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### **Road noise alters foraging duration and vigilance behaviour of three common tit species**

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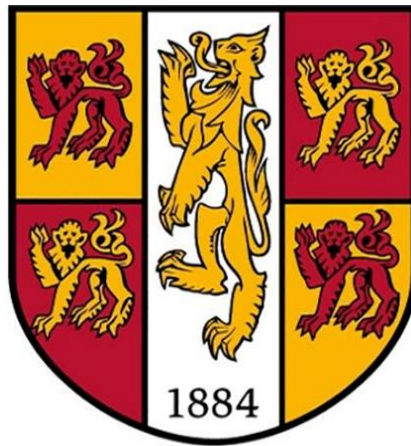
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# **Road noise alters foraging duration and vigilance behaviour of three common tit species**

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Key words: *Cyanistes caeruleus*, *Parus major*, *Pariparus ater*, anthropogenic, noise, foraging, vigilance

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## Chapter 1: Review

### Introduction

It is widely accepted that many human activities have a negative effect on the survival of wild species at both a local and global scale (Steidl and Powell, 2006). Due to the growth of human population, greater demand is placed on rates of resource extraction, urbanisation and transportation network expansion, and has led to an unprecedented rise in background noise levels (Slabbekoorn and Ripmeester, 2008; Francis, *et al.* 2009; Shannon, *et al.* 2016a). These elevated anthropogenic noise levels permeate from areas of high human population density into many natural landscapes, and their effects are raising concern for humans and wildlife alike (Bluhm, *et al.* 2007; Shannon, *et al.* 2016a; Petrelli, *et al.* 2017). The rise in background noise levels have been recognised as a major contributor to declines in wildlife population densities (Carr and Fahrig, 2001; Barber, *et al.* 2010; McLaughlin and Kunc, 2013), poor reproductive success (Barber, *et al.* 2010; Alloush, *et al.* 2011; Francis, *et al.* 2011a; Purser and Radford, 2011; Dahl, *et al.* 2012; Kight, *et al.* 2012; McLaughlin and Kunc, 2013) and reduced feeding rates (Leonard and Horn, 2012; Luo, *et al.* 2015; Payne, *et al.* 2015; Blair, *et al.* 2016). In bird species, anthropogenic noise has contributed to the homogenisation of communities (Barber, *et al.* 2010; Proppe, *et al.* 2013; McClure, *et al.* 2017), area avoidance (Slabbekoorn and Ripmeester, 2008; Francis, *et al.* 2009; Goodwin and Shriver, 2010; McClure, *et al.* 2013; McLaughlin and Kunc, 2013; Chen and Koprowski, 2015; Forney, *et al.* 2017; Shonfield and Bayne, 2017), alteration of migration routes and stop-over sites (van Opzeeland and Slabbekoorn, 2012; Tennessen, *et al.* 2014; McClure, *et al.* 2016; Kavanagh, *et al.* 2017), changes in vocalisations (Foote, *et al.* 2004; Nemeth, *et al.* 2013; Costello and Symes, 2014; McMullen, *et al.* 2014; Kern and Radford, 2016) and a shift in vigilance behaviour (Quinn, *et al.* 2006; Shannon, *et al.* 2014; Klett-Mingo, *et al.* 2016; Branstetter, *et al.* 2018). Noise has also been seen to contribute to depression and annoyance (Stansfeld, *et al.* 2000; Freitas, *et al.* 2012; Beutel, *et al.* 2016), sleep deprivation (Hume, *et al.* 2012; Halperin, 2014; Shannon, *et al.* 2016a) and cardiovascular disease (Stansfeld, *et al.* 2000; Babisch, *et al.* 2013; Shannon, *et al.* 2016a) and negative effects on long-term memory and cognitive performance (Stansfeld, *et al.* 2000; Jahncke, 2012; Klatte, *et al.* 2013) in humans.

Within the marine environment, acoustic pollution from seismic surveys and sonar can expose wildlife to noise in excess of 120dB, whilst in some areas the widespread increase in commercial shipping has caused ocean background noise to double every decade (Weilgart, 2007a). In terrestrial environments, industrial noise sources such as gas drilling stations have continued to increase in their prevalence across the landscape, producing continuous noise throughout the day and night (Blickley and Patricelli, 2010; Blickley, *et al.* 2012). Road networks also present a physical and acoustic obstacle to wildlife, with 83% of areas within the United States of America reportedly within 1km of a road (Riitters and Wickham, 2003). Not only does this fragmentation increase risk of impact from direct road mortality, but also pollution, visual disturbance, wind turbulence, ground vibration, habitat reduction and edge-effects (Arévalo and Newhard, 2011; Blickley, *et al.* 2012; Crino, *et al.* 2013; Injaian, *et al.* 2018a).

