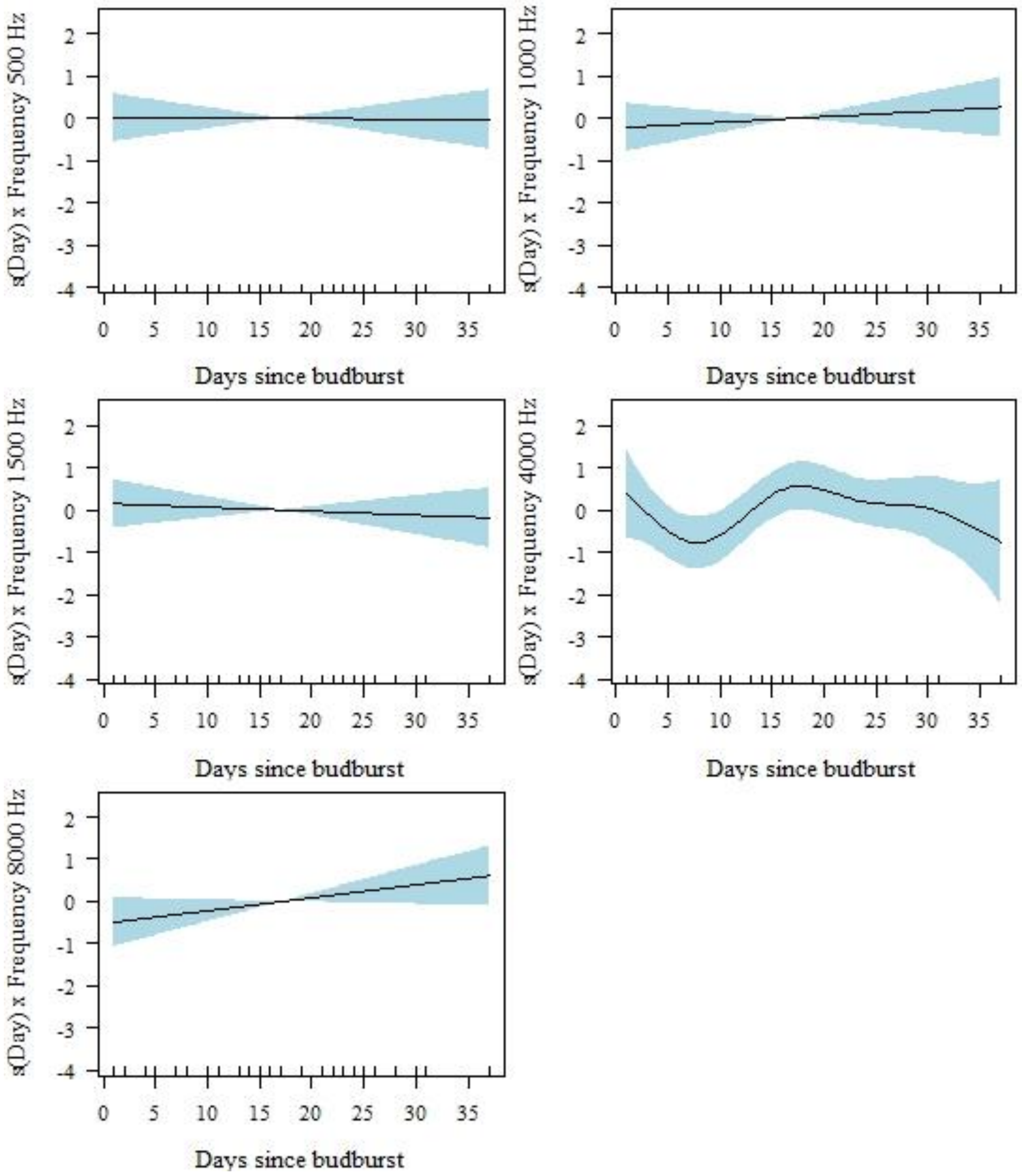


Figure C.2 Results of generalised additive models (GAMs) for the effect of the number of days since budburst (day) on the attenuation of five test sounds of different frequency played-back through a loudspeaker at two heights (1.5 m and 5 m) and received by microphones at two heights (1.5 m and 5 m) within three distance categories in a mixed deciduous woodland in Durham, UK. The smoothed effect of day was varied by frequency. The automatic smoothing applied by the *mgcv* package in R (Wood, 2019) forced linear relationships to the data for each frequency, with the exception of 4000 Hz. However, the relationship with the 4000 Hz frequency was not significant (p=0.176). The smoothed effect of background noise was also included in the GAM, but is not shown here (refer to Fig. C.1).

C.4 Coefficients of linear model

Table C.3 Results of linear model for the effect of factors influencing the attenuation of pure-tone test sounds from budburst through to full-leaf in a mixed deciduous woodland

	Estimate	SE	t	
Intercept	17.18	1.640	10.476	***
Day since budburst (Day)	0.03	0.011	2.604	**
Distance category (Distance) Mid	15.48	2.252	6.876	***
Distance category (Distance) Far	22.25	2.204	10.094	***
Frequency 1000 Hz	-0.74	0.557	-1.327	
Frequency 1500 Hz	3.89	0.659	5.904	***
Frequency 4000 Hz	7.57	0.618	12.240	***
Frequency 8000 Hz	-3.68	0.879	-4.190	***
Height of Loudspeaker 5 m (Loudspeaker)	1.34	0.376	3.558	***
Height of Microphone 5 m (Microphone)	-0.74	0.463	-1.595	
Energy in background noise (dB) (Background)	-0.05	0.027	-1.796	.
Background × Distance Mid	-0.10	0.038	-2.624	**
Background × Distance Far	-0.04	0.037	-0.975	
Day × Microphone 5 m	-0.04	0.016	-2.643	**
Distance Mid × Frequency 1000 Hz	-1.22	0.628	-1.948	.
Distance Far × Frequency 1000 Hz	-1.78	0.620	-2.878	**
Distance Mid × Frequency 1500 Hz	-5.28	0.796	-6.638	***
Distance Far × Frequency 1500 Hz	-7.40	0.778	-9.515	***
Distance Mid × Frequency 4000 Hz	-3.75	0.753	-4.975	***
Distance Far × Frequency 4000 Hz	-4.13	0.735	-5.617	***
Distance Mid × Frequency 8000 Hz	-2.18	1.158	-1.881	.
Distance Far × Frequency 8000 Hz	0.47	1.125	0.420	
Frequency 1000 Hz × Loudspeaker 5 m	-1.47	0.485	-3.038	**
Frequency 1500 Hz × Loudspeaker 5 m	-3.12	0.485	-6.430	***
Frequency 4000 Hz × Loudspeaker 5 m	-2.06	0.485	-4.239	***
Frequency 8000 Hz × Loudspeaker 5 m	-2.08	0.486	-4.287	***
Frequency 1000 Hz × Microphone 5 m	3.91	0.485	8.072	***
Frequency 1500 Hz × Microphone 5 m	-0.35	0.485	-0.712	
Frequency 4000 Hz × Microphone 5 m	-0.44	0.485	-0.906	
Frequency 8000 Hz × Microphone 5 m	1.14	0.486	2.344	*
Loudspeaker 5 m × Microphone 5 m	0.85	0.307	2.778	**

***p<0.001, **p<0.01, *p<0.05

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