Effects of anthropogenic noise on reproductive success and communication of European bird species

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This one is for me.

Abstract

Anthropogenic noise affects humans and wildlife globally. Birds, in particular are susceptible to its effects, because of their reliance on acoustic communication for survival and reproduction. Decades of research show that singers adapt their songs to noisy conditions, but much less is known about how impaired communication affects receivers, and how it affects sexual selection and fitness. Anthropogenic noise has been shown to reduce breeding success. However, not many studies have simultaneously investigated the effects of noise on settlement, population structure and breeding success at different stages of the breeding cycle. We know even less about the effects of noise on large geographical scales that transcend the population level.

This thesis aims to understand the effects of noise on the breeding success and communication of European birds. Specifically, in order to investigate the effects of noise on nest site selection together with its effects on breeding success, I studied a population of blue tits exposed to a gradient of road traffic noise. To understand the scale of the problem, I developed a methodology to combine citizen-science breeding data with government noise maps, and I tested this approach across two countries and eleven bird species. At the population level, I found that noise affected reproductive success, with negative impacts on nestling body condition and survival. Despite these effects, blue tits were more likely to breed in noisier nest sites, although these were also more likely to be occupied by first year breeders. I found that negative effects were not restricted to one population, but they were also evident at a countrywide level and on multiple species, with the most significant impact at the nestling stage.

In order to investigate a factor that might play a role in affecting breeding success, I used a playback experiments to test the assessment of performance of a territorial song under different ambient noise conditions. I found behavioural evidence that noise may affect the assessment of structural differences in signal quality of conspecifics, thus altering territory defence and, by inference, leading to suboptimal mate choice. This thesis concludes that the effects of noise on birds are significant even in species common in noisy areas, and that presence of a species should not be interpreted as a lack of effects.

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CHAPTER 1.
INTRODUCTION

1. ANTHROPOGENIC NOISE AND OVERVIEW OF ITS EFFECTS

The negative impact of anthropogenic noise on wildlife is an urgent conservation priority (Francis and Barber, 2013). While noise can originate from natural biotic sources (such as heterospecific and conspecific calls) and abiotic sources (such as wind and rain), the magnitude and extent of noise generated by humans have no rivals in the natural world. Sources of human-generated noise include transportation systems and industrial activities such as resource extraction, military bases, and windfarms (Ellis, 2011). Depending on the source, noise can vary in its amplitude, frequency profile, and spatial and temporal patterns (McGregor et al., 2013). Most types of anthropogenic noise concentrate their energy towards low frequencies (<250 Hz), which can propagate over long distances with relatively little energy loss (Wang and Pereira, 2005). The temporal patterns of noise are also important, as animal behaviours often happen at specific times of the day. Rush hour traffic often coincides with the dawn chorus of bird song, an important time for birds in terms of mate attraction and territorial defence. While industrial activities can be problematic because of the intensity and continuity of the noise that they generate, they also tend to be more localised in the landscape (Blickley and Patricelli, 2010). In contrast, transportation systems are amongst the most pervasive sources of anthropogenic noise across all habitats, as they include roads and vehicular traffic, airports and airplanes, railways, ships, and off-road vehicles.

In Europe 65% of the human population is exposed to noise levels exceeding 55 dB(A) (Chepesiuk, 2005), while across the United States 88% of the land experiences elevated sound levels of anthropogenic origin (Mennitt et al., 2013). Roads networks are rapidly increasing in their extent, and they are the most widespread source of anthropogenic noise. In the 33 member countries of the European Environment Agency, it has been estimated that road traffic alone is responsible for affecting over 100 million people with harmful noise levels (European Environment Agency 2018), while in the continental US, 83% of the land area is within c. 1 km of a road (Ritters and Wickham, 2003). The human population is expected to reach between 8 and 10.5 billion by 2050; as population and urbanisation grow, so will the extent of anthropogenic noise (United Nations, 2019).

Anthropogenic noise has created novel acoustic conditions that have no precedents in evolutionary history. Noise has been shown to be harmful for humans, with severe psychological and physiological consequences, such as sleep disturbance, higher risks of cardiovascular diseases, tinnitus, and cognitive impairments in children (Babisch 2005; Recio et al. 2016; WHO 2011). Similarly, noise constitutes a threat to other animals (Barber et al., 2010), and especially birds, which rely on vocal communication for their survival and reproduction. Acoustic communication plays a vital role in the life of many species, as vocalisations are essential to attract mates, deter rivals, or signalling the presence of predators (Bradbury and Vehrencamp, 1998). As communication is only effective when signals are propagated and broadcasted efficiently (Lohr et al., 2003), any disturbance in the transmission or the reception of acoustic signals will likely have fitness costs for both the senders and receivers.

Where animals have been exposed to natural noise patterns over many generations, populations have managed to adjust to noise disturbance to increase communication efficiency (Nemeth and Brumm, 2010). In areas with high levels of natural noise (e.g. from waterfalls or other animals) birds use a variety of strategies to avoid signal masking (the phenomenon that occurs when the perception of a biologically relevant vocalisation is affected by the presence of another sound; Ortega, 2012). These include adjustments in song timing, song structure, and performance (Brumm and Todt, 2002). Similar adaptive processes seem to have happened as a response of anthropogenic noise in birds that inhabit urbanised noisy environments. Studies have demonstrated that, in order to avoid masking traffic noise, a number of bird species shift song frequencies, duration, amplitude, and timing of singing (Rheindt, 2003; Slabbekoorn and Peet, 2003; Nemeth and Brumm, 2010). These adjustments denote adaptive responses to the evolutionary novel habitat represented by noisy environments, and probably depend upon both behavioural (learning process and plasticity of singing behaviour) and micro-evolutionary modifications (Brumm, 2006a). Indeed, while genetic differentiation may account for population specific differences, several studies have identified culturally learned differences in signal structures that reduce the impact of masking by noise as a mechanism of acoustic adaptation to anthropogenic noise (e.g. Moseley et al., 2018), which likely takes place over multiple generations (see Luther and Baptista, 2010 longitudinal study over a 30 year time gap).

However, anthropogenic habitat change and noise have generated unique environmental pressures in a short amount of time from an evolutionary perspective, and these changes in signal structure might not be efficient (Rabin and Greene, 2002) in evolutionary terms. Song adjustments in urban habitats may lead to trade-offs between natural selection, which determines signal adaptations, and sexual selection for “attractive” signals (Slabbekoorn and Ripmeester, 2008). On the other hand, some bird species, might simply not be able to adapt their signals to improve communication in noisy areas and will therefore avoid them, or pay the consequences of impaired communication (Rheindt, 2003). Noise might also contribute to the creation of population sinks in habitats otherwise suitable for feeding or nesting, with significant consequences on population viability (Schmidt et al., 2014).

Noise can have an impact on birds through several complex and non-mutually exclusive processes, which might ultimately result in declines of fitness and survival of the individuals or population affected. The same response can be induced via multifactorial and interconnected mechanisms (Figure 1). For instance, reductions in parental provisioning may be driven by a combination of stress, increased predatory perception, altered time budgets, and acoustic masking of begging calls (Quinn et al., 2006; Blickley, Word, et al., 2012; Leonard et al., 2015). Increased predatory perception can then feed back into this loop by causing increases in stress levels (Kight and Swaddle, 2011).

Here I review the literature on how birds respond to anthropogenic noise, with a particular focus on its effects that on the reproductive success and on the vocal communication of birds.

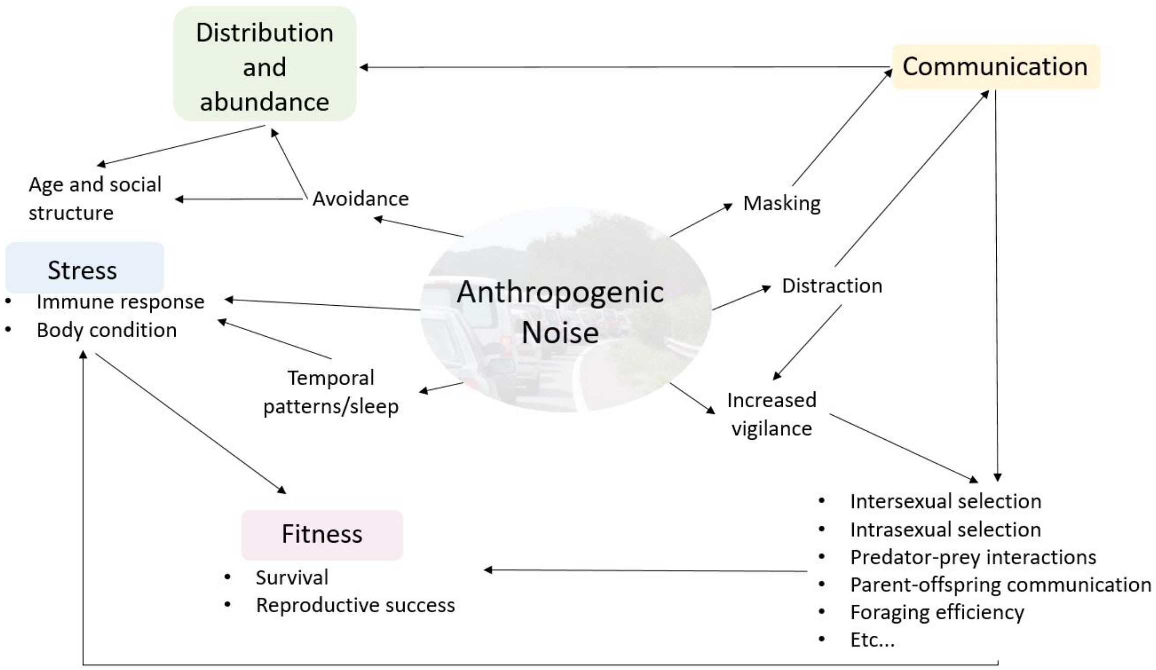


Figure 1 A simplified conceptual map of the effects of anthropogenic noise on fitness, communication, physiology, and abundance, and on how they interlink with each other. Adapted from Francis and Barber, 2013.

2. EFFECTS ON DISTRIBUTION, ABUNDANCE, AND STRUCTURE

A large amount of the evidence for the impact of anthropogenic noise comes from studies on density, abundance, and species diversity of avian populations and communities. Research on the abundance of birds near motorways has led to the conclusion that noise is a major factor explaining declines in populations near roads (Reijnen et al., 1996; Forman et al., 2002; Rheindt, 2003; Peris and Pescador, 2004; Parris and Schneider, 2009). Recent work has focused on detangling the effects of noise from other forms of disturbance associated with anthropogenic infrastructures and activities (such as visual disturbance, collisions, chemical pollution, and edge effects), and on providing evidence that noise alone can alter breeding distribution and species richness. Studies carried out around natural gas extraction sites have been the first to isolate the effect of noise, by comparing sites close to active gas compressor stations to sites where these were turned off (Ortega and Francis, 2012). Noise generated by these stations appears to be the main factor responsible for changes in songbird breeding distribution and species richness, as well as pairing success and age structure (Habib et al., 2007; Bayne et al., 2008). In fact, birds may perceive noisy territories as being of lesser quality, hence less experienced and/or younger birds might end up breeding in noisier territories where they experience less competition from socially dominant individuals (Reijnen and Foppen, 1991; Habib et al., 2007). Recently, a series of “phantom road” studies, consisting of an array of loudspeakers broadcasting road noise into a road-less landscape, have allowed to entirely isolate the effects of noise from other effects. These experiments showed a decline of bird abundance by over one-quarter, and almost complete avoidance by some species (McClure et al., 2013). The same experimental set up also showed changes in age composition (McClure et al., 2017).

3. DIRECT MEASURES OF FITNESS

Changes in species abundance or composition only provide a limited understanding of how noise can affect bird populations and communities. Measuring these changes alone can be misleading because high or normal levels of abundance do not necessarily translate into high fitness (Halfwerk and Slabbekoorn, 2014). Drawing conclusions on whether noise has a negative impact on a population based only on presence of individuals is problematic, because individuals may not have alternative areas to occupy, or might not be choosing habitats effectively. For example, individuals that were found living around the phantom road experienced a decrease in their overall body condition (Ware et al., 2015), suggesting that species that persist and might appear to be adapted to living in noisy areas, might still experience negative effects.

Noise has the potential to decrease fitness, both through acting as a direct physiological stressor, or by masking important vocalizations and leading to behavioural alterations (Francis and Barber, 2013). Studies looking at direct measures of fitness show that noise has the potential to affect breeding success at different stages of the reproduction, such as egg laying, incubation, hatching, and fledging. For example, great tits (*Parus major*) have been shown to produce fewer eggs and fledge fewer young when nesting in areas affected by high levels of traffic noise compared to quieter areas (Halfwerk, et al., 2011), and ash-throated flycatcher (*Myiarchus cinerascens*) nests exposed to noise have higher rates of abandonment at the incubation stage, and therefore lower reproductive success (Mulholland et al., 2018). House sparrows (*Passer domesticus*) breeding in noisy conditions have fewer hatchlings, with lower body mass, that ultimately result in fewer recruits than their conspecifics breeding in quiet sites (Schroeder et al., 2012). Eastern bluebirds (*Sialia sialis*) also show lower hatching rates and fledging success when breeding in noisy sites.

Finally, chestnut-collared longspur (*Calcarius ornatus*) nesting in proximity to noisy roads produce fewer fledglings, and typically fail or produce only one fledgling when within 50 meter from a road (Ng et al., 2019).

Currently, all studies on the effects of anthropogenic noise on avian breeding are based on a single or a couple of populations. So far, studies looking at multiple populations on a large geographical scale have focused on change in the vocal behaviour (eg. Slabbekoorn and den Boer-Visser, 2006; Mockford and Marshall, 2009; Gil et al., 2015) and in the abundance (eg. Patón et al., 2012) of birds at sites exposed to noise, demonstrating that changes observed are widespread amongst populations. Larger scale studies covering wide geographical areas offer a more generalised understanding of this phenomenon than single population studies. In order to be able to draw conclusions over large geographical ranges, studies on the impact on noise on breeding performance are therefore necessary.

While there is growing evidence that the negative effects of noise on reproductive success affect a wide variety of species (Halfwerk and Slabbekoorn, 2014), different species may differ greatly in their mechanisms of physiological stress response (Hofer and East, 1998), hearing abilities (Ryals et al., 1999; Dooling et al., 2000), vocal traits, and diets (Francis, 2015). For this reason, and because of how species interact within a community (Francis et al., 2009), the response to anthropogenic noise can vary significantly between species. Only a few studies so far have investigated the effects of noise on fitness by focusing on more than one species, and they found that noise can have a negative effect on some species but not on others (Kleist et al., 2018b; Mulholland et al., 2018), or that it may even facilitate reproductive success, as a result of the disruption of predator-prey interactions (Francis et al., 2009; Francis, Paritsis, et al., 2011). As the relationship between anthropogenic noise and breeding performance is likely to vary greatly amongst different species, multi-species studies are therefore necessary in order to provide a wider picture on the effect of this pollutant.

4. PHYSIOLOGICAL AND PHYSICAL CHANGES

Exposure to noise pollution can increase physiological stress levels (Kight and Swaddle, 2011), which allows animals to cope with this stressor, but has potential negative effects over time. In vertebrates, stress is responsible for the activation of the hypothalamic-pituitary-adrenal (HPA) axis, which results in an increased secretion of glucocorticoid hormones (in birds, corticosterone) (Wingfield et al., 1998). This, in the short term, may improve the survival of an individual by releasing energy, but in the long term can increase oxidative stress and inhibit growth and immune function (Kight and Swaddle, 2011), and result in other negative consequences (Kriengwatana et al., 2013), such as elevated heart rate and decreased body condition (Ortega, 2012).

While correlations between noise exposure and glucocorticoid stress responses have been shown in a wide number of species (e.g. Tempel and Gutiérrez, 2003; Cyr et al., 2007; Blickley, Word, et al., 2012; Crino et al., 2013), the effects of noise on stress response are complex, and studies investigating their links have produced very mixed evidence. Indeed, depending on a multitude of factors (such as species, context, life history stage, and type of noise exposure) different studies both in adult birds and nestlings have found that the direction and the extent of the association between corticosterone levels and noise exposure can vary substantially, or have found no association at all. In some species, elevated noise levels have been associated with elevated corticosteroid concentrations, which can be interpreted as an indication of stress, and might negatively affect fitness (Bonier et al., 2009). For example, this has been found in greater sage-grouses (*Centrocercus urophasianus*) exposed to experimental industrial noise (Blickley, Blackwood, et al., 2012), or urban house wrens (*Troglodytes aedon*) exposed to traffic noise (Davies et al., 2017). In some other species, however, chronically stressed birds might respond to acute stressors with hypocorticism (Rich and Romero, 2005), via a reduced synthesis of hormones from the HPA-axis and/or enhanced sensitivity to negative feedback of corticosterone (Fries et al., 2005). For instance, Kleist et al. (2018) found that chronic noise exposure to gas compressor depressed baseline corticosterone levels of breeding females of western bluebird (*Siala mexicana*). Similar negative correlations have also been found in adults of European blackbirds (*Turdus merula*) (Partecke et al., 2006), northern cardinals *(Cardinalis cardinalis*) (Wright and Fokidis, 2016), and breeding zebra finches

(*Taeniopygia guttata*) (Zollinger et al., 2019). Lastly, some studies have found no impact of chronic anthropogenic noise exposure on baseline corticosterone levels (Potvin and MacDougall-Shackleton, 2015b; Angelier et al., 2016; Davies et al., 2017).

The identification of the processes behind stress response and anthropogenic noise is further complicated by the fact that, to date, most studies have been conducted in the field (but see Potvin and MacDougall-Shackleton, 2015; Zollinger et al., 2019), where other factors such as chemical and light pollution (Isaksson, 2010; Swaddle et al., 2015; Dominoni et al., 2016), habitat structure (Nemeth and Brumm, 2010), avian community density and composition (McKinney, 2006), and food availability (e.g. Biard et al., 2017) might also play a role. Moreover, noise might be directly responsible for alterations in the baseline corticosterone levels through acute exposure, or it might act indirectly as a physiological stressor through alterations in the interaction between birds and their environment (reviewed in Kight and Swaddle, 2011), in particular when noise frequencies overlap with auditory environmental cues, leading to reduced detection and discrimination of key acoustic signals, and therefore causing birds to experience a state of unpredictability (Rich and Romero, 2005). Noise levels might act indirectly as a physiological stressor because of increased predatory risk perception (Quinn et al., 2006) and/or reduced foraging opportunities (Schaub et al., 2009; Ware et al., 2015). Similarly, noise induced environmental uncertainty in both parents and chicks might cause chronic activation of the HPA axis and affect both glucocorticoids and fitness (LaManna and Martin, 2016). Whether through a direct pathway or through impairment of other behaviours, chronic stress can ultimately translate into less energy to invest in the eggs and the offspring (Angelier et al., 2009; Spée et al., 2011; Thierry et al., 2013), leading to slower body size and impaired development in the chicks (Saino et al., 2005), and ultimately affecting reproductive success (Blickley and Patricelli, 2010).

Alteration of telomere dynamics is yet another pathway through which noise has been shown to have direct physiological effects on bird. Telomeres are made of repetitive sequences of non-coding DNA at the ends of chromosomes, protecting them from loss of genetic information (Monaghan and Haussmann, 2006), and their length is positively related to survival in free-living birds (Haussmann et al., 2005). Telomeres have been found to shorten in response to increases in baseline corticosterone (Haussmann et al., 2012), and to early post-natal stress exposure (Herborn et al., 2014). Urban environments (Salmón et al., 2016) and traffic noise exposure (Meillère et al., 2015) have been shown to decrease telomere length in juvenile songbirds, and anthropogenic noise alone has been found to increase telomere loss (Dorado-Correa et al., 2018).

5. EFFECTS ON COMMUNICATION

One of the main effects of noise is the disruption of vocal communication through acoustic masking (Dooling and Blumenrath, 2014). By decreasing signal to noise ratio, background noise makes signals harder to detect, discriminate and recognise for the receiver (Brenowitz, 1982; Dooling and Blumenrath, 2014). Bird song plays a central role on inter- and intrasexual selection and on social integration, and it therefore is vital for reproductive success (Catchpole and Slater, 2008). Other kinds of vocalisations (such as alarm, begging, fight, and food calls), are also crucial for breeding and survival (Marler, 2004a). Any decrease in the active space of signals could therefore reduce the fitness of individuals, and ultimately result in population declines.

5.1 SONG PERFORMANCE

In birds, songs are accurate indicators of individuals quality (Gil and Gahr, 2002), and, in many species, song performance has been shown to affect territorial defence and female mate choice (Searcy and Yaksukawa, 1996; Nowicki and Searcy, 2004; Catchpole and Slater, 2008). In order for songs to be accurate indicators of quality, their production must involve some costs, which ensures that they are honest signals (Johnstone and Grafen, 1993). Indeed, even the simple production of songs can be costly in terms of time and energy (Oberweger and Goller, 2001), and therefore the ability of an individual to produce more songs than another might be a cue of its quality or the quality of its territory (Greig-Smith, 1982; Radesater and Jakobsson, 1989). Across different species, other quantitative metrics of an individual's vocal performance that have been shown to affect female choice include the ability to sing longer songs or sing often, and the size and complexity of a male's vocal repertoire (Alatalo et al., 1990; Marcel et al., 1991; Kempenaers et al., 1997), as this might be constrained by developmental costs associated with brain growth and song learning (Nowicki et al., 2002). On the other hand, quality metrics that could potentially serve as an indicator of male condition involve the ability to sing physically demanding songs (Vallet and Kreutzer, 1995; Vallet et al., 1998; Drăgănoiu et al., 2002), or to accurately copy song models (Nowicki et al., 1998; Holveck et al., 2008). For instance, female canaries (*Serinus canaria*) are more responsive to songs including syllable types that require more complex motor patterns for their production (Vallet and Kreutzer, 1995; Vallet et al., 1998). Another indicator of vocal performance that has started getting attention since the last decade, is song consistency (reviewed in Botero and de Kort, 2011). This song feature is defined as the acoustic similarity between renditions of a given song type or syllable type within a song (Byers, 2007; Botero et al., 2009; de Kort, E. R.B. Eldermire, et al., 2009), and has been related to the singer's fitness in a large number of studies (e.g. Botero et al., 2009; de Kort et al., 2009; Rivera-Gutierrez et al., 2010, 2011; Wegrzyn et al., 2010; Moseley et al., 2018; Phillips and Derryberry, 2018).

5.2 THE SENDER'S PERSPECTIVE

Some birds in noisy environments are able to adjust their songs in order to lessen the detrimental impact of masking noise (Brumm and Zollinger, 2013), and species that have the capacity to adjust their signal are more prone to adjust to urbanisation and survive in noisy environments (Slabbekoorn, 2013). Much of the research on the effects of anthropogenic noise on the vocal communication of birds has been focusing on the behavioural adjustments and adaptations of the sender.

One way of intensifying the detectability of a vocal signal is to increase the amplitude at which they are broadcast. The involuntary elevation of voice amplitude in response to increases in background noise levels, a response known as the Lombard effect (Junqua et al., 1999), has been observed in birds (reviewed in Brumm and Zollinger, 2013). This phenomenon appears to be taxonomically widespread among birds, and has been demonstrated with psychoacoustic experiments in soundproof laboratory settings for a number of different vocal signals, such as songs and begging calls, and in a wide range of taxa (e.g. Cynx et al., 1998; Manabe et al., 1998; Oberweger and Goller, 2001; Brumm and Todt, 2002; Leonard and Horn, 2008; Templeton et al., 2016). While measuring amplitude changes in the field is complex (Zollinger and Brumm, 2015), studies on natural population show that birds occupying loud environments also modify the amplitude of their songs

(Wood and Yezerinac, 2006). For example, not only nightingales (*Luscinia megarhynchos*) sing at higher frequencies, they also adjust their amplitude to different levels of noise depending on peaks in anthropogenic noise (Brumm, 2004). Birds in the wild also adjust the amplitude of other signals, such as alarm calls. For example, noisy miners (*Manorina melanocephala*) living in areas with heavy traffic noise call louder than individuals at quieter locations (Lowry et al., 2012). In addition to simply increasing the amplitude of a vocalisation, some birds may raise the amplitude of their songs through a selective use of songs from their repertoire which are louder or contain louder elements, (Nemeth and Brumm, 2010; Nemeth et al., 2013), a phenomenon which has also been linked to adjustments in peak frequency.

Indeed, another way to improve the signal-to-noise ratio of acoustic signals is to increase their frequency, resulting in masking release, a change that is thought to be an adaptive response to the typically low-frequency anthropogenic noise (but see Nemeth et al., 2013). This phenomenon has been observed in a number of species, such as for example song sparrows (*Melospiza melodia*) (Wood and Yezerinac, 2006), great tits (Mockford and Marshall, 2009), European blackbirds (Nemeth and Brumm, 2010), and black-capped chickadees (Goodwin and Podos, 2013). While some species are able to increase the frequency of individual notes within a song (Bermúdez-Cuamatzin et al., 2011), others, such as great tits, sing at higher minimum frequency by switching to song types with higher frequency elements (Halfwerk and Slabbekoorn, 2009). However, an experimental study on great tits has recently hinted that the link between noise and pitch shifts might not be as straight forward as previously assumed (Zollinger et al., 2017); these laboratory-reared birds did not show any frequency shifts during song ontogeny or as a result of individual adult plasticity, suggesting that other factors other than noise might be involved in the vocal divergence amongst urban and forest populations, or that this divergence might be the result of slower, population-wide changes over several generation.

The temporal structure of vocalisations can also be adapted in response to noise. By increasing the repetition and duration of signals, birds might improve their detectability (Fernández-Juricic et al., 2005; Warren et al., 2006; Proppe et al., 2011). Males of vermilion flycatcher *(Pyrocephalus rubinus*) occupying territories with higher noise levels produce longer songs, whereas males in quieter places sing both long and short songs (Ríos-Chelén and Garcia, 2007). Other studies suggest that another strategy might be singing shorter, faster songs. For instance, free-living house finches (*Carpodacus mexicanus*), significantly reduce the number of notes in noisy areas (Fernández-Juricic et al., 2005). Likewise, this has also been found in great tits (Slabbekoorn and den Boer-Visser, 2006) and black-capped chickadees (*Poecile atricapillus*) (Proppe et al., 2011).

Rather than adjusting the acoustic signal, birds might change the timing or location of their vocalisations in order to ease or prevent the effects of masking noise (Mathevon et al., 2005; Halfwerk et al., 2012; Nordt and Klenke, 2013; Dominoni et al., 2016). Indeed, the levels of urban noise follow strong and predictable patterns during the day and are reduced overnight when human activities decline. Species that would normally be diurnal may therefore adjust the time at which they vocalise to minimise interference. For instance, European robins (*Erithacus rubecula*) are more likely to sing at night when noise levels are lower (Fuller et al., 2007), and in European blackbirds (*Turdus merula*) the start of the down chorus depends on traffic noise and light levels (Nordt and Klenke, 2013). Recently, the duration and the onset time of the down chorus has been linked to airport noise (Dominoni et al., 2016), and the dawn chorus of 21 species across 39 different populations has been analysed to discover that birds advance its timing in order avoid anthropogenic acoustic interference from airport noise (Gil et al., 2015).

Adjustments in the length, timing, amplitude, and frequency of vocalisations in response to anthropogenic noise can be energetically costly (Gillooly and Ophir, 2010; Oberweger and Goller, 2001; but see Zollinger et al., 2011), and may require physiological capacities and a vocal plasticity which some species might not possess (Bradbury & Vehrencamp 2011; Templeton et al. 2016). There is a large variation in the extent to which urban species can adjust the frequencies of their songs (Hu and Cardoso, 2010), and birds with vocal frequencies that can be masked by low frequency noise have been shown to avoid noisy areas (Goodwin and Shriver, 2010; Proppe et al., 2013). In fact, the detrimental impacts of anthropogenic noise on bird breeding density and reproductive seem particularly common in species with low-pitched vocalisations (Francis et al., 2009; Halfwerk, Holleman, et al., 2011). Additionally, even if birds modify their vocal behaviour in response to noise, these adjustments are not a guarantee for success in noisy areas (Moiron et al., 2015). Alterations in vocal performance are not always sufficient to avoid acoustic masking (Schmidt et al.,

2014) or, when they do produce benefits in terms of signal detection, they might be lose in terms of signal quality (Ríos-Chelén, 2009; Huet des Aunay et al., 2013).

5.3 THE RECEIVER'S PERSPECTIVE

For acoustic communication to be effective, vocal signals have to be transmitted efficiently by the sender, while also being detected and interpreted successfully by the receiver (McGregor et al., 2013). Masking by anthropogenic noise has the potential to impair the detection and the assessment of vocal signals (Lohr et al., 2003), and to alter the response of the receiver. However, the behaviour of the receiver in noise is comparatively understudied in comparison to that of the sender, and most of our understanding on the effects of anthropogenic noise on the receiver's side of acoustic communication comes from psychoacoustic studies carried out in laboratory settings. Lohr et al. (2003) showed that noise affects both the detection and the discrimination of vocal signals in zebra finches (*Taeniopygia guttata*) and budgerigars (*Melopsittacus undulatus*), and that thresholds for detection and discrimination vary with the spectral shape of noise. Similarly, studies on great tits show that noisy conditions increase the detection threshold of vocal signals by up to 18 dB, and that high-frequency songs in urban noise are more easily detected and discriminated than low-frequency ones (Pohl et al., 2009, 2012).

In the field, the effect of ambient noise on the ability of the receiver to detect and assess signals has only recently started to be investigated. Although there are few field-based experiments in this field, research suggests that receivers also adjust their behaviour to improve communication in noisy conditions. For example, males of white-crowned sparrows (*Zonotrichia leucophrys*) tend to approach more closely to songs as noise increases (Phillips and Derryberry, 2018), something that might be interpreted as increased aggression in response to urban noise, or as an adaptation in order to assess vocal performance traits that would otherwise be masked by noise. Changes in song post in response to noise have been seen in blackcaps (*Sylvia atricapilla*), which alter perch height to improve communication (Mathevon et al., 2005). Birds may also adjust their vocal behaviour. European robins exposed to playbacks masked by noise change the complexity and pitch of their songs (McMullen et al., 2014), possibly sacrificing the quality of their signals in order to increase detection (Zwart et al., 2016). Noise might also weaken the territorial response to a potential intruder by increasing the latency to respond to a playback of their songs (Kleist et al., 2016).

Decreased or delayed detections have also been observed for other vocal signals other than songs. For example, great tits fail to perceive alarm calls when exposed to traffic noise (Templeton et al., 2016). In tree swallows (*Tachycineta bicolor*) parent-offspring communication is altered, as nestling fail to perceive contact and feeding calls by the parents (Leonard and Horn, 2012), and parents fail to perceive begging calls by the nestlings (Leonard et al., 2015). As shown in the experiments carried out in laboratory conditions, the process of hearing does not simply stop at the detection of a signal (Knudsen and Gentner, 2010), but indeed involves at least two more processes. These processes consist in what Dooling and Blumenrath (2014) identify as discrimination (which in humans is defined as the ability to tell one voice from another), and recognition (defined as the ability to understand what is being said). Discrimination of a signal requires a higher signal-to-noise ratio than detection, and for recognition the signal-to-noise ratio must be even higher (Lohr et al., 2003; Freyaldenhoven et al., 2006). This means that a detectable signal might still be unintelligible because of masking noise. Most of the research conducted in the field so far, has only been focusing on the detection of vocal signals on the functional consequences of song adjustments when birds are exposed to noise. As signal discrimination and recognition are processes that allow to decode the information enclosed in such signals, and to assess their quality and content, more field research is necessary to understand how failure of the receiver to discriminate and recognise signal takes place, and to highlight the consequences of such failures in a natural context.

The section below highlights some of the fitness costs that might take place when changes in vocal behaviour are only adaptive in terms of detection but not of vocal selection, and it draws attention to the consequences that might take place when birds fail to detect, assess, and decode vocal signals appropriately.

5.4 WHEN COMMUNICATION GOES WRONG: IMPACTS ON REPRODUCTIVE SUCCESS RELATED TO SIGNAL MASKING

Any failure in the transmission and the reception of acoustic communication might ultimately result in decreased chances of survival and reproductive success, by affecting aspects related to intra- and intersexual communication, or other forms of communication among intra- and inter-specifics, such as parent-offspring interactions, food calls, and alarm calls.

In songbirds, females can tell apart individuals based on their songs, and they recognise the songs of their mates and show preferences for certain aspects of it, such as higher rates, larger repertoires and larger frequency bandwidths (Wasserman and Cigliano, 1991; Buchanan and Catchpole, 1997; Luther et al., 2015). The masking of signals important for mate attraction has been shown to have a negative impact on reproductive success by eroding pair preferences in zebra finches (Swaddle and Page, 2007), albeit in individuals of the same species exposed to levels of noise more similar to roads, extrapair paternity was not affected by traffic noise (Zollinger et al., 2019). Moreover, alterations in vocalisations to avoid signal masking might reduce the effectiveness of the signal transmitted and have significant consequences in pairing and breeding. For instance, in species where females prefer males that sing at lower frequencies, higher pitched songs might improve signal transmission but decrease their attractiveness, as shown in song sparrows (*Melospiza melodia*) and great tits (Wood and Yezerinac, 2006; Halfwerk, Bot, et al., 2011). Similarly, in species where females choose males based on their repertoire size, if males reduce their repertoire to exclude songs that would be less audible in noise, this could reduce their attractiveness (Ríos-Chelén, 2009).

Trade-offs can also occur during competition between males, as vocal inputs are used for conspecific recognition, and to assess the signaller’s motivation to fight or its physical condition (Catchpole and Slater, 2008). By affecting the ability to deter a rival, or the perception of song characteristics that give information on the level of aggressiveness or threat, anthropogenic noise could cause fewer mating opportunities and impair territorial defence (Mockford and Marshall, 2009). In European robins, the presence of wind turbine noise reduces their use of low-frequency elements in response to simulated territorial intrusions (Zwart et al., 2016), which corresponds to a weaker defence signal. As specific singing behaviours are hypothesised to be threatening, males that change their vocalisations to avoid urban noise might be interpreted as less threatening, unless there is a corresponding shift in the interpretation of the signal (Patricelli and Blickley, 2006). For example, white-crowned sparrows (*Zonotrichia leucophrys nuttalli*) increase the minimum frequency of their song in response to noise. However, the receivers perceive these songs as low performance and respond less intensely to these compromised signal (Luther et al., 2015).

The masking effect of noise on song has the potential to affect breeding success through impairing the perception of song quality, or modifications to songs that make them less preferred by females or less effective for obtaining or maintaining a territory. Females are known to breed later, allocate less energy to the eggs, or provide less maternal care to the chicks when breeding with males that they perceive to be of lower quality (Halfwerk, Holleman, et al., 2011), and males will experience reduced pairing success and breeding opportunities.

Not only songs, but also other vocalisations are crucial for the reproductive success and survival of birds (Chan and Blumstein, 2011). For example, noise has been shown to impair parent offspring-communication (Leonard and Horn, 2012; McIntyre et al., 2014; Lucass and Eens, 2016), which in turn might cause reduced parental care and provisioning, and has been linked to nest failure at the nestling stage (Schroeder et al., 2012). Nestlings use begging calls to attract their parents' attention and signal their needs, and parents use them to assess which nestling to feed (Wright and Leonard, 2002). When begging for food in noisy conditions, nestlings may need to call louder to elicit the desired response from their parents, thereby increasing the energetic cost of obtaining food and potentially decreasing fitness (Leonard and Horn, 2005). Nestlings of tree swallows (*Tachycineta bicolor*) exposed to playbacks of white noise change the frequency structure of their calls (Leonard and Horn, 2008). Yet, when exposed to noise, parents reduce their provisioning rate, and nestlings fail to respond to their parents arrival (Leonard and Horn, 2012; Lucass and Eens, 2016). House sparrows reduce provisioning frequency in the presence of noise because of two potential mechanisms: chick begging not being audible or being less audible, or chicks failing to notice their parents' arrival at the nest, resulting in them not begging for food (Schroeder et al., 2012). This was directly associated with lower fledging mass and lower fledging and recruitment success.

The detection of anti-predator signals might also be compromised or delayed by the presence of noise. This has been shown both amongst adults and between adult and nestlings. In adults of starlings (*Sturnus vulgaris*), the perception of alarm calls is impaired by the presence of a wide spectrum masking noise (Mahjoub et al., 2015). Nestlings exposed to anthropogenic noise, also fail to respond appropriately to mobbing alarm calls, such as shown in tree swallows (McIntyre et al., 2014) and great tits (Templeton et al., 2016), and are therefore more likely to be exposed to potential predators. In response to the increased predation risk in noise, species have been shown to spend more time being vigilant, which translates into less energy to devote to their eggs and offspring (Angelier et al., 2009; Spée et al., 2011). Missed detections of alarm calls might also affect non conspecifics (Grade and Sieving, 2016), as species often eavesdrop on the alarm calls of others to monitor the presence of potential predators (Magrath et al., 2015). Alarm calls are not just used to warn of the presence of predators, but they also convey information on the type of predators, depending on which birds might need to respond differently (Evans et al., 1993). While a complete failure to detect alarm calls carries obvious fitness consequences, inaccuracies in the discrimination of these vocal signals might still cause fatal errors by leading to incorrect behavioural responses through masking of subtle information about predator type or threat. Vice versa, for species that rely on their auditory system to detect prey, anthropogenic noise might decrease hunting success, such as shown in Northern saw-whet owls (*Aegolius acadius*), whose ability to catch prey is progressively affected in increasing noise and entirely compromised at noise levels above 61 dB(A) (Mason et al., 2016).

6. OUTSTANDING QUESTIONS

While it is increasingly clear that the omnipresence of noise is detrimental to wildlife, urban noise levels continue to increase in geographical spread, proportion of time exposed to high levels, and intensity (Berglund et al., 2000). The above examples illustrate the manner in which wild birds can modify their behaviour to successfully survive in noisy environments, but also how a complete or even only partial failure to do so can have important consequence for their fitness and survival, on both an individual and population level.

More research is necessary to better understand the trade-offs associated with living and breeding in noisy areas, including among those species that might appear to be tolerant to life in noisy or uban environments, as they breed and settle in close proximity to sources of anthropogenic noise (Francis et al., 2009). Indeed, while many studies focus on changes in the distribution of species exposed to noise, rarely do they simultaneously consider the reproductive success of the individuals (Shannon et al., 2016). As the mere presence of individuals in noisy areas may not be a reflection of their fitness, more studies looking at breeding site selection, and how it correlates with breeding output are necessary to understand whether species settling in noisy environments are truly noise tolerant.

To date, there is a paucity of large scale studies on the impact of noise on birds, and research on the effects on breeding performance is yet to include more than a single or a few populations. The large-scale studies that have been conducted focus on the impacts of noise on communcation or distribution (Blickley and Patricelli, 2010), but I am not aware of a study that has investigated the impact of noise on breeding success at a large geographic scale, particularly across multiple countries and species. Large scale life history data are available thanks to volunteer and citizen science programmes, and could be used to quantify impacts of noise on breeding. However, we lack a methodology to do this on a large scale.

It is clear that behavioural flexibility acts as a crucial factor when understanding the ability of species to respond to challenging environmental conditions (Lowry et al., 2013). Species may differ in their capacity to correct for novel circumstances (Schlaepfer et al., 2002). Some types of adaptive response might be either physiologically impossible (such as in the case of frequency adjustments for some species) or have a fitness cost, thus precluding some species from noisy habitats, or degrading their chances of reproductive success (Barber et al., 2010). Adjustments through plasticity may only mitigate the effect of environmental changes but not entirely compensate for them, or may only be adaptive for certain aspects but yet result in declines in fitness (Wright et al., 2007). Ultimately, a greater knowledge of how different species respond to noise pollution in terms of their fitness may be crucial to maintaining biodiversity and ecological stability in the growing number of landscapes disrupted by our artificial noise.

Finally, birds rely on vocal communication to perform vital behaviours such as mate attraction, territorial and mate defence, parental provision, and defence from predators

(Bradbury and Vehrencamp, 1998; Catchpole and Slater, 2008). The impairment of vocal communication is one of the key features linked to declines in the reproductive success and overall survival of birds (Proppe et al., 2013). However, while the detection of vocal signals has received considerable attention, little is know about the effects of masking on the discrimination and identification of vocal signals. Indeed, birds are regularly exposed to noise levels below the threshold that would cause vocal signals to be completely masked (McKenna et al., 2016). It is therefore likely that negative effects of noise via masking of information contained in a signal (informational masking) might be far more extensive than the effects of noise caused by an impaired detection of vocal signals (Rosa et al., 2015). Informational masking, in fact, can take place well beyond the spatial extent at which noise amplitude is strong enough to only affect detection (Banbury et al., 2001). Consequently, more research is needed to evaluate this phenomenon not just in laboratory settings, but in an ecological relevant context.

7. THESIS AIMS AND STRUCTURE

This thesis has the following aims:

1. To investigate nest-site selection, nest fidelity, and breeding success in a population of songbirds exposed to a gradient of traffic noise over multiple years.
2. To develop a method to test the relationship between different stages of the breeding ecology of birds with the level of anthropogenic noise around major road networks on a large geographical scale.
3. To apply the method to test the relationship between different stages of the breeding ecology with the level of anthropogenic noise around major road networks for 11 common bird species.
4. To test if blue tits recognise fine structural song differences under a variety of ambient noise conditions.

7.1 CHAPTER 2 - INFLUENCE OF NOISE ON NEST SITE SELECTION AND NESTING SUCCESS: A LOCAL POPULATION STUDY ON BLUE TITS

Chapter 2 addresses the first aim of this thesis by assessing nest-site selection, fidelity, and breeding performance of a common species of songbird. To that end, it uses long-term data from a population of blue tits breeding in nest-boxes exposed to a traffic noise gradient. The noise gradient provides an opportunity to examine the levels at which a response is initiated, and how the response changes with increasing noise levels. By looking at nest site selection across different noise levels while simultaneously exploring their relationship with breeding performance, this design can also reveal whether breeding site choice is reflected in breeding performance.