With the wealth of research focusing on the effect of anthropogenic noise on wildlife, many comprehensive reviews have been published to collate this information. Typically, review papers either focus broadly on the effects on wildlife in general (Rabin, *et al.* 2003; Wright, *et al.* 2007; Barber, *et al.* 2010; Kight, and Swaddle, 2011; Shannon, *et al.* 2016a), or specifically review the literature applying to a single taxonomic group (Patricelli and Blickley, 2006; Warren, *et al.* 2006; Hatch and Wright, 2007; Nowacek, *et al.* 2007; Weilgart, 2007b; Popper and Hastings, 2009; Ríos-Chelén, 2009; Slabbekoorn, *et al.* 2010; Ortega, 2012). In the extensive review published by Shannon, *et al.* (2016), the authors included all studies that explored the relationship between noise and wildlife published 1990-2013. In the review, Shannon, *et al.* (2016) found that across all taxonomic groups studied, most published material was on birds (37%).

Research focus on the effects of anthropogenic noise on avian species in particular has seen a real surge of interest in the past two decades (Hatch and Wright, 2007; Nowacek, *et al.* 2007; Weilgart, 2007b; Wright, *et al.* 2007; Kight and Swaddle, 2011; Ortega, 2012; Shannon, *et al.* 2016a). The increase in their popularity likely stems from their abundance in, and tolerance to, many environments across the urban gradient (Clergeau, *et al.* 1998; Slabbekoorn and Ripmeester, 2008; Shochat, *et al.* 2010; Meffert and Dziock, 2013; Salmón, *et al.* 2018). This, paired with their reliance on acoustic communications for information transfer, a behaviour that is known to be impacted by increased levels of background noise (Rheindt, 2003; Hu and Cardoso, 2009; Lowry, *et al.* 2012), makes them

a key focal taxa. Alarm calls (Templeton, *et al.* 2016), territorial song (Kleist, *et al.* 2016), mate attraction (Halfwerk, *et al.* 2011a; Luther, *et al.* 2016) and offspring cues (Leonard and Horn, 2012; Schroeder, *et al.* 2012; Lucass, *et al.* 2016) all require a reliable transmission and delivery of vocal communication between conspecifics (Grade and Sieving, 2016), easily disrupted by extraneous noise. Birds also fill many vital trophic niches, from pollinators and dispersers to providing prey and predatory species to sustain and manage populations (Francis, *et al.* 2009; Francis, *et al.* 2012). This versatility makes them excellent indicators to ecosystem health (Francis, *et al.* 2012).

From simple observations during noise events in early years (Ellis, *et al.* 1991; Delaney, *et al.* 1999) to correlative studies (Habib, *et al.* 2006; Francis, *et al.* 2009; Parris and Schneider, 2009) and finally onto incorporating noise playback (Blickley, *et al.* 2012; McClure, *et al.* 2013; Dorado-Correa, *et al.* 2018), the advance in noise research techniques is evident. As these approaches develop, it is vital that they are utilised to explore future avenues of research and bridge gaps in our current knowledge. Though simple observations provide clear evidence as to current behaviours and trends, incorporating a noise playback element into a study can allow for predictions to be made with regards future noise levels as well as controlling for confounding variables.

Investigation into noise presentation has revealed marked differences between the impact of unpredictable, high-intensity and chronic, low-frequency noise. High-intensity noise events, such as explosions from firework displays as found by Shamoun-Baranes, *et al.* (2011), often startle surrounding birds, potentially impairing hearing, causing life-preserving behaviours such as fleeing, and ultimately the rise in stress levels (Payne, *et al.* 2012; Shannon, *et al.* 2016a). Chronic, low frequency noise, such as traffic, can impact an environment for years (as found in a study by Halfwerk, *et al.* (2011a)) and can result in much longer-lasting impacts (Blickley, *et al.* 2012; Injaian, *et al.* 2018a). These impacts can include heightened long-term physiological stress levels, alteration of social interactions, reduced reproductive success and poor parent-offspring feeding rates (Halfwerk, *et al.* 2011a; Blickley, *et al.* 2012; Schroeder, *et al.* 2012; Injaian, *et al.* 2018a).

Due to the popularity of this taxonomic group and depth of existing research, this review will focus solely on avian species, providing detailed insight spanning almost three decades of literature. This review will aim to (1) successfully collate and synthesise the existing literature published on the effects of anthropogenic noise on birds from 1990-

2019, (2) identify current trends and underrepresented areas in the research, and (3) discuss the importance of bridging those gaps to form an accurate representation of anthropogenic noise issues in the future. The outcome of this review is to stimulate an increased interest in avian biological responses to anthropogenic noise levels, which might have been overlooked by the existing literature. Often these areas are over-looked due to challenges with linking behaviour directly to fitness costs, or from difficulties scaling-up noise studies to be able to investigate effects across larger spatial and temporal scales. Despite these challenges, it is hoped that this review will encourage well-advised thought for future research and encourage the inclusion of advancing research techniques. Ultimately it is hoped this interest will aid in the implementation of future conservation strategies and dilute any impact to wildlife from anthropogenic noise disturbance.



## Review Methodology

The methodology executed in this review followed that used by Shannon, *et al.* (2016) in their comprehensive review. Using the same search procedure, definitions of responses measured and noise categories, this review builds on their findings, focusing on literature published solely on birds from 1990-2019. Previously collated literature on birds spanning 1990-2013 was provided by the lead author for this review (see Shannon, *et al.* (2016) for previous methodology) ( $N = 92$ ).