7.2 CHAPTER 3 - USING LARGE-SCALE DATA TO QUANTIFY THE CONSEQUENCES OF ANTHROPOGENIC NOISE ON BREEDING SUCCESS

Chapter 3 develops a method to investigate the impact of anthropogenic noise on breeding success of birds on a countrywide scale. This method is developed using noise data generated by European Environmental Agency (EEA) member countries, and breeding data from the British Trust for Ornithology’s Nest Record Scheme, and the Sovon Dutch Centre for Field Ornithology.

7.3 CHAPTER 4 - IMPACT OF ANTHROPOGENIC NOISE ON BREEDING SUCCESS IN 11 COMMON BIRD SPECIES

Chapter 4 applies the method developed in the previous chapter to 11 different species of common European birds, and it tests the effects of anthropogenic noise on the breeding performance on a large, combined citizen science dataset from the UK and the Netherlands. This approach provides an effective method to compare the impact of anthropogenic noise on multiple species. It also allows estimating whether noise affects certain stages of the breeding cycle more than other, or which stages are more likely to be affected depending on species.

7.4 CHAPTER 5 - NOISE IMPAIRS THE PERCEPTION OF THE FINE STRUCTURE OF BIRDSONG

Chapter 5 uses an experimental playback design to investigate how noise at different amplitudes and frequency bands affects the assessment of acoustic signals in blue tits. Bird vocalisations contain subtle information in the acoustic structure that are used for quality assessment, and communication of this information may be impaired by noise, leading birds to make poor decisions regarding appropriate investments in defence behaviour. This chapter characterises how accurate recognition of fine differences within a song might be a primary mechanism driving sensitivities to noise.

7.5 CHAPTER 6 – CONCLUSIONS

Chapter 6 provides overall conclusions and recommendations for future studies, and it highlights how this research might be important to inform ecological theory, conservation and management of human-generated noise pollution on avian species.

CHAPTER 2.

INFLUENCE OF NOISE ON NEST SITE SELECTION AND NESTING SUCCESS: A LOCAL POPULATION STUDY ON BLUE TITS

Abstract

Anthropogenic noise is a rapidly expanding environmental pollutant, in particular because of the growth of transportation networks such as roads. Because of their reliance on acoustic communication for processes directly related to fitness, birds are particularly sensitive to the effects of noise exposure. Studies have found that noise can affect the chances of survival and the reproductive success of individuals, and that it can alter the abundance and structure of populations. However, some species or populations appear to successfully persist in noisy environments, and less is known about the impacts of noise on the breeding success of these. This study investigated how noise affected nest-site choice overall and over subsequent years to investigate whether younger birds are more likely to nest in noisy territories, and to assess the impact of noise on the breeding success of birds. To do so, I used long-term data from a population of blue tits (Cyanistes caeruleus) breeding in nest-boxes along a gradient of road traffic noise. I found that breeding success was reduced in noisier areas, particularly in terms of fledgling success and nestling body mass. Counterintuitively, noisy nest-boxes were more likely to be occupied by breeding pairs than quieter nest-boxes, although proportionally by younger birds. Nest-box fidelity over subsequent years decreased as noise levels increased, but there was no difference on whether birds would move to noisier or quieter nest-boxes. These results show that blue tits might not be using noise as a cue for nest-site selection, despite it having an impact on their breeding success. Noisy territories may therefore constitute an ecological trap for blue tits, and the presence of individuals in noisy territories might not necessarily reflect an absence of effects on fitness.

1. INTRODUCTION

With ever increasing global human population (ONU, 2019), urbanisation, and growth of transportation networks and resource extraction, anthropogenic noise has become one of the most widespread and pervasive environmental pollutants (Barber et al., 2010). Transportation networks, and in particular roads, are ubiquitous components of human-altered landscapes, and largely responsible for the prevalence of this pollutant on such a vast scale (Forman, 2000; Barber et al., 2010). Both individual and population level effects of roads have been documented in many taxa, including plants, mammals, reptiles, amphibians and birds (Fahrig and Rytwinski, 2009; Benítez-López et al., 2010; Holderegger and Di Giulio, 2010; Kight and Swaddle, 2011; Kociolek et al., 2011; Van Der Ree et al., 2011). In particular, there is increasing evidence that road noise is a selection pressure that affects the ecology and evolution of many species (Francis et al., 2009; Swaddle et al., 2015; Wiley, 2017), and that noise alone, rather than physical structure of roads, can constitute a source of habitat degradation (McClure et al., 2013, 2017; Ware et al., 2015; Cinto Mejia et al., 2019).

Birds are the most studied taxonomic group in terms of the impacts of anthropogenic noise, and in particular traffic noise. Human-generated alterations to the acoustic environment have been shown to reduce the quality and suitability of otherwise seemly good habitats for some bird species, and to decrease population density and cause changes in avian communities (Francis et al., 2009; Parris and Schneider, 2009; Francis, 2015), with potential cascading effects on entire ecosystems (Francis et al., 2012). A substantial amount of research has focused on the behavioural adjustments of birds in response to noise (Potvin, 2017). In particular, some species alter their vocal behaviour in order to avoid masking of their vocal signals, by modifying features of their signals relative to amplitude and frequency, or changing timing and/or rate of delivery (Patricelli and Blickley, 2006; Luther and Gentry, 2013). Despite these adaptations, birds that successfully persist in noisy areas might still be sensitive to the detrimental effects of noise.

A large amount of research reports reductions in the density, abundance and diversity of species in response to high levels of anthropogenic noise (Reijnen et al., 1995; Bayne et al., 2008; Francis et al., 2009). Declines in abundance and changes in population and community structure are a clear measure of the impact of anthropogenic noise. However, the presence of a species in a noisy area cannot be used as a sole indicator that noise does not affect negatively that species or specific population. Indeed, the individuals and species that persist in noisy areas do not always represent healthy populations or communities (Halfwerk and Slabbekoorn, 2014). For example, if individuals with better fitness avoid breeding in noisy areas (Halfwerk, Holleman, et al., 2011), noise might have an effect on the age structure of breeding populations. In willow warblers (*Phylloscopus trochilus*), first year birds are more likely to breed near roads (Reijnen and Foppen, 1994, 2006), and male ovenbirds (*Seiurus aurocapilla*) exposed to chronic industry noise are relatively lower quality and younger than males that occupy quieter areas (Habib et al., 2007). While species declines in noisy areas are well documented, the impact of anthropogenic noise on nest site selection, especially over multiple seasons, is much less studied (but see Kleist et al., 2017), and the link between noise and demographic distribution of breeding individuals is poorly understood. Nest site selection is a critical component of habitat selection and is directly linked to reproductive success (Jones, 2001). For this reason, long-term studies that combine data on nest site selection with demographic and reproductive success data are fundamental to give a full picture of the effects of noise on breeding populations, and to understand how individuals respond to noise over time.

Reduced reproductive success in birds exposed to anthropogenic noise has been observed in species where breeding population size does not appear to be affected, such as great tits (*Parus major*; Halfwerk et al., 2011), eastern bluebirds (*Sialia sialis*; Kight et al., 2012), house sparrows (*Passer domesticus*; Schroeder et al., 2012), and western bluebird (*Sialia mexicana;* Kleist et al., 2018). This is another example of the fact that presence or abundance of breeding individuals is not sufficient to assess fitness of populations exposed to noise, and that investigating the breeding performance of a population is necessary to assess the impact of noise on species that would otherwise appear to be tolerant to this pollutant. This is also important in order to pinpoint which life-history stages are most vulnerable to noise. Declines in breeding success might be taking place on only one or on multiple stages of the reproductive performance depending on which phases of the breeding performance are impacted by noise. Optimal mate choice may be affected because females may not be able to assess a male's quality through song performance because of acoustic masking (Halfwerk, Bot, et al., 2011). This may result in reduced parental investment and smaller clutches (Habib et al., 2007; Halfwerk and Slabbekoorn, 2014). Anthropogenic noise might also alter stress levels (Crino et al., 2013; Kleist et al., 2018) either acting as a direct stressor, or by altering the perception of predation risk (Quinn et al., 2006; Ware et al., 2015), which might result in altered incubation and provisioning. Masking of alarm calls or predators' sound might also leave nestlings and parents more vulnerable to predators (McIntyre et al., 2014; Templeton et al., 2016) or result in a trade-off between feeding the nestlings or vigilance (Quinn et al., 2006). Noise might also interfere with parent-offspring communication (Leonard and Horn, 2012; Leonard et al., 2015; Lucass and Eens, 2016) and therefore affect feeding rate at the nest.

Long-term field studies of monitored populations exposed to noise are fundamental to understand how anthropogenic noise acts on breeding success and nest site selection over multiple breeding seasons. Studying populations over multiple generations also allows to understand how nest-site selection relates to the demographics of the population, which is a critical component of habitat selection, and directly linked to reproductive success (Halfwerk et al., 2016; Kleist et al., 2017). The present study looks at reproductive success in order to investigate nest-site selection and breeding output of a population of blue tits (*Cyanistes caeruleus*) breeding in nest-boxes exposed to a natural gradient of traffic noise over multiple years. The first aim was to assess nest-site preference and age distribution of blue tits breeding along a noise gradient. A second aim was to quantify nest-site fidelity over subsequent breeding seasons, and to establish whether movement to different nest-boxes in subsequent years could be linked to noise levels. Finally, this study aimed to underline any potential effects of traffic noise on the breeding performance of this population. By focusing on different phases of the breeding performance, it aimed to identify which stages are more susceptible to the damaging effects of noise, and to link them to the processes through which noise might affect reproductive success.

2. METHODS

2.1 STUDY SITE

The data used for this chapter are part of an ongoing project (Leech et al., 2001; M. C. Mainwaring and Hartley, 2008; Mainwaring et al., 2010; Deeming et al., 2012) on the nesting biology of a population of blue tits breeding in nest-boxes and located on Lancaster University campus, UK (Figure 1), and have not been personally collected by me. The study site comprises several woodland patches in which 111 wooden nest boxes have been installed as part of long-term study into the breeding biology of blue tits (Mainwaring and Hartley, 2016). The nest-boxes have an entrance hole of 25 mm in order to restrict access to other potentially competitive species, such as great tits (*Parus major*), and have been fitted with a metal plate around the entrance hole, and with galvanised wire mesh sheets on the external walls, in order to prevent predators of eggs and nestlings from gaining access (Mainwaring and Hartley, 2008). The areas where the nest-boxes are located consist largely of mixed deciduous woodland. Vegetation composition is roughly the same across the site, largely consisting of deciduous and mixed woods that primarily comprise sycamore (*Acer pseudoplatanus*) and common beech trees (*Fagus sylvatica*), and some coniferous trees interspersed throughout the study site, although they are more abundant in the woodland patch containing nest-boxes 88 to 92 (Mainwaring et al., 2011). Although some areas are more mature than others, the majority of the trees were planted when the University was established and are thus about 60 years old (Hartley, 2018 *unpublished raw data*). Two main roads and a railway line run on each side of the campus, and they generate a gradient of anthropogenic noise on the study site (Figure 2). The M6 motorway is located east of the campus, while the A6 and the railway line run parallel to the M6 west of the campus.

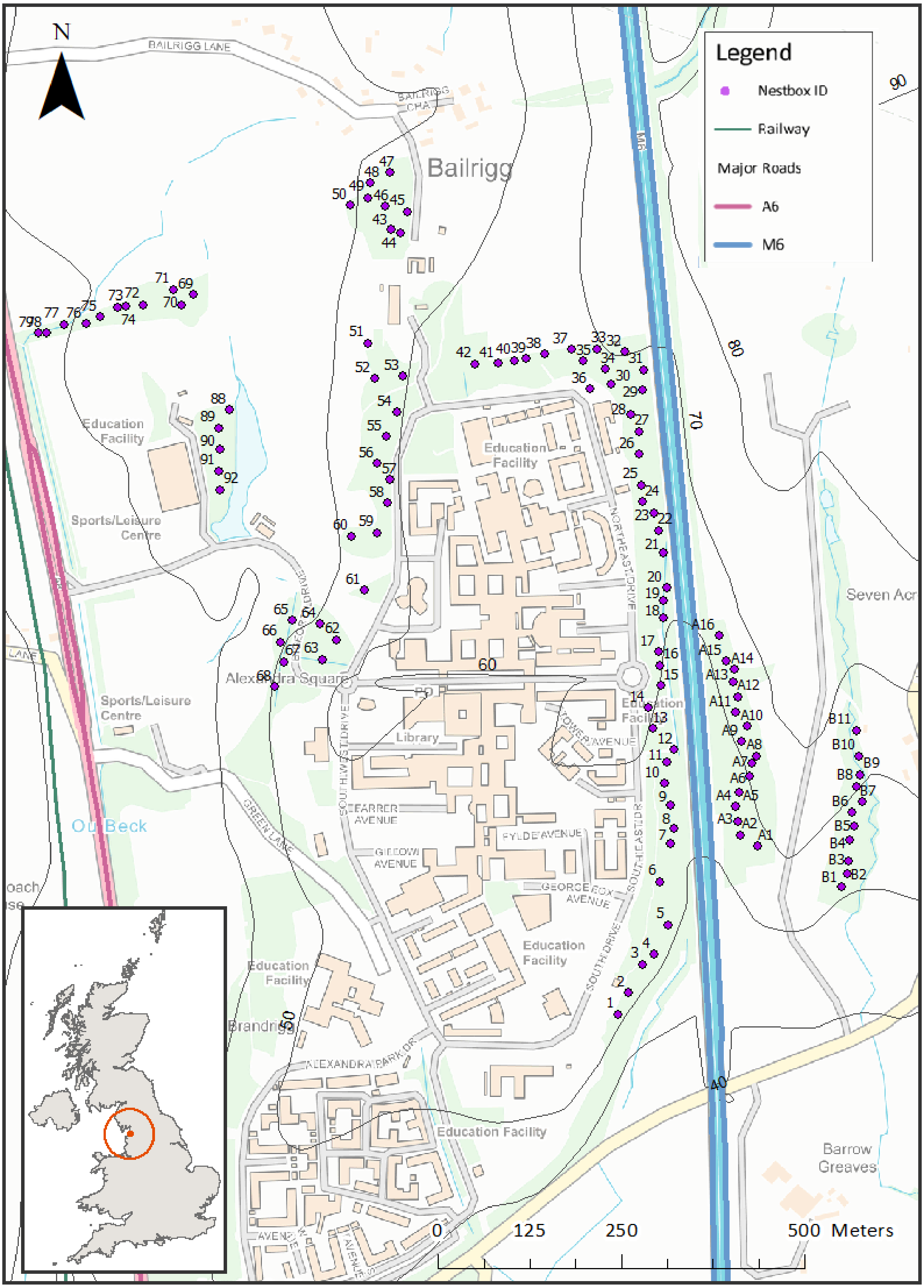


Figure 1 Study site at Lancaster University campus in north-west England. EDINA Digimap Ordnance Survey: Service OS VectorMap® Local; OS MasterMap Highways Network; OS Terrain® 50 topographic contours.

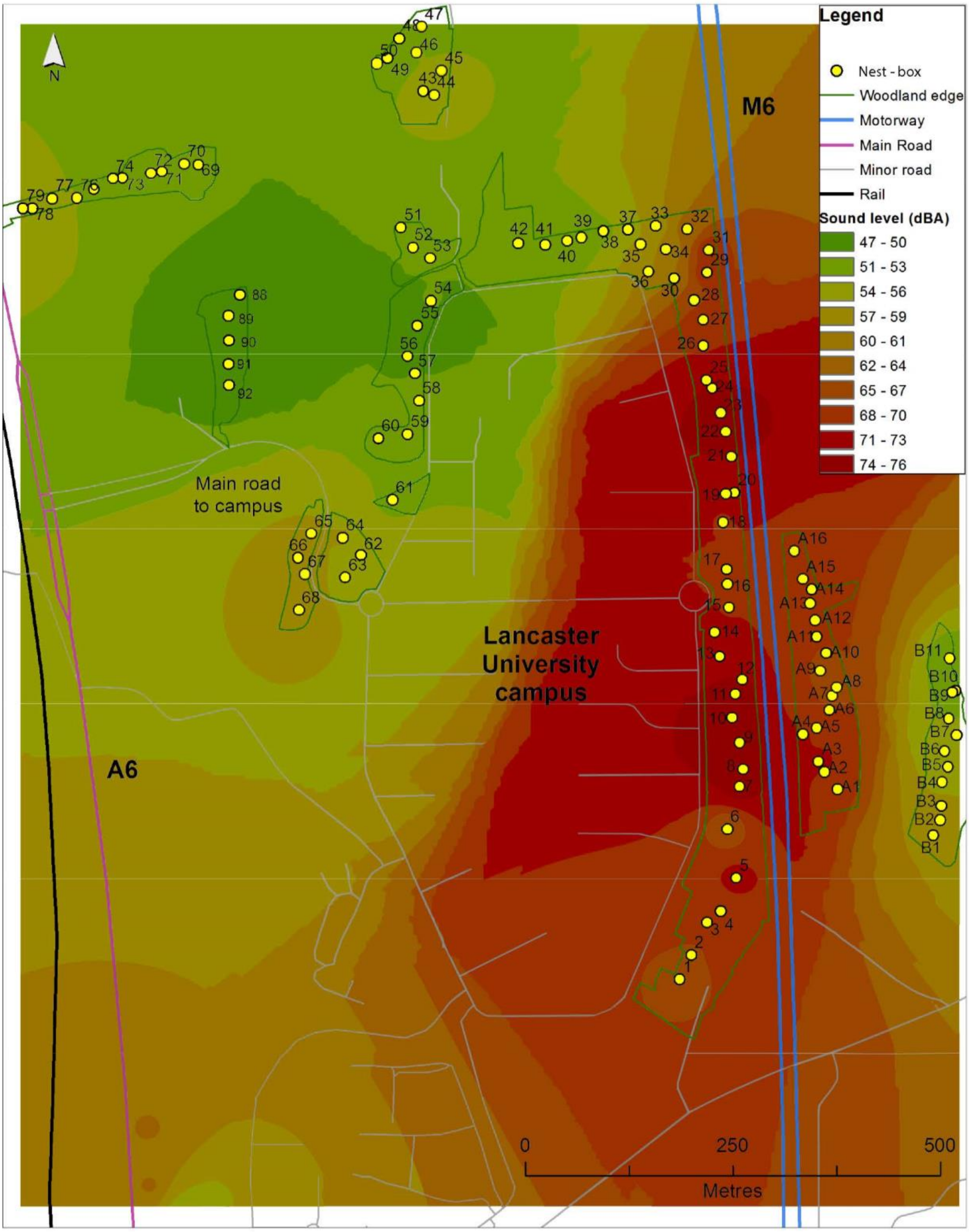


Figure 2 Map of sound levels for study site at Lancaster University, England, interpolated from point measurements at the nest-boxes.

2.2 BREEDING DATA

Blue tit breeding data were collected between 2010 and 2018. The parameters used for this study were nest-box occupancy (whether a nest had been built in the nest-box or not), laying date, clutch size, number of fledglings, and pre-fledging mass (average weight of chicks for the brood when chicks are 15 days old). In total, the dataset used for the analysis consisted of 663 clutches produced by 310 different females. Data on nestling mass were only available for the years 2011 and 2015 to 2018 (Table 1). Although nest-box occupancy in all woodland patches is usually high, it varies from year to year, and not all nest-boxes are occupied each year (Mainwaring and Hartley, 2016). The majority of blue tits in the population are marked with a unique combination of three coloured bands and a metal ring, which allows for age estimation and individual identification. The birds form territories between late winter and early spring, and breed between April and June, producing a single brood each year. Regular nest-box checks took place each year from the beginning of April in order to establish the date on which the first egg was laid, assuming one egg being laid per day (Cramp and Perrins, 1993). Body mass (±0.1 g) measurements were taken on 15 days old chicks with an electronic balance (Mainwaring et al., 2010). Finally, nests were checked at day 20 (± 1) to establish fledging success, defined as the number of fledged nestlings.

Table 1 Number of clutches laid, first egg date (1 = 1 April), clutch size, number of fledglings, and average brood mass at 15 days for each breeding season sampled. Values are means and standard deviations.

Breeding season	No clutches	Laying date	Clutch size	Fledglings	Average mass (g)
2010	63	26.1 ± 5.92	9.97 ± 1.90	8.30 ± 2.27	-
2011	83	18.8 ± 4.37	9.86 ± 1.54	6.58 ± 3.58	10.7 ± 0.912
2012	66	20.7 ± 7.65	9.74 ± 2.08	5.88 ± 3.85	-
2013	57	36.2 ± 5.83	9.07 ± 2.03	6.42 ± 3.29	-
2014	65	18.9 ± 7.09	9.63 ± 2.13	7.46 ± 3.76	-
2015	78	28.0 ± 4.71	9.08 ± 2.02	4.24 ± 3.57	10.4 ± 0.995
2016	71	27.2 ± 5.26	9.13 ± 1.69	7.81 ± 2.35	10.4 ± 0.842
2017	77	22.4 ± 5.27	8.91 ± 1.87	5.75 ± 3.02	9.86 ± 1.28
2018	73	26.1 ± 4.03	8.97 ± 1.83	5.26 ± 3.41	10.4 ± 1.22

2.3 NOISE MEASUREMENTS

Noise measurements were collected in 2016 by Andrew Wolfenden (Wolfenden, 2016 *unpublished*), following a similar procedure to that adopted by Kleist et al. (2016). Sound amplitude levels were recorded from the top of each nest-box over five minutes, with the microphone pointing towards the nest-box entrance. Measurements were taken using a Tenma 72-947 data logging sound level meter (A-weighting, fast response, and 30–100 dB(A) settings; accuracy ±1.4 dB(A) and were calculated as an Leq (equivalent continuous sound level). While the A-weighting scale is a human-centric (as it is based on equal loudness contours for human hearing) (Francis and Barber, 2013), it was chosen because auditory hearing curves for this species are not available, and because it provides a conservative estimate of bird hearing and is the best readily-available weighting for bird studies (Dooling and Popper, 2007). The sound measurements took place during the breeding season between 10:00 and 15:00 to avoid peaks in traffic, and only on days without rain or strong wind, since such atmospheric events might affect sound levels (Ovenden et al., 2009). It was assumed that sound levels did not change considerably over the nine-year period. Measurements of temporary sources of noise, such as machinery and human activities, were also avoided.

2.4 ENVIRONMENTAL VARIABLES

All breeding data were modelled including averages of the atmospheric conditions for the years considered, as these environmental variables have been shown to impact the breeding behaviour and reproductive output (Deeming et al., 2012; Bleu et al., 2017; Britt et al., 2017). Specifically, average mean temperature (maximum plus minimum value divided by two; °C) and rainfall (mm) for the months of April and May were considered. Local weather conditions were obtained from Lancaster University's Hazelrigg meteorological station, located within 1 km of the study area.

Distance from the nearest main road (either the M6 or the A6) was initially considered for input into the models, in addition to the noise level. As such, the planar distance from the closest main road was calculated from all nest-boxes to the nearest point on the main road. Most nest-boxes were closer to the M6 motorway, with only 25 out of the 111 nest-boxes located closer to the A6 road. However, distance from road and noise level were very highly correlated (*r*=-0.90, *p*<0.001) and so only noise was included in the models (Hair et al., 2014).

2.5 STATISTICAL ANALYSIS

All analyses were conducted using R version 3.6.1 (R Core Team, 2019). Initial data exploration was carried out following the protocol described by Zuur et al. (2010). The presence of outliers was investigated, and correlation between predictors was assessed using multi-panel scatterplots, correlation tests, and variance inflation factors (VIF). For each life history trait, generalised linear mixed models (GLMM) were used to analyse the data using the package *lme4* (Bates et al., 2015).

Nest-box occupancy rates were analysed using a GLMM (binomial error distribution, logit-link function) with occupancy as dependent variable (0=empty or 1=occupied), noise levels measured at the nest-box as a fixed effect, and year and nest-box ID as a mixed effects to account respectively for yearly differences in number of breeders and for repeated measures. A logistic regression approach was also used to analyse age distribution (yearling=1, older=0) across the noise gradients, with sex as a predictor in order to control for differences between sexes. Site loyalty and movement to quieter or noisier nests were measured for individuals that were identified over breeding events in subsequent years. Each pair of subsequent years was treated as a separate unit and analysed using a binomial GLMM, with noise levels, age, sex, and number of fledglings as fixed effects, and nest-box ID as a mixed effect to account for repeated measures.

Finally, to analyse breeding performance a set of generalised linear mixed models (GLMM) was built for each variable (Bolker et al., 2009). Models for clutch size and nestling mass used a Gaussian distribution, while models for number of fledglings and laying date used a Poisson distribution. Nest-box ID and breeding year were always included as random factors. The package *segmented* (Muggeo, 2017) was used to conduct further analysis and estimate breakpoints in the regression model. Depending on the model, other reproductive traits were included as explanatory variables (Wilkin et al., 2006). Laying date was included in all models to account for time of the breeding event and to control for the correlation between laying date and other breeding variables. For the number of fledglings clutch size was included in the model. Clutch size was also included in the fledging mass model, as it is known to have an effect on fledging mass (Wilkin et al., 2006; Halfwerk, Holleman, et al., 2011).

3. RESULTS

3.1 NEST BOX OCCUPANCY

Noise level was a significant predictor of nest-box occupancy, with the probability of blue tits breeding in a nest-box increasing slightly as noise level increased (p = 0.026, Table 2a). Noise level was also a significant predictor of distribution by age, with the likelihood of yearling presence increasing with higher values of noise, irrespective of sex (Table 2b).

Table 2 Generalized linear mixed model (GLMM; binomial errors with logit link) investigating the relationship between sound level measured at the nest-box and nest-box occupancy, with a) year as a mixed effect, and b) year and Nest-box ID as mixed effects. Significant effects are in bold.

a) Nest-box Occupancy	*Predictors*	*Estimates*	*Std. Error*	*CI*	*z-value*	*p*
N=1016	(Intercept)	-0.559	0.57	0.19 – 1.76	-0.97	0.331
	Noise	0.019	0.01	1.00 – 1.04	2.23	**0.026**
b) Age Distribution	*Predictors*	*Estimates*	*Std. Error*	*CI*	*z-value*	*p*
N=892	(Intercept)	-1.624	0.71	0.05 – 0.79	-2.29	**0.022**
	Noise	0.022	0.01	1.00 – 1.04	2.09	**0.036**
	Sex (male)	0.159	0.14	0.89 – 1.55	1.13	0.259

3.2 NEST-BOX FIDELITY

Out of 331 consecutive breeding events for individuals that bred in nest-boxes for at least two consecutive years, 56.2% moved to a different nest and 43.8% stayed in the same nest-box the consecutive year. Regardless of sex, age (yearling or older) or number of chicks fledged in year 1 of the two consequential years, noise was a significant predictor of nest-box fidelity, with higher probability of movement as noise increased (p=0.003) (Table 3a). However, there was no difference in the proportion of birds moving to a quieter nest or a noisier one (X2= 2.667, df = 1, p=0.103), with 55.6% moving to a quieter nest-box and 44.4% moving to a noisier one (216 breeding events). Further analysis also showed no evidence for noise being a significant predictor of whether blue tits would move to a quieter or a noisier nest-box (Table 3b).

Table 3 Generalized linear mixed model (GLMM; binomial errors with logit link) investigating the relationship between sound level measured at the nest-box and a) nest site fidelity (where stay=0 and move=1), and b) movement to either a quieter or a noisier nest site (where quieter=0 and noisier=1). Significant effects are in bold.

a)	**Nest-box Fidelity**	*Predictors*	*Estimates*	*std. Error*	*CI*	*z-value*	*p*
	N=352	(Intercept)	-5.39657	2.19	0.00 – 0.33	-2.46	**0.014**
		Noise	0.10306	0.03	1.04 – 1.19	3.02	**0.003**
		Age(yearling)	0.21656	0.32	0.67 – 2.31	0.68	0.495
		Sex(male)	-0.45106	0.30	0.35 – 1.16	-1.48	0.138
		No. Fledglings	-0.04920	0.06	0.84 – 1.07	-0.81	0.420
b)	**Lower or Higher Noise Level**	*Predictors*	*Estimates*	*std. Error*	*CI*	*z-value*	*p*
	N=211	(Intercept)	3.21007	2.48	0.19 – 3195.08	1.29	0.195
		Noise	-0.04335	0.04	0.89 – 1.03	-1.18	0.236
		Age(yearling)	-0.06315	0.42	0.41 – 2.13	-0.15	0.880
		Sex(male)	-0.29780	0.40	0.34 – 1.63	-0.74	0.458
		No. Fledglings	-0.02566	0.08	0.83 – 1.15	-0.31	0.756

3.3 BREEDING PERFORMANCE

Noise had a negative effect on fledgling mass at 15 days, which declined in nest-boxes exposed to higher noise levels. While the GLMM on the number of fledglings did not show noise to be a significant predictor of fledgling success, further graphical investigation suggested that both number of fledglings and fledgling mass started declining at a threshold located above 70 dB(A) (Figure 3). In particular, for number of fledglings the breakpoint for the full regression model was estimated to be at a noise level of 74.12 ±0.74 (SE) dB(A). Reanalysing the data including only the nest-boxes for which noise levels were above 70 dB(A), resulted in noise being a strong negative predictor for the number of fledglings (Table 4).

Laying date had a strong effect on clutch size as well as the number of fledglings and nestling mass, with birds that started laying later having lower number of offspring and lower offspring mass (Table 4). In addition, average temperature was a significant negative predictor of clutch size and laying date, and average rainfall was a strong negative predictor of number fledglings. Noise level was not a significant predictor for clutch size and first egg date (Table 4).

Table 4 Generalized linear mixed model (GLMM) investigating the relation between sound level measured at the nest-box and a) Clutch size, b) Laying date, c) Number of fledglings and d) Average mass of nestlings at day 15. Significant effects are in bold.

	*Predictors**	*Estimates*	*std. Error*	*CI*	*t-value*	*p*
Clutch Size	(Intercept)	9.38	0.17	9.05 – 9.71	56.29	**<0.001**
	Noise	0.1	0.08	-0.06 – 0.26	-1.25	0.219
N=633	Laying Date	-1.08	0.09	-1.25 – -0.91	-12.39	**<0.001**
	Average Temp.	-0.49	0.16	-0.82 – -0.17	-3.01	**0.003**
	Average Rainfall	-0.17	0.16	-0.49 – 0.14	-1.09	0.281
Laying Date	(Intercept)	3.184	0.05	21.96 – 26.54	65.84	**<0.001**
	Noise	-0.006	0.01	0.97 – 1.02	0.56	0.576
N=667	Average Temp.	-0.135	0.05	0.80 – 0.96	-2.87	**0.004**
	Average Rainfall	-0.055	0.05	0.86 – 1.04	-1.11	0.266
Number Fledglings	(Intercept)	1.797	0.04	5.54 – 6.57	41.14	**<0.001**
	Noise	0.007	0.02	0.97 – 1.05	0.34	0.737
N=581	Laying Date	-0.138	0.03	0.83 – 0.92	-5.19	**<0.001**
	Average Rainfall	-0.152	0.04	0.79 – 0.93	-3.61	**<0.001**
	Average Temp.	-0.059	0.04	0.87 – 1.03	-1.36	0.175
	Clutch Size	0.166	0.02	1.13 – 1.23	7.86	**<0.001**
Number Fledglings >70 dB(A)	(Intercept)	1.819	0.05	5.60 – 6.79	36.97	**<0.001**
	Noise	-0.109	0.03	0.85 – 0.95	-3.65	**<0.001**
	Laying Date	-0.122	0.04	0.82 – 0.95	-3.36	**0.001**
N=240	Average Rainfall	-0.100	0.05	0.82 – 0.99	-2.12	**0.034**
	Average Temp.	-0.045	0.05	0.87 – 1.06	-0.89	0.374
	Clutch Size	0.161	0.03	1.10 – 1.25	5.02	**<0.001**
Average Mass	(Intercept)	10.374	0.19	10.00 – 10.73	55.58	**<0.001**
	Noise	-0.150	0.06	0.02 – 0.25	2.21	**0.027**
N=231	Laying Date	-0.560	0.08	-0.69 – -0.38	-6.82	**<0.001**
	Average Rainfall	0.280	0.2	-0.19 – 0.61	1.04	0.3
	Average Temp.	-0.120	0.2	-0.53 – 0.27	-0.66	0.51
	Clutch Size	-0.279	0.06	-0.41 – -0.16	-4.37	**<0.001**

*all fixed effects are scaled

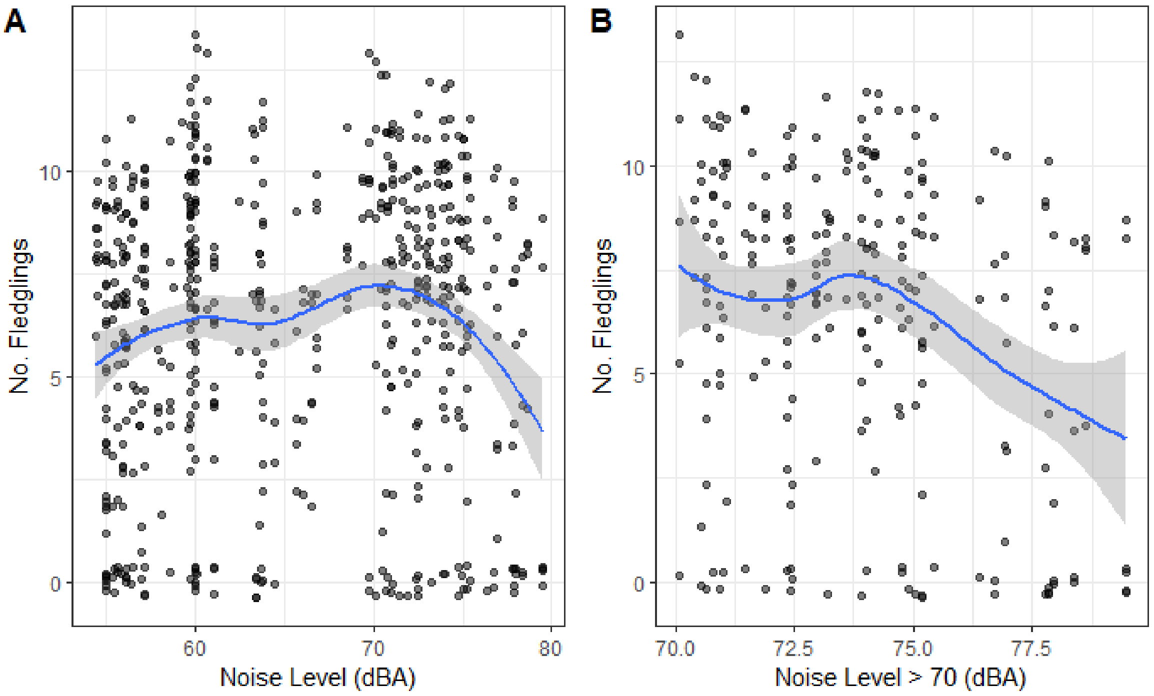


Figure 3 Relationship between the (A) number of fledglings and Noise Level and (B) number of fledglings at Noise Level > 70 dB(A). A *LOESS* smoother was added to aid visual interpretation.

4. DISCUSSION

This long-term study tested nest site choice, nest site fidelity, and breeding performance at different breeding stages along an existing gradient of anthropogenic noise. Counterintuitively, blue tits were more likely to breed in nest-boxes exposed to higher noise levels, and this was especially prevalent in first year breeders. Nevertheless, breeding success was lower in locations exposed to higher noise levels, which was evidenced by lower nestling body mass and smaller number of fledglings. Blue tits were more likely to move in subsequent breeding seasons if they bred in noisy locations, but they did not move to quieter areas.

4.1 NOISE HAS A NEGATIVE IMPACT ON NESTLING MASS AND FLEDGLING SUCCESS

A negative effect of anthropogenic noise was only detected in the late stages of reproductive cycle, and especially above 70 dB(A). In some other species, negative responses have been reported even at levels below 50 dB (reviewed in Shannon et al., 2015), and therefore well below the threshold detected in this study. However, it is not surprising that blue tits, which have been shown to persist in noisy environments (Rheindt, 2003), would only start experiencing negative effects at high noise levels. The finding that nestlings are particularly vulnerable to anthropogenic noise lends support to a number of studies. In a study on birds exposed to noise from gas field compressors, the species that was more likely to nest in the noisiest sites, western bluebird (*Sialia mexicana*), was also the only one to experience reduced hatching success and body condition (Kleist et al., 2018). Interestingly, the results of the current study share a number of similarities with Kleist et al. (2018), which also observed a non-linear effect of noise on feather growth and body size, which only started showing a decline at levels above ~70dB(F) (Leq, dB un-weighted measurements). Kight et al. (2012) found reduced number of fledglings in a population of Eastern bluebirds (*Sialia sialis*) exposed to noise, while Schroeder et al. (2012) found that both fledgling success and mass were negatively associated with noise in a population of house sparrows (*Passer domesticus*).

One explanation for the negative impact of noise on nestlings is the impaired chick development hypothesis (Kight and Swaddle, 2011; Schroeder et al., 2012), and in particular the possibility that noise might mask acoustic communication between offspring and parents, and therefore result in reduced provisioning frequency (Leonard and Horn, 2008, 2012; McIntyre et al., 2014; Leonard et al., 2015). Indeed, impaired parent-offspring communication has been specifically shown in blue tits (Lucass and Eens, 2016). Experimentally introduced highway noise increased the chances of “missed detections” by the chicks, which failed to beg once the parents arrived at the nest, resulting in a decreased rate of parental provisioning. The link between increasing noise levels and poorer nestling condition and fledgling success found in the current study might therefore be the result of an interference with feeding effort, caused by compromised parent-offspring communication. Noise might also affect predator-prey interactions in a number of ways that could leave nestlings more vulnerable to predators. For example, noise might break down communication of predation risk between parents and offspring and leave nestlings vulnerable to predators (McIntyre et al., 2014), or generally affect the detection of anti-predation signals (Zhou et al., 2019) or the presence of predators by parents (Quinn et al., 2006; Huet des Aunay et al., 2013; but see Pettinga et al., 2016). On the other hand, noise might mask nestling begging calls and thus reduce detection by predators (Mason et al., 2016).

4.2 NEST-SITE PREFERENCE INCREASES WHILE NEST-SITE FIDELITY DECREASES WITH NOISE

Blue tits showed a preference for breeding in noisier nest-boxes. While this finding might initially appear counterintuitive, it is consistent with previous experimental studies that have found noisy nest-boxes to be more likely to be occupied (Halfwerk et al., 2016), and observational studies that found blue tits to be more abundant where traffic noise was at its highest (Rheindt, 2003). One of the most plausible explanations for this result is that blue tits are more likely to breed in noisier areas where they experience reduced interspecific competition. In Halfwerk et al.'s (2016) work, this was explained by the fact that blue tits, which had to compete with great tits for access to nest boxes, were being forced out of quieter nest-boxes and had to settle for the remaining noisy ones. While in the present study the nest-boxes were designed so that only blue tits could access the nest-box, blue tits are also known to compete with great tits over access to food resources (Dhondt and Eyckerman, 1980; Halfwerk and Slabbekoorn, 2009). The reduced abundance of less noise-tolerant species that compete over food resources might therefore be responsible for their preference for noisier sites. Another hypothesis is that blue tits might prefer noisier habitats because potential predators, such as spotted woodpecker (*Dendrocopos major*) and sparrowhawk (*Accipiter nisus*), might be absent or reduced in numbers in noisy areas (Rheindt, 2003). Species such as blue tits might therefore benefit from reduced predatory risk in noisy areas, where predators are less abundant (Francis et al., 2009; Francis, Ortega, et al., 2011a). While it has been shown that abundance of woodpecker decreases by 76% in areas with greater traffic noise (Rheindt, 2003), surveys would be required to confirm such changes in community composition at this site.

First year blue tits were more likely to breed in noisy territories. Noise has indeed been shown to alter the local age structure within species that do not otherwise appear to be affected by noise in terms of abundance (McClure et al. 2017). Studies on noise-impacted areas often found younger birds to be more abundant than more experienced ones in noisier areas (Reijnen and Foppen, 1991; Habib et al., 2007), and more common at noisy stopover migration sites (McClure et al., 2017). One explanation for these findings is that younger, lower quality birds have to settle for noisy habitats that are perceived as more disturbed. However, when looked in combination with the patterns of nest site fidelity and the breeding data, the results of the present study suggest that this explanation might not be true for blue tits. In fact, while nest site fidelity decreased with increasing noise levels, blue tits did not show a preference for moving to quieter territories rather than noisier ones. Moreover, laying date and clutch size did not appear to be affected by noise. Both laying date and clutch size have been shown to be related to true or perceived territory and mate quality (Pearson and Lack, 1992; Joly and Marmignon, 1996). Females adjust their parental investment by laying fewer eggs or breeding later when breeding with lower quality males or in lowered quality territories (Halfwerk, Bot, et al., 2011). While noise was found to be a significant predictor of age distribution, it is therefore unlikely that this was due to individuals' territorial perception.

4.3 A Mismatch Between Choice of Breeding Habitat and Breeding Success

Nest site selection is an important component of the individual fitness of birds, as the choice of nest site can have an impact on the chances to maximise the breeding output. Cues directly related to habitats, such as habitat structure, are known to be used to assess habitat quality in order to inform nest site selection (Chalfoun and Schmidt, 2012), as the choice of breeding site will ultimately affect reproductive output. Birds also use their individual breeding performance (Winkler et al., 2004; Citta and Lindberg, 2007) and public information, such as fledgling quantity and quality, in order to choose breeding site (Parejo et al., 2007).

The results of this study suggest that anthropogenic noise might not be a primary factor for blue tits when deciding on their breeding location. Their inability to judge territory quality reliably when confronted with anthropogenic noise is most markedly supported by the mismatch between territory occupancy and reproductive success. Blue tits appeared to be more inclined to breed in noisier territories. However, in these territories they were also more likely to experience reduced reproductive success. Following a non-optimal breeding attempt, blue tits might be using their individual reproductive success to assess nest-site quality and decide whether to breed at the same site or not. Nevertheless, if blue tits do not identify noise as the cause of their lowered reproductive success, they might still move to equally noisy or even noisier territories. The reason for this might be that this species has not yet evolved to recognise noise as a negative cue when assessing habitat quality, and therefore falls into an anthropogenically-induced ecological trap (Schlaepfer et al., 2002). Indeed, this term originates specifically to describe a situation in which the choice of nesting habitat might lead a bird to nest failure because of a recent anthropogenic change in the environment that disrupted the normal cue-habitat quality correlation (Gates and Gysel, 1978). It has long been recognised that sudden environmental alterations driven by anthropogenic change might result in the responses of individuals no longer being adaptive (Schlaepfer et al., 2002). Anthropogenic noise has emerged swiftly on a global scale, and has only recently started to grow in its intensity and extent (Francis et al., 2009). While birds have developed strategies to respond to natural sources of environmental noise (Slabbekoorn and Smith, 2002), anthropogenic noise is often louder, more common and frequent, and has a different frequency spectrum than natural sources of ambient sounds (McKenna et al., 2016). It is therefore likely that birds might not yet have evolved an appropriate adaptive response to this novel evolutionary pressure. Given the relatively rapid increase in anthropogenic noise and its spectral and temporal differences in comparison to natural noise, organisms may not perceive it as an indicator of poor habitat quality and instead rely on other cues to evaluate habitat quality.

However, in drawing conclusions on the association between breeding success, choice of nesting site, and anthropogenic noise levels at the nest, it is not possible to rule out other unmeasured factors that might have played a role. While the study site is homogenous in terms of vegetation and comprises mostly mixed, deciduous woodland, local differences may be important. Some of the more mature woodland areas (between boxes 20 and 42) have higher numbers of oak trees *Quercus spp*., which are favoured by blue tit (Perrins, 1979). However, some areas which appear to comprise comparatively young vegetation, such as the area between box 4 and 12, had a high level of occupancy. Ground surveys measuring habitat characteristics could be included to account for what could potentially be a significant factor (Wilkin et al., 2006). Moreover, blue tits may choose to breed in natural cavities even when there is a surplus of boxes (Perrins, 1979), so nest-box occupancy may not entirely reflect true breeding densities.

Furthermore, traffic collisions or other forms of pollution linked to roads, including chemical contamination and artificial light emissions, might have been responsible for some of the negative effects seen on the fitness of this population (Isaksson, 2018). In birds, light pollution is often associated with changes in biological rhythms, which can ultimately affect breeding behaviours and fitness (Dominoni et al., 2013, 2014; Dominoni and Partecke, 2015). Indeed, blue tits exposed to artificial light during the night have for example been shown to lay eggs earlier than individuals living in darker areas (Kempenaers et al., 2010), something that might have indirectly effected the clutch size of this population. Small, insectivorous birds such as blue tits might also be particularly vulnerable to increased levels of bioaccumulation of heavy metals because of their metabolic rate and diet, as shown in many common bird species (eg. Swaileh and Sansur, 2006; Hofer et al., 2010; Isaksson, 2010; Bichet et al., 2013). Young individuals are likely to be even more sensible to chemical pollution, and suffer from higher mortality, and decreased body mass and condition (Janssens et al., 2003; Turzańska-Pietras et al., 2018).

Further work, accounting for these other factors that might covary with noise, but also for vegetation structure and habitat type, food availability, presence of predators, and extra-specific competition (Maícas et al., 2012), would help understand what might be driving species to fall into this ecological trap, while also teasing apart the effects of noise pollution from those of other forms of pollution associated with noise.

4.4 CONCLUSIONS

This study provides evidence that, when choosing breeding sites, blue tits do not avoid settling in territories with high levels of anthropogenic noise. This could be one of the causes leading to an impaired reproductive success of species that appear to be well adjusted to breeding in noisy environments. This study shows that, while blue tits were more likely to breed in noisy sites, their breeding success was compromised in terms of pre-fledgling nestling mass and fledgling success. The present findings also highlight evidence for which stages of the breeding cycle might be more vulnerable to noise, and they give valuable evidence for informed mitigation and management strategies in human-altered landscapes. If even species that persist in noisy environments are sensitive to noise during the period between hatching and fledgling, simple surveys to measure abundance of breeding birds will not be sufficient to monitor bird populations for noise management purposes. Moreover, if the phenomenon observed in this study is common in other species, it might be one of the mechanisms behind the decline in species whose decline has been directly linked to decreases in breeding success (Leech et al., 2004). While this study found that traffic noise played a negative role in the reproductive success of this population, we are yet to know what the scale of this problem is, and there is a need for studies assessing the effects of anthropogenic noise on a much larger spatial scale and on a much larger number of species. Noise pollution is rapidly increasing throughout much of the World. Expanding our understanding of how species respond to this novel selection pressure and which life history stages are more susceptible may be critical to maintaining healthy ecological communities.

CHAPTER 3.

USING LARGE-SCALE DATA TO QUANTIFY THE CONSEQUENCES OF ANTHROPOGENIC NOISE ON BREEDING SUCCESS.

Abstract

Anthropogenic noise is a widespread and pervasive environmental pollutant that affects behaviours crucial for the fitness of animals, and that has been directly linked to declines in the reproductive success of birds. However, research so far has only been population-specific, and no studies have yet explored the effects of noise on reproduction at a countrywide and non-population-dependent scale. I aimed to develop a large-scale approach to test the relationship between the breeding performance of birds and the intensity of anthropogenic noise around major road networks, which could be used and integrated over different datasets. This was achieved by combining traffic noise soundscape data with two large citizen science datasets on the reproductive output of blue tits (Cyanistes caeruleus), obtained from the British Trust for Ornithology (BTO) in the United Kingdom, and the Dutch Centre for Field Ornithology (Sovon) in the Netherlands. Applying the same method on different datasets and on different types of traffic noise data delivered analogous results. In this chapter, I show that the impact of noise on birds' reproduction is not restricted to population-specific conditions, and I deliver a method that can be applied to multiple datasets across different countries. This method allows to combine datasets in order to provide a much-needed international overview of the impacts of large-scale patterns in the breeding behaviour of birds exposed to noise.

1. INTRODUCTION

The alteration of ecosystems caused by human activities is one of the greatest threats to global biodiversity (Hooper et al., 2012). In particular, human-generated noise is a growing source of habitat fragmentation and alteration, and a major driver behind the environmental impacts of roads and other transportation systems (Summers et al., 2011). This environmental pollutant is related to human population density, and is therefore predicted to become more widespread as human populations increase (Ortega, 2012). Transportation systems, energy development, and motorised recreation are major contributors to modern ambient sound levels (Warren et al., 2006). While urban and suburban areas are noisier than less developed areas, with the expansion of transportation networks (Farina, 2013) the problem has spread to rural and remote areas, and even protected natural areas are now being exposed to noise pollution (Barber et al., 2011). Addressing the impact of these growing sources of anthropogenic disturbance on wildlife is therefore of vital importance.

Birds can function as sensitive ecological indicators of environmental change and pollution, and especially noise pollution, due to their reliance on acoustic communication for vital processes related to individual and population fitness (eg. Kight et al., 2012; Schroeder et al., 2012; Davies et al., 2017; Halfwerk et al., 2018; Injaian et al., 2018). In the last two decades, a considerable number of studies have addressed the impact of anthropogenic noise on birds (Radford et al., 2011; Shannon et al., 2016). While species might persist in urban and noisy areas (Farina, 2017), the cumulative effects of anthropogenic noise can include population declines, and contribute to local extinctions in urban environments (Blickley and Patricelli, 2010; Shannon et al., 2016), especially in species that are already experiencing habitat degradation due to other factors, and will avoid noisy areas, which would otherwise be suitable habitats (Potvin, 2017). In particular, noise affects bird distribution, reducing species richness and abundance (Bayne et al., 2008; Francis, Ortega, et al., 2011b, 2011c; Halfwerk et al., 2016; Perillo et al., 2017), and changing community and population structure (Habib et al., 2007; Francis et al., 2009; Proppe et al., 2013; McClure et al., 2017).

In order to provide appropriate conservation plans and to identify actions to recover declining populations, it is therefore of vital importance to monitor and to understand the demographic processes behind changes in population abundance (Aebischer et al., 2000), and in particular to investigate crucial life stages, such as breeding. One of the main ways noise affects birds is through its impact on breeding success (Injaian et al., 2018). Noise driven changes in reproductive success have been shown in terms of egg production, incubation, brooding strategies, and nest abandonment, and have been linked to the masking effect of noise on signals used to alert conspecifics of predators, defend territories, attract a mate, or hear and respond to chicks' begging calls (Halfwerk et al. 2011; Kight et al. 2012; Ortega 2012).

Prior to nesting, masking of acoustic signals could compromise the ability of competing males and of potential mates to assess male quality (Halfwerk, Holleman, et al., 2011; Chapter 5). During incubation and chick development, noise is associated with altered stress hormone levels in parents or offspring, likely due to an impairment on predation risk perception via masking or distraction (Crino et al., 2013; Kleist et al., 2018). Furthermore, increased vigilance and anti-predator behaviour, coupled with a decreased foraging efficiency due to noise, have been observed in both captive and free-living birds (Quinn et al., 2006; Ware et al., 2015; McClure et al., 2017; Evans et al., 2018). Throughout the nestling stage, noise can also inhibit parent-offspring communication by interfering with begging calls and detection of the parents by the chicks (Leonard and Horn, 2012; Lucass and Eens, 2016), although whether this is directly linked to changes in reproductive success remains to be confirmed. Finally, birds may settle non-randomly across environments with different levels of anthropogenic noise, such that individuals in good condition occupy quiet environments and less experienced or less fit individuals are forced into noisy territories (Habib et al., 2007).

Although there is evidence linking noise to a decline in the breeding success and overall fitness of birds (Kight et al., 2012; Schroeder et al., 2012; Read et al., 2014; Potvin and MacDougall-Shackleton, 2015b; Injaian et al., 2018; Kleist et al., 2018; Mulholland et al., 2018; Zollinger et al., 2019), currently only a few studies have attempted to explore the effects of noise on a large spatial scale (Shannon et al., 2016). The effect of noise on songbird abundance and occurrence has been examined at a multi-country scale in four studies, by using large-scale datasets to determine whether vocal frequency or particular life history traits were associated to presence or abundance in urbanised areas (Hu and Cardoso, 2009; Cardoso, 2014; Francis, 2015; Moiron et al., 2015). However, the effects of noise on breeding performance have so far only been researched on single populations or by comparing a few populations (Halfwerk and Slabbekoorn, 2014). Large-scale patterns of breeding performance in noisy habitats, important for a better understanding of the cumulative effects of noise exposure, are not well understood, and the effects of noise on breeding performance have yet to be assessed in a way where they can be disentangled from population-specific factors. Additionally, studies on breeding success that investigate a gradient of noise exposure rather than quiet versus noisy treatments are rare, and again limited to single populations (Francis, Paritsis, et al., 2011; Halfwerk, Holleman, et al., 2011; Schroeder et al., 2012).

The purpose of this study was to develop a large-scale method to test the relationship between different stages in the breeding ecology of birds (for hypotheses see Table 1) with the level of anthropogenic noise around major road networks. The main aims were to be able to apply and to be able to integrate this method across other bird-monitoring datasets and different maps of soundscape, in order to provide an easily accessible and fast approach for assessing the effects of noise on an international scale. For this reason, the method was initially developed by combining traffic noise data (modelled as part of the EU Environmental Noise Directive 2002/49/EC) with a large citizen science dataset on reproductive output of blue tits (*Cyanistes caeruleus*) obtained from the British Trust for Ornithology (BTO) in the UK. It was then further applied and tested to breeding data obtained from Sovon Bird Research in the Netherlands. The results were then compared in order to exclude the possibility that systematic differences in the way breeding data were collected or in the way the noise data were modelled might prevent working with one unified dataset.

Table 1 Hypotheses and predicted effect of noise for variables included in models.

Breeding variable	Predicted effect	Rationale	Supporting Evidence
Laying days	Delayed laying (accompanied by reduced clutch size)	*Parental investment is lower in noisy areas.* *Noisy territories are (or are perceived as) lower quality/are held by lower quality males.*	Laying date is primarily determined by conditions at the breeding sites (Joly and Marmignon, 1996). If males or territories in noisier areas are (or are perceived) as lower quality, females adjust their parental investment (Halfwerk, Holleman, et al., 2011; Potvin and MacDougall-Shackleton, 2015b).
Clutch size	Reduced clutch	*Parental investment is lower in noisy areas.* *Noisy territories are lower quality/are held by lower quality males.*	Non-random nest site choice, so that less experienced or less fit individuals are forced into noisy territories (Habib et al., 2007).
Brood size	Reduced brood	*Parental investment is lower in noisy areas.* *Anthropogenic noise is a physiological stressor for parents.*	Females with elevated stress levels may produce low quality offspring (Saino et al., 2005). Increased stress levels in females because of increased predatory risk perception (Quinn et al., 2006) and/or reduced foraging opportunities (Schaub et al., 2009; Ware et al., 2015) translating into less energy to invest in their eggs.
Failure at egg stage	Increased failure rate	*Parental investment is lower in noisy areas. Noisy territories are (or are perceived as) lower quality/are held by lower quality individuals. Anthropogenic noise is a physiological stressor for parents.*	Parents with elevated stress levels show reduced incubation and/or increase nest abandonment (Strasser and Heath, 2013; Thierry et al., 2013).
Failure at chick stage	Increased failure rate	*Anthropogenic noise is a physiological stressor for parents. High levels of background noise mask parent-offspring communication. High levels of background noise mask predator sounds.*	Masking of parental-offspring communication by noise resulting in reduced feeding rates by parents (Schroeder et al., 2012; Ng et al., 2019) or parental alarm calls. Parents with elevated stress levels may decrease nestling feeding rates (Angelier et al., 2009).

2. METHODS

This study was initially developed for the British Trust for Ornithology's (BTO) data on 11309 reproductive events over 11 subsequent years (2006-2017) (Figure 1; Appendix B Table 2). It was then later replicated on 1118 breeding events for the Sovon Dutch Centre for Field Ornithology data, across the same time-period (Appendix Table 2). Blue tits have the highest number of records of all species in the BTO data and the second highest in the Sovon data. These data, together with territorial noise levels for areas adjacent to major roads, were used to quantify the relationship between reproductive success and traffic noise. Reproductive success was analysed at different stages using the following variables: laying date, clutch size, brood size, and nest failure at the egg and nestling stage. Records were selected for each of the variables depending on accuracy of data (see below for further explanation), and this resulted in smaller effective sample sizes.

2.1 STUDY SPECIES

Blue tits are an excellent model species because they breed readily in nest boxes, which makes their reproductive performance particularly easy to track. Blue tits are widespread across Europe, both in rural and urban habitats (Cramp and Perrins, 1993). They can be commonly found in areas affected by anthropogenic noise, such as alongside motorways and in cities (Solonen and Hildén, 2014; Vaugoyeau et al., 2016). The conservation status of blue tits is globally classified as least concern (BirdLife International, 2019).

2.2 BTO'S NEST RECORD SCHEME

The British Trust for Ornithology's (BTO) Nest Record Scheme (NRS) offers the opportunity to study large-scale effects on breeding performance across the UK. The main aim of the NRS is to annually monitor the breeding performance of over 80 species of birds, interpreting changes and undertaking studies of rare or declining species, in order to inform conservation and management policies (Baillie, 2008). Across the UK, circa 30000 records are submitted to the NRS each year. Volunteers collect and record the progress of individual nests (Greenwood, 2009), providing a number of parameters for each nest: location, year, habitat type, dates of each visit, numbers of eggs and/or chicks, and standardised codes to describe the development of nests (Crick et al., 2003).

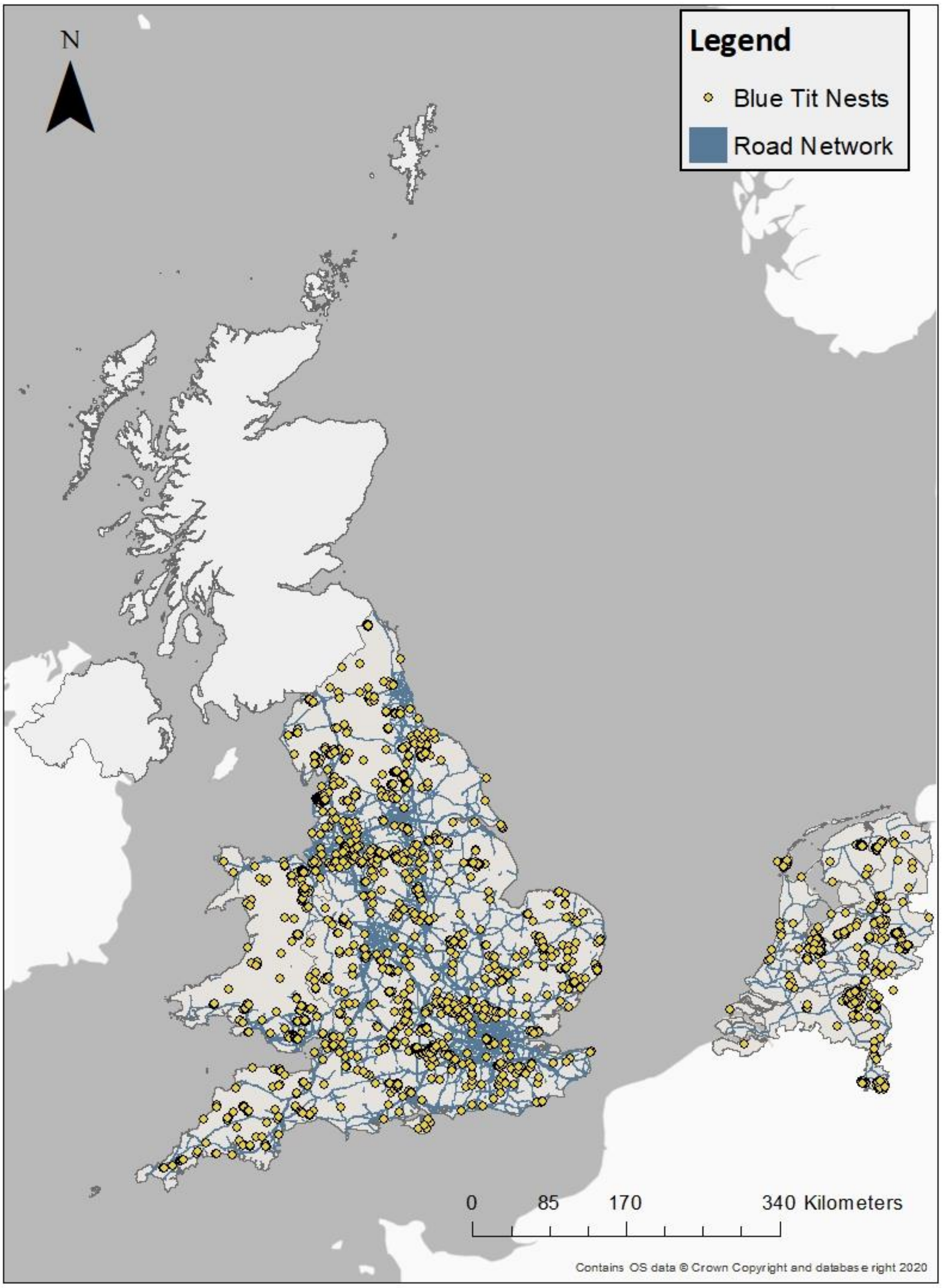


Figure 1 Location of breeding data on the nests of blue tits (*Cyanistes caeruleus*) and extent of road network considered for this study.

2.3 BREEDING DATA

The NRS data were analysed using the following parameters: first egg date, clutch size, brood size, and nest failure rates at the egg and nestling stage. Acronyms for the corresponding parameters as used in the NRS are provided in brackets below.

2.3.1 LAYING DATE

The laying date parameter used for the analysis was the first egg date (*feg*), calculated as the mid-point between the minimum estimated first egg date (*minfeg*) and maximum estimated first egg date (*maxfeg*). Records were only included in the analysis if they allowed a precise estimate of first egg date, and the interval between minimum and maximum possible first egg date did not exceed 10 days. The laying date was encoded such that day 1 was equivalent to 1 January.

2.3.2 CLUTCH SIZE

Clutch size (*maxclu*) was defined as the maximum number of eggs found in a nest. Entries were discarded whenever this parameter had a smaller value than the maximum nest content (*maxco*), which includes the chick stage, as this suggested that the clutch was not complete at the time of the maximum egg count and egg laying was still in progress after the last recorded visit. Records were also discarded if a nest had only been visited only once or if observations began after egg hatching. Finally, records where the maximum clutch size was zero, or larger than the maximum clutch size observed for blue tits (16 eggs) (Nur, 1986), were also discarded.

2.3.3 BROOD SIZE

Brood size (*maxyng*) was defined as the maximum number of young found in nests that had progressed from the egg stage. Nests where this value was smaller than one and larger than 16 were omitted from the analysis (following Halfwerk et al., 2010 protocol).

2.3.4 NEST FAILURE

Whether a nest fails or succeeds is a key variable in demographic studies of birds. However, estimating nest success requires particular techniques in order to handle the incomplete nature of data collected through the Nest Record Scheme. Failure rates were therefore estimated using Shaffer's adaptation (Shaffer, 2004) of the Mayfield method (Mayfield, 1961, 1975). The Mayfield method can be applied to any nest visited at least twice, and it allows to correct for problems arising from nests that were not observed to an outcome. Omitting these records would cause failure rates to be too high because, while all nests that failed at early stages are more likely to be included, nests that might have been successful but were not observed throughout the whole nesting period would be excluded. On the other hand, simply including nests with an unknown outcome would overestimate success.

Mayfield developed an ad hoc estimator of nesting success that overcomes the bias associated with estimates of apparent nesting success. His approach calculates the daily survival probability for only the days during which nests were under observation (the *nest-days*). To calculate the daily nest failure rate, the number of nests that fail during the observation period are added, and then divided by the total nest-days over which observations were taken.

$$Daily\ nest\ failure\ rate\ m\ = \frac{\text{No. of failures}}{\text{nest days}}$$

In this equations, *No. of failures* refers to the sum of all the nests that are known to have failed, while *nest days* is the total number of days during which the nests were observed active and hence were susceptible to failure (“exposure” days) (Crick et al., 2003).

For this chapter, following Shaffer's approach to Mayfield method (Shaffer, 2004), success or failure of the nests were modelled as a binary variable in a logistic-exposure regression model.

2.4 NOISE LEVELS

2.4.1 DEFRA NOISE MAPS

The Defra (Department for Environment Food & Rural Affairs) noise maps identify the main sources of environmental noise (Large Urban Areas, Major Airports, Major Railways and Major Roads), and are generated as part of the strategic noise mapping undertaken to meet the requirements of the EU Environmental Noise Directive (END) 2002/49/EC (European Parliament and Council of the European Union, 2002). The aim of the Environmental Noise Directive is to manage the impact of environmental noise (Defra, 2018). This requires, on a 5-year cycle, the creation of strategic noise maps estimating the levels of exposure to environmental noise, followed by the preparation of relevant action plans based on the noise maps and on public consultations.

Data are available for England and Wales as a geospatial vector data. For this study, data produced for Round 3 on Major Roads and Agglomerations was utilised. These datasets cover roads with more than 3 million vehicle passages per year, and local roads within agglomerations with a population of more than 100,000.

The noise values for the maps are calculated by using computer-modelling techniques. Such values are based on traffic flow data, road type, and vehicle type data, and account for 3D environmental data, which affect the spread of noise. These include digital ground model data (defining the profile and height of the terrain), building data (defining the position and height of buildings), bridge data (describing the location and height of bridges supporting relevant sources), noise barrier data (defining location and height of noise barriers), and finally ground cover data (defining whether the ground over which noise propagates is acoustically absorbent or reflective) (Defra, 2015). The maps quantify sound at a receptor height of 4 m above ground on a 10- meter grid, which is then used to produce polygons that identify sound level calculated in 5-decibel A-weighted noise classes or contour bands: 75.0+ dB, 70.0-74.9 dB, 65.0-69.9 dB, 60.0-64.9 dB, 55.0-59.9 dB.

Noise levels are calculated as annual averages described using the metric Equivalent Average Sound Levels (LEQ), over a specific time-period. The Equivalent Average Sound Levels, also called noise indicators, are based on the scale LAeq, described as the equivalent sound level that, if maintained, would cause the same sound energy to be received as the actual sound over the same period (Abbott and Nelson, 2002). Based on what periods of time the Equivalent Average Sound Levels are calculated for, the maps can be available as:

- Lden: the average sound level over a whole day, with a penalty of 10 dB(A) for night-time noise (23.00-7.00) and an additional penalty of 5 dB(A) for evening noise (i.e., 19.00-23.00).

- Lnight: the average sound level for the 8-hour period from 23.00 to 07.00.

- LAeq16: the average sound level for the 16-hour period from 07.00 to 23.00.

The average sound level for the 16-hour period from 07.00 to 23.00 (LAeq16) was considered the most representative in order to estimate the effects of noise levels in blue tit territories, as it gave the closest approximation of the active hours of passerine birds, such as blue tits, during the breeding period (Lees, 1948; Fitzpatrick, 1997). However, country-specific legislation regulates which noise metrics are to be produced, and some EU countries (such as the Netherlands) only generate Lnight and Lden noise distribution maps.

As this study was designed to develop a method that could be applied on a multinational scale, the same BTO's breeding data was tested under the two noise long-term average indicators Lden and LAeq16, and results were compared in order to assess whether using two different noise indicators would deliver equivalent results. Energy-based noise metrics are often highly correlated (Brink et al., 2018). This was also confirmed by selecting 1000 random nest points and testing for correlation between the noise scores derived from the two noise indicators considered.

2.4.2 TERRITORIAL NOISE LEVELS AND SCORING METHODOLOGY

Nest locations and noise maps were imported in ArcMap 10.3.1 (Environmental Systems Resource Institute 2012). All maps were projected into an equal area projection (Transverse Mercator, GCS_OSGB_1936).

Locations for each single nest are described as either a 4-figure grid reference (which identifies a 1-km square) or a 6-figure grid reference (which identifies a point to the nearest 100 m), based on the Ordnance Survey National Grid system. In order to include nest records for which locations are described as a 4-figure grid reference, nests were mapped inside the OSGB British National Grid for 1 km square, and noise exposure levels were calculated at a 1 km square definition (Figure 2). While noise at the nest is important (see studies on nest boxes Halfwerk et al., 2016; Mulholland et al., 2018), noise present across the territory also plays a significant role on behaviours linked to breeding success, and has been shown to have a stronger effect than noise at the nest site on nest box occupancy (Kleist et al., 2017). This is especially true when considering that acoustic communication is involved in processes that take place outside of the nest box, such as prey detection (foraging behaviour), vigilance (predator detection) (Shannon et al., 2014), and mate selection (Ríos-Chelén, 2009).

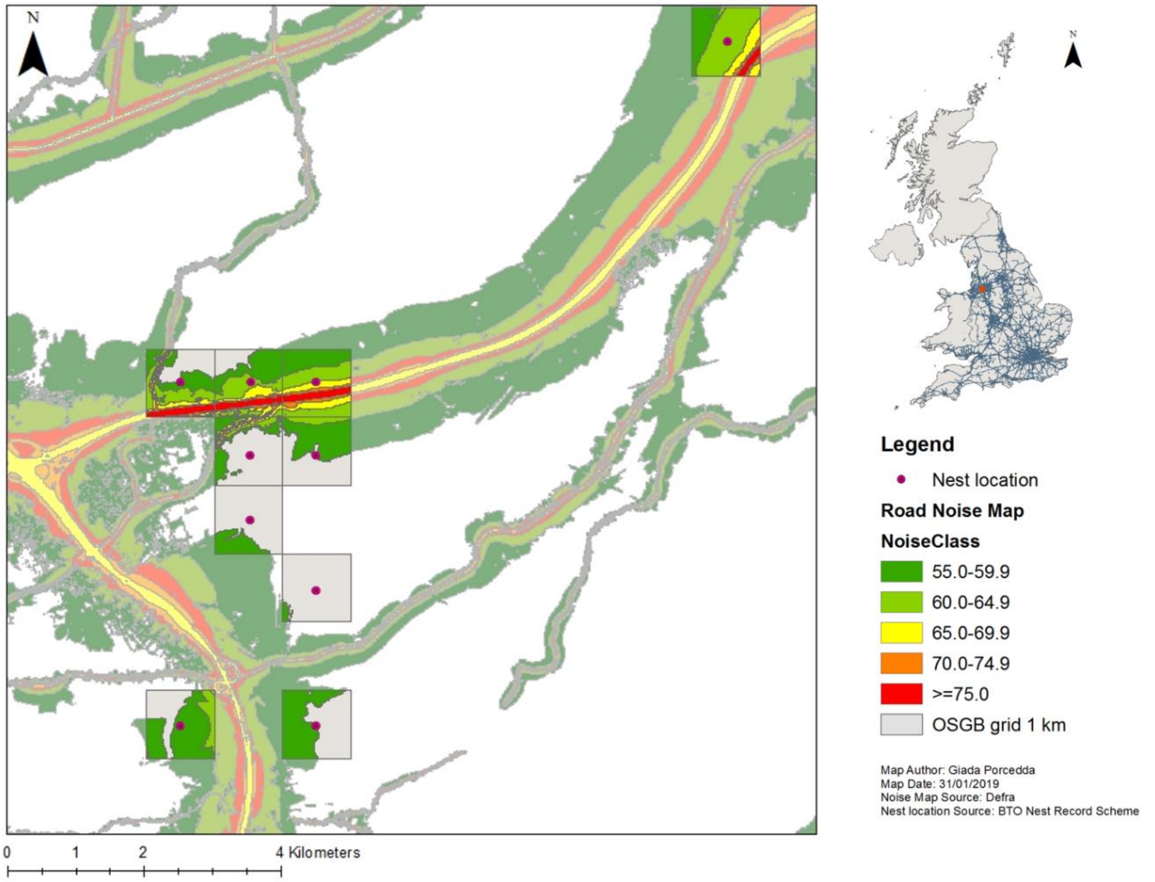


Figure 2 Example of NRS data nest locations within OSGB British National Grid squares that overlap with Defra noise maps.

Only nests located within squares that overlapped with the noise maps were selected, and each square was assigned an evaluation score, based on the following procedure. For each square, I calculated in square meters the surface area of each of the five noise classes, and of the areas that did not fall into the noise maps. Then, in order to account for the correlation between the intensity of noise and the severity of its impact (Francis and Barber, 2013), I applied a Simple Additive Weighting method (SAW). This method is also known as a weighted linear combination or scoring method. It is a simple and the most often used method for multi-attribute decision technique, and it is based on the weighted average using arithmetic mean (Abdullah and Adawiyah, 2014). To apply the SAW method, each noise band was assigned an increasing value, or weight, based on the average noise level for each noise band (see Table 2). Finally, the evaluation score was calculated by multiplying the square meters occupied by each noise band with the weight assigned to the noise bands, and then summing the products. An analogous method has been utilised before by Ciach and Fröhlich (2017) in order to evaluate a noise emission parameter from maps of road noise emission.

Table 2 Weights assigned to each noise class based on Simple Addictive Weighting method (SAW).

Criterion	Noise band	Criterion Weight
Noise Class	<55.0- dB	52.45
	55.0-59.9 dB	55.45
	60.0-64.9 dB	62.45
	65.0-69.9 dB	67.45
	70.0-74.9 dB	72.45
	>=75.0 dB	77.45

2.5 OTHER FACTORS INFLUENCING BREEDING PERFORMANCE

An initial set of biologically relevant predictors other than territorial noise exposure were selected, as they have the potential to affect the breeding performance. These included year, laying date, latitude, habitat type, and regional seasonal conditions (rainfall and mean temperatures).

2.5.1 YEAR

Year was included as a random effect in all analyses to control for long-term trends and changes in productivity (Winter et al., 2005). For example, rising ambient temperatures as a consequence of climate change have resulted in earlier egg laying in a number of birds species in the United Kingdom (Crick et al., 1997).

2.5.2 LAYING DATE

Laying date was included to control for seasonal variations in clutch size. The clutch size of single-brooded species generally declines as the season advances, while multi-brooded species usually show a mid-season peak in clutch size (Crick et al., 1993). In Britain, blue tits are single brooded species (Perrins, 1979), therefore this variable was included to control for clutch size declines as the season progressed. Including this predictor also allowed to control for potential age-specific variations in clutch size related to the parents, as it is common for younger and less experienced birds to lay smaller clutches and later in the season (Sæther, 1990).

2.5.3 LATITUDE

For some bird species, including blue tits, latitude is correlated with laying date (Evans, Leech, et al., 2009; Mainwaring et al., 2012) and clutch size (Sanz, 1998). Birds (and in particular passerines) show a striking trend towards an increase in clutch size as latitude increases (Jetz et al., 2008). To account for this, coordinates for latitude of the nest locations were included in the models.

2.5.4 HABITAT TYPE

The models used to calculate noise levels in the Defra noise maps correct for sound transmission differences between different habitat types. Nevertheless, the suitability of a particular habitat can affect the reproductive performance and population dynamics of each species, as well as the dispersion of individuals within a species' range (Alerstam et al., 1982; Okes et al., 2008; Evans, Newson, et al., 2009), and habitat has been shown to influence laying dates in tits (Dhondt et al., 1984). Including habitat types is important when measuring the effects of human activity on bird populations, and it was therefore included as an explanatory variable in the current analysis. Using data from the Nest Record Scheme, the habitat types surrounding each nest were derived by simplifying the hierarchical coding system developed by the BTO, which provides a non-technical description of bird-habitats (Crick, 1992). In order to account for rare habitat types, this categorical variable was reduced to 3 main types: i) woodland, habitats dominated by trees generally greater than 5 m tall; ii) urban and suburban, habitats consisting of densely urbanised areas and town centres, including urbanised areas directly adjacent to rural ones or containing large gardens, municipal parks, or recreational areas; iii) open habitats, including any open habitat not classified as woodland or urban/suburban, such as scrubland, grassland, marshland, farmland, rural, and wetland and coastal habitats (see Appendix Table 3 for conversion of BTO categories).

2.5.5 SPRING TEMPERATURES AND RAINFALL

The timing of reproduction in birds is determined by day length (Dawson et al., 2001) and temperature (Visser et al., 2009). The effects of temperature on food availability, energetic costs and physiological state, are important determinants of reproductive success (Mares et al., 2017). Changes in rainfall patterns also have the potential to affect breeding phenology through delays in the start of breeding during wet springs, or the reproductive output through alterations in foraging patterns and energetic demands (Öberg et al., 2015), resulting in reduced juvenile growth rates and increased offspring mortality (Arlettaz et al., 2010). Spring temperature and rainfall data were therefore used in this study in order to account for these effects. These data were obtained from the British Atmospheric Data Centre, using the 'Met Office – Historic station data' dataset based on the nearest available meteorological stations to each of the nest sites (mean ± SD distance between nests and nearest meteorological station 44.30 km ± 30.30 km) (Met Office, 2018). Spring temperatures were calculated as an average of the minimum and maximum temperatures recorded for the months of March, April, and May. Rainfall was calculated as the average of the same three months.

2.6 METHOD APPLICATION

In order to test whether the method developed for the BTO's Nest Records Scheme could be applied and integrated over similar datasets, the approach developed on the BTO's Nest Record Scheme was employed on breeding data of the same species obtained from the Sovon's Nest Record Scheme in the Netherlands. This programme is coordinated by the Sovon Dutch Centre for Field Ornithology in collaboration with Statistics Netherlands (Versluijs et al., 2016). The Dutch Nest Record Scheme citizen science programme, established to monitor reproductive parameters of breeding birds, has been set-up to be easily comparable to its British equivalent (Crick et al., 2003). It was therefore possible to apply to same methods of selection and modelling to this data. Environmental factors such as habitat type and latitude were available as part of the nest records, while weather data for the Netherlands were acquired from the Royal Netherlands Meteorological Institute (KNMI) historical monthly time series (KNMI, 2019). The noise score was calculated using noise maps obtained from the executive agency of the Ministry of Infrastructure and Water Management, Rijkswaterstaat. The noise maps are made in the context of the EU Environmental Noise Directive (END) (European Parliament and Council of the European Union, 2002). Since 2014, European environmental agencies follow the same CNOSSOS-EU (Common Noise Assessment Method for Europe) guidelines, resulting in a common noise assessment methodology. Because of these similarities, the same procedure used to score territorial noise levels explained in section 2.4.2 of this chapter could be applied to calculate noise scores.

2.7 STATISTICAL ANALYSIS

All analyses were performed using R version 3.5.2 (R Core Team, 2018). Data exploration was applied following Zuur et al. (2010) protocol. The presence of outliers was investigated using boxplots, while collinearity was assessed using scatterplots, Pearson correlation coefficients, and variance inflation factors (VIF). In case of collinearity among predictors, terms with an absolute r greater than 0.5 were not included in the same model (Appendix B Figure 2). All continuous variables fitted as fixed terms were scaled by subtracting the mean of all data points from each individual data point, and dividing those points by the standard deviation of all points. This was done in order to allow the direct comparison of their corresponding estimated effect sizes, and to facilitate the interpretation of the effects of variables involved in interactions (Hilbe, 2015). All responses were modelled using the package lme4 (Bates et al., 2015). The breeding variables were fitted against the selected predictors by using generalised linear mixed models (GLMM), with year as a random intercept term to account for repeated measures. For the continuous breeding variables (clutch size, brood size, first egg date), GLMMs with a Poisson error distribution and a log link function were applied. Daily nest failure rates at the incubation and the nestling stage were estimated using Shaffer's (2004) logistic exposure method, an adaptation of the Mayfield method. The response variable consisted in nest fate (0: success, i.e., at least one chick fledged; 1: failure, i.e., no chicks fledged) for the nests where at least one egg was laid. Failure or success were estimated with a GLMM with binomial errors and a custom logit-link function adjusted for exposure days (Bolker, 2014). Model validation was applied to each model to verify the underlying assumptions. Specifically, residuals versus fitted values were plotted in order to assess homogeneity of variance, and residuals versus each covariate were plotted to investigate model misfit. Finally, likelihood ratio tests, comparing likelihood for models that included noise score with null models where the latter had been removed, were used for statistical inference. In order to test whether the same approach would deliver analogous results, all sets of data were analysed separately.

3. RESULTS

3.1 BTO'S NEST RECORD SCHEME

Statistical significance of likelihood ratio tests, estimates, and p-values for the GLMM were analogous between the models where the noise score was calculated on noise maps based on the long-term average noise indicator LAeq16 and those based on the noise indicator Lden (Figure 3; Table 3). Noise scores assigned based on the two noise indicators also showed a high correlation for 1000 randomly selected nests (Pearson r= 0.991, p<0.001).

As models based on noise indicator LAeq16 and Lden were highly comparable, model outputs reported below are derived from the models where noise scores were obtained from the noise indicator LAeq16, for model outputs based on noise indicator Lden see Appendix B Table 4. Significant changes in breeding performance with increasing levels of territorial noise were detected for all the measures of breeding performance except clutch size and brood size (Table 3). Territorial noise was a significant predictor of nest failure rate at the egg stage (EFR) ($\chi^2(1)= 8.443$, $p<0.001$), with more nests surviving with higher noise levels (estimate -0.084 ± 0.03). The territorial noise was also a significant predictor of nest failure rates at the nestling stage (NFR) ($\chi^2(1)= 11.079$, $p<0.001$). At this stage, however, more nests failed as noise levels increased 0.077 ± 0.022.Territorial noise had no effect on clutch size ($\chi^2(1)= 0.0022$, $p=0.96$) or brood size ($\chi^2(1)= 2.30$, $p=0.13$). The noise score did however have an effect on first egg date ($\chi^2(1)= 11.79$, $p<0.001$) lowering the average value by 0.14 days ± 0.006 (standard errors) (see Table 4 for full estimate parameters).