The remaining search for literature on birds published 2013-2019 was conducted via ISI *Web of Science*, restricted to areas 'Ecology', 'Multidisciplinary Sciences', 'Zoology', 'Behavioral Sciences', 'Urban Studies', 'Acoustics', 'Environmental Sciences', 'Evolutionary Biology', 'Ornithology', 'Environmental Studies' and 'Biodiversity Conservation'. These areas differed slightly to those used by Shannon, *et al.* (2016) to avoid excluding relevant studies, but also to keep the search relevant to avian species. The specific search terms used were '(TS=(bird AND noise))', excluding the other taxa used in the original search by Shannon, *et al.* (2016) and excluding 'sonar', which did not apply to birds ( $N = 540$ ). Papers were filtered to include only empirical studies focused on documenting the effects of anthropogenic noise on birds, and combined with those found by Shannon, *et al.* (2016) to generate the final data set ( $N = 225$ ).

The relevant studies were categorised by year of publication, study type (playback, natural or theoretical), whether the study was performed in the field or laboratory, geographic region, response measured and noise stimulus used. Additional categories added for this review were: taxonomic order of focal species, whether noise levels used were via dosage or binary presentation and the playback noise levels used, in decibels (dB).

A playback study was defined as using projected noise from an artificial source in the environment, such as a speaker, set up by researchers. A natural experiment was therefore defined as a study which tested the response to sound already existing within the environment, which had not been introduced for the purpose of the study. Responses measured were categorised as: ecosystem, life history/reproduction, mating behaviour, movement behaviour, physiological, population, vocal behaviour and vigilance behaviour. Categories for noise stimulus used were: environmental, industrial, military, recreation, transportation and other. Following the categorisation of noise studies by

Shannon, *et al.* (2016), studies assigned to the environmental category concentrated on general acoustic energy present within an environment, typically referred to as 'background noise'. The industrial categories included studies focused on noise from construction and industrial work sites, such as those involving pile driving, wind turbines and gas compressor sites. Military noise was defined as gunshot, explosions, sonic booms and military aircraft. Recreation included noise generated by transport used for leisure, such as helicopter tours, ecotourism and large-scale celebratory events. The transportation category was kept for commercial and privately owned road (cars, motorbikes and heavy-goods vehicles) and air transport (passenger aircraft and helicopters). The 'other' category comprised of the remaining sound studies; largely those involving simulated white- and pink-noise. White- and pink-noise is defined as synthetic noise which features sound frequencies at varying intensities. White-noise ( $1/f^0$ ) features all sound frequencies at equal amplitude, whereas in pink-noise ( $1/f^1$ ), higher-frequency sounds are quietened (Stoyanov, *et al.* 2011). A study was deemed as using binary playbacks if it used a single level of noise to test whether there is a response present. Dose-response playbacks were defined as a study using two or more noise levels which increased in relatively equal increments to test for a change in behaviour.

## **Trends in Current Knowledge**

### *Geographic Region*

Of the 225 empirical scientific papers published on the effects of anthropogenic noise on birds 1990-2019, 52% of those were based in North America (Table 1). With a further 30% based in Europe, 82% of all studies were restricted to the northern hemisphere. Continents such as South America (6%), Australia (5%), Asia (5%) and Africa (0%) were largely underrepresented despite accounting for a significant proportion of landmass and biodiversity, totalling only 16% of studies. In spite of their underrepresentation, developing nations are those most likely to undergo the greatest changes in their acoustic environment in the future through rapid population growth and urbanisation (Shannon, *et al.* 2016a). These developing countries with vast populations currently, renowned for their noisy cities, would provide vital contribution to representing global sound levels, but are typically missing from the literature.

India, a developing country well-known for its vast population, was found in a study by Lynch (2019) to have anthropogenic noise levels that greatly exceed those typically found in western urban areas. India therefore may be a typical example of a developing country which would provide vital insight into regional noise levels, but due to geographical bias, many like it may be absent from the literature. As in many other countries, religious events in India are often accompanied by celebratory music, fireworks and amplified speeches, with noise from these public festival events known to reach levels higher than 120dBA (Lynch, 2019). These noise levels occur despite the Indian Noise Pollution (Control and Regulation) Rules 2000, which aim to restrict noise to 40-75dBA depending on the time and location of events (Lynch, 2019). During Diwali celebrations 2014-2016, the Maharashtra Pollution Control Board (MPCB) recorded average daytime ambient noise levels ranging from 62-91dBA, and night-time noise levels from 58-86dBA (Lynch, 2019). These noise levels are capable of spanning over days or weeks depending on the festival, and are at levels which have the potential to cause significant disturbance to both humans and wildlife (Lynch, 2019). The recorded noise levels however are suspected of bias, with the MPCB reportedly limiting noise level recording to select buildings, often located away from the noise source, failing to provide an accurate reflection on the impact of the noise on those nearer the source (Lynch, 2019). Non-governmental organisations (NGOs) however appear to report noise levels with opposing bias, often selecting the

loudest sources of noise at which to take and report noise readings (Lynch, 2019). Ideally, a non-biased scientific approach should be taken to provide a true reflection of how loud urbanised areas in developing countries and the southern hemisphere can be, and how this may impact the behaviour and disturbance of their highly biodiverse bird populations.