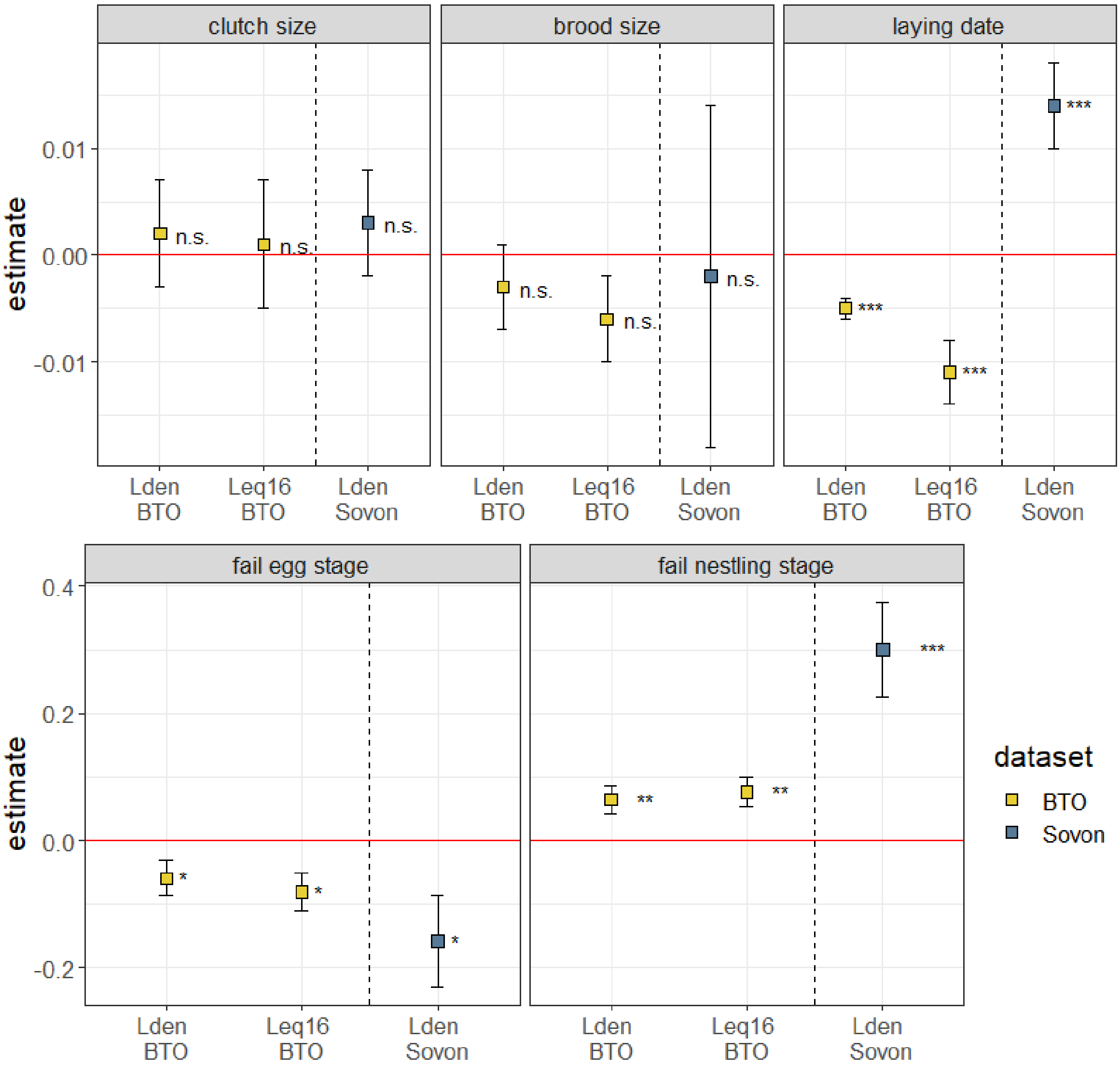


Figure 3 Estimates with standard errors for the noise score parameter for models on clutch size, brood size, laying date, failure at the egg stage, and failure at the nestling stage, for BTO dataset (where noise score is derived from noise indicator Lden or LAeq16), and for Sovon dataset (where noise score is derived from noise indicator Lden). Estimates show direction and significance of the effect. Significance of marginal tests (Wald test) is indicated as * for p ≤ 0.05, ** for p ≤ 0.01, * for p ≤ 0.001.**

Table 3 Statistical significance of likelihood ratio tests comparing the models without noise score as a factor (*null*) to the models with Noise score as a factor (*full*) where noise score were derived from the noise indicator LAeq16 and noise indicator Lden.

BTO data									
Noise indicator	Breeding variable			Df	AIC	logLink	deviance	χ^2	p-value
Leq16	Clutch Size	*Noise score + Latitude + Habitat + FED + Rainfall + Min temp*	Null	8	14933	-7458.3	14917		
			Full	9	14935	-7458.3	14917	0.018	0.894
	Brood Size	*Noise score + Latitude + Habitat + FED + Rainfall + Min temp*	Null	8	34436	-17210	34420		
			Full	9	34436	-17209	34418	1.911	0.167
	First Egg Date	*Noise score + Habitat + Mean Temp + Rainfall*	Null	7	38009	-18998	37995		
			Full	8	37995	-18990	37979	15.67	< 0.001
	Egg Failure Rate	*Noise score + Habitat + Latitude + FED + Rainfall + Min temp*	Null	8	1582.7	-783.37	1566.7		
			Full	9	1577.1	-779.56	1559.1	7.610	0.006
	Nestling Failure Rate	*Noise score + Habitat + Latitude + FED + Rainfall + Min Temp*	Null	8	3224.6	-1604.3	3208.6		
			Full	9	3215.6	-1598.8	3197.6	10.988	< 0.001
Lden	Clutch Size	*Noise score + Latitude + Habitat + FED + Rainfall + Min temp*	null	8	19746	-9864.9	19730		
			full	9	19748	-9864.8	19730	0.155	0.6933
	Brood Size	*Noise score + Latitude + Habitat + FED + Rainfall + Min temp*	null	8	38234	-19109	38218		
			full	9	38236	-19109	38218	0.448	0.5034
	First Egg Date	*Noise score + Habitat + Mean Temp + Rainfall*	null	7	40547	-20266	40533		
			full	8	40535	-20260	40519	13.586	< 0.001
	Egg Failure Rate	*Noise score + Habitat + Latitude + FED + Rainfall + Min temp*	null	8	1782.7	-882.35	1764.7		
			full	9	1785.3	-884.67	1769.3	4.634	0.031
	Nestling Failure Rate	*Noise score + Habitat + Latitude + FED + Rainfall + Min temp*	null	8	3455.2	-1719.6	3439.2		
			full	9	3448.9	-1715.5	3430.9	8.266	0.004

Table 4 Estimated regression parameters, standard errors, *z* values, and *p*-values for Poisson GLMMs on continuous breeding variables clutch size, brood size, and first egg date and binomial GLMMs on daily nest failure rate at the egg stage and at the nestling stage. Noise score was derived from the noise indicator LAeq16. Significance of marginal tests (Wald test) is indicated as * for p ≤ 0.05, ** for p ≤ 0.01, * for p ≤ 0.001.**

			BTO data				
Breeding Variable	n	Predictor*	Estimate	Std. Error	*z* value	*p*-value	
Clutch size	3378	(Intercept)	2.172	0.016	132.539	< 0.001	***
		Noise score	0.001	0.006	0.134	0.894	
		Latitude	0.022	0.007	2.978	0.003	**
		Open habitat	-0.018	0.014	-1.321	0.186	
		Urban habitat	-0.078	0.017	-4.619	< 0.001	***
		Laying date	-0.129	0.008	-16.867	< 0.001	***
		Rainfall	-0.004	0.009	-0.417	0.677	
		Min temp	-0.011	0.011	-1.006	0.314	
Brood size	7445	(Intercept)	2.006	0.022	89.097	< 0.001	***
		Noise score	-0.006	0.004	-1.379	0.168	
		Latitude	-0.035	0.010	-3.644	< 0.001	***
		Open habitat	-0.189	0.013	-13.973	< 0.001	***
		Urban habitat	0.013	0.005	2.425	0.015	*
		Laying date	-0.139	0.006	-24.382	< 0.001	***
		Rainfall	-0.007	0.007	-1.037	0.300	
		Min temp	-0.007	0.008	-0.965	0.3344	
First Egg Date	5268	(Intercept)	3.229	0.040	80.516	< 0.0001	***
		Noise score	-0.011	0.003	-3.941	< 0.001	***
		Latitude	0.068	0.003	20.546	< 0.001	***
		Open habitat	0.031	0.006	4.921	< 0.001	***
		Urban habitat	-0.023	0.008	-2.907	0.004	**
		Rainfall	0.056	0.004	12.928	< 0.001	***
		Min temp	-0.013	0.005	-2.738	0.006	**
Egg Failure Rate	6542	(Intercept)	1.202	0.072	16.749	< 0.001	***
		Noise score	-0.081	0.030	-2.687	0.007	**
		Open habitat	-0.202	0.066	-3.060	0.002	**
		Urban habitat	-0.137	0.083	-1.657	0.097	.
		Latitude	-0.066	0.0338	-1.945	0.052	.
		Laying date	0.111	0.034	3.246	0.001	**
		Rainfall	0.056	0.041	1.388	0.165	
		Min temp	-0.040	0.045	-0.894	0.372	
Nestling Failure Rate	4186	(Intercept)	1.590	0.064	25.000	< 0.001	***
		Noise score	0.077	0.023	3.288	< 0.001	**
		Open habitat	0.415	0.052	8.011	< 0.001	***
		Urban habitat	0.330	0.064	5.139	< 0.001	***
		Latitude	-0.100	0.028	-3.517	< 0.001	***
		Laying date	0.109	0.028	3.877	< 0.001	***
		Rainfall	0.077	0.034	2.278	0.023	*
		Min temp	0.003	0.039	0.066	0.948	

*All fixed effects are scaled

3.2 DUTCH NEST RECORD SCHEME

Analysis of the Dutch Nest record scheme showed similar result compared to the British data, territorial noise influenced breeding performance (Table 5). Territorial noise had no effect on clutch size ($\chi^2(1)= 1.42$, $p=0.23$) or brood size ($\chi^2(1)= 2.13$, $p=0.14$). The noise score did however have an effect on first egg date ($\chi^2(1)= 12.68$, $p<0.001$, bringing it forward increasing the average value by -0.014 days ± 0.004 (SE) (see Table 6 for full estimate parameters).

Territorial noise had a weak positive effect on nest failure rate at the egg stage ($\chi^2(1)= 5.09$, $p=0.024$) with more nests surviving with higher noise levels (estimate 0.16 ± 0.07). The territorial noise score also had an effect on nest failure rates at the nestling stage ($\chi^2(1)= 14.01$, $p<0.001$). At the nestling stage, the effect of noise was strongly negative, increasing failure rate by 0.29 ± 0.08.

Table 5 Statistical significance of likelihood ratio tests comparing the models without Noise score as a factor (*null*) to the models with Noise score as a factor (*full*).

			Sovon data					
Breeding variable			Df	AIC	logLink	deviance	χ^2	p-value
Clutch Size	Noise score + Latitude + Habitat + FED + Rainfall + Min temp	Null	8	4168.3	-2076.1	4152.3		
		Full	9	4170.3	-2076.1	4152.3	0.005	0.941
Brood Size	Noise score + Latitude + Habitat + FED + Rainfall + Min temp	Null	8	3041.7	-1512.8	3025.7		
		Full	9	3043.7	-1512.8	3025.7	0.020	0.887
First Egg Date	Noise score + Habitat + Mean Temp + Rainfall	Null	7	6972.6	-3479.3	6958.6		
		Full	8	6962	-3473	6946	12.687	**<0.001**
Egg Failure Rate	Noise score + Habitat + Latitude + FED + rains + Min temp	Null	8	502.35	-243.18	486.35		
		Full	9	499.25	-240.63	481.25	5.098	**0.024**
Nestling Failure Rate	Noise score + Habitat + Latitude + FED + Rainfall + Min temp	Null	8	255.72	-119.86	239.72		
		Full	9	242.73	-112.36	224.73	14.994	**<0.001**

Table 6 Estimated regression parameters, standard errors, *z* values, and *p*-values for Poisson GLMMs on continuous breeding variable clutch size, brood size, and first egg date and binomial GLMMs on daily nest failure rate at the egg stage (EFR) and at the nestling stage (NFR).

Sovon data							
Breeding Variable	n	Predictor*	Estimate	Std. Error	*z* value	*p*-value	
Clutch size	908	(Intercept)	2.162	0.013	165.628	< 2e-16	***
		Noise score	0.003	0.005	0.541	0.589	
		Latitude	-0.007	0.006	-1.073	0.283	
		Open habitat	-0.031	0.012	-2.564	0.010	*
		Urban habitat	-0.066	0.015	-4.332	< 0.001	***
		First egg date	-0.061	0.006	-9.297	< 2e-16	***
		Rainfall	-0.015	0.007	-2.046	0.041	*
		Min temp	-0.009	0.008	-1.028	0.304	
Brood size	650	(Intercept)	2.192	0.024	91.686	< 0.001	***
		Noise score	-0.002	0.016	-0.142	0.887	
		Latitude	0.009	0.017	0.537	0.591	
		Open habitat	0.057	0.041	1.377	0.168	
		Urban habitat	-0.056	0.081	-0.692	0.489	
		Laying date	-0.170	0.019	-8.879	< 0.001	***
		Rainfall	-0.012	0.021	-0.565	0.572	
		Min temp	-0.083	0.024	-3.529	< 0.001	***
First Egg Date	993	(Intercept)	4.666	0.012	393.840	< 0.001	***
		Noise score	0.014	0.004	3.585	< 0.001	***
		Latitude	-0.004	0.004	-0.992	0.321	
		Open habitat	0.001	0.010	0.025	0.980	
		Urban habitat	0.001	0.015	0.058	0.953	
		Rainfall	-0.024	0.008	-3.047	0.002	**
		Min temp	0.014	0.007	1.928	0.054	.
Egg Failure Rate	958	(Intercept)	1.178	0.219	5.373	< 0.001	***
		Noise score	-0.158	0.071	-2.219	0.026	*
		Latitude	0.029	0.091	0.320	0.749	
		Other habitat	0.328	0.177	1.846	0.065	.
		Urban habitat	-0.547	0.484	-1.130	0.258	
		First egg date	0.274	0.070	3.939	< 0.001	***
		Rainfall	-0.241	0.138	-1.750	0.080	.
		Min temp	0.452	0.191	2.374	0.018	*
Nestling Failure Rate	678	(Intercept)	1.654	0.420	3.936	< 0.001	***
		Noise score	0.300	0.074	4.070	< 0.001	***
		Latitude	0.555	0.201	2.760	0.006	**
		Other habitat	0.279	0.381	0.732	0.464	
		Urban habitat	-0.160	0.086	-1.853	0.064	.
		First egg date	0.038	0.085	0.445	0.656	
		Rainfall	0.032	0.089	0.366	0.714	
		Min temp	-0.154	0.094	-1.643	0.100	

*All fixed effects are scaled

4. DISCUSSION

This chapter presents an approach to the analysis of large-scale bird breeding data, in order to quantify variations in reproductive performance and relate them to environmental factors of anthropogenic origin such as noise. While there are other large-scale multi-country studies looking at the impact of human-generated environmental alteration on birds (Cardoso, 2014; Francis, 2015; Hu and Cardoso, 2009; Moiron et al., 2015), this method focuses on the use of large citizen science datasets, and specifically on direct indicators of breeding performance rather than vocal traits or other life history traits. This approach delivered comparable outputs when applied to different noise indicator metrics, and it was further validated on breeding data originating from a different bird-monitoring scheme in the Netherlands. Environmental noise was found to affect failure rates at crucial stages of the breeding cycle of blue tits, and this result was replicated on the same breeding dataset for the UK over two noise maps based on different equivalent sound pressure levels, and on a geographically separate breeding dataset for the Netherlands. The findings from all datasets show similar patterns in terms of failure rates at the incubation stage and at the nestling stage. At the incubation stage, failure rates significantly decreased in increasing noise, suggesting that, at the early stages of their reproductive cycle, breeding in noisier territories might be advantageous for blue tits. However, after hatching, failure rates of the nestlings increased as territorial noise score increased, meaning that, at a later stage, noise might play a negative role on their fitness.

4.1 A NOVEL APPROACH TO INVESTIGATING THE EFFECTS OF NOISE ON LARGE SCALE ECOLOGICAL DATA

This study reports on a novel method to address a substantial gap in large spatial scale published data on the effects of anthropogenic noise on birds' breeding success. Volunteer-based monitoring programmes such as the BTO's or the Sovon's Nest Record Schemes are powerful tools to provide an insight into the effects of anthropogenic change at large spatial scales, and they can be applied across a range of species. More importantly, this approach has the potential to be extended to other countries with comparable nest record schemes, and to any available large-scale data of environmental factors of anthropogenic disturbance. Similar breeding data are in fact collected in North America, Australia, New

Zealand, and several other European countries (Spina, 1999; Gregory et al., 2005; Saracco et al., 2008; Cooper et al., 2015). Spatially extensive, long-term monitoring schemes through citizen science, are becoming increasingly valuable for monitoring the impact of environmental change and for their potential conservation applications, especially when used in conjunction with large-scale data of environmental anthropogenic pollutants, such as noise.

Although programmes such as Nest Record Scheme are invaluable for the volume of data collected, there are inevitable trade-offs between such scale and the accuracy and resolution of information available. The main sources of possible bias is characterised by seasonal variation in the timing and the proportion of nests found, caused by changes in search effort and nest detectability (Crick et al., 2003), which might have played a role in affecting the results in terms of laying date. Finer quality in the spatial resolution of the data could provide a smaller margin of error for the estimated levels of noise exposure, and would allow to measure distance from the road, helping to control for some of the factors associated with roads, such as traffic collisions, and atmospheric and light pollution (Kociolek et al., 2011). On this account, it is important to mention that experimental evidence in the field has repeatedly concluded that noise alone has can have negative consequences on birds' fitness (McClure et al., 2017; Cinto Mejia et al., 2019). While the method developed in this chapter does not provide causational evidence on the effects of noise, it provides an effective and immediate instrument to assess anthropogenic impact on a scale that would otherwise not be possible to achieve. The findings of this study largely mirror experimental evidence, and they provide suggestive data that the extent of the effects previously observed experimentally both in field and laboratory conditions are taking place on a much larger scale than any other study has been able to achieve.

4.2 HIGHER FAILURE RATES AT THE NESTLING STAGE

In blue tits, increasing territorial noise scores corresponded to higher rates of failure at the nestling stage. These results support the hypothesis that noise might reduce breeding success by impairing the development of the nestlings. Indeed, noise might lead to poor chick development, and affect blue tits only at a later stage of their breeding performance by means of at least four potential pathways. Firstly, it is possible that noise might induce psychological stress in the chicks, which in return might lead to reduced growth rates (Cyr et al., 2007; Crino et al., 2013; Kleist et al., 2018). The other possibilities are related to the acoustic masking effects of noise. In particular, begging calls indicate the nestling's needs, and parents use them to select which nestling to feed (Wright and Leonard, 2002), meaning any masking of this type of communication would result in parents reducing their provisioning rates, therefore increasing the chances of nest failure at this stage. In some species, noise has indeed been shown to cause chick begging calls to be less audible (Schroeder et al., 2012; Naguib et al., 2013; Lucass and Eens, 2016; Kleist et al., 2018). In other species, noise has been linked to failure of the chicks to notice their parents arrival at the nest, resulting in them not begging for food (Leonard and Horn, 2008, 2012; Lucass and Eens, 2016). Another possibility is that noise might hamper auditory cue detection of potential predators or alarm calls (McIntyre et al., 2014; Templeton et al., 2016), therefore playing a role as a component of the trade-off between vigilance and feeding (Quinn et al., 2006), or resulting increased predation risk (Antze and Koper, 2018).

4.3 LOWER FAILURE RATES AT THE EGG STAGE

Territorial noise levels were however correlated with lower rates of nest failure at the egg stage. Noise has been shown to affect embryonic development in some species (Potvin and MacDougall-Shackleton, 2015b), possibly through a trade-off between incubating and increased vigilance. Studies on other species, however, have led to contradictory results, suggesting that hatching success in relation to noise exposure might be species-dependent or related to other local conditions. Kleist et al., 2018a reported that only one of three species exposed to noise from gas fields showed a negative association with noise at the incubation stage, while another showed a trend towards positive effects. Similarly, ash throated flycatchers (*Myiarchus cinerascens*), but not western bluebirds (*Sialia mexicana*) showed higher rates of nest abandonment at the incubation stage when exposed to ambient sound (Mulholland et al., 2018). A possible explanation for the results found in this study is that higher quality, more experienced blue tits might be more likely to breed in noisier territories because of reduced number of predators or heterospecific competition (Halfwerk et al., 2016) over nesting sites, roosting sites, and food resources (Dhondt and Eyckerman, 1980; Kempenaers and Dhondt, 1991). This would in turn decrease the chances of nest failure at the egg stage (Slagsvold and Lifjeld, 1990), while still leaving the nests exposed to potential negative consequences of noise at later stages of their reproduction.

4.4 NO EVIDENCE FOR NOISE PLAYING A ROLE ON THE QUALITY OF THE BREEDER OR THE TERRITORY

This study did not show any evidence that low quality blue tits might end up occupying noisier territories. Indeed, if noisier territories are lower quality or are held by lower quality individuals, clutch size should decrease in increasing noise and laying date should be delayed (Huet des Aunay et al., 2017). Clutch size, however, did not change across different territorial noise conditions, suggesting that, in blue tits, it is unlikely that low quality or less experienced individuals are being relegated to noisier territories by more competitive ones (Habib et al., 2007). Apart from few exceptions (Halfwerk, Holleman, et al., 2011; Huet des Aunay et al., 2017), previous studies have also not been able to find any conclusive relationship between noise levels and clutch size (Kight et al., 2012; Schroeder et al., 2012; Halfwerk et al., 2016; Mulholland et al., 2018).

First egg date showed opposite patterns across the two datasets, although the level of variation for this variable was minimal for both the BTO's and the Sovon's data. As mentioned above, it is highly plausible that biases might be arising from the accuracy with which this variable is obtained. It is also possible that laying date might instead be influenced by other anthropogenic factors associated with roads, such as artificial night light (Lambrechts et al., 1997; Kempenaers et al., 2010), and it may not be a reliable measure of the effects of noise on breeding performance. Indeed, this breeding variable has only been included as a fitness measure in two previous field studies (Halfwerk, Holleman, et al., 2011; Schroeder et al., 2012), both of which found no links with anthropogenic noise.

Brood size also did not change with increasing noise exposure levels. These results are consistent with the literature, where brood size does not appear to be a breeding measure significantly affected by noise (Kight et al., 2012; Angelier et al., 2016; Halfwerk et al., 2016). If noise were a physiological stressor for parents, they would reduce their parental investment and their breeding attempts would show higher levels of embryo mortality (Thierry et al., 2013), resulting in smaller broods. Contrarily, the results of this study suggest that noise induced stress does not play a role at this stage of the breeding performance of blue tits, which is further indicated by the lack of an effect of noise on clutch size, and a decrease in nest failure rates at the egg stage.

4.5 HABITAT SUITABILITY MIGHT DECREASE AT THE NESTLING STAGE

To summarise, this study finds evidence for the hypothesis that failure rates at the nestling stage increase at higher noise levels, but no evidence for negative effects on earlier stages of breeding. The findings support the possibility that, at the incubation stage, breeding in noisier territories might constitute an advantage for blue tits. These results parallel what found in the population study carried out for Chapter 2, giving further support to fact that the changes that have so far been observed in single populations reflect a much bigger and widespread issue.

Two possible hypotheses could explain what might be happening to blue tits breeding in noisier environments: one is of an ecological trap with initial preference for poor-quality habitats, and the other is of an equal preference ecological trap. The first explanation is that noisier territories are initially more attractive because of reduced hetero-specific competition (Halfwerk et al., 2016). Blue tits might be preferentially choosing noisier territories, but eventually suffer reproductive costs at a later stage of their breeding performance. While this hypothesis is supported by the lower rate of egg failure in territories with higher noise levels, if noisier territories were initially perceived as attractive, this would also reflect in a larger clutch size for individuals settling there, which was not the case for this study. The second and more conservative hypothesis of an equal-preference ecological trap (Robertson and Hutto, 2006) is more likely to be accurate. In this case, blue tits settle non-preferentially across noisier, lower quality habitats compared to quiet, higher quality habitats. This is also suggested by the fact that clutch size, which in tits are affected by fitness parameters of females (Slagsvold and Lifjeld, 1990), did not vary in increasing noise. While a lower level of competition might initially play a role in decreasing failure rates at the incubation stage, the suitability of the habitat for reproduction is decreased at the nestling stage, possibly when noise starts playing a role in parent-offspring communication.

4.6 CONCLUSIONS

The proposed method provides the first multi-country study to correlate breeding parameters and intensity of exposure to road traffic noise, providing a large-scale indication that noise affects breeding performance of an urban dweller such as the blue tit. Similar or even worse effects are likely to be taking places in other species, even more so in species that have already been identified as noise sensitive. As anthropogenic noise penetrates even the most remote locations (Ortega, 2012) and secluded areas (Barton and Holmes, 2007; Barber et al., 2011), expanding our understanding the relationship between this environmental pollutant and reproductive success in as many as possible species becomes increasingly important. This study provides a valuable method for monitoring and managing the impact of environmental pollutants by using spatially extensive, long-term monitoring schemes in conjunction with large-scale data of anthropogenic pollutants such as noise. In particular, the method tested in this chapter has the potential to be adapted to generate predictive models on the impact of noise, and potentially other urban pollutants, on birds' fitness but also distribution, and especially to be used a quick assessment tool to predict the impact of road infrastructure development projects.

CHAPTER 4.

IMPACT OF TRAFFIC NOISE ON THE BREEDING SUCCESS OF 11 COMMON BIRD SPECIES

Abstract

Anthropogenic noise is a pervasive environmental pollutant that affects behaviours crucial for the fitness of animals. Noise has been associated to declines in the breeding performance of birds, but our understanding of species-specific responses is still limited, and mostly restricted to a local-population level. Studies encompassing a wide variety of species and at a large spatial scale are thus necessary to reflect patterns over large geographical ranges and taxa. In this study, I merged breeding data from the Nest Record Schemes of two separate countries, the UK and the Netherlands, and applied the approach developed in Chapter 3 in order to study the reproductive output of 11 common breeding European species. Results show complex, species- and stage-specific relationships between noise and breeding performance. The nestling phase emerges as particularly vulnerable, as most of the species negatively affected experienced increased failure at this stage. This study highlights the importance of considering the stage of breeding when studying the effects of noise on birds. By transcending population level, this study shows that the effects of anthropogenic noise encompass much larger scale than ever shown before, and it highlights an even more pressing need for the implementation of noise mitigation measures around roads.

1. INTRODUCTION

Noise generated by human activities has seen a dramatic increase over recent decades as a result of population growth, urbanisation, and increase of resource extraction and transportation networks. While railways, air traffic, and industry are major sources of noise, the most widespread source of noise pollution in both urban and non-urban areas is road traffic. In the European Union, 100 million people are estimated to be exposed to annual average noise levels above 55 dB(A) (European Environment Agency, 2018), a level at which some negative responses begin to appear in both humans and wildlife (Babisch, 2003; Dooling and Popper, 2007; Jarup et al., 2008; Kight and Swaddle, 2011).

Anthropogenic noise is a prominent force affecting the ecology and evolution of different species (Slabbekoorn and Ripmeester, 2008; Francis et al., 2009; Kight and Swaddle, 2011; Shannon et al., 2016), and birds have been shown to be particularly sensitive to its effects, possibly because of their reliance on vocal communication (Slabbekoorn and Ripmeester, 2008). Research has shown that traffic noise may alter habitat use and cause changes in abundance and density of birds (Reijnen et al., 1996; Rheindt, 2003; Peris and Pescador, 2004; McClure et al., 2013). Noise may also interfere with acoustic communication (Brumm, 2006a; Patricelli and Blickley, 2006; Barber et al., 2010; Brumm and Zollinger, 2013), and trigger physiological stress responses such as elevated plasma glucocorticoids, leading to depressed immune function and increased oxidative stress (reviewed in Kight and Swaddle, 2011).

Each of these negative effects may ultimately result in fitness costs for the individuals affected. There are several ways through which noise can decrease reproductive success, related to shifts in habitat use, communication, behaviour, and physiological response. Alterations in reproductive success might be taking place through changes in age and fitness structure of the populations, with less experiences birds occupying noisier territories and being less successful in attracting mates (eg. Habib et al., 2007). Another possibility is that noise might interfere with acoustic signals related to sexual selection (eg. Habib et al., 2007; Huet des Aunay et al., 2013; Kleist et al., 2016; Phillips & Derryberry, 2018; Swaddle & Page, 2007), or with parent-offspring communication (eg. Leonard & Horn, 2012; Lucass & Eens, 2016; McIntyre et al., 2014). Noise might also alter other behavioural aspects such as vigilance levels (Evans et al., 2018) and time allocation (Meillere et al., 2015; Ware et al., 2015), or interfere with sounds playing a role in predator-prey interactions (Antze and Koper, 2018). Moreover, noise might affect breeding through physiological stress (Crino et al., 2013; Potvin and MacDougall-Shackleton, 2015a; Injaian et al., 2018, 2019; Zollinger et al., 2019). While high corticosterone levels might help parents cope with stressors (Bonier et al., 2011), maternal stress has been linked to smaller fledglings and slower plumage development (Saino et al., 2005). High levels of corticosterone in parents have also been shown to affect the amount of time parents spent incubating eggs (Spée et al., 2011), to increase the chances of nest abandonment (Thierry et al., 2013), and to reduce feeding rates (Angelier et al., 2009).

Studies on the behavioural and physiological changes triggered by noise are fundamental to understand the mechanisms through which noise affects the fitness of birds. However, unambiguous evidence on the fitness costs of noise can only be supported by directly addressing the effects of noise on reproductive success. Research on this topic has only recently been growing in numbers, giving evidence that the behavioural and physiological responses to noise exposure in birds might ultimately result in decreased fitness (Halfwerk, Holleman, et al., 2011; Potvin and MacDougall-Shackleton, 2015b; Halfwerk et al., 2016; Huet des Aunay et al., 2017; Injaian et al., 2018). Evidence from correlational field studies comparing noisy and less noisy sites suggest that noise might affect reproductive success in some species. High levels of environmental noise have been related to smaller clutch and brood size in great tits (*Parus major*) (Halfwerk, Holleman, et al., 2011), reduced productivity in Eastern bluebirds (*Sialia sialis*) (Kight et al., 2012), reduced hatching success in Western bluebirds (*Sialia mexicana*) (Kleist et al., 2018), higher rates of abandonment at the incubation stage in ash-throated flycatchers (*Myiarchus cinerascens*) (Mulholland et al., 2018), and smaller clutches and delayed egg-laying date in tree swallows (*Tachycineta bicolor*) (Injaian et al., 2018).

Negative effects of noise on breeding performance have been observed in species from diverse ecological and taxonomic groups, suggesting that noise has the potential to impact a wide variety of species. However, the susceptibility and response to elevated noise levels is likely to have interspecific differences, depending on variation in, for example, mechanisms of physiological stress response (Hofer and East, 1998), hearing ability (Ryals et al., 1999; Dooling et al., 2000), vocal traits, and diets (Francis, 2015). Direct comparisons of species in response to the same noise sources are therefore necessary in order to facilitate a comprehensive understanding of the impacts of anthropogenic noise on multiple species. To date, however, only few studies have approached the impact of noise on the reproductive performance of birds by looking at multiple species. Such studies found noise to have a negative effect on some species but not on others (Kleist et al., 2018b; Mulholland et al., 2018), and that noise may even facilitate reproductive success as a result of the disruption of predator-prey interactions (Francis et al., 2009; Francis, Paritsis, et al., 2011).

Additionally, not many studies have investigated the effects of anthropogenic noise at larger spatial scales, despite these having the potential to offer a more complete and general understanding on the impact of noise than single population studies. So far, multiple population studies have focussed on how noise affects the vocal behaviour of birds and their abundance (Slabbekoorn and den Boer-Visser, 2006; Mockford and Marshall, 2009; Patón et al., 2012), but not on the impacts on breeding performance. In order to demonstrate that the changes observed through single population studies and controlled experiments actually reflect wider patterns over large geographical ranges, large-scale studies that encompass a wide variety of species and that transcend the population scale are thus necessary.

The aim of this study was to relate the breeding ecology of birds to the intensity of road traffic noise at a large geographical scale. This was achieved by analysing the breeding performance of 11 common European bird species in relation to the level of territorial noise experienced. The hypothesis tested was that higher levels of territorial noise would have a negative impact on the reproductive output of the species considered. This study further investigated whether noise affected some stages of the breeding cycle more than others. Depending on which processes might be at play, it was also expected that noise would affect some stages of the reproductive performance, while being neutral or even positive for others. These hypotheses were tested on a large, combined dataset originating from two large citizen science programmes, the British Trust for Ornithology’s (BTO) Nest Record Scheme in the United Kingdom, and the Sovon’s Nest Record Scheme in the Netherlands.

2. METHODS

2.1 STUDY SPECIES

The relationship between variation in the breeding performance and levels of territorial noise generated by roads was investigated for 11 resident avian breeders (McInerny et al., 2018) that can be found along motorways: stock dove *Columba oenas*, barn owl *Tyto alba*, tawny owl *Strix aluco*, kestrel *Falco tinnunculus*, blue tit *Cyanistes caeruleus*, great tit *Parus major*, starling *Sturnus vulgaris*, blackbird *Turdus merula*, song thrush *Turdus philomelos*, house sparrow *Passer domesticus*, and tree sparrow *Passer montanus*. These species were selected based on the number of record available in the databases. In addition, they encompass a variety of breeding ecology, preferred habitats, population statuses, and diets (Table 1).

Blue tit and great tit had the highest number of nesting events available from the Nest Record Schemes. Both are small insectivorous, hole-nesting birds that are known to breed readily in noisy urban areas and along motorways and roads (Reijnen et al., 1995), and have been extensively studied in the context of anthropogenic noise (eg. Ciach and Fröhlich, 2017; Corsini et al., 2017; Halfwerk et al., 2011a; Halfwerk and Slabbekoorn, 2009; Klett-Mingo et al., 2016; Lucass and Eens, 2016; Mockford and Marshall, 2009; Naguib et al., 2013; Pohl et al., 2012, 2009; Salmón et al., 2016; Silva et al., 2014; Templeton et al., 2016; Wiacek et al., 2015). Great tits have been shown to have reduced clutch size and number of fledglings in locations with high traffic noise (Halfwerk, Holleman, et al., 2011), although experimental evidence does seem to show that noise alone does not affect the breeding performance of this species (Halfwerk et al., 2016).

Tree sparrow and house sparrow are two closely related species with similar habitats and diets (Summers-Smith, 1998a, 1998b). While both species are of least concern globally, their European populations have declined by over 20% since the 1970s (Summers-Smith, 2003; Staneva and Burfield, 2017). Experimental evidence shows that house sparrows reduce parental provisioning (Schroeder et al., 2012) and increase vigilance (Meillere et al., 2015) in a noisy environment, but there is no conclusive evidence for a clear effect on their reproductive performance (Meillere et al., 2015; Angelier et al., 2016). Tree sparrows show a decline in density (Ciach and Fröhlich, 2017) and an increase in corticosterone levels (Zhang et al., 2011) with increasing urbanisation, but no studies have directly looked at noise effects on their fitness.

Blackbird and song thrush are related species that regularly inhabit urban areas. While for both species there is currently no information on their breeding success in relation to traffic noise, it has been show that both song thrushes and blackbirds breed in lower densities in close proximity to main roads (Reijnen et al., 1995; Rheindt, 2003). Blackbirds, however, have been shown to adapt to urbanisation by changing their breeding strategies. In particular, urban blackbirds have a smaller clutch size, longer nestling periods, and slower growth of chicks than their woodland counterparts, but a higher number of fledglings in human-populated habitats, where they likely benefit from lower rates of predation (Ibáñez-Álamo and Soler, 2010). European populations of starling have also been declining (Peterjohn, 2006; Staneva and Burfield, 2017); however, this species has been observed to occur in higher numbers at noise levels where other species show declines (González-Oreja, 2017).

Stock dove is found in urbanised, and therefore potentially noisy, areas, however its numbers decline in proximity to densely built-up areas (Mörtberg and Wallentinus, 2000). Stock doves are among those species that vocalise at lower frequencies, which are more likely to overlap with anthropogenic noise. Such species have been shown to avoid noisy areas more than species that vocalise at higher frequencies (Cardoso, 2014; Francis, 2015; although see also Moiron et al., 2015); the reduced ability of doves to modify their signals (Patricelli and Blickley, 2006; Guo et al., 2016) might make them even more vulnerable to the effects of anthropogenic noise (Ríos-Chelén et al., 2012).

Three species of raptors were also considered in the analysis. Eurasian kestrel is a fairly common and adaptable diurnal raptor known for settling and breeding in noisy urban areas, where it has however been observed to experience reduced breeding performance (Sumasgutner et al., 2014). Barn owl and tawny owl are nocturnal raptors that hunt using auditory cues. Consequently, their hunting efficiency might be reduced with increasing noise levels (Knudsen and Konishi, 1979; Siemers and Schaub, 2011; Mason et al., 2016). While there are no studies directly linking anthropogenic noise to the breeding performance of these two species, the probability of occurrence of tawny owl in urban areas has been shown to be determined by the availability of basic breeding habitat and ambient noise intensity (Fröhlich and Ciach, 2018).

Table 1 European population status, main habitat and months included for weather averages based on average first clutch for each species chosen for breeding performance analysis.

English Name	Scientific name	European population status*	Average first clutch laid	Main habitat	Months for weather averages
Stock dove	*Columba oenas*	Favourable	4 Jun	rural	April-July
Barn owl	*Tyto alba*	Depleted	6 May	woodland	April-May
Tawny owl	*Strix aluco*	Favourable	23 Mar	woodland	March-April
Kestrel	*Falco tinnunculus*	Declining	1 May	rural	April-May
Blue tit	*Cyanistes caeruleus*	Favourable	26 Apr	woodland, urban, rural	March-May
Great tit	*Parus major*	Favourable	26 Apr	woodland, urban, rural	March-May
Starling	*Sturnus vulgaris*	Declining	19 Apr	rural	April-May
Blackbird	*Turdus merula*	Favourable	22 Apr	woodland, urban, rural	April-June
Song Thrush	*Turdus philomelos*	Favourable	21 Apr	rural	April-June
House sparrow	*Passer domesticus*	Declining	14 May	rural	April-July
Tree sparrow	*Passer montanus*	Depleted	17 May	rural	April-May

**according to BirdLife International* (Staneva and Burfield, 2017)

2.2 ENVIRONMENTAL VARIABLES

The relationship between territorial noise levels and breeding performance was analysed using five breeding variables: clutch size, brood size, laying date, and failure rates for the whole nest at the egg and nestling stages. Breeding data in the UK were derived from the Nest Record Scheme (British Trust for Ornithology) and in the Netherlands from Dutch Nest Record Scheme (Sovon Dutch Centre for Field Ornithology, in collaboration with Statistics Netherlands). Both are volunteer-based programmes for monitoring reproductive parameters and nest success of breeding birds, that collect data on the location, habitat, laying date, and content of the nests at each visit, together with evidence for success or failure (see Chapter 3 and Crick et al., 2003 for more detailed description).

Nest record data were analysed in terms of clutch size (the maximum number of eggs found in a nest), brood size (the maximum number of young found in a nest), laying date, and daily nest failure rates at the egg and nestling stage. Data on clutch size was rejected when the maximum content was larger than the maximum number of eggs, suggesting clutches might not have be complete at the time of recording. Brood size comprises the maximum number of chicks found in a nest at any time after hatching, and it is therefore likely to overestimate the actual number of fledglings, but it does give a good estimate of number of hatchlings. Laying date was calculated as an average between the earliest and the latest possible laying date, based on information on clutch size and the age or stage of the nest contents on each visit (Crick et al., 2003). For multi-brooded species, the data did not allow to establish whether nests found were a first or a second or third brood. Laying date was therefore only used as a breeding parameter for single brooded species. Finally, daily nest failure rates at the egg and nestling stage were estimated as the ratio of total number of failures to the total number of days during which a nest was observed for the stage considered (exposure days). This was based on Shaffer's (2012) adaptation of the Mayfield method (Mayfield, 1961). For a more detailed description of breeding variables, see Chapter 3.

Decision about inclusion of data points in the analysis differed between breeding parameters, and it depended on systematic errors and on the number and timing of visits in each breeding stage. For instance, nest records on clutch size had to be omitted if there was evidence that laying was still in progress on the last visit, or the number of eggs recorded was not within the range for each specific species. Therefore, not all breeding parameters could be derived from the raw data in equal number for each nest, and, as a result, sample sizes differ between breeding parameters. In the UK, the barn owl is listed under Schedule 1 of the Wildlife & Countryside Act (1981), so details for nest locations on this species were not freely accessible. Therefore, data for this species came exclusively from the Dutch Nest Record Scheme. This meant that for barn owl data was only sufficient to perform analysis on the clutch size, brood size, and laying date.

In order to avoid the confounding effects of long-term changes in breeding performance (Crick et al., 1997; Siriwardena et al., 2000), but also to reduce the effect of major changes in the noise levels modelled for road traffic, the time span of the data analysed was restricted to the 11-year period between 2006 and 2017. The territorial noise parameter was determined from the maps of exposure to environmental noise from major roads, produced by the Department for Environment, Food and Rural Affairs (Defra) in the UK and the Rijkswaterstaat in the Netherlands. Both maps have been developed as part of the EU Noise Directive 2002/49/EC (END) and, since 2014, follow the same CNOSSOS-EU (Common

Noise Assessment Method for Europe) guidelines. For this study, I used noise maps modelled in 2017 based on the equivalent noise level Lden (day-evening-night noise level), an A-weighted, equivalent noise level over a whole day, but with a penalty of +10 dB(A) for night-time noise (22.00-07.00) and +5 dB(A) for evening noise (19.00-23.00). The maps show the noise level in the form of a vector layer, expressed in 5 classes of sound intensity (dB(A)): 75.0+ dB, 70.0-74.9 dB, 65.0-69.9 dB, 60.0-64.9 dB, 55.0-59.9 dB.

Using ArcGIS, nests were mapped within a 1 km square of each country's respective national grid. For each 1 km square containing a nest and overlapping with the noise maps, each area identified by a noise class was weighted by the average dB(A) levels of the corresponding noise class, and the sum of the values was used to assign a score of noise to each square. This value was then associated to any nest located within that square, giving a measure of territorial noise levels (Noise score).

A set of control variables likely to affect the breeding performance of the study species was selected. These included mean minimum temperatures and rainfall during the breeding period (this varied with species, see Table 1), latitude, year, laying date, and habitat. Year (modelled as a mixed effect) and latitude were included to account for temporal and spatial variations in breeding phenology. Spring temperature and rainfall data were used to account for their influence on the success rate and timing of breeding. Laying date can indeed be delayed by temperature (Visser et al., 2009) or rainfall patterns (Öberg et al., 2015). Temperature and rainfall might also play a role on food availability, energetic costs, and physiological state, and they are important determinants of reproductive success (Mares et al., 2017) resulting in reduced juvenile growth rates and increased offspring mortality (eg. Arlettaz et al., 2010; Mainwaring and Hartley, 2016; Mares et al., 2017; Öberg et al., 2015). Temperature and rainfall data were obtained from meteorological data based on the nearest available stations to each of the nest sites (mean±SD distance between nests and meteorological stations 43.50 km ± 10.30 km for the UK, and 27.58 ± 12.35 km for the Netherlands). They were calculated as averages during the breeding months, defined as the months comprising at least 90% of the breeding events included in the analysis. Weather data for the UK were obtained from the British Atmospheric Data Centre, using the 'Met Office – Historic station data' dataset (Met Office, 2018), while data for the

Netherlands were obtained from the Royal Netherlands Meteorological Institute (KNMI) historical monthly time series (KNMI, 2019).

Laying date was introduced as a control variable for seasonal variations in clutch size and brood size (Crick et al., 1993). For several species included in this study, breeding performance varies over the breeding season (Perrins and McCleery, 1989; Feare, 1996; Summers-Smith, 1998b; Korpimäki et al., 2006; Gosler and Clement, 2007; Snow, 2008), so laying date was also included in the analysis of nest failure rates in order to control for time of the occurrence of the breeding event. Habitat (classified as either woodland, urban, or open) was assigned to species for which the nests were distributed approximately equally between habitats (blue tit, great tit, and blackbird). For all the other species, the majority of nests included in the analysis were recorded in a single habitat (Table 1), and habitat type was excluded from the model.

2.3 STATISTICAL ANALYSIS

All analyses were performed using R version 3.6.0 (R Core Team, 2019). Data exploration was applied following the Zuur et al. (2010) protocol. The presence of outliers was investigated using boxplots and Cleveland dot plots, while collinearity was assessed using scatterplots, Pearson correlation coefficients, and variance inflation factors (VIF). In case of collinearity among predictors, terms with an absolute r greater than 0.5 and VIF value exceeding 3.0, were not included in the same model. In order to allow the direct comparison of their corresponding estimated effect sizes, and to facilitate the interpretation of the effects of variables involved in interactions (Hilbe, 2015), all continuous variables were scaled before inclusion in the models as fixed factors.

The breeding performance of each species was analysed separately for each breeding variable. The breeding variables were fitted against the selected predictors by using generalised linear mixed models (GLMM), with year as a random intercept term. First egg date was analysed using GLMMs with a Poisson error distribution and a log link function, using the package *lme4* (Bates et al., 2015). The same function was used for clutch size and brood size models in species where these followed a Poisson distribution. Other species where clutch and brood size followed a strongly skewed distribution that did not fit a Poisson regression, were analysed using quasi-Poisson GLMM models with the package

MASS (Venables and Ripley, 2002). Daily nest failure rates at the incubation and the nestling stage were estimated using a logistic exposure method, Shaffer's variation of the Mayfield method (Mayfield, 1961, 1975; Shaffer, 2004), where complete failure or success were estimated using a binomial distribution (where failure=1 and success=0) with custom logit-link function adjusted for exposure days (Bolker, 2014). During the analysis, all models were kept whole, and non-informative parameters were not dropped. Polynomial or interaction terms were not included in these models because this would have given rise to increased problems of model interpretation. Tables describing the output of each model for each species were generated using the package *sjPlot* (Lüdecke, 2019). In the figures summarising the effect of Noise Score for each breeding variable (Figure 1. to Figure 5.), the estimates and standard errors of each model were standardised to facilitate visual comparison across species. This was done by dividing them by the standard deviation (SD) of Noise Score in each species' dataset and then multiply them by the SD of Noise Score of the dataset including all species.

3. RESULTS

3.1 CLUTCH SIZE

Increasing levels of territorial noise had a significant effect on the clutch size in three out of the eleven species considered (Figure 1, Table 2; see Appendix C Table for full estimate parameters). Clutch size decreased with increasing levels of territorial noise in house sparrow (p=0.001), but it increased in blue tit (p=0.022) and common starling (p=0.021). In all remaining species, there was no significant increase or decrease in the number of eggs in relation to noise. Laying date was a significant predictor of clutch size in all species except stock dove and starling, and, in single brooded species, nests initiated earlier in the season tended to have larger clutch sizes.

3.2 BROOD SIZE

Noise score was a significant predictor for brood size in three of the eleven species (Figure 2; see Appendix C Table) for full estimate parameters). Brood size decreased with increasing noise score for kestrel (p=0.017), but it increased for starling (p<0.001) and tree sparrow (*p*=0.021). In blue tits, an increase in noise score resulted in a marginally non-significant trend (*p*=0.071) of decreasing number of chicks in the nest.

3.3 LAYING DATE

As it was not possible to separate first broods from second or third broods, statistical analysis of the breeding variable laying date was only meaningful for four species of single or mostly single brooded birds: blue tit, great tit, kestrel, and tawny owl. Noise was a significant predictor for only one species, great tit, where egg laying took place earlier in territories with increasing noise score (p=0.032) (Figure 3; see Appendix C Table for full estimate parameters). Kestrel and tawny owl showed marginally non-significant trends for earlier first egg date with increasing noise score (kestrel, p=0.064; tawny owl, p=0.08), while no effect was detected for blue tits.

3.4 FAILURE RATES EGG STAGE

Increasing levels of territorial noise had a significant influence on nest failure rate at the egg stage in five of the eleven species (Figure 4; see Appendix C Table). In blue tit (*p*<0.001), great tit (*p*=0.002), starling (*p*=0.003), and tawny owl (*p*=0.025) the likelihood of a nest failing at the egg stage decreased with increasing noise scores. For tree sparrow, the likelihood of nest failure at the egg stage increased with increasing noise score (*p*<0.001).

3.5 FAILURE RATES NESTLING STAGE

There was a significant effect of noise on nest failure rate at the nestling stage in five of the eleven species (Figure 5; see Appendix C Table). Blue tits (*p*=<0.001), starlings (*p*=0.048), stock doves (*p*=0.002), and kestrels (*p*<0.001) showed a higher likelihood of nest failure at the nestling stage with increasing noise scores in their territories. In contrast, the likelihood of nest failure at the nestling stage for tree sparrows decreased as territorial noise increased (*p*<0.001).

Table 2 Summary of effects of noise score for each species on each of the breeding variables. Signs *+* and - symbolise the direction of the effect caused by increasing noise score. For clutch size and brood size, *+* means an increase in number of eggs and chick found in the nest, and - means a decrease. For laying date, the sign *+* means later laying date and the sign - earlier laying date. For nest failure rates at the egg and nestling stage *+* means increased failure and – decreased failure. *no* means no significant effect was detected.

	clutch size		brood size		laying date		failure rate egg stage		failure rate nestling stage	
Species	effect	sample size	effect	sample size	effect	sample size	Effect	sample size	effect	sample size
Stock dove	no	422	no	950	Not available		No	324	+	193
Barn owl	no	155	no	56	Not available		Not available		Not available	
Tawny Owl	no	174	no	468	no	267	-	123	no	238
Kestrel	no	195	-	802	no	800	No	443	+	392
Blue tit	+	4496	-	8955	no	6716	-	8319	+	5585
Great tit	no	4359	no	4359	-	5112	-	7258	no	4103
Starling	+	117	+	532	Not available		-	216	+	257
Blackbird	no	1498	no	1883	Not available		No	1594	no	1343
Song Thrush	no	426	no	404	Not available		No	383	no	295
House sparrow	-	289	no	517	Not available		No	329	no	371
Tree sparrow	no	1066	+	1328	Not available		+	1204	-	672

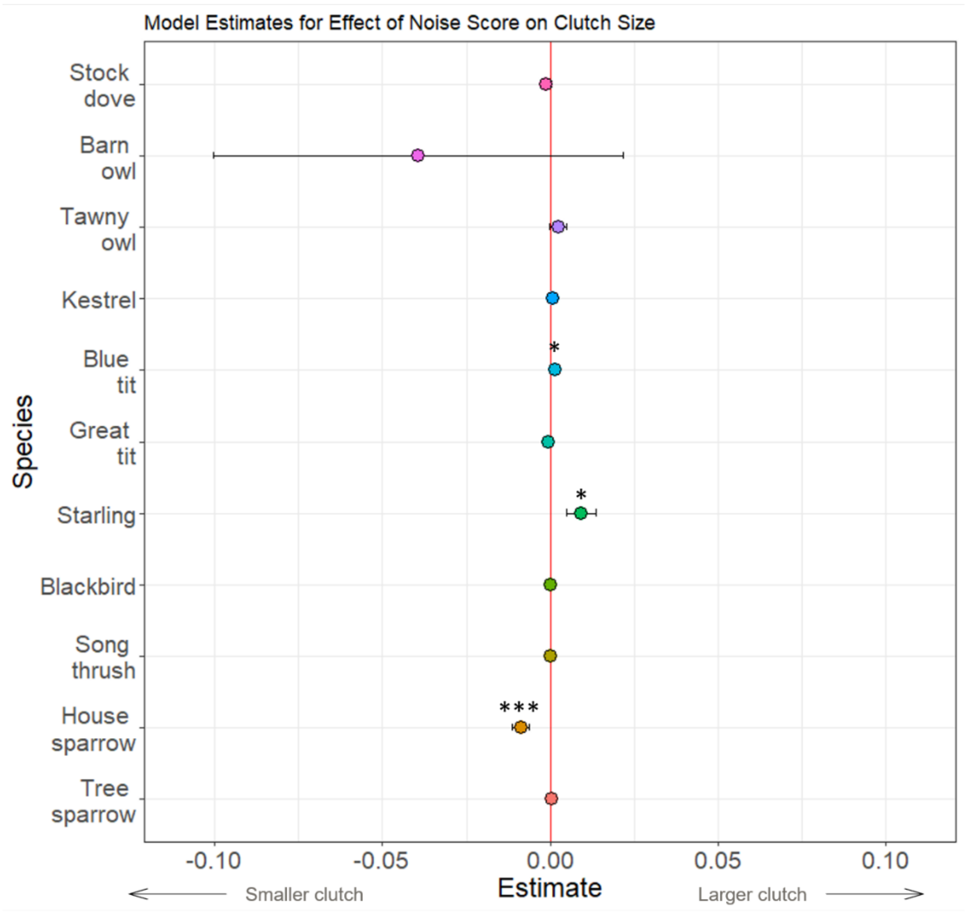


Figure 1 Estimates with standard errors (SE) for Noise Score for models on clutch size, showing direction and significance of the effect. Significance of marginal tests (Wald test) for the Noise Score parameter is indicated as * for p ≤ 0.05, ** for p ≤ 0.01, *** for p ≤ 0.001. Estimates and SE have been standardised to facilitate comparison between species.

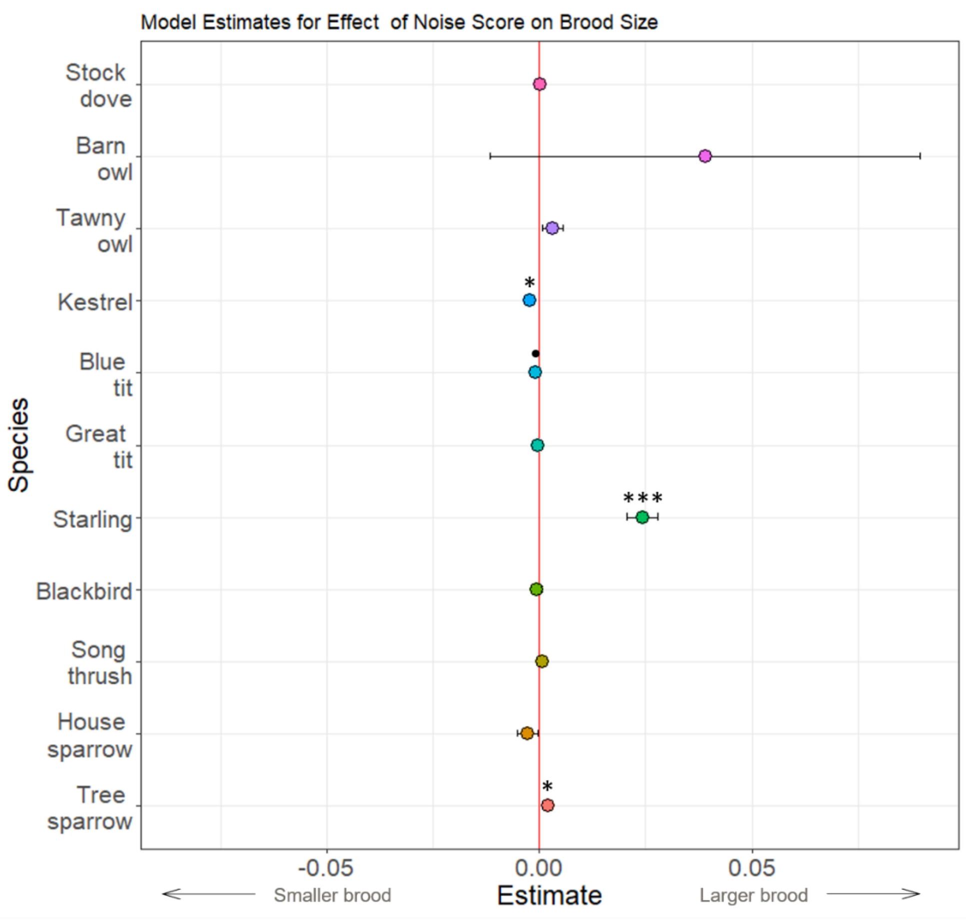


Figure 2 Estimates with standard errors (SE) for Noise Score for models on brood size, showing direction and significance of the effect. Significance of marginal tests (Wald test) for the Noise Score parameter is indicated as * for p ≤ 0.05, ** for p ≤ 0.01, *** for p ≤ 0.001. Estimates and SE have been standardised to facilitate comparison between species.

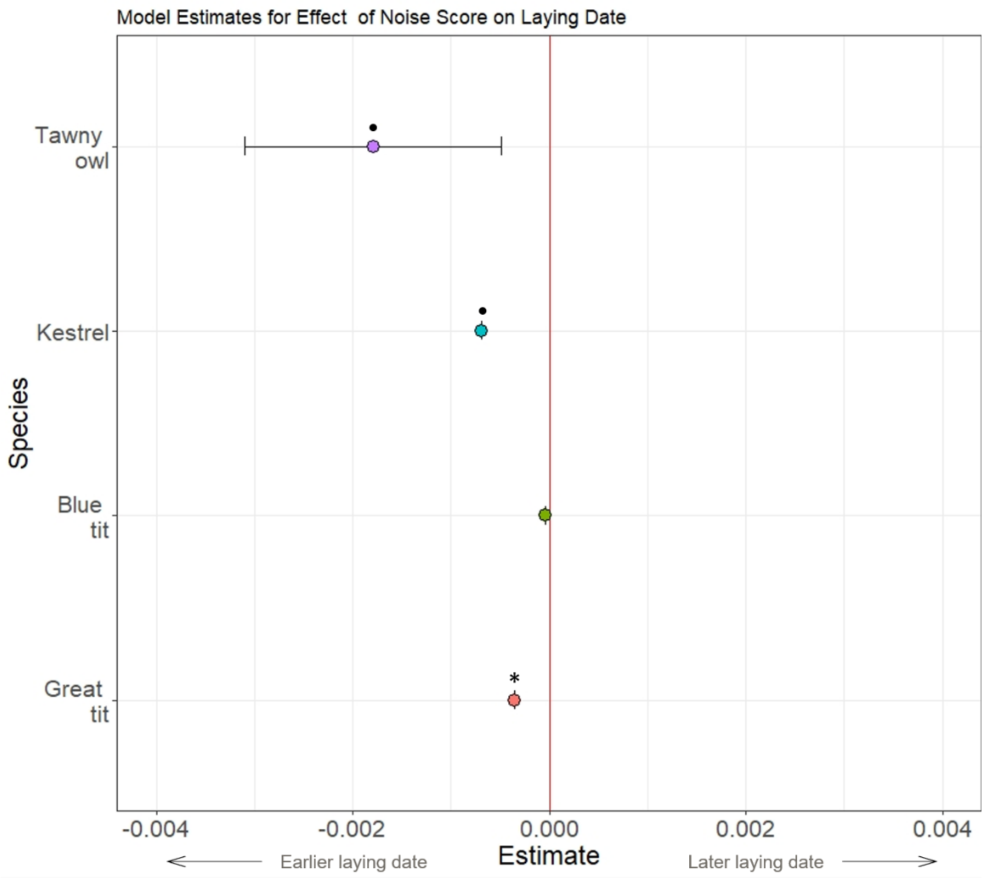


Figure 3 Estimates with standard errors (SE) for Noise Score for models on laying date, showing direction and significance of the effect. Significance of marginal tests (Wald test) for the Noise Score parameter is indicated as * for p ≤ 0.05, ** for p ≤ 0.01, * for p ≤ 0.001. Estimates and SE have been standardised to facilitate comparison between species.**

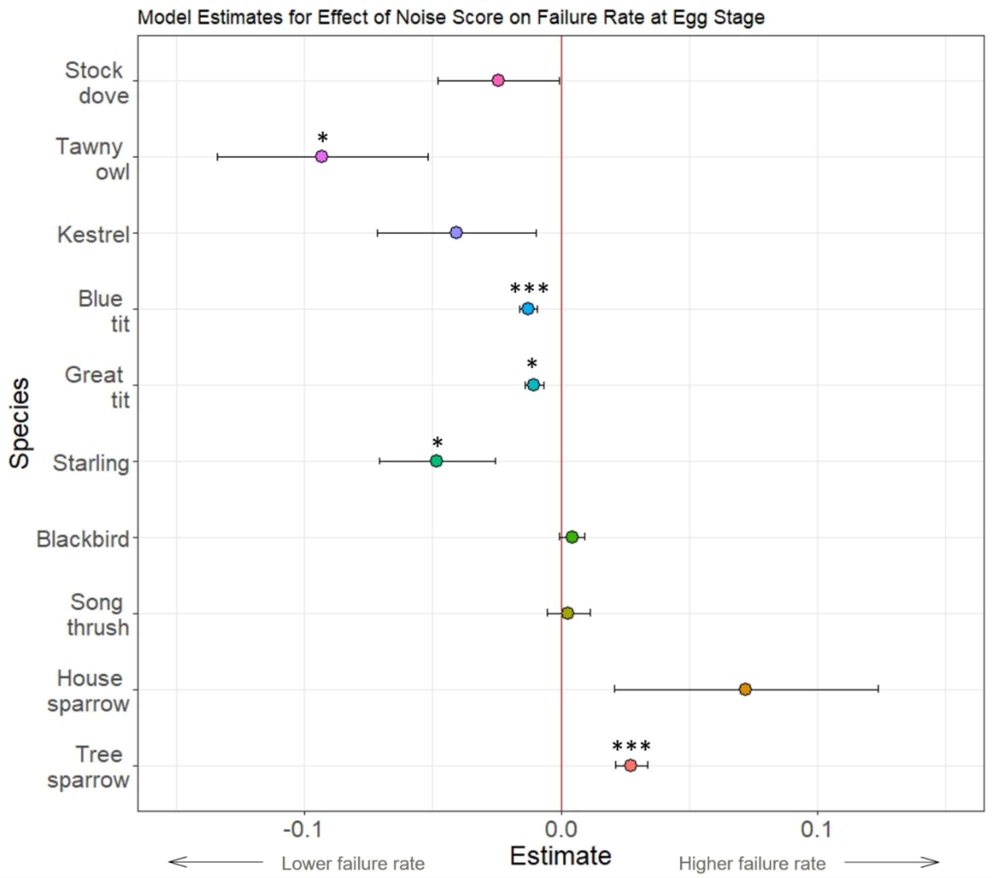


Figure 4 Estimates with standard errors (SE) for Noise Score for models on nest failure rate at the egg stage, showing direction and significance of the effect. Significance of marginal tests (Wald test) for the Noise Score parameter is indicated as * for p ≤ 0.05, ** for p ≤ 0.01, * for p ≤ 0.001. Estimates and SE have been standardised to facilitate comparison between species.**

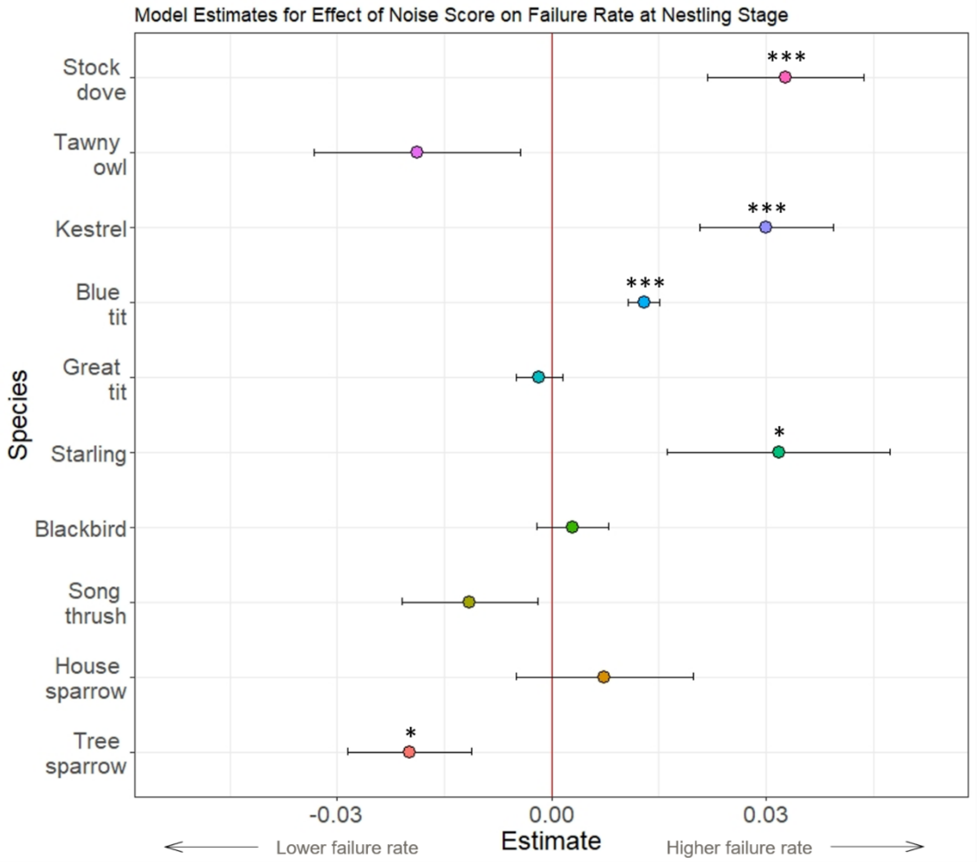


Figure 5 Estimates with standard errors for Noise Score for models on nest failure rate at the nestling stage, showing direction and significance of the effect. Significance of marginal tests (Wald test) for the Noise Score parameter is indicated as * for $p \leq 0.05$, ** for $p \leq 0.01$, * for $p \leq 0.001$. Estimates and SE have been standardised to facilitate comparison between species.**

4. DISCUSSION

4.1 THE EFFECTS OF NOISE DEPEND ON SPECIES AND BREEDING VARIABLES.

Of the eleven species whose reproductive success was analysed for this study, six exhibited negative effects in response to higher levels of territorial noise on at least one stage of their breeding cycle. Negative effects of traffic noise were found across all breeding parameters except laying date, but the most common negative effects were detected at the nestling stage, as four species experienced increased failures at higher levels of traffic noise.

4.2 THE NESTLING STAGE IS THE MOST VULNERABLE TO FAILURE

Nest failure at the nestling stage emerged as particularly vulnerable in relation to territorial noise, as four species with quite different phylogeny, vocal behaviour, and diets (blue tit; starling; stock dove; kestrel) experienced increased failure rates with increasing levels of territorial noise. Indeed, previous studies have found the post-hatching stages of the reproductive performance of birds to be vulnerable to anthropogenic noise. For example, noise has been associated with reductions in productivity in eastern bluebird (*Sialia sialis*) (Kight et al., 2012), impaired chick development in house sparrows (Schroeder et al., 2012), and reduced body condition in chicks of white-crowned sparrow (*Zonotrichia leucophrys oriantha*) (Crino et al., 2013). Noise has also been shown to affect nestling physiology, by altering corticosterone stress levels (Crino et al., 2013; Mulholland et al., 2018; Injaian et al., 2019), reducing immune response (Raap et al., 2017), and decreasing telomere length (Meillère et al., 2015; Salmón et al., 2016, 2017; Dorado-Correa et al., 2018).

The increased rates of failure at the nestling stage observed in the present study could be arising from alterations on different aspects of the biology of the birds. However, reduced parental care and provisioning rate is the most likely process behind the failures observed in blue tit, starling, kestrel, and stock dove. Reduced parental care might be taking place through alteration of behavioural time budgets in the parents because of increased vigilance (Quinn et al., 2006), or through alterations in parent-offspring communication through acoustic masking (McIntyre et al., 2014). Noise has been shown to increase missed detections of parent’s arrival by the chicks (Leonard and Horn, 2012), and to affect the perception of begging calls, therefore decreasing food provisioning rates by the parent

(Schroeder et al., 2012). Masking might also be responsible for impaired communication of alarm calls, leaving nests more vulnerable to predation (Barber et al., 2010). Stock dove and kestrel were not negatively affected in the earlier stages of their breeding cycle, while blue tit and starling showed lower egg failure with increasing noise levels. The negative effects of anthropogenic noise on these species are therefore more likely the result of events taking place post hatching, rather than the result of pre-laying and pre-hatching noise-induced stress in the parents or of demographic patterns. In fact, if that had been the case, the earlier stages of the breeding cycle would likely have been negatively affected as well.

Remarkably, increased failure at the nestling stage was found in species that have all been shown to breed in heavily urbanised or noisy areas (Stone, 2000; Sumasgutner et al., 2014). It is therefore possible that the fact that these species might be less likely to avoid noisy environments might be the reason why they are ultimately affected negatively at the nestling stage, when noise plays a role in affecting communication of vital vocal signals between offspring and parents. Direct evidence of impaired parent-offspring communication in high levels of traffic noise has indeed been found in blue tits, which show an increase in missed detections of parent arrival by the chicks, and a decrease in parental provisioning (Lucass and Eens, 2016).

4.3 OTHER BREEDING STAGES CAN ALSO BE VULNERABLE

Higher levels of noise exposure had deleterious consequences on all other breeding variables except laying date, suggesting that, depending on species, breeding performance can be adversely affected at all stages. Negative effects on other breeding variables, however, were much rarer and only associated with single species. Only house sparrows showed a decrease in clutch size with increasing anthropogenic noise levels. In this species, there is evidence for a decrease in telomere length (Meillère et al., 2015) and a decrease in the metabolic rate of nestlings exposed to noise (Brischoux et al., 2017), suggesting a direct effect of noise exposure, rather than an indirect effect through the quality of parental care. In these experimental studies, however, house sparrows were not able to choose quiet nesting sites, which might have otherwise resolved in noise avoidance or in a non-random distribution of individuals. Noise can change the age structure of populations, resulting in younger and inexperienced birds breeding in noisier territories (McClure et al., 2017). The finding that house sparrow laid smaller clutches in increasing noise levels might therefore mean that noisy territories are occupied by less experienced or less fit individuals, which are more likely to lay fewer eggs (Habib et al., 2007).

Negative effects of noise on brood size were only found in kestrels. Smaller broods have been associated with lower parental investment, but also to anthropogenic noise being a physiological stressor for parents (Saino et al., 2005; Ware et al., 2015), resulting in less energy being invested in the offspring. In kestrels, noise was also associated with increased failures at the nestling stage, suggesting that nutritional stress, possibly deriving from disruptions in communication, could be the most likely mechanism behind the negative effects seen for this species.

Increases in failures at the egg stage were only detected in tree sparrows. Given that the same species showed larger clutch size and decreased nest failure at the nestling stage, this seems like a rather contradictory result. Higher rates of failure at the egg stage caused by noise might be linked to pre-zygotic mechanisms related to parental quality, connected with the hypothesis that lower reproductive success might result from female investments being lower in response to actual or perceived male quality via male song performance (Halfwerk and Slabbekoorn, 2014). It is also possible that noisy territories might occur in concomitance with high levels of chemical pollutants such as heavy metals, which might affect male behaviour and fertility (Gorissen et al., 2005; Jackson et al., 2011). In captive breeding birds, nest failures at the egg stage have been linked to incubation failure (Birkhead et al., 2008), or might be due to poor egg quality, which is related to female condition and investment (Hayward and Wingfield, 2004; Krištofík et al., 2014). The specific results for this species, with clutch size being positively associated with increasing territorial noise scores, suggest that it is unlikely that male quality and consequent female investment played a role in increasing the rates of failure at the egg stage. Studies on free living populations suggest that failure at the egg stage might also be linked to reduced incubation effort and/or increased nest abandonment triggered by noise-induced higher stress levels in the parents (Spée et al., 2011; Thierry et al., 2013), or a trade-off between incubation and increased vigilance in noisy areas (Quinn et al., 2006; Meillere et al., 2015). This could indeed be a possibility for tree sparrows. As each breeding stage could involve different mechanisms through which traffic noise may have an effect, it is also likely for each breeding stage to have different noise thresholds, and to respond to changes in noise amplitude and frequency in a different way.

4.4 NOISE MIGHT HAVE A POSITIVE EFFECT THROUGH REDUCED COMPETITION AND PREDATION RISK

Tree sparrow was not the only species that showed a correlation between breeding in noisier areas and higher success for some of the breeding variables. Positive effects of noise on breeding success were also observed in blue tits, starlings, and tawny owl, although for these species the effects mainly took place at the egg stage. This is not the first study to conclude that breeding birds might benefit from noise: spotted towhees (*Pipilo maculatus*), chipping sparrows (*Spizella passerina*) (Francis et al., 2009), and grey flycatcher (*Empidonax wrightii*) (Francis, Paritsis, et al., 2011) show increases in nest success with increased noise amplitudes, while nestlings of mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) exposed to traffic noise have lower glucocorticoid levels and improved condition (Crino et al., 2013).

A large number of studies suggests that noise from roads may exclude some species from otherwise suitable areas (Reijnen et al., 1995; Forman et al., 2002; Rheindt, 2003; Francis, Ortega, et al., 2011b), while simultaneously playing a positive role for noise-tolerant species through reduced competition for food and nesting sites, and reduced predation risk (Francis, Paritsis, et al., 2011; Halfwerk et al., 2016). It is also possible that road structure, rather than noise, might have a positive effect by providing foraging habitat, song-posts, and perching spots for hunting activities (reviewed in Morelli et al., 2014). Yet, the same species might also suffer detrimental effects of road noise on their reproductive output, through the potential negative effects on parental care mentioned above. As breeding birds may benefit from noise while also experiencing harmful effects, quantifying the impact of noise on populations and communities becomes a particularly complex task. Further work is needed in order to assess how and if noise affects breeding habitat assessment and choice in relation to other environmental cues, and on how the interaction between anthropogenic noise and the abundance of competitors, prey, and predators might affect the breeding performance of birds.

4.5 UNAFFECTED SPECIES OR UNDETECTED EFFECTS?

For some of the species considered (barn owl, blackbird, and song thrush) there was no evidence for an effect of traffic noise on their breeding success. This is somewhat surprisingly for blackbird and song thrush, as these are two highly vocal species for which noise has been associated to change in vocal behaviour (Mendes et al., 2011). However, for barn owl, the sample size was as small as 56 breeding events for brood size, so caution should be applied in interpreting a lack of detectable effect in the models as an actual lack of effect.

While previous experimental studies have found a lack of effect on the reproductive output and chicks of some noise-tolerant species (Meillere et al., 2015; Angelier et al., 2016; Halfwerk et al., 2016; Casasole et al., 2017), it is also possible that some effects might still be taking place on aspects of the breeding performance that this correlative study could not measure. For example, Injaian et al., 2018 found that anthropogenic noise affected parental behaviour, body condition, and oxidative stress in nestlings of tree swallows (*Tachycineta bicolor*), but ultimately found no effect on fledging success. The data used for this study does not allow any consideration on nestling condition, on fledging success, or on post fledging survival, which have been shown to be negatively associated with anthropogenic noise in a number of species (Kight et al., 2012; Schroeder et al., 2012; Crino et al., 2013).

It is also possible that unaffected species might be entirely absent from noisier areas, and that the breeding events recorded largely took place in relatively quiet territories. Vice versa, in species particularly sensitive to noise, territories classified with a low score might have already been above the threshold at which negative effects would take place, and therefore a lack of effect might simply have reflected a negative effect on the entire population breeding around roads. For example, a series of experiments replicating the soundscape of a highway while controlling for other road effects, showed that even a noise level considered moderate (~55 dB(A), 24Leq at 50 meters) was enough to alter the distribution (McClure et al., 2013), age structure (McClure et al., 2017), and body condition of birds (Ware et al., 2015).

4.6 CONCLUSIONS

This is the first large-scale study that, using citizen-data, shows a complex, species-specific relationship between intensity of anthropogenic noise and breeding performance. The underlying mechanisms for the relationships between breeding history and intensity of traffic noise remain to be determined; however, by looking at which stages of the breeding cycle are most affected, it is possible to infer hypotheses on how traffic noise might play a role in affecting reproduction. The prevalence of negative effects on the nestling stage suggests this period might be particularly vulnerable to the negative impacts of anthropogenic noise. Birds depend on acoustic communication for both their reproduction and their survival (Catchpole and Slater, 2008), and the potential of urban noise to acoustically mask parent–offspring communication might be one of the leading causes for some of the negative effects observed.

This chapter highlights the importance of considering the stage of breeding when studying the effects of noise on birds, as species that might appear not to be affected by noise when looking at a specific stage might be experiencing negative effects on another. By transcending individual and population level, this study gives evidence for the fact that the ecological effects of anthropogenic noise exposure extend over a much larger scale than ever shown before, and it highlights an even more pressing need for the implementation of noise mitigation measures around roads.

CHAPTER 5.

NOISE IMPAIRS THE PERCEPTION OF THE FINE STRUCTURE OF BIRDSONG

Abstract

Bird song can have extremely complex acoustic structures, details of which may convey a variety of information, including pertinent information about the signaller's quality. Perception of these details may affect decisions made by receivers in territorial defence and mate choice. The fine structure of songs makes birds susceptible to masking by background noise, and whether the message that they convey is perceived or not may have major consequences for their reproductive success. This chapter uses a series of playback experiments to test whether song consistency, a performance trait conveyed in the fine structure of song and important in sexual selection, is perceived under different noise conditions. I found that blue tits (Cyanistes caeruleus) are affected in the assessment, but not in the detection of conspecific song stimuli under noisy conditions, depending on noise level and frequency range. In particular, high-level white noise and high-frequency noise that overlapped with the spectrum of the songs were responsible for degrading song assessment, which instead took place when no background noise was added to the playbacks, and in low-level and low-frequency background noise. This study shows that one of the processes through which noise affects birds might be the masking of the fine structure of songs. The consequent loss of information conveyed in the fine structure can lead to decreased fitness, highlighting the importance of further understanding the effects of noise on communication from a receiver's perspective.

1. INTRODUCTION

Anthropogenic noise is an invisible source of habitat degradation that has become increasingly pervasive and detrimental for wildlife (Francis and Barber, 2013), and that is mainly produced by transportation systems, industrial plants, resource extraction, and urban development (Ellis, 2011). In particular, transportation networks (such as airports, roads and railways) are widespread sources of noise across many habitats, and traffic noise has become a significant selection pressure on acoustic communication in birds occupying noisy territories (Slabbekoorn and Ripmeester, 2008). While animals have evolved to communicate in the presence of natural noise, this novel source of acoustic pollution differs from natural noise in temporal, spectral and amplitude patterns (Barber et al., 2010), and may therefore make adaptive responses problematic or impossible.

Acoustic communication plays a vital role in mediating many aspects of the life of animals related to survival and reproductive success (reviewed in Bradbury and Vehrencamp, 1998). In particular, birds rely on complex, species-specific songs for vital behaviours such as territorial defence and mate attraction (Catchpole and Slater, 2008). Birds also use vocalisations for parent-offspring communication (Kilner and Johnstone, 1997), communication with flock members (Ritchison, 1983), and for warning other individual of predators (Marler, 2004b). Reliance on acoustic communication for these crucial behaviours renders birds vulnerable to any disruption of efficient transmission and clear perception of acoustic information. One of the main mechanisms through which ambient noise affects communication is through acoustic masking. This phenomenon occurs when the perception of a signal is altered by the presence of background noise, and can be defined as the impairment of detection and discrimination of sounds by other sounds (Kleist et al., 2016).

Because of the fundamental functions of vocal signals in birds, any interference in the transmission of vocalisations can have fitness costs. These include increased risk of predation when the detection of alarm calls is impaired (Francis et al., 2009; Lowry et al., 2012), and decreased breeding success when parent–offspring or parent–parent communication is disturbed (Leonard and Horn, 2008; Halfwerk et al., 2012). Ambient noise may for example mask the sender's signal when females are choosing a mate, leading to suboptimal mate choice and lower reproductive success (Halfwerk, Holleman, et al., 2011). Birds also use songs to signal their fighting ability and motivation to attack in the context of territorial and mate defence (Lambrechts and Dhondt, 1986). Subtle acoustic variation may mediate aggressive interactions and prevent physical conflicts, risk of injuries, and waste of energy (Smith and Price, 1973; McGregor, 2000). Any deterioration in the recognition of such signals might mean that males are no longer able to efficiently deter competitors and avoid costly physical conflicts, with fitness consequences for both the owner of the territory and the intruder.

Much of the literature on communication in anthropogenic noise has focussed on the behavioural adjustments and adaptations of the sender, and on the importance of conveying vocal information less likely to be masked by anthropogenic noise. Several studies have shown that anthropogenic noise influences the distribution of species based on the frequency of their songs, where especially bird species that sing songs with lower frequencies, that are more likely to overlap with anthropogenic noise, avoid noisy habitats (Goodwin and Shriver, 2010; Francis, Ortega, et al., 2011b; Proppe et al., 2013; Francis, 2015). Moreover, it is now well established that urban-dwelling birds are able to adjust the structure and performance of their singing behaviour, by which they compensate for high levels of anthropogenic noise (reviewed in Brumm and Zollinger, 2013). For example, a number of bird species are able to shift song frequencies, duration, amplitude, and timing of singing (eg. Nemeth and Brumm, 2010; Rheindt, 2003; Slabbekoorn and Peet, 2003).

In order to understand the effects of fluctuating ambient noise on acoustic communication, it is equally important to study the receiver's ability to detect, discriminate and recognise different vocalisations under different noise conditions. Laboratory based studies have shown that, under urban noise conditions, detection thresholds increase by up to 18 dB and vary with the spectral shape between signal and experimental noise bands, (Lohr et al., 2003; Pohl et al., 2009). Thresholds for discrimination with low-frequency noise maskers were shown to be better when high-frequency elements were present in the signal (Pohl et al., 2012). Acoustic energy in or near the frequency range of the signal plays a greater role in raising the masked threshold of a signal than in spectral ranges far from the signal (see Dooling, Fay and Popper, 2000 for review). It is however important to mention that these laboratory studies did not seek to replicate realistically natural conditions of birds exposed to real traffic noise, but rather focused on understanding the main principles behind it. Under field conditions, the ability of receivers to perceive vocal signals is highly variable, and depends on the spectral and temporal variations of traffic noise, but also on the type of habitat and vegetation, on the weather conditions, and on the behavioural changes that both signallers and receiver might implement in order to improve communication (reviewed in Dooling and Blumenrath, 2014). For example, traffic noise is not continuous (Klump, 1996), and some birds might take advantage of quieter windows to communicate (Brumm, 2006b; Arroyo-Solís et al., 2013; Dominoni et al., 2016), or comodulate their vocal signals to noise amplitude fluctuations.

The effect of ambient noise on receivers has only began to be studied in the field in the last decade (eg. Phillips and Derryberry, 2018). Evidence that ambient noise levels affects the entire process of communication, and not just the behaviour of the sender, has come from field-based experiments in European robins (*Erithacus rubecula*), which have shown that the songs in response to playbacks of conspecific songs decreased in complexity and increased in pitch in simulated traffic noise conditions (McMullen et al., 2014). Other field playbacks have shown that territorial defence behaviours in response to conspecifics' songs are altered by noise from wind turbines (Zwart et al., 2016) and compressor sites (Kleist et al., 2016).

While these studies support the hypothesis that receivers must modify their behaviour to adjust to noise, they only explore one aspect of masking, which is the detection of vocal signals. However, hearing is a more complex process than the simple detection of a sound. Birds do not only need to detect acoustic signals, but they also have to discern between signal senders (discrimination), and assess the quality of the signal (recognition) (Dooling and Blumenrath, 2014). Such processes come with different thresholds, which might mean that, even when songs are detected, the information they convey (such as the quality of the singer, its fighting ability, and its motivation) might be lost, as this information is often carried in subtle spectral and temporal characteristics of the song (Podos, 1997; Botero et al., 2009; de Kort, E. R.B. Eldermire, et al., 2009).

Birds' vocalisations may include a variety of simple and complex signals, which comprise of short notes and calls, but also long and elaborated songs (reviewed in Catchpole and Slater, 2008). Birds have the ability to perceive the complexity and fine details of these vocalisations, especially their own species-specific vocalisation (Lohr et al., 2003), and are sensitive to fine-grained, multidimensional acoustic differences (Brown et al., 1988). Research shows that birds use vocal production as an honest signal of quality, in order to achieve a quick assessment of other individuals (Gil and Gahr, 2002). Indeed, vocal production requires fine and accurate coordination of the respiratory airflow, and modulation of their syrinx and other vocal trait structures (Riede and Goller, 2010). Vocal displays are therefore subject to physical constraints, such as biomechanical limits occurring during their production or during song learning and development, so that their execution might be linked to information about the condition, quality, and motivation of the signaller (reviewed in Podos et al., 2009). Different traits of birdsong might be subject to vocal constraints and function as indicators of vocal performance. For example, the production of larger and more complex song repertoires (Nowicki et al., 1998; S. et al., 2002), the rate of vocal production (Geberzahn et al., 2010), and the ability to produce physically challenging signals, such as low-pitch songs (Geberzahn et al., 2009; Hall et al., 2013), high amplitude songs (Brumm and Todt, 2004), or the consistency in performing recurring vocal elements (Botero et al., 2009; de Kort, E. R.B. Eldermire, et al., 2009) have all been identified as indicators of condition in birds (Nowicki et al., 1992, 1998; Gil and Gahr, 2002).