Table 1 - An overview of literature focusing on the effects of anthropogenic noise on birds, published 1990-2019 ( $N = 225$ ).

**Number of Papers Published**

1990-1999	2000-2009	2010-2019	1990-2019
4	24	197	225

**Geographic Region**

North America	Europe	South America	Australia	Asia	Africa	Global
52%	30%	6%	5%	5%	0%	1%

**Biological Response Measured**

Vocal	Population	Physiological	Life History/ Reproduction	Movement	Vigilance	Mating	Ecosystem
49%	17%	9%	8%	7%	7%	2%	1%

**Noise Source Studied**

Environmental	Transportation	Industry	Military	Recreation	Other
41%	30%	14%	2%	2%	10%

*Biological Response Measured*

As predicted, the vast majority of published avian studies focused on vocal communication and adjustment in response to anthropogenic noise (49%) (Table 1). The popularity and interest in these vocal studies increased dramatically in 2009, with a steadily increasing number of studies published in subsequent years (Fig. 1) (Appendix 1). Alterations in song timing, frequency and amplitude in response to transport noise levels have been a popular research topic (10%,  $n = 23$ ). To help overcome vocal masking due to road noise, Brumm (2004) found that male nightingales (*Luscinia megarhynchos*) from noisier areas sang at higher amplitudes than those from areas less affected by noise. It was also found that nightingale males do not automatically maximise their call amplitude, but regulate it flexibly in response to background noise levels (Brumm and

Todt, 2002). Though this vocal adjustment will aid in vital song transmission for mate attraction and territory defence, there will be an increased energetic cost for singing at a higher level (Brumm, 2004). In a vocal frequency study by Parris and Schneider (2008) comparing two Australian species, the lower-pitched singing species were seen to increase their minimum frequencies with proximity to road noise, whereas the higher-pitched species did not. This increase in the frequency of songs has been well-documented among a range of species, and has proven effective at reducing the overlap in frequency with traffic noise (Rheindt, 2003; Slabbekoorn and Peet, 2003; Slabbekoorn and den Boer-Visser, 2006; Nemeth and Brumm, 2009; Bermúdez-Cuamatzin, *et al.* 2011; Halfwerk, *et al.* 2011b; Ríos-Chelén, *et al.* 2017). However, lower-frequency songs are often still preferred by females, despite this apparent adaptive success (Halfwerk, *et al.* 2011b). There is the hypothesis that, in response to noisy areas, an increase in vocal amplitude will often result in an involuntary call frequency increase (along with rate and duration of syllables), known as the Lombard effect (Lombard, 1911; Bermúdez-Cuamatzin, *et al.* 2011; Potvin and Mulder, 2013). Despite both vocal adjustments improving the success of carrying signals above background noise, both come at a cost to energy and attraction (Brumm, 2004; Halfwerk, *et al.* 2011b).

Aside from the popularity of vocal studies, those focused on population metrics, such as abundance, density and occupancy, account for 17% of publications, seeing a spike in interest in 2011 (Table 1) (Fig. 1) (Appendix 1). These studies often investigate the impact of noise on species diversity, richness and assemblage at community-level, and have increased in interest alongside the growing concern that exposure to anthropogenic noise may contribute to species homogenisation by favouring those most bold and adaptable (Patricelli and Blickley, 2006; Hinsley, *et al.* 2009; Slabbekoorn and Halfwerk 2009; Fontana, *et al.* 2011; Meffert and Dziock, 2013; Proppe, *et al.* 2013).

Other areas such as physiological responses (9%), life history/reproduction (8%), vigilance (7%) and mating (2%), are largely underrepresented, forming just 26% of studies (Table 1). By investigating these areas further, evidence as to how current individuals deal with noise as a global pollutant may suggest how the increased stress and distraction may impact future generations.

Of the studies concentrating on vigilance behaviour, research has revealed that many species have a finite attention-span, and must split it between necessary simultaneous

tasks (Dukas, 2004; Chan, *et al.* 2010; Chan and Blumstein, 2011; Walsh, Arnott and Kunc, 2017). These tasks can include foraging whilst also executing antipredator, vigilance behaviour. Dukas (2004) found that foraging blue jays (*Cyanocitta cristata*) reacted much more slowly to an object in their peripheral vision when focused on finding more cryptic prey. Had this object been predatory, the birds may have taken longer to react and flee when more of their attention was dedicated to another task (Dukas, 2004). Similarly, a study investigating the impact of boat motor noise on Caribbean hermit crabs (*Coenobita clypeatus*) found that crabs exposed to the heightened noise allowed a simulated predator to approach more closely before hiding (Chan, *et al.* 2010). These results show the possibility that food availability and increase in environmental noise can distract individuals to an extent that may lead to compromised threat detection and avoidance.