One song trait that can function as an indicator of birds' vocal performance is the ability to produce virtually identical repetitions of songs or song components, known as song consistency (Botero and de Kort, 2011). Song consistency has been shown to provide reliable information about the quality of a signaller, and can be correlated with males' phenotypic quality and competitive abilities, such as body size, condition, or age (Gil and Gahr, 2002). This song performance trait has been linked to age (Lambrechts and Dhondt, 1986; Botero et al., 2009; de Kort, E. R.B. Eldermire, et al., 2009; Rivera-Gutierrez et al., 2010), social status (Christie et al., 2004; Botero et al., 2009), and better early-life conditions in a number of species (Lambrechts, 1997; Nowicki et al., 1998; Holveck et al., 2008). In white-crowned sparrows (*Zonotrichia leucophrys*), song consistency has also been shown to vary in response to infection from parasites, suggesting that, in some species, it might reflect variations in the physical and health conditions of the singer (Gilman et al., 2007). Evidence also suggests that consistency plays a role in sexual selection (Byers, 2007; Cramer et al., 2011) and that birds that sing with high consistency fare better in relation to reproductive success (Byers, 2007). It is likely that this song trait might be perceived and used by the receivers in sexual selection as an indicator of the quality of a conspecific. For example, male receivers of banded wrens (*Thryophilus pleurostictus*) and great tit (*Parus major*) respond differentially to playback stimuli that vary only in song consistency (de Kort, E. R.B. Eldermire, et al., 2009; Rivera-Gutierrez et al., 2011), and females of banded wrens prefer extra-pair mates with more consistent songs (Cramer et al., 2011).

For this study, I focused on trill consistency, a song trait that has received particular attention in recent years (eg. Moseley et al., 2013; Phillips and Derryberry, 2018, 2017; reviewed in Podos et al., 2009; Botero and de Kort, 2011;). The trill of a song is a section consisting of rapidly repeated, almost identical short notes (Podos and Nowicki, 2004). Because the production of identical repetitive notes requires a precise coordination of vocal tract movement and airflow (Riede et al., 2006), trill performance is the result of a trade-off between how quickly a bird can repeat the trill notes and the frequency bandwidth of each note (Podos, 1997). Given that the assessment of the quality (a process hereby defined as recognition) of a trilled vocal signal would depend on the assessment of fine changes in the temporal and spectral structure or the trill, it is possible that this process might be particularly vulnerable to masking by noise.

In the current study, I conducted two field experiments to test whether territorial blue tits (*Cyanistes caeruleus*) recognise differences in song consistency at different levels (Experiment 1) and different frequency bands (Experiment 2) of background noise. In experiment 1, the aim was to determine if blue tits recognise variations in trill consistency under natural, ambient noise conditions (referred to as no-noise) and two experimentally elevated levels of anthropogenic noise (referred to as low- and high-level noise). In experiment 2, the aim was to test if blue tits recognise variation in trill consistency with two different types of noise with the same bandwidth but energy at non-overlapping and overlapping frequencies (referred to as low- and high-frequency noise respectively).

2. METHODS

2.1 STUDY SITE AND POPULATION

The study was conducted over two breeding seasons in 2017 and 2018. Experiment 1 was conducted over both breeding seasons, while experiment 2 was conducted entirely over the 2018 breeding season. The subjects belonged to a nest-box breeding population within the grounds of Lancaster University, United Kingdom (54°0' N, 02°7' W). The site contains several woodland patches, in which 115 wooden nest boxes have been installed as part of ongoing research into the breeding biology of blue tits (Leech et al., 2001; M. C. Mainwaring and Hartley, 2008). The majority of blue tits in this population are colour ringed for individual identification. This allowed to avoid accidentally sampling the same individual twice for the same noise treatment. However, some individuals were sampled twice across different noise treatments.

Blue tits are small passerines that readily nest in boxes when these are provided. Females select the site and build the nest, which usually consist of a base layer of moss and plant matter, and a nest cup lining materials such as grass, hair, and feathers (Britt et al., 2017). Male blue tits are facultatively polygynous (Kempenaers et al., 1997), and they reach their peak in singing activity shortly before and during the first few days of egg laying, which coincides with the fertile period of females (Poesel et al., 2001).

Nest-boxes were visited at least once every 4 days from the beginning of April in order to establish when the first eggs were laid, assuming a laying rate of one egg per day (Cramp and Perrins, 1993; Mainwaring and Hartley, 2016). All experiments were conducted on territorial males whose nests were complete, or in which egg laying had started. This breeding phase corresponds to a period of high responsiveness towards conspecific song, as blue tits are more motivated to defend their territory and mates from potential intruders, in order to avoid extra pair copulations (Amrhein et al., 2008), which in this population occur at a rate of 11.7% of chicks, or 39.8% of broods (Leech et al., 2001). Experiments were only performed on individuals whose nest-boxes were located in relatively quiet areas, where the average noise levels measured were less than 55 dB(A). Ambient noise amplitude levels had been previously measured by Andrew Wolfenden (Wolfenden, 2016 *unpublished*) after the dawn chorus and between the hours of 7 and 8 am. Measurements were taken from the top of the nest-boxes at each site using a Tenma

72-947 data logging sound level meter (A-weighting, fast response, and 30–100 dB settings; accuracy ±1.4 dB).

2.2 STIMULI DESIGN

In order to test whether blue tits recognise variation in song performance under different noise conditions, two sets of song stimuli varying in consistency were created: a control and a consistent set of songs. The stimuli were generated by using songs with a clear, high-pitched trill or tremolo, consisting of a quick repetition of short notes at a very rapid rate (Doutrelant et al., 2000; 1). The ability to repeat such trill notes with the minimum amount of variation is defined as trill consistency (de Kort, E. R.B. Eldermire, et al., 2009).

In order to avoid pseudo-replication (Kroodsma et al., 2001), a total of 10 songs were selected from recordings of different males. These recordings were made in 2012 at the same site using a Marantz PMD661 professional solid-state recorder and a Sennheiser ME67 directional microphone (WAVE format, 44.1 kHz sampling rate, 16-bit amplitude encoding). Upon visual assessment of the spectrograms, songs were selected only from recordings with high signal to noise ratio, by using the software package Avisoft-SASLab Pro (5.2.09; R. Specht, Berlin). A high pass filter (lower cut-off frequency at 1.0 kHz) was applied to the trilled songs in order to eliminate low frequency background noise from the recordings.

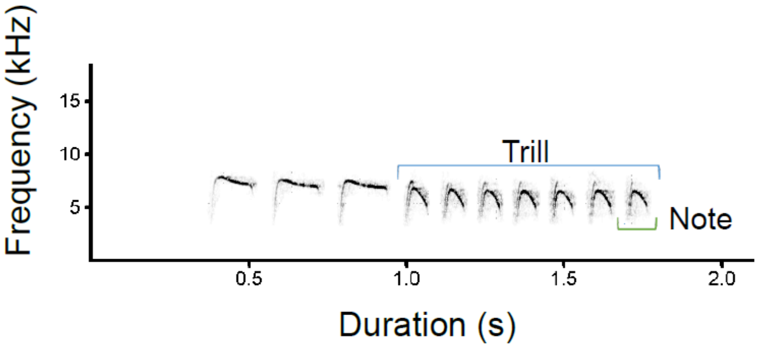


Figure 1 Spectrogram of song stimuli used in consistency experiments. Spectrogram was created in Avisoft (Avisoft Bioacoustics, Berlin, Germany) using the following parameters: fast Fourier transform 512, frequency resolution 8 Hz, Hamming window, overlap 8.

A pair of song stimuli (treatment and control) was created by manipulating the same song, using Avisoft-SASLab Pro, in order to control for effects on responsiveness by any other song variable (such as syllable type, song structure, broad frequency, and syntax). In this way, I also controlled for other variables that may influence territorial response strength, such as sound intensity, song rate, and song length (Kroodsma et al., 2001). In order to simulate the natural maximum sound intensity of vocalising blue tits, the output sound pressure level was adjusted for the stimuli to be broadcast at 64 dB(A) at 10 metres (Poesel et al., 2004), measured with a sound pressure level meter. All selected songs had three introductory notes followed by eight trill notes, and subsequent songs were separated by an interval of 1.8 to 2.0 seconds, which is within the range of natural songs recorded in 2012.

For the control song stimulus, trill consistency of the song was measured as the average spectral cross-correlation (SPCC) of individual trill notes (1) with the software Avisoft-CORRELATOR. Only songs with a mean SPCC ≤ 0.8 (i.e., low consistency) were used as controls. The consistent song stimulus was generated using Avisoft-SASLab Pro (5.2.09; R. Specht, Berlin) by replacing all trill notes in the control song with its 3rd trill note at the same rate and the same number of times. This resulted in a consistent song stimulus with an SPCC of 1. To control for potential effects caused by this operation, the control stimulus was also manipulated by copying the trill notes of the original song and placing them back in the same order and rate. Similar stimulus design has been used before in playback experiments (Ríos-Chelén and Garcia, 2007; de Kort, E. R.B. Eldermire, et al., 2009; Rivera-Gutierrez et al., 2011; Cramer, 2013; Reichert and Ronacher, 2015).

2.3 PLAYBACK PROCEDURE

The same playback procedure was applied for both experiment 1 and experiment 2. The song playback trials simulated territorial intrusions and were carried out at least 60 minutes after sunrise (between 0600 and 1200 hours DST) and at dusk (between 1800 and 2100 hours DST), after locating focal individuals in proximity to their nest-boxes. For each trial, the subject was exposed to both stimuli, the consistent songs and the control songs, using a FoxPro Fusion portable field speaker (FOXPRO Inc., Lewistown, Pennsylvania 17044, USA). This paired design controlled for individual differences in behaviour and other variables that may affect response strength, such as time of the day and atmospheric conditions. Subsequent trials were never conducted on a neighbouring territory. Trials were ended whenever a subject was out of sight for longer than 30 seconds, and the same subject was not re-tested within 24 hours.

The trials started with a pre-playback observation period of one minute. In the playbacks with background noise, this time was also used as a habituation phase during which the noise gradually increased, reaching its maximum amplitude by the time the first song stimulus started. This pre-playback period was then followed by two consecutive sets of playbacks and post-playback observation periods (Figure 2). The first playback period consisted of one minute of either control or consistent songs, followed by a 2 and a half minutes post-playback observation period. After this time, the second playback period started, with either a set of control or consistent songs, depending on what type of song had been presented in the first playback period. In fact, to allow for testing of order effects, the order in which they were presented was alternated between subsequent trials. Through preliminary tests, it was established that the 2.5 minutes allocated for the observation period would also provide sufficient time for the behaviours elicited by the first playback to avoid carryover effects. This is within the range used in other similar playback studies in blue tits, e.g. 1 min (Bolton, 2007), 5 to 15 minutes (Poesel et al., 2006), 10 min (Ríos-Chelén and Garcia, 2007).

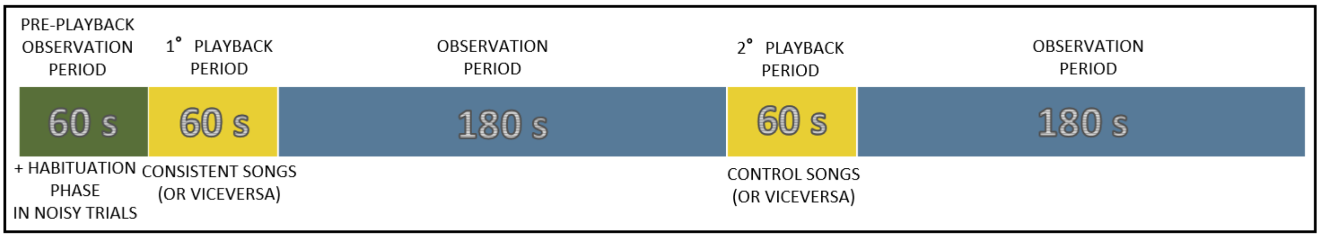


Figure 2 Experimental design of a song playback trial in paired design that included a pre-playback observation period, two stimulus presentation periods, followed by response observation periods.

2.4 EXPERIMENT 1 – NOISE LEVEL EXPERIMENT

Experiment 1 was carried out over the two breeding seasons 2017 and 2018. It consisted of a total of three sets of playbacks in different noise conditions: ambient noise (defined as no-noise), low-level noise, and high-level noise, to test for recognition of consistent and control song stimuli for three signal-to-noise ratios (**Error! Reference source not found.**3 A). As explained in the playback procedure, for each noise condition, the response of individual birds was tested for both control and consistent stimuli. However, no same individual was tested across the different noise conditions. For example, individuals tested under ambient noise condition were not tested under low-level or high-level noise.

Ambient noise. The first set of playbacks presented the song stimuli (control and consistent) at normal ambient noise conditions, with no additional noise.

The other two sets of playbacks presented the song stimuli in combination with a full spectrum (0 – 22 000 Hz) masking white noise (WAVE format, 44.1 kHz sampling rate, 16 bit amplitude encoding), which was synthesised digitally using the software Audacity (Audacity Team, 2018). The stimuli playbacks were merged into a single track with the white noise. The choice of full spectrum white noise rather than a band-pass filtered noise, aimed at focusing exclusively on the effects of noise at different noise amplitudes excluding other potential factors.

High-level noise. For the high-level noise, the root mean square of the masking noise was 15 decibels lower than the maximum of the stimulus. This noise level was based on studies on speech recognition in humans, which have found that word recognition is best achieved at a signal to noise ratio (SNR) between 10 dB to 15 dB range (Rogers et al., 2003; Freyaldenhoven et al., 2006). The upper limit of SNR for speech recognition in humans was chosen because assessment of trill performance requires the ability to recognise fine spectral structural differences which go beyond speech recognition in humans (Dooling, 2004).

Low-level noise. For the low level noise playbacks, the root mean square of the noise was 25 decibels lower than that of the stimulus, a value that in humans allows for comfortable speech recognition (Cooper and Cutts, 1971).

2.5 EXPERIMENT 2 – NOISE FREQUENCY BAND EXPERIMENT

Experiment 2 consisted of two sets of playbacks in different noise conditions: high-frequency noise and low-frequency noise, to test for recognition of consistent and control song stimuli with non-overlapping and overlapping noise spectra (Figure 3 B). For both sets, the background noise was set to 15 dB below the maximum sound level in the stimulus, which is the same level as for the high-level noise playbacks in Experiment 1. As for experiment 1, for each noise condition the response of individual birds was tested for both control and consistent stimuli. No same individual was tested across the different noise conditions.

High-frequency noise. For the high frequency noise playbacks, the background noise was created in order to overlap the spectral range of the signal. The minimum and maximum frequency for the trill notes of the songs were measured to generate a noise spectrum that overlapped the trill frequency distribution of the songs used as stimuli. The minimum frequency across all song trills was 3530 Hz, and the maximum frequency was 7750 Hz. A masking noise with a bandwidth of 3500 Hz was generated by band passing the white noise from experiment 1 between 3670 and 7170 Hz (roll-off of 6 dB per octave), using a TDT PF1 module in Audacity software (Audacity Team, 2018). This particular frequency distribution was selected in order to allow for spectral overlapping of the trill while also keeping the same bandwidth for high and low frequency noise.

Low-frequency noise. For the low frequency noise playbacks, the background noise was created in order to avoid overlap in the spectral range of the signal. The bandwidth for this masking noise was also 3500 Hz, but shifted towards lower frequencies. The white noise was band-passed between 0 and 3500 Hz (roll-off of 6 dB per octave), using a TDT PF1 module. Because traffic noise is weighted towards lower frequencies (<1400 Hz) (Wood and Yezerinac, 2006), this bandwidth resembles the frequencies encountered in noisy traffic conditions. In mammals, noise energy concentrated in lower frequencies can still have masking effects on higher-frequency channels due to the upward spread of masking (Moore, 1997), while the reverse is less likely to be true (Lohr et al., 2003). By using low-frequency noise, this experiment may help understanding the effect of traffic noise on avian acoustic communication.

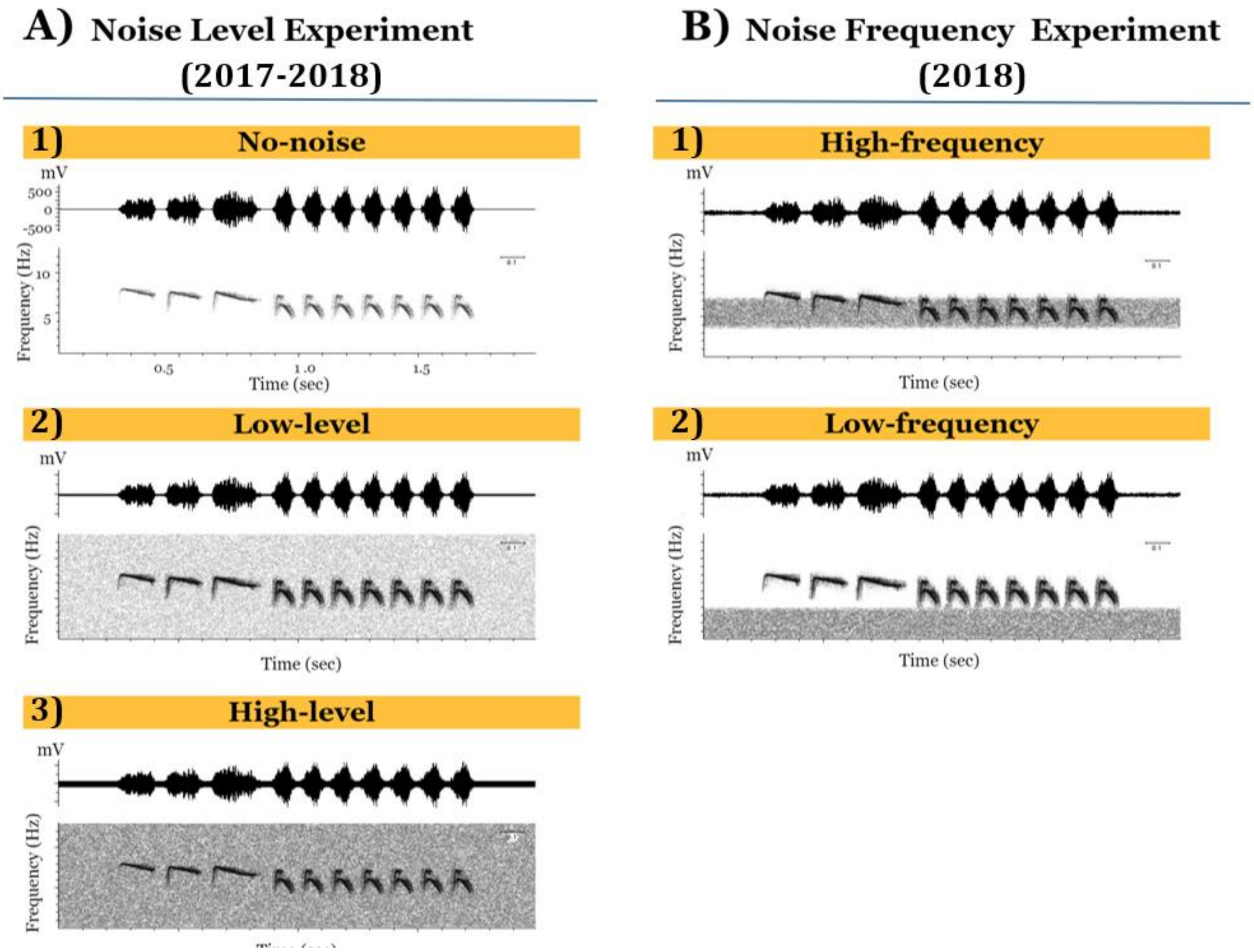


Figure 3 Spectrogram and waveform of song stimuli and background noise used in A) Noise level experiment and B) Noise frequency experiment. Spectrograms were created in Avisoft using the following parameters: fast Fourier transform 512, frequency resolution 8 Hz, Hamming window, overlap 8.

2.6 RESPONSE MEASURES TO PLAYBACK

During each trial, vocal behaviour and spoken observations of other behaviours of the focal male were recorded (WAVE format, 44.1 kHz sampling rate, 16-bit amplitude encoding) using a Marantz (Longford, Middlesex, UK) PMD661 professional solid-state recorder connected to a Sennheiser ME67 (Wedemark, Lower Saxony, Germany) directional microphone. The following response parameters were measured: the number of songs, the time spent within a 5-meter radius from the speaker, the number of flights directed towards the speaker, and the response latency, measured as the time between the start of a stimulus and the first occurrence of a vocalisation or flight.

2.7 STATISTICAL ANALYSIS

The behavioural response data were checked for having a normal distribution using a Shapiro-Wilk test. Because the data were not normally distributed, non-parametric tests were used for statistical analysis. To test whether the stimuli elicited a response regardless of noise condition in the playback, Wilcoxon signed-rank tests with continuity correction were used to compare the 60 seconds pre-playback period with the first 60 seconds of the first playback periods. Wilcoxon signed rank tests with continuity correction were used in order to examine differences in response to each of the playback treatments (consistent and control). The sequential Bonferroni correction (Rice, 1989) was used to correct for multiple testing across different behavioural response parameters. All test results reported reflect two-tailed tests and were performed using R (R Development Core Team, 2015).

3. RESULTS

3.1 EXPERIMENT 1– NOISE LEVEL EXPERIMENT

In total, 65 individuals were tested for both consistent and control stimuli presented in alternating order. Of these individuals, 22 were tested in no-noise conditions, 22 in low-level noise conditions, and 21 in high-level noise. No effect of order of exposure to stimuli was found on any of the response variables (number of songs: $W = 436.5, n_1 = n_2 = 65, p = 0.94$; number of flights: $W = 417, n_1 = n_2 = 65, p = 0.71$; time spent within 5 m: $W = 334, n_1 = n_2 = 65, p = 0.34$; response latency: $W = 495, n_1 = n_2 = 65, p = 0.41$).

To establish whether the stimuli were detected in all background noise conditions, blue tit behaviour was compared between the pre-playback and the first minute of the first trial. Comparing the pre-playback to the first minute of the first trial period showed that, in all three levels of background noise, the stimuli elicited an increase in the three response measures (See

Appendix D Table ; Figure 4). For no-noise conditions, the stimuli elicited an increase in the number of territorial songs ($W = 169, n_1 = n_2 = 22, p < 0.001$), the number of flights ($W = 190, n_1 = n_2 = 22, p < 0.001$), and the time spent within a 5 m radius from the speaker ($W = 43, n_1 = n_2 = 22, p < 0.05$). Likewise, in the low-level noise condition the stimuli elicited an increase in the number of songs ($W = 154, n_1 = n_2 = 22\ p < 0.001$); number of flights ($W =$

$190, n_1 = n_2 = 22, p < 0.001$); and time spent within a 5-meter radius ($W = 21, n_1 = n_2 = 22\ p < 0.05$). For the high-level noise condition, the stimuli elicited an increase in the number of songs ($W = 170, n_1 = n_2 = 21, p < 0.001$); number of flights ($W = 230, n_1 = n_2 = 21, p < 0.001$); and time spent within a 5-meter radius ($W = 54, n_1 = n_2 = 21, p < 0.05$).

When tested for recognition between songs with different levels of consistency, blue tits produced more songs in response to consistent than control stimuli under the no-noise condition ($W = 181.5, N = 22, p < 0.05$) and the low-level noise condition ($W = 244, N = 22, p < 0.05$), but not for the high-level noise conditions ($W = 118, N = 21, p = 0.94$). No differences were observed in the other response parameters under any of the treatments (Figure 5; see Appendix D Table 2 for details of test statistics).

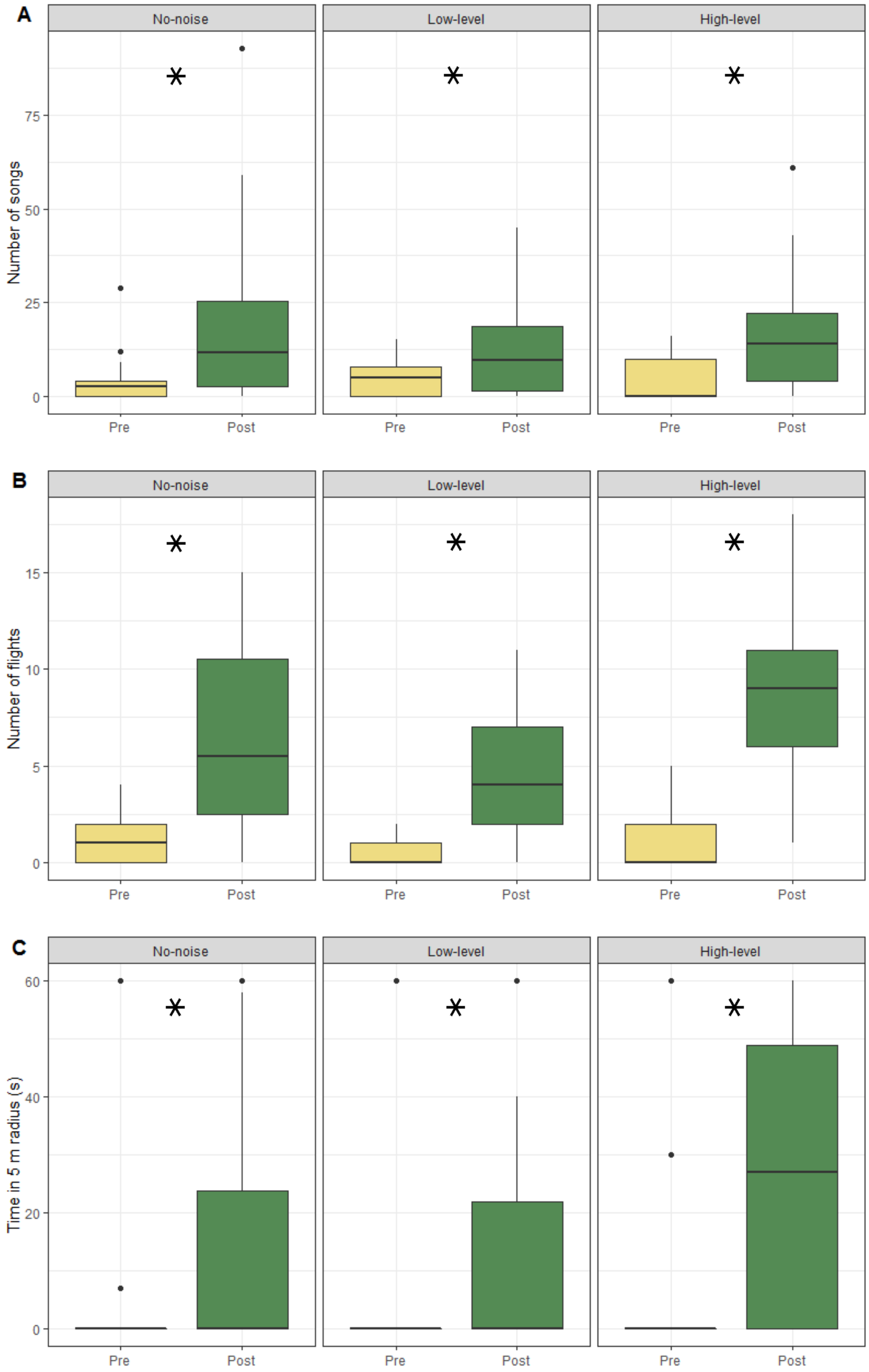
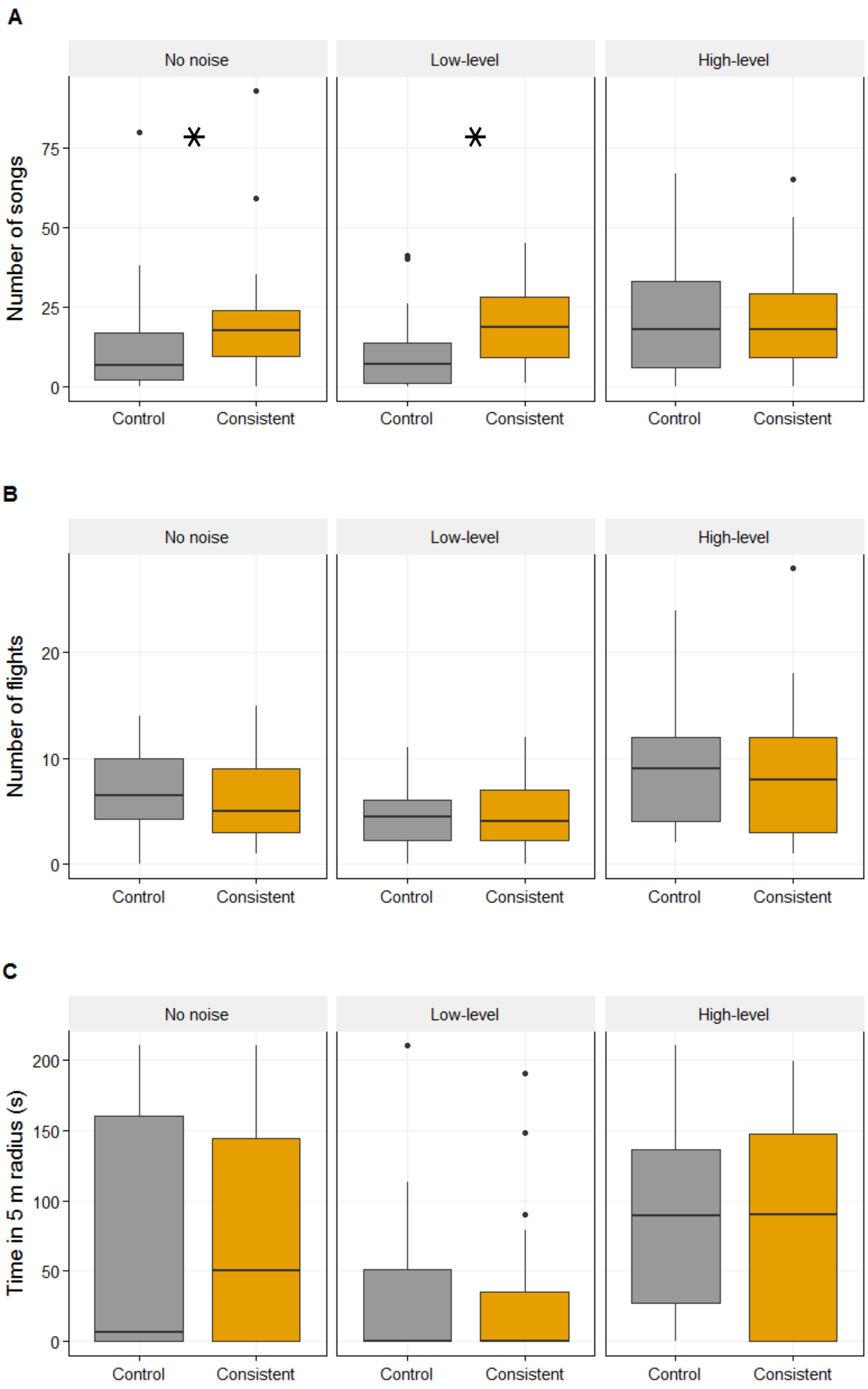


Figure 4 Comparison of (A) number of songs, (B) number of flights and (C) time within 5 m of playback speaker following playback of conspecific songs to blue tits (*Cyanistes caeruleus*) under different noise conditions, namely no-noise, low-level and high-level noise. In all three levels of background noise, there are significant differences between the pre-playback and the playback periods for all three response measures. * indicates a significant difference between pre playback and post playback period after sequential Bonferroni correction for multiple testing.


A
No noise
Low-level
High-level
Number of songs
0
25
50
75
*
*
Control
Consistent
B
No noise
Low-level
High-level
Number of flights
0
10
20
Control
Consistent
C
No noise
Low-level
High-level
Time in 5 m radius (s)
0
50
100
150
200
Control
Consistent

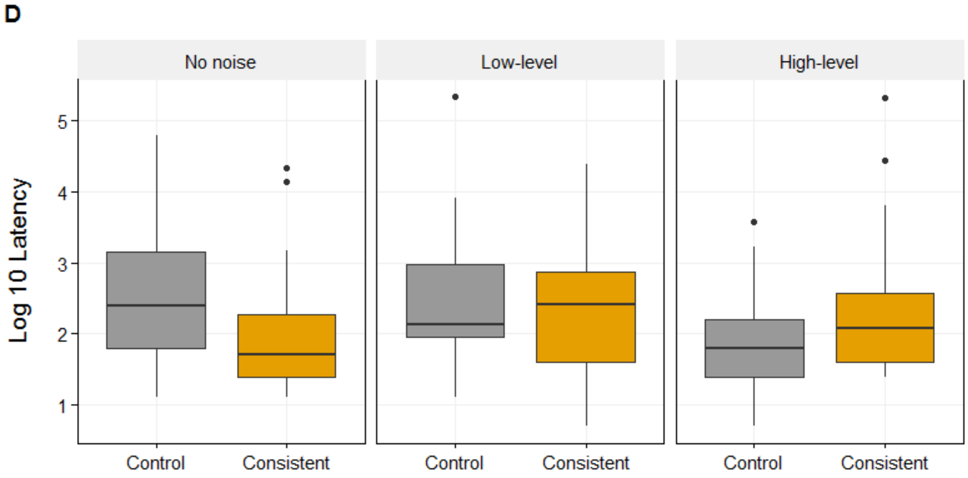


Figure 5 Comparison of (A) number of songs, (B) number of flights and (C) time within 5 m of playback speaker and (D) response latency in response to control and consistent conspecific songs to blue tits (*Cyanistes caeruleus*) under different noise conditions, namely no-noise, low-level and high-level noise. Blue tits produce more songs in response to consistent than control stimuli under the no-noise condition and the low-level noise condition ($W = 244, N = 22, p < 0.05$), but not for the high-level noise conditions * indicates significant a difference between control and consistent stimuli after sequential Bonferroni correction for multiple testing.

3.2 EXPERIMENT 2 – NOISE FREQUENCY BAND EXPERIMENT

In total, 41 individuals were tested for both consistent and control stimuli. No effect of order was found on any of the response variables measured. Of the 41 individuals tested, 20 were tested in high-frequency background noise, and 21 in low-frequency background noise conditions.

Comparing the pre-playback to the first minute of the first trial period showed that, for both types of background noise, the stimuli elicited an increase in all three response measures recorded (Figure 6; Appendix D Table 3). For high-frequency conditions there was an increase in the number of territorial songs ($W = 20, n_1 = n_2 = 20, p < 0.05$), the number of flights ($W = 6.5, n_1 = n_2 = 20, p < 0.001$), and the time spent within a 5 m radius from the speaker ($W = 3, n_1 = n_2 = 20, p < 0.05$). Likewise, under low- frequency conditions there was a significant increase in the number of songs ($W = 34, n_1 = n_2 = 21, p < 0.05$); number of flights ($W = 16.5, n_1 = n_2 = 21, p < 0.001$); and time spent within a 5-meter radius ($W = 3, n_1 = n_2 = 21, p < 0.05$).

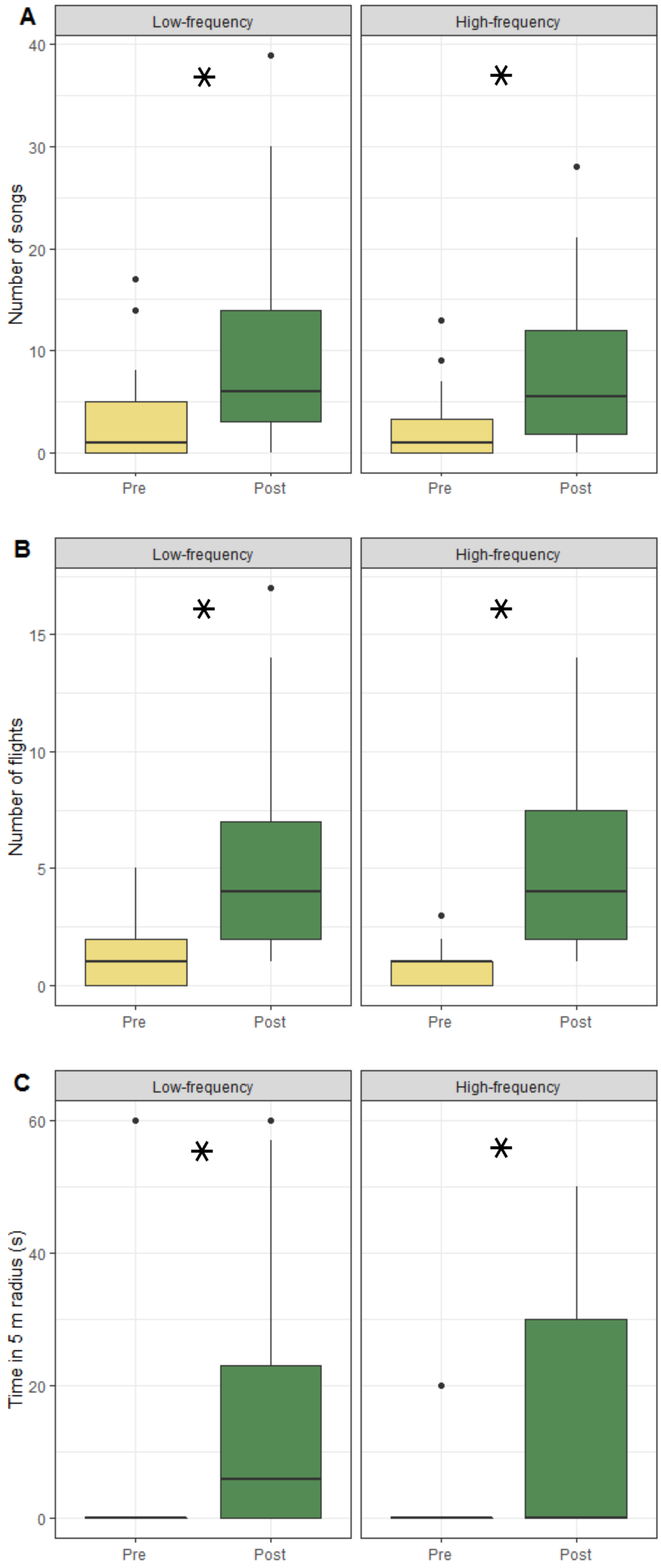
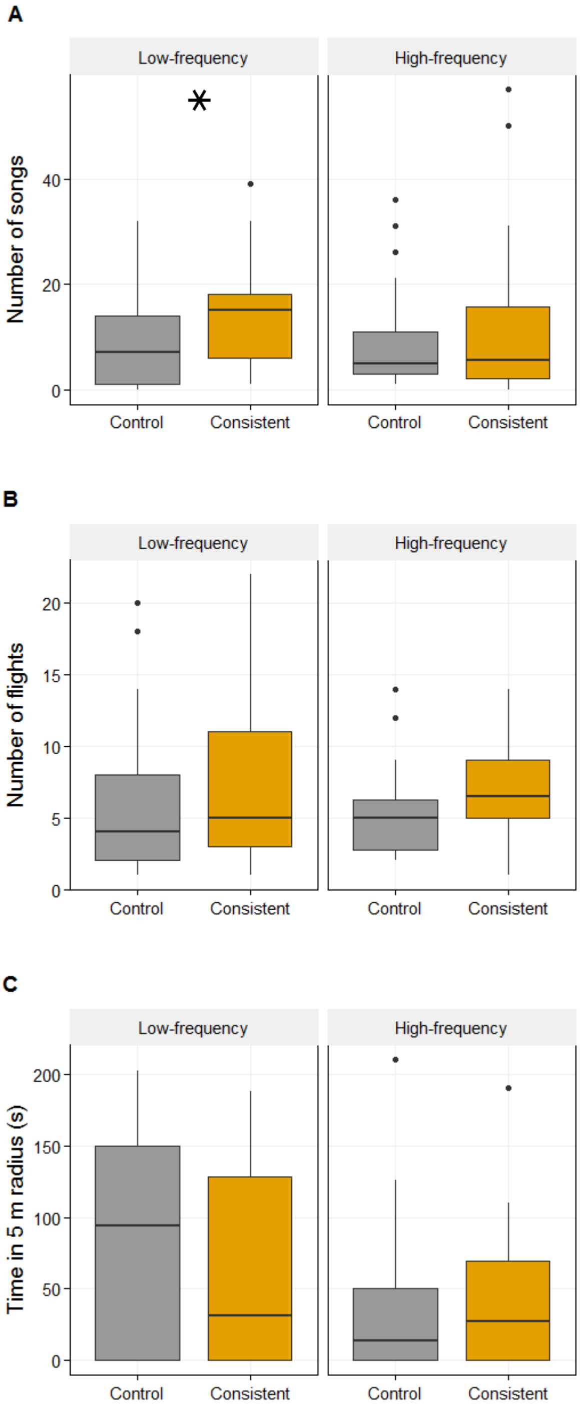


Figure 6 Comparison of (A) number of songs, (B) number of flights and (C) time within 5 m of playback speaker following playback of conspecific songs to blue tits (*Cyanistes caeruleus*) under High frequency and low frequency noise conditions. In all three levels of background noise, there are significant differences between the pre-playback and the playback periods for all three response measures. * indicates a significant difference between pre-playback and post-playback period after sequential Bonferroni correction for multiple testing.

When tested for detection of acoustic variation between two songs with different levels of consistency, blue tits produced more songs in response to consistent than control stimuli under low frequency noise conditions (*W = 190, N = 21, p < 0.05)*, but not under high frequency noise conditions (*W = 113.5, N = 20, p = 0.23*). No differences were observed in the other response parameters under any of the treatments (Figure 6; see Appendix D Table 4 for details of test statistics).