Increased background noise level can also increase an individual's perceived level of risk in the environment, and as a result, alter behaviours accordingly (Klett-Mingo, *et al.* 2016). An increase in perceived risk heightens vigilance, increases scan time and decreases the inter-scan interval (Quinn, *et al.* 2006; Klett-Mingo, *et al.* 2016). Due to the heightened vigilance, individuals have been seen to reduce feeding intake rate as a consequence, leading to a direct fitness cost (Quinn, *et al.* 2006; Klett-Mingo, *et al.* 2016). Individuals may also be reluctant to make as many visits to the nest to feed young and deter predators when under increased perceived risk, threatening the survival of fully-dependent offspring (Schroeder, *et al.* 2012; Antze and Koper, 2018). Ultimately, these behaviours could directly lead to reduced fitness and survival in viable breeding individuals and/or poor fecundity and fledging success. Understanding their relationship with noise is therefore vital for conservation. However, clearly demonstrating these links can be challenging.

Accounting for only 1% of the existing literature, whole ecosystem effects proved the least popular biological response within the published studies (Table 1); possibly due to the difficulty of scaling-up noise studies to be able to investigate entire system effects. The study by Francis, *et al.* (2012) successfully investigated the indirect effect of natural gas well compressor noise on ecosystem health by investigating the disturbance of key pollinators and seed dispersers. Authors measured the effect of gas well compressor noise on the pollination visit rates of black-chinned hummingbirds (*Archilochus alexandri*), known to nest in noisy environments, and the seed-removal rates of western

scrub-jays (*Aphelocoma californica*), a species known to avoid noisy areas (Francis, *et al.* 2012). As predicted, compressor noise had an indirect positive effect on flower pollination by hummingbirds, and an indirect negative effect on *Pinus edulis* seed-removal by scrub-jays; seen exclusively to remove seeds from the control site in the absence of compressor noise (Francis, *et al.* 2012). It was therefore hypothesised that noisy habitat provides refugia for the hummingbird species, which are able to forage in the absence of nest-predating species that avoided the area (Francis, *et al.* 2009; Francis, *et al.* 2012). Though beneficial to one species, the absence of a key seed-disperser may eventually result in fewer mature trees in noisier areas due to poor seed-recruitment (Francis, *et al.* 2009; Francis, *et al.* 2012). Eventually, the decline in slow-maturing tree species such as *P. edulis* and reduction in woodland diversity may threaten the survival of species which rely on them for survival (Mueller, *et al.* 2005; Francis, *et al.* 2012).