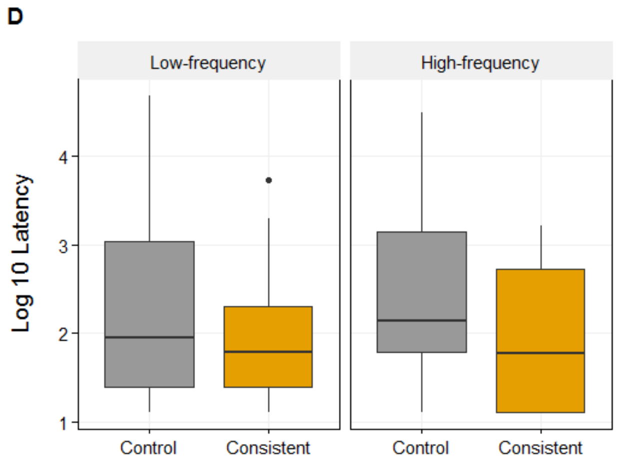


Figure 7 Comparison of (A) number of songs, (B) number of flights and (C) time within 5 m of playback speaker and (D) response latency in response to control and consistent conspecific songs to blue tits (*Cyanistes caeruleus*) under low-frequency and high frequency noise conditions. Blue tits produce more songs in response to consistent than control stimuli under low frequency noise conditions but not under high frequency noise conditions. * indicates a significant difference between control and consistent stimuli after sequential Bonferroni correction for multiple testing.

4. DISCUSSION

Blue tits are affected in the recognition, but not in the detection of conspecific song stimuli under noisy conditions, depending on noise level and frequency range. Since subtle spectral information in bird song plays a role in sexual selection, these results imply that anthropogenic noise may cause suboptimal decision making in blue tits. Blue tits sang more songs in response to consistent compared to control stimuli under no-noise, low-level noise, and low-frequency noise. This difference in behaviour was not found under high level and high frequency background noise. Both the level dependent and frequency dependent results, show that the impact is related to reduced audibility and not to other potential factors such as distraction, agitation, or anxiety.

4.1 MASKING OF PERCEPTION IN THE FIELD

The results of this study provide field-based evidence that background noise has the potential to affect the assessment of vocal performance by the receiver. Most research on the impact of background noise on songbird auditory perception has been conducted in controlled laboratory conditions by using operant conditioning techniques (Lohr et al., 2003; Pohl et al., 2009, 2012). However, while this approach provides the best instrument to accurately measure detection and discrimination thresholds (Langemann et al., 1998;

Lohr et al., 2003; Pohl et al., 2012), the perception of vocal signals is deprived of its context, and therefore prevents accurate understanding of the ecological consequences of signal disruption. This study focuses on the effects of acoustic masking from experimentally introduced noise in a natural population, and thus provides an understanding of the biological relevance of noise-induced failure to recognise differences in vocal performance in a natural context.

The results show detection of song in the presence of masking noise, but noise-dependent lack of song recognition. Blue tits responded to the stimuli under all treatments, showing that detection of the signal occurred under all noise conditions. Previous studies on song detection of natural vocalisations have shown that a signal to noise ratio (SNR) as little as 3 dB is sufficient for detection in background noise (Brenowitz, 1982; Lohr et al., 2003). While actual SNRs for effective detections in the field are likely to be higher than values measured in laboratory conditions (Lohr et al., 2003), the noise levels in the current masking experiment were well below the recorded thresholds for signal detection.

In no-noise and low-level noise conditions, blue tits exhibited a different response to the stimuli differing in consistency, showing the ability to discriminate between different levels of vocal performance. Blue tits gave stronger responses to high-consistency songs, by singing more in response to the consistent stimuli (Searcy and Beecher, 2009). The playbacks simulated a territorial intrusion, so the differential response can be interpreted as a difference in the focal individual’s perception of the simulated competitor’s ability and motivation. An intruder with a high-consistency song may pose a stronger threat than an individual with a low-consistency song, and it might therefore motivate blue tits to protect their territory and breeding mate. These results are consistent with those observed in earlier studies focusing on the importance of song consistency during male-male encounters in songbirds. For example, banded wrens also show a different vocal response to simulated intruders with different levels of consistency (de Kort, Erin R.B. Eldermire, et al., 2009), and great tits respond more aggressively and approach more closely in response to more consistent songs (Rivera-Gutierrez et al., 2011).

4.2 MASKING OF RECOGNITION, BUT NOT DETECTION

The results for playbacks complement earlier research that addressed detection and discrimination as a trade-off, and it show that noise has the potential to affect the assessment of vocal performance. This study shows that, at noise levels that allow for comfortable detection of an intruder’s vocal signal, the message carried in the fine acoustic structure of the signal (which allows the receiver to assess the quality of another individual) might still be lost. In the context of mate-choice, several studies have suggested that, in noisy conditions, there might be a shift in favour of detection of vocal signals rather than their discrimination. High-frequency songs are better audible in low-frequency noise, but low-frequency songs may be an honest signal of quality, and therefore high-quality males may become unable to distinguish themselves spectrally from competitors under noisy conditions (Ríos-Chelén, 2009; Halfwerk, Bot, et al., 2011; Huet des Aunay et al., 2013). In the context of male competition and territorial defence, increases in background noise levels also appear to affect behaviour through noise-dependent disruption of the acoustic signals reaching the receiver (McMullen et al., 2014; Kleist et al., 2016). In particular, a recent study on white-crowned sparrows (*Zonotrichia leucophrys*), suggests that ambient noise might affect the assessment of vocal traits related to individual performance, as this species had to approach the simulated intruders closer in the presence of noise (Phillips and Derryberry, 2018).

4.3 MASKING AND NOT DISTRACTION?

It has been suggested that it is possible that distraction from noise plays a role in causing changes in territorial behaviour, and combined with masking, may have an additive effect in degrading the recognition of the information conveyed within a signal (Chan et al., 2010). Nevertheless, results from the frequency band experiment suggest the possibility that masking could have been solely responsible for the failure to recognise differences in trill consistency in blue tits. For the same overall noise level, assessment of consistency only occurred in low-frequency masking noise without spectral overlap. One limitation to this interpretation is that high-frequency overlapping noise might have been more distracting than low-frequency noise. However, while masking occurs primarily when noise is at a similar acoustic frequency to that of the signal (Brumm and Slabbekoorn, 2005), distraction can occur regardless of the acoustic frequency of noise (Francis and Barber, 2013). The results from this study on wild birds are consistent with laboratory masking studies, showing that noise energy overlapping the frequency region of a vocal signal has a much stronger effect in raising the masked thresholds for detection, discrimination and recognition, when compared to noise energy at spectral regions distant from the signal (Dooling and Blumenrath, 2014). Because masking ratios are highly variable among species, frequencies, and type of noise and signal (Dooling, 2004), it is difficult to compare these specific results of this study directly with laboratory studies. However, laboratory studies generally show a monotonic decline in the intensity of the response with increasing amplitude of overlapping white noise, up to a threshold past which birds no longer respond to a signal (Lohr et al., 2003; Dooling and Blumenrath, 2014). On the other hand, the degree of distraction is not necessarily related to the amplitude in the same way as signal masking and can be affected in a much different way by characteristics of noise such as its constancy in time and frequency (Naguib, 2013). For example, while fluctuating noise might facilitate signal detection and recognition during periods of lower noise amplitudes, the same fluctuations, when unpredictable, can instead be more distracting and take away attention from the signal (Talling et al., 1998; Purser and Radford, 2011).

4.4 FREQUENCY SHIFTS MAY ALSO IMPROVE RECOGNITION

These findings also support the observation that the shifts of vocal signals towards higher frequencies might be a strategy in order to avoid masking by anthropogenic noise, which is typically biased to low frequencies in the 0–3 kHz range (Wood and Yezerinac, 2006; Goodwin and Podos, 2013). Several observational and experimental studies have hypothesised that birds might deliberately increase the minimum frequency of their songs to avoid masking by low-frequency anthropogenic noise (reviewed in Brumm and Slabbekoorn, 2005; Gil and Brumm, 2013; Patricelli and Blickley, 2006; Ríos-Chelén, 2009). Studies have found that, under noisy conditions, high pitched songs are indeed easier to detect and discriminate, and are more effective in triggering female responses (Halfwerk, Bot, et al., 2011; Pohl et al., 2012). However, whether the extent to which an increase in pitch is a response to noise or a by-product of singing at higher amplitudes in noise has been the subject of debate (Nemeth and Brumm, 2010; Cardoso and Atwell, 2011; Zollinger et al., 2012; Nemeth et al., 2013). Indeed, studies have found that, at least in some species, frequency and amplitude are coupled in bird vocalisations, so that as vocal amplitude increases due to the Lombard effect, so does frequency (Amador et al., 2008; Amador and Margoliash, 2013; Beckers et al., 2003; but see Cardoso and Atwell, 2011; Zollinger et al., 2017). It is also possible that, in the low-frequency noise typical of cities, higher pitched songs are simply more likely to be heard because of partial masking release, and therefore more likely to be learned and to be transmitted across generations (reviewed in Blickley and Patricelli, 2012). Whether a deliberate change in pitch, a coincidental by-product of higher amplitude, or the result of noise-related cultural or microevolutionary shifts, if recognition of vocal signals is mainly driven by frequency masking, frequency shifts towards higher pitched songs may constitute an advantage not only in terms of detection, but also in terms of assessment of vocal performance by the receiver.

When discussing potential implications of frequency-dependent masking, it is important to bear in mind that, while the frequency spectrum of most types of anthropogenic noise tends to be concentrated towards lower frequencies, it also encompasses frequencies that could overlap with vocalisations located at relatively high frequencies (Can et al., 2010). While it appears that only the high-frequency masking noise affected the ability to recognise differences in song consistency in blue tits, the background noise levels for this playback were well below the levels that birds living near busy roads might be exposed to. Birds exposed to high levels of anthropogenic noise might still encounter masking of recognition through the high frequency contained in traffic noise. A further field study using digitally synthesised noise with an acoustic spectrum designed to simulate traffic noise, such as that designed by Lohr et al. (2003), would be important in order to explore this aspect. Finally, another question that this study leaves unanswered is whether low frequency noise at a higher level than that used for this playback, might have masked recognition. In this study, birds were presented with playbacks in which the amplitude was regulated based on the A frequency weighting scale. While this filter provides an estimate of bird hearing (Dooling and Popper 2007), it was developed to approximate human loudness perception and may not have been the most appropriate for this species (Swaddle et al., 2015). It is therefore possible that blue tits might not have perceived the low-frequency noise used in this study as loudly as the high-frequency noise. Moreover, because of the upward spread of masking, noise energy concentrated in lower frequencies can have masking effects at higher-frequency channels (Kinsler et al., 1999). In future studies, it would be interesting to test the ability of birds to assess song quality at higher levels of low-frequency background noise.

4.5 CONCLUSIONS

In many birds species, song plays a vital role in processes directly related to their fitness, such as mate choice and territorial defence (reviewed in Collins, 2004). The complexity and the structural details of songs are what birds ultimately use to mediate sexual selection. Any alteration in the perception of songs can therefore lead to significant fitness consequences. This study shows that some of these fine structural details (trill consistency) can be masked by anthropogenic noise above certain levels with overlapping frequencies. Noise has therefore the potential to affect sexual selection, with potentially far-reaching consequences on the reproductive success and overall fitness of the individuals affected. The results of this study add to a growing body of evidence showing noise-induced changes in the behaviour of receivers in natural conditions, in the context of mate-choice (Halfwerk, Bot, et al., 2011; Halfwerk, Holleman, et al., 2011; Huet des Aunay et al., 2013), territorial defence (McMullen et al., 2014; Kleist et al., 2016; Phillips and Derryberry, 2018), and parent-offspring communication (Leonard et al., 2015; Lucass and Eens, 2016). This research highlights the importance of understanding the receiver's role when studying the effects of noise pollution on wildlife, not just in its ability to detect signals, but also in more complex processes such as discrimination and recognition.

CHAPTER 6.
DISCUSSION

1. KEY FINDINGS AND THEIR IMPLICATIONS

The primary aim of this thesis was to address some of the outstanding questions in our understanding of the effects of noise on birds' reproductive success and communication. This is the first study to provide evidence on a large geographical scale and for a heterogeneous number of species that anthropogenic noise affects the reproductive performance of birds, and that the nestling stage is particularly susceptible to this pollutant. This thesis also gives experimental evidence that noise impairs the ability of birds to recognise fine structural differences in their songs, suggesting that anthropogenic noise affects processes of sexual selection and possibly reduces optimal mate choice, and therefore highlighting to importance of better understanding communication on the sender and the receiver's side.

1.1 A MISMATCH BETWEEN NEST STE SELECTION AND BREEDING PERFORMANCE

The first aim was to investigate nest-site selection, nest-site fidelity, and breeding success in a population of songbirds exposed to traffic noise over multiple years. This was addressed in Chapter 2, which found that, although blue tits were more likely to breed in nest-boxes exposed to higher noise levels, the number and the body weight of chicks fledged declined at higher levels of noise exposure. Although blue tits' nest site fidelity decreased in noisier areas, they did not move to quieter nest boxes, suggesting that relocating individuals did not use noise level for decisions about resettlement in subsequent years. These results highlight how there might be a mismatch between nest-site choice and breeding performance. As anthropogenic noise constitutes a relatively novel environmental pressure, species might not have had sufficient time to evolve adaptive responses. Noise level may therefore not be used as an indicator of habitat quality, and instead blue tits may be relying on other environmental cues, such as foraging opportunities and presence of predators, to evaluate territory quality and select nest sites (Francis and Barber, 2013). If birds do not respond adaptively to anthropogenic noise, by settling in noisy habitats that would otherwise appear to be suitable, they might end up being caught in an ecological trap, causing them to experience lower breeding success (Schlaepfer et al., 2002).

The presence and abundance of species are common metrics used for the environmental impact assessment of anthropogenic activities. While these measures are fundamental to assess the status of populations, the results of this thesis imply that simple surveying techniques might not be sufficient to measure the full spectrum of effects of such a novel environmental pollutant, and that they should therefore be accompanied by programmes monitoring direct measures of fitness.

1.2 A WIDER LOOK AT THE CORRELATION BETWEEN NOISE AND BREEDING PERFORMANCE

A second aim of this thesis was to develop a methodology to investigate the effects of traffic noise at a large geographical scale, in order to be able to apply it to a number of different breeding monitoring schemes and test the relationship between traffic noise and potential changes at various stages of breeding in different species. Chapter 3 established a valuable method to monitor the impact of noise pollution using data that, thanks to the efforts of volunteers on monitoring programmes, is available on a national scale for multiple countries. As anthropogenic noise exposure has emerged as an environmental priority for human health and wellbeing (Berglund et al., 2000), environmental agencies worldwide have been developing soundscape maps around major roads, airports, and railways. These can be implemented to assess the effects of anthropogenic noise not just in terms of changes in spatial distribution, but also in terms of fitness, and to provide a cost-effective way to predict the impact of noise as urbanisation and transportation networks expand.

Chapter 4 applies the method developed in Chapter 3 to increase our understanding of species-specific responses, providing results that help generalise the consequences of noise exposure on the reproductive success of birds. This chapter shows that negative effects of noise on breeding performance are common amongst different taxonomic groups and can be present at all the stages of reproduction monitored for this study. The nestling stage stands out as the most vulnerable, as it emerged that most of the species affected experienced negative effects in terms of fledgling success. Remarkably, the one common aspect shared by these taxonomically diverse species (namely blue tits, starlings, kestrels, and stock doves) is their persistence in noisy and heavily urbanised areas (Patón et al., 2012; Strasser and Heath, 2013; González-Oreja, 2017). This corresponds to the findings of Chapter 2 on blue tits, emphasising how species presence in noisy environments should not be confused with successful breeding and fitness in noisy conditions. As proposed in Chapter 2, this is likely taking place through alterations in parental care towards the chicks, whether in terms of food provisioning, number of visits, or time spent with the chicks. As anthropogenic noise can mask crucial vocalisations such as food, alarm, and begging calls, the impairment of parent-offspring communication might play a key role in causing breeding efforts to be more likely to fail as noise levels increase (McIntyre et al., 2014; Leonard et al., 2015). It is indeed possible that species defined as "noise-tolerant" because they are commonly found in noisier environments, might be the ones where the impact of noise on breeding is more likely to take place at the nestling stage, when communication between parents and their chicks is most important. In species that do avoid anthropogenic noise, any negative effects might instead occur at earlier stages, either via a non-random distribution of individuals, resulting in higher quality birds breeding in quieter areas, or alternatively through individuals that persist in noisier areas experiencing stress, or seeing their ability to defend territories and attract mates decreased (Halfwerk and Slabbekoorn, 2014).

The findings of this chapter emphasise the importance of considering all stages of breeding when assessing the consequences of noise on reproductive success. What might appear as a species not vulnerable to noise when looking at one specific aspect of their breeding, might actually be experiencing negative effects at a different stage. Understanding what stages of reproduction are most susceptible to noise is therefore important to inform conservation, so that efforts to limit the effects on human-generated noise can be focused on times during which each specific species are most vulnerable.

Moreover, the results of this thesis also suggest the need to understand the fitness implications of noise on a more diverse set of species. Unfortunately, current studies of the impacts of anthropogenic noise have focused on only a small subset of bird taxa. Because noise pollution is so pervasive, examining only a subset of families does not allow us to fully understand the effects of anthropogenic noise. Exploring a more diverse set of families with differing traits will allow for a more robust analysis in determining how traits contribute to responses to anthropogenic noise. My results confirm the view that more data exploring the impacts of anthropogenic noise on a wider set of species is needed (Francis et al. 2012).

1.3 A POTENTIAL MECHANISM AFFECTING REPRODUCTIVE SUCCESS

The aim of Chapter 5 was to test if songbirds are able to recognise fine structural difference in the song of a conspecific under different noise conditions. This allowed to explore the effects of noise not only in term of detection, but also on the ability of birds to assess song quality, a process just as vital as detection in terms of territorial and mate defence and mate attraction. This chapter provides new field-based evidence that masking noise affects the receiver by impairing their assessment of a potential intruder's vocal performance. It is therefore important to consider the fact that impairment of vocal communication can take place at noise levels where the detection of acoustic signals is possible while their assessment is difficult or even impossible (Dooling and Popper, 2007). Birds inhabiting noisy habitats are more likely to be exposed to noise levels that impair the assessment of songs and other vocalisations rather than their detection. It is therefore possible that masking of elements that allow signal assessment, rather than masking of their detection, is the main culpable for the decrease in survival and reproduction that have been linked to impairment of acoustic communication. While the study in this thesis focused on song, similar processes might also be occurring for other vocal signals such as begging or alarm calls. Poor assessment of these signals might affect individual fitness as a result of decreased antipredator behaviour, poor flock cohesion, or reduced parental care (McGregor et al., 2013).

1.4 COMBINED MEANING OF THE FINDINGS AND CONSERVATION IMPLICATIONS

Although an ever-growing body of studies show negative effects of anthropogenic noise on bird fitness and reproductive success, this thesis wanted to pin down the scale of these effects. I developed a big data approach, informed by citizen science, to monitor any correlations between the intensity of traffic noise and the reproductive output of common European bird species. By looking at individuals in a natural population, I explored some of the potential processes driving the correlations between anthropogenic noise and changes in reproductive success. By simultaneously looking at nest site selection and reproductive success in a natural population exposed to a noise gradient, I aimed at getting a better insight into what might happen to populations that settle in noisy habitats. For the same species and population, I also looked at how noise might affect the correct transmission of important vocal sexual signals.

Together, the findings of the thesis suggest the presence of widespread negative effects on reproduction, which likely transcend differences in traits and which might even apply to species that, based on their presence in urban environments, have been identified as urban adapters or exploiters (Conole, 2014). I showed that a species typically found in urban and noisy habitats, the blue tit, might be experiencing a mismatch between the choice of nesting site and the fledging success and body mass of their fledglings. This indeed opens up the possibility that some species considered urban adapters might instead be in the presence of an ecological trap, whereas there is a discrepancy between the environmental cues they use to select habitats and the actual habitat quality (Schlaepfer et al., 2002). This is of particular concern, because in the presence of an ecological trap populations tend toward extinction, as animals abandon better quality habitats to settle in inferior ones (Battin, 2004). Finally, this thesis supports the possibility that the negative impact of noise on reproduction could be associated to its impact on communication. I show that, through masking, anthropogenic noise could be inhibiting the efficient assessment of vocal performance and therefore interfere with territorial and mate defence, and with mate selection (reviewed in Kight and Swaddle, 2011). While not tested in this thesis, other types of vocal communication essential for survival might also be impacted by noise, which can affect not only the detection but also the discrimination and recognition of vocal signals. For example, communication between parents and their offspring, essential to offspring survival (Lucass and Eens, 2016), might also be affected in similar ways to those tested in the last chapter of this thesis. Linking the impairment of the correct assessment of vocal signals to reproduction and reproductive success is therefore fundamental for a deeper understanding of the downstream effects of anthropogenic noise.

As decreased individual fitness may translate into severe consequences in terms of population viability (Francis and Barber, 2013), it becomes important to relate the adverse impacts of noise to conservation and noise management. The work of this thesis is relevant to policy makers and conservationists in their decisions about noise mitigating efforts related to environmental impact assessment. Legislation on wild birds in Europe already prohibits the deliberate disturbance of breeding and rearing birds (EU Birds Directive; Council of the European Union, 2009). Given the spatial extent of the problem identified in this thesis, it would be essential to extend this legislation to specifically incorporate anthropogenic noise. Seasonal restrictions to traffic or other noise-generating human activities in locations where declining species are known to breed could greatly help mitigate the impacts of noise. This study also gives some indicative threshold of sensitivity to noise. Noise levels above 70 dB(A) have significant impact on breeding success of blue tits, a species commonly found in noisy and urban environments. In species that are more sensitive this threshold is likely to be lower. Furthermore, at lower noise levels, difficulties in signal assessment arise, and communication between individual is affected, most likely with indirect effects on their fitness.

1.5 CAN BIRDS TRULY ADAPT TO ANTHROPOGENIC NOISE?

The results of this thesis suggest that the reproductive success of species that persist in noisy environment and that might display vocal adjustments in the presence of anthropogenic noise might nevertheless be affected. In this light, it is important to understand if their vocal adjustments truly are adaptive. Avian species have long been exposed to loud natural sounds caused by physical processes such as wind, rain, or other forms of moving water (e.g., streams, waterfalls, surf). Noise can also be the result of the vocalisations of other conspecifics or heterospecific, which might lead to an even greater acoustic overlap than that of noise from abiotic sources. Where birds have been exposed to similar noise patterns over multiple generations and existed in these noisy environments for a long time, populations have succeeded in adjusting to these natural physical constraints to increase communicative efficiency (Nemeth and Brumm, 2010). Birds use a variety of strategies to avoid signal masking in areas with high levels of natural noise, including adjustments in song timing, structure, and performance. For instance, the large-billed leaf warbler (*Philloscopus magnirostris)* (Martens and Geldudig, 1990) and the white-throated dippers (*Cinclus cinclus*) (Brumm and Slabbekoorn, 2005) use particularly high frequencies well above those generated by the fast-running streams and torrents in their habitats. This is thought to be the result of these abiotic noise sources acting as a selection pressure and driving the evolution of their vocalisations. Although there are many other benefits to singing at dawn (reviewed in Catchpole & Slater, 2008), it has also been observed that, in habitats where the occurrence of rain and wind follow somehow predictable patterns, the singing activity of some species might be linked to these noise patterns (Henwood and Fabrick, 1979). Biotic sources of noise might constitute an even greater pressure on birds' vocal communication, inducing them to adjust their songs and calls (Tobias et al., 2010), and to develop strategies to improve communication on both the signaller and the receiver end (eg. Aubin & Jouventin, 2002; Greenfield, 2005; Schmidt & Balakrishnan, 2014).

Given the fact that birds have successfully adapted to cohabiting with non-human noise, it is possible that similar processes might be taking place as an adaptation to anthropogenic noise. As highlighted in the introduction to this thesis, changes in vocal signals in response to anthropogenic noise have been observed both as a result of individual plasticity and of microevolutionary changes (reviewed in Brumm & Zollinger, 2013). For example, many studies provide evidence for a link between song frequency use and anthropogenic noise (reviewed in Slabbekoorn, 2013). This could mean that singing at high frequencies, or at least reducing the use of low frequencies that are more likely to be masked by traffic noise, may provide signalling and fitness benefits in noisy urban areas. One compelling example of the adaptive value of song adjustment is the work of Halfwerk et al., 2011, which showed experimentally that, although low-frequency songs are preferred by females of great tits and are and linked to female fecundity, exposure to traffic noise impairs the effectiveness of low-frequency songs and favours higher-pitched songs.

It is however important to be particularly careful when drawing conclusions on whether signal adjustments are indeed adaptations to anthropogenic noise. Firstly, the correlations between song characteristics and an increased signal to noise ratio observed in the field might not always be the result of an adaptation to human-generated noise. For example, it has been demonstrated that increases in song frequency are less effective at reducing masking by anthropogenic noise than increases in amplitudes(Nemeth and Brumm, 2010). At least in some species, the higher frequencies observed in urban birdsong could be a physiological side-effect of singing louder (eg. Verzijden et al., 2010; Zollinger et al., 2017; but see Cardoso & Atwell, 2011) . Moreover, song adjustments in urban habitats may lead to trade-offs between natural selection, which determines signal adaptations, and sexual selection for attractive signals (Slabbekoorn and Ripmeester, 2008). Indeed, even when vocal adjustments are efficient in decreasing signal-to-noise ratio, changes in these sexually selected traits might be associated with losses in vocal performance, and therefore the costs of song adjustments may outweigh their benefits. For example, males of white-crowned sparrow (*Zonotrichia leucophrys nuttalli*) occupying louder territories increase the minimum frequency of their songs in response to anthropogenic noise by reducing the bandwidth of their trills. This results in lower performance songs (Luther et al., 2015; Phillips and Derryberry, 2018) and might negatively affects male-male interactions. In male house wrens (*Troglodytes aedon*) (Grabarczyk et al., 2018) only paired males increase their peak frequency in response to noisy playbacks while unpaired males do not, suggesting that unpaired males may sacrifice detectability for attractiveness, with a trade-off between vocal performance and transmission distance.

Anthropogenic noise constitutes an very recent challenge on an evolutionary level, and, while it is true that some species might be more likely to tolerate noisy environments based on their vocal traits (eg. Cardoso et al., 2018; Hu & Cardoso, 2010; Rheindt, 2003), this does not necessarily mean that these species might thrive in noisy environments. Indeed, while birds do possess a wide range of strategies to mitigate the effects of anthropogenic noise, these adaptations most likely originate from adaptations to non-anthropogenic noise, and might fall short in the face of this novel environmental pollutant (McGregor et al., 2013). Urban, noisy environments pose a fundamentally different challenge than natural environments (Isaksson, 2018), as they keep changing as human populations expand and develop. Even when birds might adapt, or at least adjust, to living in urban environments, the constant alteration of these environments poses and ever-changing challenge to wildlife.

2. MOVING FORWARD: CONSIDERATIONS FOR FUTURE RESEARCH

The effective discrimination and detection of vocal signals other than songs (such as copulation, alarm, begging, contact, and alarm calls) is just as vital in determining the chances of survival and reproductive success of individuals. While not much research in the field has worked on teasing apart song assessment and detection, even less in known about this aspect when it comes to other important vocalisations (Ortega, 2012). Throughout this thesis, parent-offspring communication was often brought up as a possible explanation as to why the nestling stage consistently emerged as particularly susceptible to anthropogenic noise exposure. While there is evidence that detection of parental calls and begging calls is affected by noise (eg. McIntyre et al., 2014; Templeton et al., 2016), little is known about the consequences of alterations in the discrimination and recognition of these vocal signals. Differences in begging calls influence parental feeding decisions (Leonard and Horn, 2001), and alarm calls contain information about the type of threat (Evans et al., 1993), which might require different behavioural responses. Playback experiments testing not only detection, but also the assessment of the messages conveyed in these kinds of vocal signals would help highlight some of the additional mechanisms that play a role in determining fitness declines in noisy environments.

Taken together, the results of the chapters on breeding success show an overall negative association between noise and breeding performance. However, while the design of this thesis allowed exploring the effects of noise over a large international scale, it is important to acknowledge the fact that it does not allow drawing definite conclusions about the causes of the negative relationships observed. In order to provide conclusive evidence on the causal relationship between anthropogenic noise and changes in breeding success, an experimental approach would be required. A possible method would be to create a playback study with a design similar to the “phantom road” developed by McClure et al. (2013), which simulated traffic noise in an otherwise road-less landscape. The authors used this method in a series of studies to show that traffic noise alone could cause avoidance, changes in age structure, and changes in body conditions (McClure et al., 2013, 2017; Ware et al., 2015), but the same experimental design could be used to test the effects of traffic noise on nest-site choice and breeding over multiple generations.

Another possible area of future research would be to use the same method developed in Chapter 3 to integrate other environmental pollutants (such as atmospheric and light pollution) that can exert a pressure on fitness, and that may have played a role in enhancing some of the changes observed in relation to noise. This would help to disentangle the effects of noise from those related to other environmental factors that might co-vary with noise. Light levels and atmospheric pollution are also being monitored and can be modelled in order to assess the extent of their impact on humans. This might open up possible interdisciplinary collaborations between GIS experts, environmental agencies, and biologists. Integrating this information could also potentially generate a predictive instrument to calculate the impact of transportation networks before they are developed, and to contain their effects. Given that urbanisation is predicted to grow, such a model could be particularly useful to assist scientists, natural resource managers, industry, and policy makers to predict the potential outcomes of urban planning on biodiversity, and to promote sustainable growth as well as implementing meaningful thresholds and help mitigate the negative impact of urbanisation.

2. CONCLUSIONS

The results of this thesis address fundamental questions in behavioural ecology, and applied questions relevant to environmental impact assessment and government policy concerning noise pollution and conservation biology. Anthropogenic noise might cause birds to fall into ecological traps by choosing to breed in otherwise suitable habitats, leading to decreased breeding performance and degraded communication. Even species that might appear less sensitive to noise might experience negative consequences. It therefore becomes critical to assess the effects of noise beyond presence or absence, in the context of other measures of impacts such as reproductive success and changes in communication. By introducing a novel observational approach, and extending the experimental approach to aspects of acoustic communication that have yet to be fully understood, this thesis widens our understanding of what we know about the effects of noise exposure. As habitat loss and the effects of human-induced changes in climate currently threaten many species across the globe with an uncertain future, accurately understanding the effects of changes in the acoustic environment will increasingly become an essential element to guarantee habitat suitability for vulnerable populations and communities.

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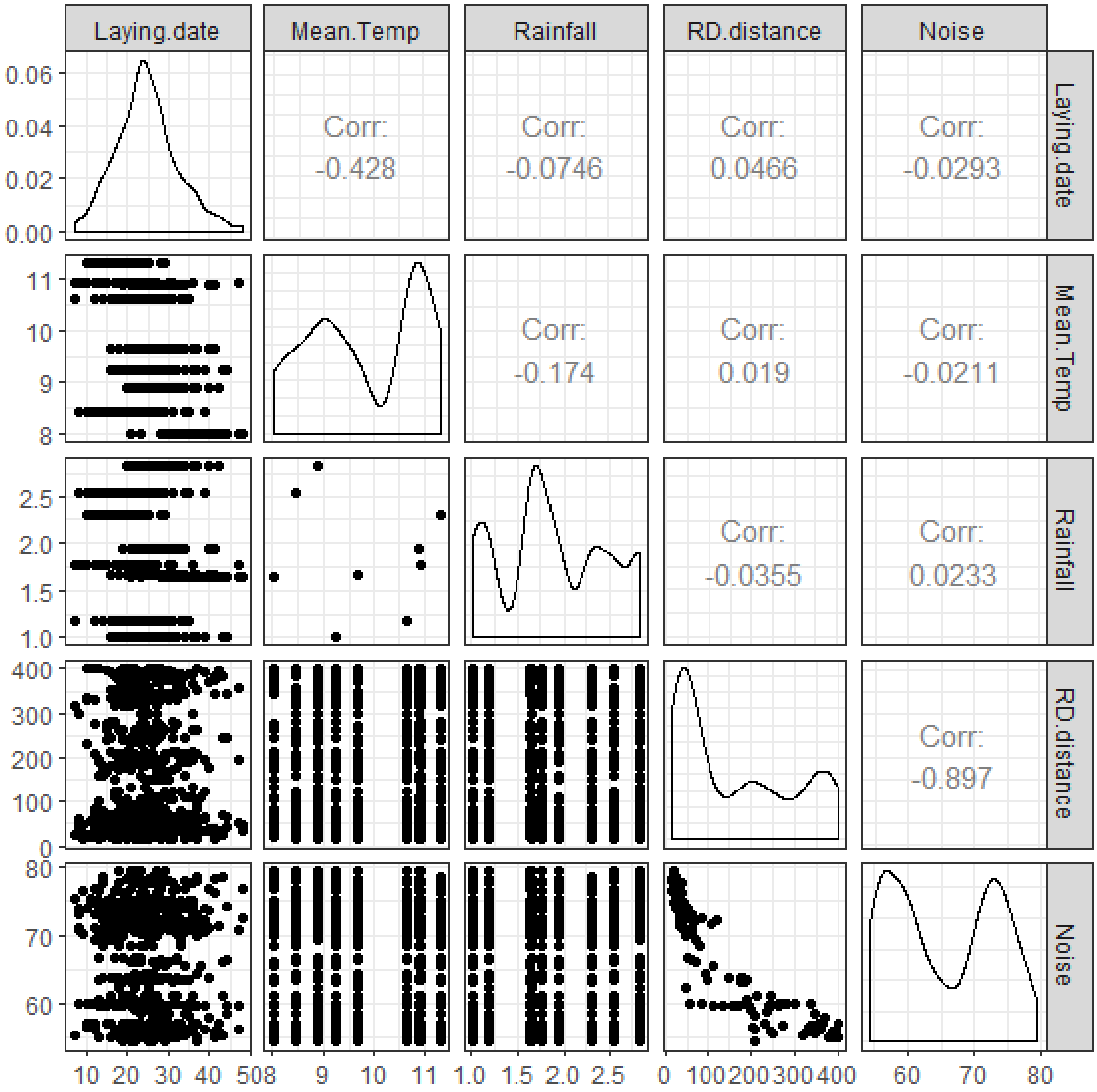
APPENDICES

Appendix A



Appendix A Figure 1 Correlation Matrix of predictors initially considered for GLMMs on breeding variables. On top are shown the correlation values. On bottom, the bivariate scatterplots, with a fitted line. P-values of the correlation test are given in the table below.

Appendix A Table 1 Table of correlation coefficients and relative p-values of predictors initially considered for GLMMs on the breeding variables.

	Laying date	Mean Temp	Rainfall	Road distance	Noise
Laying date		-0.42834	-0.07459	0.046563	-0.02926
Mean Temp	0		-0.17435	0.018978	-0.02107
Rainfall	0.0541761	5.92E-06		-0.03554	0.023274
Road distance	0.2297695	6.25E-01	3.60E-01		-0.89651
Noise	0.4506478	5.87E-01	5.48E-01	0	

Appendix A Table 2 Generalized linear mixed model (GLMM) investigating the relation between sound level measured at the nest-box and a) Clutch size, b) Laying date, c) Number of Fledglings and d) Average Mass of nestlings at day 15. Only breeding events that took place in nest-boxes for which the closest road was the M6 are included. Significant effects are in bold.

Clutch size	*Predictors**	*Estimates*	*std. Error*	*CI*	*t-value*	*p*
N=497	(Intercept)	9.265	0.18	8.90 – 9.63	50.4	<0.001
	Noise	-0.480	0.23	-0.93 – -0.03	-2.11	0.035
	Road Distance	-0.729	0.23	-1.18 – -0.28	-3.17	0.002
	Laying Date	-0.986	0.1	-1.18 – -0.80	-10.18	<0.001
	Average Temp.	-0.400	0.18	-0.76 – -0.04	-2.2	0.028
	Average Rainfall	-0.153	0.18	-0.51 – 0.20	-0.85	0.394
No. Fledglings	*Predictors**	*Estimates*	*std. Error*	*CI*	*z-value*	*p*
N=454	(Intercept)	1.914	0.468	2.71 – 16.96	4.093	4.26E-05
	Noise	-0.128	0.059	0.78 – 0.99	-2.177	0.0295
	Road distance	-0.146	0.061	0.77 – 0.97	-2.406	0.0161
	Laying Date	-0.143	0.029	0.82 – 0.92	-4.889	1.01E-06
	Average Rainfall	-0.219	0.077	0.69 – 0.93	-2.848	0.0044
	Average Temp.	-0.053	0.040	0.88 – 1.03	-1.332	0.1829
	Clutch Size	0.087	0.013	1.06 – 1.12	6.866	6.59E-12
Average mass	*Predictors**	*Estimates*	*std. Error*	*CI*	*t-value*	*p*
	(Intercept)	10.376	0.22	9.95 – 10.81	47.41	<0.001
N=231	Noise	-0.161	0.16	-0.48 – 0.15	-1	0.316
	Road Distance	-0.342	0.16	-0.66 – -0.02	-2.11	0.035
	Laying Date	-0.557	0.09	-0.72 – -0.39	-6.51	<0.001
	Average Rainfall	0.274	0.24	-0.19 – 0.74	1.15	0.25
	Average Temp.	-0.115	0.24	-0.59 – 0.36	-0.48	0.634
	Clutch Size	-0.294	0.07	-0.44 – -0.15	-4.05	<0.001

*all fixed effects are scaled

Appendix B

Appendix B Table 1 The annual number of blue tit nests contributing to estimates of first egg date, brood size, clutch size, and failure rates at the egg and nestling stage, for the UK (Wales and England).

Region	Parameter	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	All Years
England	*Laying days*	183	259	217	191	356	343	443	456	478	515	529	456	4426
	Clutch size	132	162	145	173	227	300	390	343	359	380	439	332	3382
	Brood size	296	357	324	332	458	632	571	591	707	727	756	714	6465
	Egg fail	214	287	282	280	431	482	490	540	615	653	689	584	5548
	Yng fail	275	333	312	316	455	575	531	585	638	691	691	630	6032
	Total	414	508	423	486	635	798	824	808	932	997	1038	977	8840
Wales	*Laying days*	26	34	43	43	54	56	69	59	88	158	134	86	850
	Clutch size	16	25	16	18	27	35	39	22	62	109	96	75	1120
	Brood size	35	50	68	52	56	67	69	60	158	187	178	140	540
	Egg fail	32	51	50	44	49	69	73	53	148	171	171	106	1117
	Yng fail	33	45	38	48	56	66	69	52	150	147	136	100	940
	Total	42	70	93	62	70	85	99	71	200	238	231	163	1424

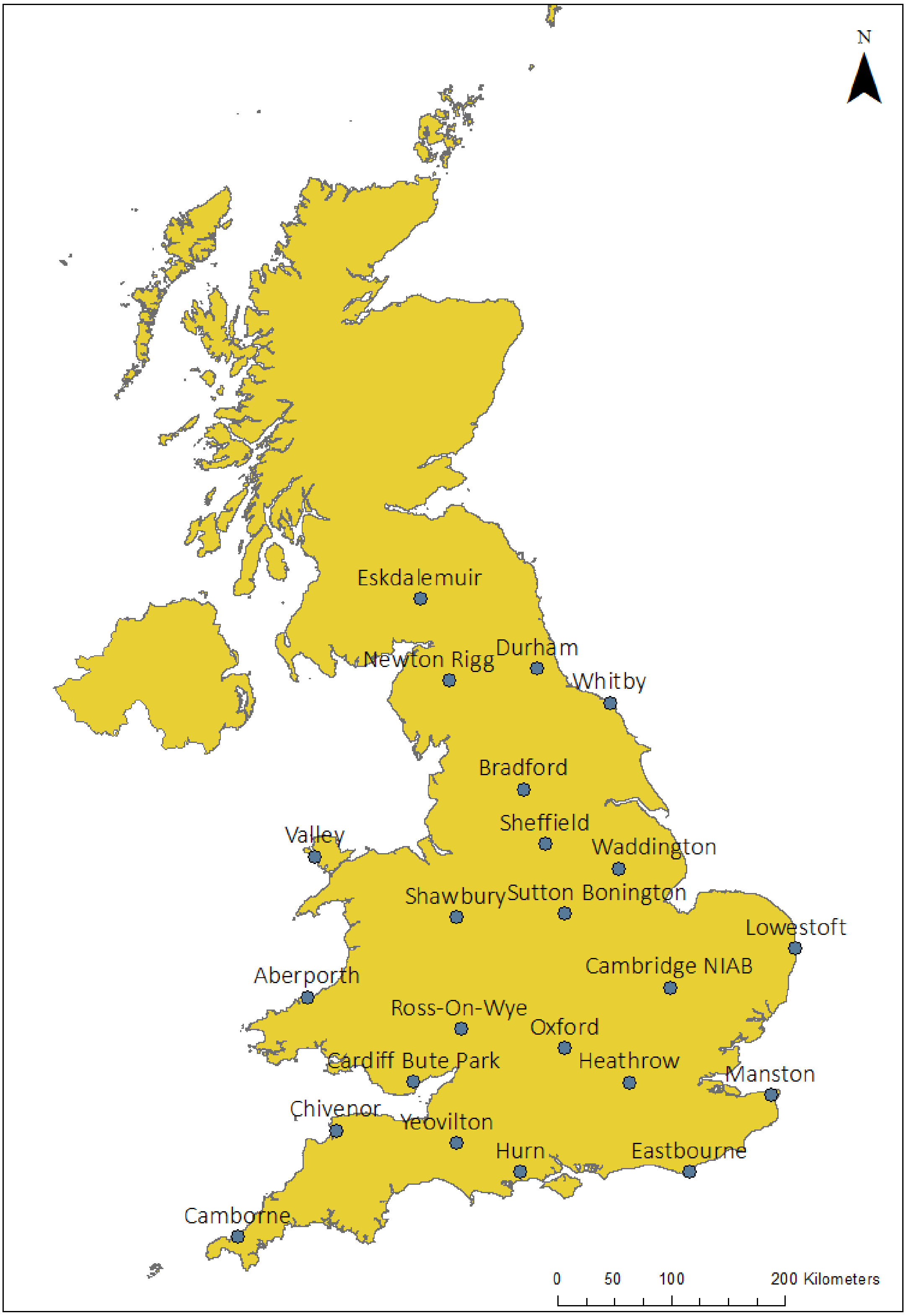
Appendix B Table 2 The annual number of blue tit nests contributing to estimates of first egg date, brood size, clutch size, and failure rates at the egg and nestling stage, for the Netherlands.