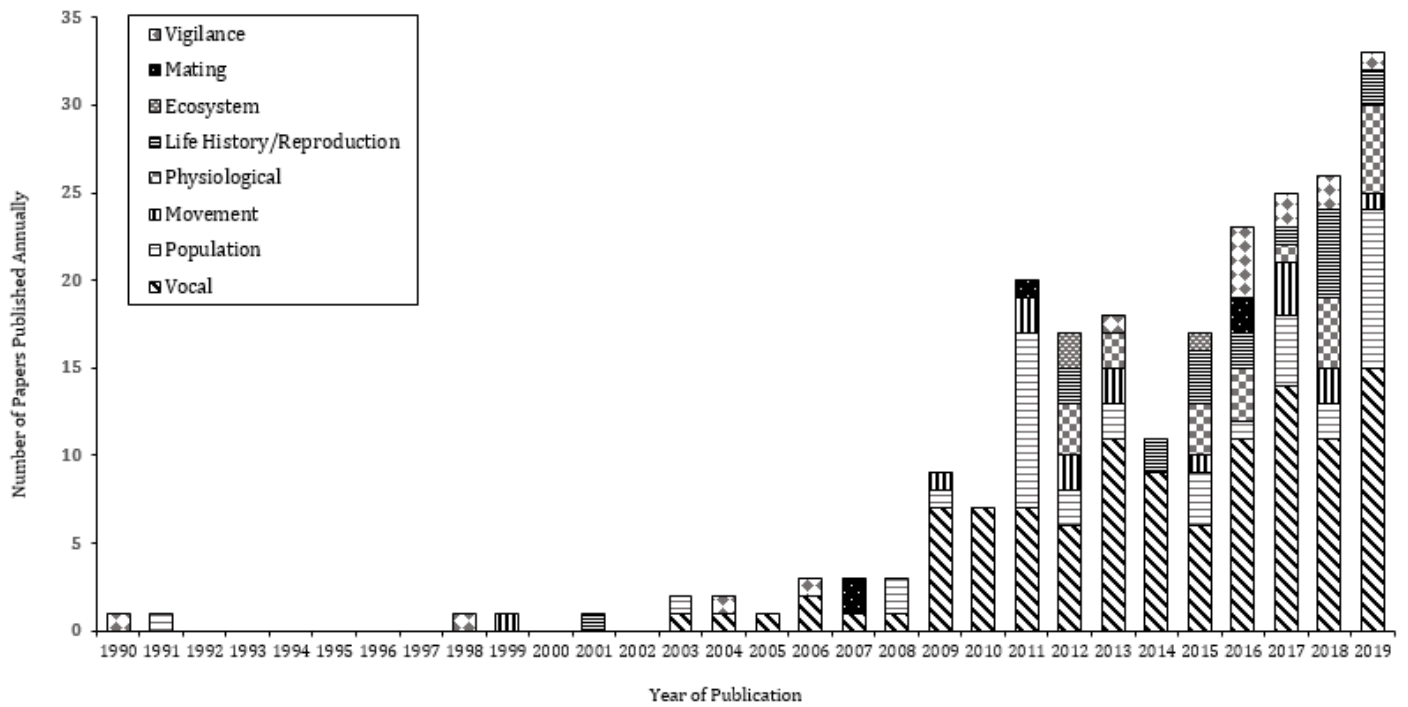


Figure 2 - Number of publications published annually focused on the effects of anthropogenic noise on birds, spanning 1990-2019. Papers are divided into the biological response measured: vocal, population, movement, physiological, life history/reproduction, ecosystem, mating and vigilance. ( $N = 225$ ).

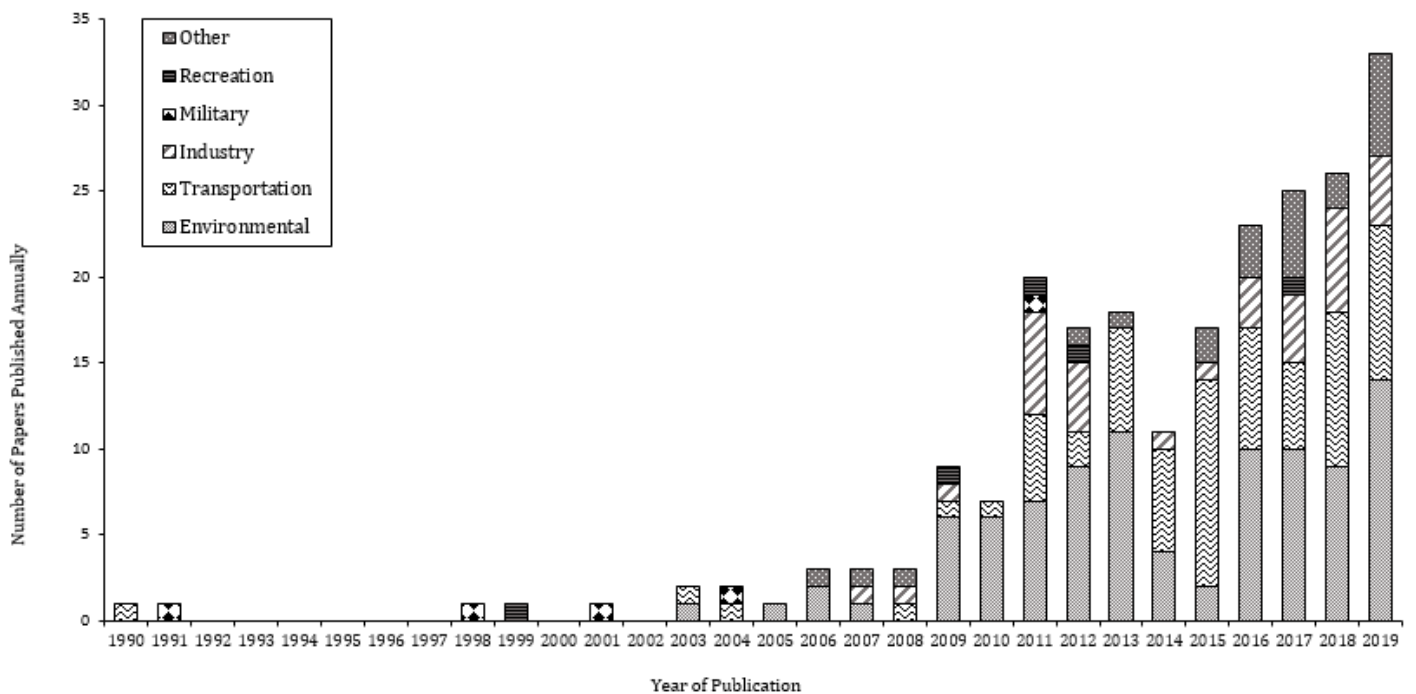


Figure 1 - Number of publications published annually focused on the effects of anthropogenic noise on birds, spanning 1990-2019. Papers are divided into the noise source studied: environmental, transportation, industry, military, recreation and other. ( $N = 225$ ).



### *Noise Stimulus Studied*

Environmental sound studies have been a popular focus since the mid-2000s (Fig. 2) (Appendix 2). Typically, these studies aim to investigate how birds respond to the general environmental sound emitted by urban areas, without a specific focus on differing noise sources frequently associated with urbanisation; such as transportation, industry or recreation. These broad environmental studies of typical “noise” are the most popular amongst the categories of sound stimulus studied, accounting for 41% of the published literature (Table 1).