Region	Parameter	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	All Years
Netherlands	*Laying days*	41	37	28	43	34	91	88	90	96	170	92	87	96	993
	Clutch size	38	31	6	34	19	86	77	88	95	164	91	87	92	908
	Brood size	9	9	4	27	18	68	67	71	62	105	72	65	73	650
	Egg fail	41	37	22	35	28	92	85	88	95	167	93	81	94	958
	Yng fail	41	29	18	30	31	75	69	67	55	82	68	45	68	678
	Total	41	37	28	43	34	91	88	90	96	170	92	87	96	1003

Appendix B Table 3 Habitat classification system used for GLMMs, compared to BTO habitats and habitat codes as used in the Nest Record Scheme (Crick, 1992)**. Habitats in light grey did not appear in the records used for the analysis.**

Habitats as grouped for analysis	BTO Main Habitat	BTO Habitat Codes	BTO Habitats
Woodland	Woodland (more than 5 m tall)	A	Woodland
		A1	Broad-Leaved Woodland
		A2	Coniferous Woodland
		A3	Mixed Woodland
		A4	Broadleaved Water-Logged Woodland
		A5	Coniferous Water-Logged Woodland
		A6	Mixed Broadleaved And Coniferous Water-Logged Woodland
Urban/Suburban	Human sites	F	
		F1	Human Sites
		F2	Suburban
Open	Human sites	F3	Rural
	Scrubland (or very young woodland less than 5 m tall)	B	Scrubland
		B1	Devastated/Regenerating Woodland/Scrub.
		B2	Chalk Downland Scrub
		B3	Heath Scrub
		B4	Young Coppice
		B5	New Plantation Scrub
		B6	Clear-Felled Woodland With/Without New Saplings
		B7	Other Scrub
	Semi-Natural Grassland and Marsh	C	Semi-Natural Grassland And Marsh
		C1	Chalk Downland
		C2	Upland Grassland/Grass Moor (Unenclosed)
		C3	Grass Moor Mixed With Heather (Unenclosed)
		C4	Machair
		C5	Other Dry Grassland
		C6	Wet Field Vegetation/ Water Meadow, Grazing Marsh
		C7	Reed swamp
		C8	Fen, Other Open Marsh
		C9	Saltmarsh
	Heathlands & Bogs	D	Heathlands And Bogs
	Farmland	E	Farmland
		E1	Apparently Improved Grassland
		E2	Apparently Unimproved Grassland
		E3	Mixed Grass/Tilled Land
		E4	Tilled Land
		E5	Orchard
		E6	Other Farming
	Water-bodies (freshwater)	G	Waterbodies (Freshwater)
		G1	Pond (Less Than 50 m^2)
		G2	Small Water-Body (50-450 m^2)
		G3	Lake/Unlined Reservoir
		G4	Lined Reservoir
		G5	Gravel Pit, Sand Pit, etc.
		G6	Stream (Less Than 3 m Wide)
		G7	River (More Than 3 m Wide)

		G8	Ditch With Water (Less Than 2 m Wide)
		G9	Small Canal (2-5 m Wide)
		G10	
	Coastal	H	Coastal
		H1	Marine -Open Shore
		H2	Marine Shore - Inlet/Cove/Loch
		H3	Estuarine
		H4	Brackish Lagoon
		H4	Brackish Lagoon
	Inland rock	I	Inland Rock
		I1	Cliff
		I2	Scree/Boulder
		I3	Limestone Pavement
		I4	Other Rock Outcrop
		I5	Quarry
		I6	Mine/Spoil/Slag Heap
		I7	Cave
	Miscellaneous	J	Miscellaneous



Appendix B Figure 1 Map of weather stations from the 'Met Office – Historic station data' dataset, providing annual spring temperature and precipitation data for each breeding event. Weather data was joined based on the nearest available (44.30 km ± 30.30 km) meteorological stations to each of the nest sites.

Appendix B Figure 2 Correlation matrix displaying Pearson's correlation coefficient for continuous variables considered for the GLMMs. Positive correlations are displayed in blue and negative correlations in red colour. Colour intensity and the size of the circle are proportional to the correlation coefficients.

Appendix B Table 4 Estimated regression parameters, standard errors, *z* values, and *p*-values for Poisson GLMMs on continuous breeding variables clutch size, brood size, and first egg date and binomial GLMMs on daily nest failure rate at the egg stage and at the nestling stage. Noise score was derived from the noise indicator Lden.

		Predictor	Estimate	Std. Error	z value	p-value	
Clutch Size	4323	(Intercept)	2.175	0.014	152.930	< 0.001	***
		Noise score	0.002	0.005	0.395	0.693	
		Open habitat	-0.034	0.012	-2.772	0.006	**
		Urban habitat	-0.068	0.015	-4.477	< 0.001	***
		Rainfall	-0.006	0.007	-0.883	0.377	
		Latitude	0.001	0.006	0.243	0.808	
		Laying date	-0.086	0.007	-13.130	< 0.001	***
		Min Temp	-0.007	0.009	-0.793	0.428	
Brood Size	8232	(Intercept)	2.017	0.020	102.917	< 0.001	***
		Noise score	-0.003	0.004	-0.669	0.504	
		Open habitat	-0.041	0.009	-4.413	< 0.001	***
		Urban habitat	-0.200	0.013	-15.450	< 0.001	***
		Latitude	0.003	0.005	0.658	0.511	
		Laying date	-0.114	0.005	-22.388	< 0.001	***
		Rainfall	-0.017	0.007	-2.554	0.011	*
		Min Temp	-0.014	0.007	-1.884	0.060	.
First Egg Date	5754	(Intercept)	4.714	0.012	404.223	< 0.001	***
		Noise score	-0.005	0.001	-3.680	< 0.001	***
		Open habitat	0.006	0.003	2.169	0.030	*
		Urban habitat	-0.006	0.004	-1.775	0.076	.
		Latitude	0.017	0.002	10.852	< 0.001	***
		Rainfall	0.013	0.002	6.625	0.001	***
		Min Temp	-0.003	0.002	-1.570	0.116	
Egg Failure Rate	7201	(Intercept)	1.206	0.071	16.966	< 0.001	***
		Noise score	-0.059	0.028	-2.120	0.034	*
		Open habitat	-0.180	0.062	-2.918	0.004	**
		Urban habitat	-0.117	0.078	-1.502	0.133	
		Laying date	0.087	0.034	2.572	0.010	*
		Rainfall	0.111	0.038	2.947	0.003	**
		Min Temp	-0.061	0.043	-1.422	0.155	
		Latitude	-0.060	0.032	-1.865	0.062	
Nestling Failure Rate	4529	(Intercept)	1.598	0.061	26.245	< 0.001	***
		Noise score	0.064	0.022	2.861	0.004	**
		Open habitat	0.369	0.050	7.435	< 0.001	***
		Urban habitat	0.326	0.062	5.228	< 0.001	***
		Latitude	-0.114	0.027	-4.249	< 0.001	***
		Laying date	0.113	0.030	3.783	< 0.001	***
		Rainfall	0.073	0.032	2.314	0.021	*
		Min Temp	-0.005	0.037	-0.127	0.899	

Appendix C

Appendix C Table 1 GLMM model estimates, standard errors (SE), and *p*-values for the score test before and after standardisation, standard deviation (SD_noisetotal) of Noise Score across the entire dataset (including all species and variables) and standard deviation of Noise Score (SD_noise) for each species and breeding variable specific dataset. Standardised values were used to aid direct comparison between species in Figure 1 to Figure 5 of chapter 4.

Breeding var.	Species	Estimate	SE	p	SD_noise	SD_noisetotal	Scaled_estimate	Scaled_SE
clutch	blue_tit	0.012037	0.01	0.022	2790487	330203.1	0.001424	0.001183
clutch	great_tit	-0.00469	0.01	0.446	2939381	330203.1	-0.00053	0.001123
clutch	house_sparrow	-0.06674	0.02	0.001	2514423	330203.1	-0.00876	0.002626
clutch	tree_sparrow	0.004091	0.01	0.609	3188627	330203.1	0.000424	0.001036
clutch	blackbird	0.001669	0.01	0.78	2646926	330203.1	0.000208	0.001247
clutch	song_thrush	0.000679	0.01	0.945	3302663	330203.1	6.79E-05	0.001
clutch	starling	0.084578	0.04	0.021	2986757	330203.1	0.009351	0.004422
clutch	stock_dove	-0.00764	0.01	0.45	2126451	330203.1	-0.00119	0.001553
clutch	kestrel	0.005637	0.01	0.631	2772274	330203.1	0.000671	0.001191
clutch	tawny_owl	0.017906	0.02	0.448	2492586	330203.1	0.002372	0.002649
clutch	barn_owl	-0.01928	0.03	0.467	162094.2	330203.1	-0.03929	0.061113
brood	blue_tit	-0.00717	0	0.071	2999757	330203.1	-0.00079	0
brood	great_tit	-0.00469	0.01	0.446	3495564	330203.1	-0.00044	0.000945
brood	house_sparrow	-0.02334	0.02	0.216	2704934	330203.1	-0.00285	0.002441
brood	tree_sparrow	0.020154	0.01	0.021	3040663	330203.1	0.002189	0.001086
brood	blackbird	-0.00516	0.01	0.468	2650996	330203.1	-0.00064	0.001246
brood	song_thrush	0.006511	0.01	0.629	3058143	330203.1	0.000703	0.00108
brood	starling	0.200506	0.03	<0.001	2734265	330203.1	0.024214	0.003623
brood	stock_dove	0.002176	0.01	0.753	3788820	330203.1	0.00019	0.000872
brood	kestrel	-0.0248	0.01	0.017	3495564	330203.1	-0.00234	0.000945
brood	tawny_owl	0.026009	0.02	0.113	2769296	330203.1	0.003101	0.002385
brood	barn_owl	0.02318	0.03	0.495	195797.1	330203.1	0.039092	0.050594
feg	blue_tit	-0.00037	0	0.753	2790590	330203.1	-4.35E-05	0
feg	great_tit	-0.00303	0	0.032	2790590	330203.1	-0.00036	0
feg	house_sparrow	0.045085	0.01	<0.001	na	330203.1	na	na
feg	tree_sparrow	-0.02845	0.01	<0.001	na	330203.1	na	na
feg	blackbird	-0.00338	0	0.14	na	330203.1	na	na
feg	song_thrush	-0.01213	0	0.944	na	330203.1	na	na
feg	starling	0.01226	0.01	0.019	na	330203.1	na	na
feg	stock_dove	0.39094	0.13	0.002	na	330203.1	na	na
feg	kestrel	-0.00652	0	0.064	3097152	330203.1	-0.0007	0
feg	tawny_owl	-0.01371	0.01	0.08	2529395	330203.1	-0.00179	0.001305
feg	barn_owl	-0.01989	0.01	0.006	na	330203.1	na	na
eggfail	blue_tit	-0.10636	0.03	<0.001	2773839	330203.1	-0.01266	0.003571
eggfail	great_tit	-0.08553	0.03	0.002	2703579	330203.1	-0.01045	0.003664
eggfail	house_sparrow	0.5201	0.37	0.156	2380451	330203.1	0.072145	0.051324
eggfail	tree_sparrow	0.26256	0.06	<0.001	3155950	330203.1	0.027471	0.006278
eggfail	blackbird	0.0359	0.04	0.309	2703579	330203.1	0.004385	0.004885
eggfail	song_thrush	0.0265	0.08	0.736	3139194	330203.1	0.002787	0.008415
eggfail	starling	-4.1806	1.95	0.032	2852940	330203.1	-0.04839	0.02257
eggfail	stock_dove	-0.2801	0.27	0.291	3799619	330203.1	-0.02434	0.023464
eggfail	kestrel	-0.26218	0.2	0.2	2130252	330203.1	-0.04064	0.031001
eggfail	tawny_owl	-0.7229	0.32	0.025	2565797	330203.1	-0.09303	0.041182
chickfail	blue_tit	0.11626	0.02	<0.001	2967121	330203.1	0.012938	0.002226
chickfail	great_tit	-0.01522	0.03	0.57	2967121	330203.1	-0.00169	0.003339
chickfail	house_sparrow	0.05969	0.1	0.536	2665881	330203.1	0.007393	0.012386
chickfail	tree_sparrow	-0.18256	0.08	0.026	3039427	330203.1	-0.01983	0.008691
chickfail	blackbird	0.02313	0.04	0.575	2607184	330203.1	0.002929	0.005066
chickfail	song_thrush	-0.10869	0.09	0.232	3127866	330203.1	-0.01147	0.009501
chickfail	starling	0.24517	0.12	0.048	2544520	330203.1	0.031816	0.015572
chickfail	stock_dove	0.39094	0.13	0.002	3941268	330203.1	0.032753	0.010892
chickfail	kestrel	0.32288	0.1	0.001	3545976	330203.1	0.030067	0.009312
chickfail	tawny_owl	-0.15648	0.12	0.184	2752399	330203.1	-0.01877	0.014396

Appendix C Table 2 GLMM model estimates, standard errors (SE), test statistics, and *p*-values for the score test explaining clutch size. All models included Year as random effect. Strong effects indicated in bold.

Clutch size					
Predictors	Estimates	SE	Statistic	p	Observations
Blue tit					4496
Intercept	2.152	0.01	180.09	**<0.001**	
Noise score	0.012	0.01	2.29	**0.022**	
Open habitats	-0.031	0.01	-2.57	**0.01**	
Urban habitats	-0.091	0.01	-6.12	**<0.001**	
Rainfall	-0.014	0.01	-2.04	**0.042**	
Latitude	-0.014	0.01	-2.24	**0.025**	
Laying date	-0.057	0.01	-9.52	**<0.001**	
Mean min. temp.	-0.017	0.01	-2.06	**0.04**	
Great tit					4359
Intercept	2.050	0.02	100.51	**<0.001**	
Noise score	-0.005	0.01	-0.76	0.446	
Open habitats	-0.031	0.01	-2.4	**0.017**	
Urban habitats	-0.069	0.02	-3.24	**0.001**	
Rainfall	-0.035	0.01	-3.86	**<0.001**	
Latitude	-0.042	0.01	-4.97	**<0.001**	
Laying date	-0.068	0.01	-11.02	**<0.001**	
Mean min. temp.	-0.071	0.01	-7.26	**<0.001**	
House sparrow					289
Intercept	1.459	0.02	70.4	**<0.001**	
Noise score	-0.067	0.02	-3.25	**0.001**	
Laying date ^{2}	-0.065	0.01	-4.35	**<0.001**	
Laying date	0.034	0.02	2.02	**0.044**	
Rainfall	-0.009	0.02	-0.57	0.572	
Latitude	0.006	0.02	0.31	0.76	
Mean min. temp.	-0.008	0.02	-0.45	0.653	
Tree sparrow					1066
Intercept	1.614	0.01	137.17	**<0.001**	
Noise score	0.004	0.01	0.51	0.609	
Laying date	0.022	0.01	3.03	**0.003**	
Rainfall	-0.021	0.01	-1.99	**0.046**	
Latitude	-0.014	0.01	-1.85	0.065	
Mean min. temp.	-0.014	0.01	-1.63	0.104	
Blackbird					1498
Intercept	1.393	0.02	79.09	**<0.001**	
Noise score	0.002	0.01	0.28	0.78	
Open habitats	-0.006	0.02	-0.3	0.762	
Urban habitats	-0.045	0.02	-2.49	**0.013**	
Laying date	0.099	0.01	13.81	**<0.001**	
Laying date ^{2}	-0.078	0.01	-14.01	**<0.001**	
Rainfall	0.001	0.01	0.09	0.929	
Latitude	-0.001	0.01	-0.14	0.892	
Mean min. temp.	0.007	0.01	0.83	0.407	
Song thrush					426
Intercept	1.459	0.01	119.01	**<0.001**	
Noise score	0.001	0.01	0.07	0.945	
Laying date	0.082	0.01	7.28	**<0.001**	

Laying date ^{2}	-0.072	0.01	-8.51	**<0.001**	
Rainfall	0.010	0.01	1.08	0.282	
Latitude	0.006	0.01	0.5	0.62	
Mean min. temp.	-0.004	0.01	-0.33	0.739	
Starling					117
Intercept	1.516	0.04	40.54	**<0.001**	
Noise score	0.085	0.04	2.34	**0.021**	
Laying date	-0.010	0.02	-0.43	0.668	
Rainfall	0.016	0.03	0.5	0.619	
Latitude	-0.017	0.05	-0.33	0.743	
Mean min. temp.	-0.073	0.04	-1.73	0.087	
Stock dove					422
Intercept	0.760	0.01	51.09	**<0.001**	
Noise score	-0.008	0.01	-0.76	0.45	
Laying date	-0.001	0.01	-0.12	0.905	
Laying date ^{2}	-0.015	0.01	-1.43	0.153	
Rainfall	0.001	0.01	0.06	0.949	
Latitude	-0.003	0.01	-0.28	0.776	
Mean min. temp.	0.017	0.01	1.49	0.137	
Kestrel					195
Intercept	1.552	0.02	95.32	**<0.001**	
Noise score	0.006	0.01	0.48	0.631	
Laying date	-0.164	0.02	-7.34	**<0.001**	
Rainfall	0.021	0.01	1.78	0.076	
Latitude	0.000	0.01	0.03	0.978	
Mean min. temp.	-0.030	0.02	-1.78	0.076	
Tawny Owl					174
Intercept	1.052	0.03	35.72	**<0.001**	
Noise score	0.018	0.02	0.76	0.448	
Laying date	-0.098	0.03	-3.52	**0.001**	
Rainfall	0.043	0.03	1.6	0.112	
Latitude	0.016	0.03	0.62	0.534	
Mean min. temp.	0.099	0.03	3.46	**0.001**	
Barn owl					155
Intercept	1.621	0.03	62.01	**<0.001**	
Noise score	-0.019	0.03	-0.73	0.467	
Laying date	0.032	0.03	1.17	0.245	
Rainfall	0.026	0.03	0.9	0.367	
Mean min. temp.	-0.035	0.03	-1.28	0.204	

Appendix C Table 3 GLMM model estimates, standard errors (SE), test statistics, and *p*-values for the score test explaining brood size. All models included Year as random effect. Strong effects indicated in bold.

Brood size					
Predictors	Estimates	SE	Statistic	p	Observations
Blue tit					8955
Intercept	2.038	0.02	107.47	**<0.001**	
Noise score	-0.007	0	-1.8	0.071	
Open habitats	-0.051	0.01	-5.8	**<0.001**	
Urban habitats	-0.205	0.01	-16.26	**<0.001**	
Latitude	0.004	0	0.8	0.421	
Laying date	-0.105	0	-24.18	**<0.001**	
Rainfall	-0.017	0.01	-2.75	**0.006**	
Mean min. temp.	-0.001	0.01	-0.17	0.862	
Great tit					4359
Intercept	2.050	0.02	100.51	**<0.001**	
Noise score	-0.005	0.01	-0.76	0.446	
Open habitats	-0.031	0.01	-2.4	**0.017**	
Urban habitats	-0.069	0.02	-3.24	**0.001**	
Rainfall	-0.035	0.01	-3.86	**<0.001**	
Latitude	-0.042	0.01	-4.97	**<0.001**	
Laying date	-0.068	0.01	-11.02	**<0.001**	
Mean min. temp.	-0.071	0.01	-7.26	**<0.001**	
House sparrow					517
Intercept	1.167	0.04	32.83	**<0.001**	
Noise score	-0.023	0.02	-1.24	0.216	
Laying date	0.004	0.02	0.25	0.802	
Laying date ^{2}	-0.048	0.02	-2.95	**0.003**	
Rainfall	0.070	0.02	3.01	**0.003**	
Latitude	-0.011	0.02	-0.56	0.575	
Mean min. temp.	-0.048	0.02	-2.18	**0.03**	
Tree sparrow					1328
Intercept	1.408	0.02	81.61	**<0.001**	
Noise score	0.020	0.01	2.32	**0.021**	
Laying date	0.023	0.01	2.75	**0.006**	
Rainfall	-0.011	0.01	-0.75	0.456	
Mean min. temp.	-0.041	0.01	-4.12	**<0.001**	
Latitude	-0.052	0.01	-5.8	**<0.001**	
Blackbird					1883
Intercept	1.219	0.02	51.74	**<0.001**	
Noise score	-0.005	0.01	-0.73	0.468	
Open habitats	0.045	0.02	1.94	0.053	
Urban habitats	-0.028	0.02	-1.2	0.23	
Laying date	0.047	0.01	5.94	**<0.001**	
Laying date ^{2}	-0.049	0.01	-7.43	**<0.001**	
Rainfall	0.015	0.01	1.74	0.082	
Latitude	-0.001	0.01	-0.08	0.939	
Mean min. temp.	-0.008	0.01	-0.74	0.46	
Song thrush					404
Intercept	1.324	0.02	70.88	**<0.001**	
Noise score	0.007	0.01	0.48	0.629	
Laying date	0.035	0.02	2.27	**0.024**	

Laying date ^{2}	-0.057	0.01	-4.4	**<0.001**	
Rainfall	0.026	0.01	1.86	0.064	
Latitude	-0.001	0.02	-0.08	0.937	
Mean min. temp.	-0.004	0.02	-0.25	0.801	
Starling					532
Intercept	1.111	0.07	16.21	**<0.001**	
Noise score	0.201	0.03	7.63	**<0.001**	
Laying date	-0.029	0.02	-1.21	0.229	
Rainfall	-0.148	0.04	-3.42	**0.001**	
Latitude	-0.176	0.04	-4.97	**<0.001**	
Mean min. temp.	-0.302	0.04	-7.54	**<0.001**	
Stock dove					950
Intercept	0.618	0.01	64.2	**<0.001**	
Noise score	0.002	0.01	0.31	0.753	
Laying date	-0.004	0.01	-0.55	0.582	
Laying date ^{2}	0.001	0.01	0.1	0.922	
Rainfall	0.011	0.01	1.52	0.13	
Latitude	-0.012	0.01	-1.51	0.131	
Mean min. temp.	-0.011	0.01	-1.43	0.152	
Kestrel					802
Intercept	2.149	0.08	26.16	**<0.001**	
Noise score	-0.025	0.01	-2.39	**0.017**	
Laying date	-0.007	0	-9.31	**<0.001**	
Rainfall	0.012	0.01	1.02	0.309	
Latitude	0.020	0.01	1.92	0.055	
Mean min. temp.	0.003	0.01	0.21	0.837	
Tawny owl					468
Intercept	0.767	0.02	44.71	**<0.001**	
Noise score	0.026	0.02	1.59	0.113	
Laying date	-0.290	0.05	-6.18	**<0.001**	
Rainfall	-0.025	0.02	-1.36	0.173	
Latitude	-0.012	0.02	-0.69	0.491	
Mean min. temp.	0.030	0.02	1.63	0.105	
Barn owl					56
Intercept	1.625	0.03	52.1	**<0.001**	
Noise score	0.023	0.03	0.69	0.495	
Laying date	-0.050	0.03	-1.56	0.126	
Rainfall	-0.029	0.03	-0.84	0.405	
Mean min. temp.	-0.021	0.03	-0.67	0.508	

Appendix C Table **4 GLMM model estimates, standard errors (SE), test statistics, and *p*-values for the score test explaining laying date. All models included Year as random effect. Strong effects indicated in bold.**

			Laying date		
Predictors	Estimates	SE	Statistic	p	Observations
Blue tit					6716
Intercept	4.705	0.01	453.29	**<0.001**	
Noise score	0.000	0	-0.31	0.753	
Open habitats	0.012	0	4.53	**<0.001**	
Urban habitats	0.000	0	-0.1	0.921	
Latitude	0.014	0	9.74	**<0.001**	
Rainfall	0.012	0	7	**<0.001**	
Mean min. temp.	-0.012	0	-6.11	**<0.001**	
Great tit					5112
Intercept	4.708	0.01	366.64	**<0.001**	
Noise score	-0.003	0	-2.14	**0.032**	
Open habitats	0.001	0	0.19	0.853	
Urban habitats	-0.012	0.01	-2.32	**0.02**	
Latitude	0.018	0	8.04	**<0.001**	
Rainfall	0.005	0	2.03	**0.043**	
Mean min. temp.	0.001	0	0.55	0.585	
House sparrow					662
Intercept	4.932	0.01	465.97	**<0.001**	
Noise score	0.045	0.01	5.29	**<0.001**	
Rainfall	0.029	0.01	3.08	**0.002**	
Latitude	0.013	0.01	1.43	0.154	
Mean min. temp.	-0.021	0.01	-2.24	**0.025**	
Tree sparrow					1596
Intercept	4.908	0.01	335.2	**<0.001**	
Noise score	-0.028	0.01	-4.7	**<0.001**	
Rainfall	0.010	0.01	1.03	0.301	
Latitude	0.003	0.01	0.61	0.544	
Mean min. temp.	0.065	0.01	9.48	**<0.001**	
Blackbird					1733
Intercept	4.731	0.01	463.55	**<0.001**	
Noise score	-0.003	0	-1.48	0.14	
Open habitats	-0.004	0.01	-0.47	0.638	
Urban habitats	0.021	0.01	2.9	**0.004**	
Rainfall	0.013	0	4.28	**<0.001**	
Latitude	0.001	0	0.41	0.682	
Mean min. temp.	-0.025	0	-7.15	**<0.001**	
Song thrush					1049
Intercept	0.000	0.02	288.99	**<0.001**	
Noise score	-0.012	0	-0.07	0.944	
Rainfall	-0.012	0.01	-2.32	**0.02**	
Latitude	-0.019	0	-3.05	**0.002**	
Mean min. temp.		0	-3.87	**<0.001**	
Starling					593
Intercept	4.678	0.01	439.78	**<0.001**	
Noise score	0.012	0.01	2.34	**0.019**	

Rainfall	-0.002	0.01	-0.35	0.723	
Mean min. temp.	-0.010	0.01	-1.55	0.122	
Latitude	0.029	0.01	4.71	**<0.001**	
Stock dove					193
Intercept	2.936	0.13	23.28	**<0.001**	
Noise score	0.391	0.13	3.07	**0.002**	
Rainfall	0.131	0.14	0.93	0.35	
Laying date	-0.062	0.12	-0.53	0.597	
Latitude	-0.345	0.13	-2.74	**0.006**	
Kestrel					800
Intercept	4.700	0.02	292.03	**<0.001**	
Noise score	-0.007	0	-1.85	0.064	
Latitude	0.009	0	2.33	**0.02**	
Rainfall	-0.003	0.01	-0.62	0.533	
Mean min. temp.	-0.005	0.01	-0.89	0.371	
Tawny owl					267
Intercept	4.231	0.01	357.03	**<0.001**	
Noise score	-0.014	0.01	-1.75	0.08	
Rainfall	-0.022	0.01	-2.32	**0.02**	
Latitude	0.037	0.01	4.48	**<0.001**	
Mean min. temp.	-0.049	0.01	-5.37	**<0.001**	
Barn owl					211
Intercept	4.745	0.02	227.48	**<0.001**	
Noise score	-0.020	0.01	-2.77	**0.006**	
Rainfall	-0.009	0.02	-0.41	0.681	
Mean min. temp.	-0.018	0.02	-0.82	0.41	

Appendix C Table 5 GLMM model estimates, standard errors (SE), test statistics, and *p*-values for the score test explaining nest failure at the egg stage. All models included Year as random effect. Strong effects indicated in bold.

	Failure rate at egg stage				
Predictors	Estimates	SE	Statistic	p	Observations
Blue tit					8319
Intercept	1.219	0.08	15.4	**<0.001**	
Noise score	-0.106	0.03	-4.14	**<0.001**	
Open habitats	-0.128	0.05	-2.41	**0.016**	
Urban habitats	-0.192	0.08	-2.53	**0.011**	
Laying date	0.080	0.03	3.09	**0.002**	
Rainfall	0.097	0.03	3	**0.003**	
Mean min. temp.	0.098	0.04	2.57	**0.01**	
Latitude	-0.021	0.03	-0.71	0.475	
Great tit					7258
Intercept	1.317	0.09	15.44	**<0.001**	
Noise score	-0.086	0.03	-3.05	**0.002**	
Open habitats	0.024	0.05	0.5	0.619	
Urban habitats	-0.646	0.11	-5.97	**<0.001**	
Laying date	-0.323	0.02	4.85	**<0.001**	
Rainfall	0.100	0.04	-0.87	0.385	
Mean min. temp.	-0.036	0.04	-8.35	**<0.001**	
Latitude	-0.374	0.04	-8.08	**<0.001**	
House sparrow					329
Intercept	-2.693	1.61	-1.68	0.094	
Noise score	0.520	0.37	1.42	0.156	
Rainfall	0.676	0.51	1.32	0.186	
Laying date	-0.156	0.18	-0.85	0.396	
Mean min. temp.	0.345	0.33	1.05	0.293	
Tree sparrow					1204
Intercept	0.700	0.12	5.77	**<0.001**	
Noise score	0.263	0.06	4.34	**<0.001**	
Latitude	-0.132	0.07	-1.99	**0.047**	
Rainfall	0.080	0.1	0.79	0.428	
Laying date	-0.121	0.06	-1.89	0.059	
Mean min. temp.	0.212	0.08	2.65	**0.008**	
Blackbird					1594
Intercept	1.671	0.1	17.01	**<0.001**	
Noise score	0.036	0.04	1.02	0.309	
Open habitats	-0.258	0.12	-2.24	**0.025**	
Urban habitats	-0.141	0.11	-1.29	0.198	
Latitude	0.092	0.05	2.01	**0.045**	
Rainfall	-0.109	0.04	-2.64	**0.008**	
Laying date	-0.193	0.04	-4.86	**<0.001**	
Mean min. temp.	-0.051	0.05	-1.1	0.27	
Song thrush					383
Intercept	1.561	0.08	19.14	**<0.001**	
Noise score	0.027	0.08	0.34	0.736	
Latitude	-0.147	0.09	-1.57	0.115	
Rainfall	-0.035	0.09	-0.41	0.679	
Laying date	-0.129	0.08	-1.69	0.092	
Mean min. temp.	-0.042	0.09	-0.46	0.647	

Starling					216
Intercept	-5.744	3	-1.92	0.055	
Noise score	-4.181	1.95	-2.14	**0.032**	
Latitude	3.220	1.62	1.99	**0.046**	
Rainfall	2.039	1.1	1.85	0.065	
Laying date	1.327	0.75	1.76	0.079	
Mean min. temp.	-0.114	0.84	-0.14	0.892	
Stock dove					324
Intercept	0.700	0.32	2.21	**0.027**	
Noise score	-0.280	0.27	-1.06	0.291	
Rainfall	0.104	0.2	0.51	0.61	
Laying date	0.120	0.13	0.93	0.355	
Mean min. temp.	-0.212	0.16	-1.34	0.18	
Latitude	-0.264	0.19	-1.36	0.175	
Kestrel					443
Intercept	-0.425	0.53	-0.81	0.42	
Noise score	-0.262	0.2	-1.28	0.2	
Latitude	0.691	0.16	4.22	**<0.001**	
Rainfall	0.255	0.19	1.32	0.188	
Laying date	1.177	0.14	8.3	**<0.001**	
Mean min. temp.	0.052	0.17	0.3	0.761	
Tawny owl					123
Intercept	1.235	0.39	3.14	**0.002**	
Noise score	-0.723	0.32	-2.24	**0.025**	
Rainfall	0.484	0.26	1.83	0.067	
Laying date	0.426	0.22	1.95	**0.051**	
Mean min. temp.	0.116	0.23	0.5	0.616	

Appendix C Table 6 GLMM model estimates, standard errors (SE), test statistics, and *p*-values for the score test explaining nest failure at the nestling stage. All models included Year as random effect. Strong effects indicated in bold.

Failure rate at nestling stage

Predictors	Estimates	SE	Statistic	p	Observations
Blue tit					5585
Intercept	1.407	0.07	20.6	**<0.001**	
Noise score	0.116	0.02	5.63	**<0.001**	
Open habitats	0.478	0.05	10.26	**<0.001**	
Urban habitats	0.394	0.06	6.63	**<0.001**	
Latitude	-0.142	0.03	-5.62	**<0.001**	
Laying date	0.194	0.03	7.11	**<0.001**	
Rainfall	0.052	0.03	1.77	0.077	
Mean min. temp.	-0.098	0.04	-2.72	**0.006**	
Great tit					4103
Intercept	1.775	0.08	17.12	**<0.001**	
Noise score	-0.015	0.03	-0.57	0.57	
Open habitats	-0.162	0.06	7.33	**<0.001**	
Urban habitats	-0.405	0.08	2.89	**0.004**	
Latitude	0.073	0.04	1.96	**0.05**	
Laying date	0.000	0.03	-0.01	0.989	
Rainfall	0.153	0.04	3.78	**<0.001**	
Mean min. temp.	0.287	0.05	6.08	**<0.001**	
House sparrow					371
Intercept	1.943	0.18	11.06	**<0.001**	
Noise score	0.060	0.1	0.62	0.536	
Latitude	-0.354	0.12	-3.06	**0.002**	
Rainfall	0.350	0.13	2.71	**0.007**	
Mean min. temp.	0.157	0.13	1.18	0.238	
Laying date	0.165	0.09	1.94	0.052	
Tree sparrow					672
Intercept	1.278	0.13	9.56	**<0.001**	
Noise score	-0.183	0.08	-2.23	**0.026**	
Latitude	-0.250	0.06	-3.99	**<0.001**	
Rainfall	0.077	0.11	0.68	0.494	
Mean min. temp.	-0.106	0.11	-0.95	0.344	
Laying date	0.152	0.06	2.37	**0.018**	
Blackbird					1343
Intercept	1.298	0.13	10.21	**<0.001**	
Noise score	0.023	0.04	0.56	0.575	
Open habitats	0.367	0.14	2.61	**0.009**	
Urban habitats	0.362	0.14	2.57	**0.01**	
Latitude	0.001	0.06	0.02	0.986	
Rainfall	0.033	0.05	0.74	0.46	
Laying date	-0.107	0.04	-2.66	**0.008**	
Mean min. temp.	-0.042	0.08	-0.54	0.588	
Song thrush					295
Intercept	1.699	0.09	19.95	**<0.001**	
Noise score	-0.109	0.09	-1.19	0.232	
Latitude	-0.042	0.11	-0.39	0.694	
Mean min. temp.	0.089	0.1	0.85	0.397	
Rainfall	0.201	0.08	2.41	**0.016**	

Laying date	-0.020	0.09	-0.23	0.815	
Starling					257
Intercept	1.721	0.28	6.16	**<0.001**	
Noise score	0.245	0.12	1.97	**0.048**	
Rainfall	-0.049	0.22	-0.22	0.828	
Laying date	0.269	0.13	2.1	**0.036**	
Mean min. temp.	0.948	0.17	5.47	**<0.001**	
Stock dove					193
Intercept	2.936	0.13	23.28	**<0.001**	
Noise score	0.391	0.13	3.07	**0.002**	
Rainfall	0.131	0.14	0.93	0.35	
Laying date	-0.062	0.12	-0.53	0.597	
Latitude	-0.345	0.13	-2.74	**0.006**	
Kestrel					392
Intercept	2.356	0.39	6.07	**<0.001**	
Noise score	0.323	0.1	3.27	**0.001**	
Latitude	0.014	0.08	0.18	0.861	
Rainfall	0.420	0.12	3.57	**<0.001**	
Laying date	-0.169	0.11	-1.58	0.115	
Mean min. temp.	1.929	0.16	11.88	**<0.001**	
Tawny owl					238
Intercept	3.376	0.15	23.13	**<0.001**	
Noise score	-0.156	0.12	-1.33	0.184	
Latitude	0.222	0.13	1.73	0.083	
Mean min. temp.	-0.343	0.14	-2.49	0.013	
Rainfall	-0.066	0.16	-0.42	0.672	
Laying date	0.037	0.12	0.3	0.763	

Appendix D

Appendix D Table 1 Pre vs post playback for noise level experiment (Experiment 1)

	Playback type	Treatment	n	Mean	Sd.	Wilcoxon z	Effect size, r	W	p
Number of songs	noise No-noise	pre	22	3.82	6.51				
		after	22	18.77	22.45	-3.6168	-0.7711	169.0	0.0003
	High-level noise	pre	21	4.00	5.80				
		after	21	16.81	16.32	-3.6595	-0.7986	170.0	0.0003
	Low-level noise	pre	22	5.18	4.91				
		after	22	13.09	13.55	-2.9664	-0.6324	154.0	0.003
Number of flights	No-noise	pre	22	1.09	1.19				
		after	22	6.64	4.68	-3.8071	-0.8117	190.0	0.0001
	High-level noise	pre	21	1.00	1.38				
		after	21	8.67	4.19	-3.9777	-0.8680	230.0	0.0001
	Low-level noise	pre	22	0.50	0.80				
		after	22	4.45	3.10	-3.8091	-0.8121	190.0	0.000
Time spent within 5 m (s)	No-noise	pre	22	3.05	12.81				
		after	22	14.14	21.77	-2.3694	-0.5052	43.0	0.018
	High-level noise	pre	21	10.00	21.91				
		after	21	26.95	24.23	-2.6502	-0.5783	54.0	0.008
	Low-level noise	pre	22	2.73	12.79				
		after	22	12.18	20.59	-2.1024	-0.4482	21.0	0.036

Appendix D Table 2 Control vs consistent stimuli for noise level experiment (Experiment 1)

	Playback type	Treatment	n	Mean	Sd.	Wilcoxon z	Effect size, r	W	p
Number of songs	No-noise	consistent	22	20.50	21.24				
		control	22	12.68	18.15	-2.8390	-0.6195	181.5	0.005
	High-level noise	consistent	21	21.48	18.41				
		control	21	21.29	18.96	-0.0696	0.0152	118.0	0.945
	Low-level noise	consistent	22	18.73	13.54				
		control	22	10.18	11.97	-3.8017	-0.8105	244.0	0.0014
Response latency (s)	No-noise	consistent	22	11.91	19.05				
		control	22	19.64	26.38	-1.4959	-0.3189	72.00	0.135
	High-level noise	consistent	21	22.86	45.85				
		control	21	8.33	8.61	-0.9533	-0.2080	131.0	0.340
	Low-level noise	consistent	22	14.59	17.84				
		control	22	21.14	43.78	-0.0650	-0.0139	124.0	0.948
Number of flights	No-noise	consistent	22	6.23	4.22				
		control	22	6.77	3.95	-0.2408	-0.0513	79.5	0.810
	High-level noise	consistent	21	8.86	6.58				
		control	21	9.10	5.52	-0.6102	0.1332	97.5	0.542
	Low-level noise	consistent	22	4.55	3.02				
		control	22	4.45	2.96	-0.1320	-0.0281	101.0	0.895
Time spent within 5 m (s)	No-noise	consistent	22	69.45	76.33				
		control	22	66.91	84.51	-0.1420	-0.0303	63.0	0.887
	High-level noise	consistent	21	80.52	75.60				
		control	21	86.00	67.86	-0.1960	-0.0428	80.5	0.845
	Low-level noise	consistent	22	30.00	52.38				
		control	22	32.00	56.58	-0.0445	0.0095	32.0	0.965

Appendix D Table 3 Pre vs post playback for noise frequency band experiment (Experiment 2)

	Playback type	Treatment	n	Mean	Sd.	Wilcoxon z	Effect size, r	W	p
Number of songs	Low-frequency	pre	21	3.67	5.35				
		after	21	9.67	10.68	-2.2229	-0.4851	34	0.026
	High-frequency	pre	20	2.50	3.59				
		after	20	7.90	7.79	-3.0041	-0.6717	20	0.003
Number of flights	Low-frequency	pre	21	1.29	1.52				
		after	21	5.00	4.46	-3.4687	-0.7569	16.5	0.001
	High-frequency	pre	20	0.80	0.89				
		after	20	5.05	3.73	-3.5521	-0.7943	6.5	0.0004
Time spent within 5 m (s)	Low-frequency	pre	21	8.57	21.51				
		after	21	17.14	23.43	-1.9022	-0.4151	6	0.057
	High-frequency	pre	20	1.00	4.47				
		after	20	12.95	18.62	-2.2529	-0.5038	3	0.024

Appendix D Table 4 Control vs consistent stimuli for noise frequency band experiment (Experiment 2)

	Playback type	Treatment	n	Mean	Sd.	Wilcoxon z	Effect size, r	W	p
Number of songs	Low-frequency	consistent	21	14.29	9.95				
		control	21	9.05	10.18	-2.5771	-0.5624	190	0.010
	High-frequency	consistent	20	13.20	16.47				
		control	20	9.65	10.47	-1.1993	-0.2617	113.5	0.230
Number of flights	Low-frequency	consistent	21	7.38	5.85				
		control	21	6.05	5.35	-0.6476	-0.1413	134.5	0.517
	High-frequency	consistent	20	6.75	3.39				
		control	20	5.50	3.61	-0.2588	-0.2588	112.5	0.247
Response latency (s)	Low-frequency	consistent	21	8.71	9.51				
		control	21	19.38	28.87	-0.6052	-0.1321	79.5	0.545
	High-frequency	consistent	20	8.15	7.18				
		control	20	21.60	27.53	-1.8499	-0.4137	55	0.064
Time spent within 5 m (s)	Low-frequency	consistent	21	66.38	74.59				
		control	21	83.71	74.08	-0.9232	-0.2015	56.5	0.356
	High-frequency	consistent	20	41.40	50.03				
		control	20	38.15	55.74	-1.3295	-0.2973	65	0.184