Within the topic of environmental noise, many studies have chosen to focus on the importance of species richness and occupancy within urban areas, and how species cope alongside stressful noise conditions. Studies conducted by Fontana, *et al.* (2011), Rodrigues, *et al.* (2018) and Lee, *et al.* (2019) focus on impacts caused by urban variables on species richness and assemblage within city environments, and how the presence of green spaces may prove beneficial. Despite expectations, building height, building density and human population density had no marked impact on species richness or distribution; whereas background noise levels, presence of green spaces and tree density did (Fontana, *et al.* 2011; Rodrigues, *et al.* 2018; Lee, *et al.* 2019). Due to the strong negative impact of background noise, positive influence of green spaces and higher tree densities, and little impact caused by human population density, it was deemed possible that with detailed planning to reduce noise effects, urban areas could successfully support complex avian communities (Fontana, *et al.* 2011; Rodrigues, *et al.* 2018; Lee, *et al.* 2019). Despite these results, there are often more indicators to successful city-inhabitation than the presence or absence of species; such as body condition and breeding success (Beale and Monaghan, 2004; Phillips, *et al.* 2018). In the study by Phillips, *et al.* (2018), male white-crowned sparrow (*Zonotrichia leucophrys*) survival and body condition in city habitats was compared to that of their counterparts in rural settings. Territory noise played a vital role in condition, and males holding territory within louder city areas were found to be of poorer body condition than those in quieter rural areas (Phillips, *et al.* 2018). This reduction in body condition may be a direct response to disrupted feeding or due to poor-quality males settling in noisy areas; dominant individuals often defend quieter, higher-quality habitat where mating calls are more audible (Reijnen and Foppen, 1994). Though often capable of living amongst raised environmental noise, it is clear that species can be

detrimentally effected by the increase in anthropogenic noise associated with urbanisation (Fontana, *et al.* 2011; Phillips, *et al.* 2018; Rodrigues, *et al.* 2018; Lee, *et al.* 2019).

As popularity in anthropogenic noise research has grown, studies have moved away from those focused on military sound events (2%), which initially proved a popular topic (four studies 1990-2004 (44% of the published literature from that time period) to only a single study 2005-2019 (0.46% of the published literature from that timescale)), and began manipulating and experimenting with artificial white- and pink-noise ('other' 10%). As their prevalence grew in our soundscape, attention was then turned to transport (30%) and industrial noise (14%). When compared with other recreational noise (2%), noise emitted from transportation is dominant in many environments (Öhrström, *et al.* 2006), and birds are often exposed to varying intensities (Blickley, *et al.* 2012).

Within the popular topic of transportation, many studies have focused on the impact of roads and air traffic, with significant results supporting that both impact on multiple avian behaviours and biological responses found. In studies conducted by Gil, *et al.* (2015) and Dominoni, *et al.* (2016), European bird species were seen to change the timings of their dawn chorus songs to reduce overlap with aircraft noise. In the surrounding areas of major airports, birds that sing later in the morning, and therefore overlap with the greatest volume of aircraft noise, were most affected, and moved the timings of their songs to much earlier in the morning (Gil, *et al.* 2015). Birds were also seen to avoid singing during plane take-offs, opting to sing only during times when vocalisations would be unimpaired by plane noise (Dominoni, *et al.* 2016). Some bird species have also been seen to change singing times in response to peak road traffic noise. Two out of six species studied by Arroyo-Solís, *et al.* (2013) were found to advance their singing before the onset of high road noise. This alteration in song timings however is not known to be solely detrimental to species, with early singing blue tits (*Cyanistes caeruleus*) often deemed more attractive by conspecifics (Poesel, *et al.* 2006; Arroyo-Solís, *et al.* 2013). It is however clear that traffic noise is capable of impacting timings of bird vocal behaviour (Arroyo-Solís, *et al.* 2013; Gil, *et al.* 2015; Dominoni, *et al.* 2016).

An issue amongst traffic noise studies however can stem from the duration of which birds are exposed to the study stimuli and relative sensitivity of species. In contrast to the

typical agreement regarding the effect of traffic noise on vocal behaviours, the impact of noise on breeding success and stress levels is often disputed. Studies by Halfwerk, *et al.* (2011a) and Injaian, *et al.* (2018) both found negative impacts on clutch size, number of fledglings, nestling body condition and stress corticosterone levels when exposed to increased levels of road noise. A study by Crino, *et al.* (2013) however, found lower glucocorticoid stress levels in nestlings when exposed to road noise.

The study by Halfwerk, *et al.* (2011a) used naturally occurring sound in the environment and studied great tits (*Parus major*) from an area which had been exposed to un-altered motorway noise for 14 years. The study by Injaian, *et al.* (2018) used noise playback of road noise to tree swallow (*Tachycineta bicolor*) nestlings over 91 days. The study by Crino, *et al.* (2013) studied white-crowned sparrow (*Zonotrichia leucophrys*) nestlings, but only exposed individuals to five days of road noise playback. It is therefore vital that anthropogenic noise studies are conducted over a realistic time-frame and consider the noise sensitivity of species to ensure comparable results. As traffic noise is typically a chronic, long-term noise source, this must be reflected in study methodologies.

There has also been concern raised about discrepancies when analysing vocal recordings. In studies conducted by Brumm, *et al.* (2017) and Ríos-Chelén, *et al.* (2017), authors found that there were often inconsistencies within the analysis of studies investigating whether a shift in minimum frequency of bird song is present in response to noise. Comparing two techniques used to measure pitch under varying levels of anthropogenic noise, Ríos-Chelén, *et al.* (2017) found that studies analysing spectrograms using “by eye practise” (BEP) were more likely to yield a false positive. This is due also to observer error, with low-frequency vocalisations increasingly masked by high-intensity, low-frequency background noise, reducing detectability by eye on spectrograms (Ríos-Chelén, *et al.* 2017). Therefore, as the signal-to-noise ratio between birdsong and background noise decreases, error using BEP is more likely (Ríos-Chelén, *et al.* 2017). Using a similar technique, Brumm, *et al.* (2017) found that observers analysing spectrograms by eye, whom had been informed of the hypothesised results, repeatedly recorded higher minimum vocal frequencies in birdsong when in the presence of noise. These results are particularly problematic as it is commonly predicted that vocal frequency will increase with background noise level, but it is possible that this conclusion could be reached or exaggerated solely due to the limitations and bias of using BEP

(Brumm, *et al.* 2017; Ríos-Chelén, *et al.* 2017). However, Brumm, *et al.* (2017) and Ríos-Chelén, *et al.* (2017) found the power/amplitude spectra “threshold method” (TM) more reliable; using a threshold value to pre-select a significant drop in amplitude which, when exceeded by the vocalisation energy at the lowest frequency value, provides the minimum frequency of the call (Ríos-Chelén, *et al.* 2017). Though TM use is limited to high-quality noise recordings with high signal-to-noise ratios, results yielded would prove more consistent; primarily due to the full range of the vocalisation being analysed without observer-expectancy biases, not only parts which would be most detectable when using the BEP methodology (Brumm, *et al.* 2017; Ríos-Chelén, *et al.* 2017). Careful consideration must therefore be taken when selecting recording techniques and analytical procedure for vocal studies to prevent the chances of exaggerating the relationship between variables or indicating a false positive.

### *Taxonomic focus*

77% of all studies focused on at least one species from the Passeriformes order (Table 1); the largest avian order comprising almost half (~5,700) of all extant bird species (Barker, *et al.* 2004). As these birds are numerous in many environments, with multiple species often cohabiting the same area, it is clear why this order is popular for research. These species are also predominantly singing birds (oscines), and so the nature of individuals from this order may also contribute to the large number of studies focused on vocal behaviours. Because of their small bodies, passerines are known to sing at a relatively high pitch, with songs of higher frequencies capable of being produced at higher amplitudes for transfer between conspecifics (Wallschläger, 1980; Rheindt, 2003; Bermúdez-Cuamatzin, *et al.* 2009; Nemeth, *et al.* 2013; Ríos-Chelén, *et al.* 2017). This provides passerines with the ability to communicate messages efficiently, with low rates of distortion (Hansen, *et al.* 2005). The high frequency also helps to avoid overlap with lower-frequency sounds which may also be present; common biotic sounds such as animal calls, and abiotic sounds such as wind, waterfalls and transport noise (Rheindt, 2003; Ríos-Chelén, *et al.* 2017). Therefore, the smaller-bodied birds are at an advantage vocally, and those with the highest-frequency songs have been seen capable of successfully living amongst roadway noise (Rheindt, 2003; Francis, *et al.* 2011b). Larger-bodied birds however often produce lower frequency calls, more susceptible to masking,

but are largely absent from the literature by comparison (Wallschläger, 1980; Francis, *et al.* 2011b).

Table 2 – The taxonomic focus of published literature focused on the effects of anthropogenic noise on birds, spanning 1990-2019 ( $N = 228$ ).

Taxonomic Focus			
Passeriformes 77% <b>154</b>	Galliformes 3% <b>6</b>	Anseriformes 3% <b>5</b>	Columbiformes 2% <b>4</b>
Charadriiformes 2% <b>3</b>	Piciformes 1% <b>2</b>	Accipitriformes 1% <b>2</b>	Strigiformes 1% <b>2</b>
Cuculiformes <1% <b>1</b>	Opisthocomiformes <1% <b>1</b>	Pelecaniformes <1% <b>1</b>	Caprimulgiformes <1% <b>1</b>
Falconiformes <1% <b>1</b>	Otidiformes <1% <b>1</b>	Suliformes <1% <b>1</b>	Community 22% <b>43</b>

*Parentheses in bold show sample size.*

The ‘Community’ order category in this review was defined as the species assemblage in an area being researched, not a specific target species, and therefore species were not selected by choice and bias was not a factor (Table 2). The largest species studied by mass were the black swan (*Cygnus atratus*), lesser snow goose (*Chen caerulescens caerulescens*) and greater sage-grouse (*Centrocercus urophasianus*), represented by a single study of each. Similarly, of the 15 orders included in the literature, only eight were represented by more than a single study (Table 2); with 154 studies conducted on Passeriformes alone. Because of popularity of vocal research, it is possible that unintended bias towards smaller species for studies has become the norm. Combined with their added abundance and ability to adapt to living amongst humans, it is easy to see why passerines are a popular focal order. It is also possible, due to the geographic bias in existing studies (with North America and Europe responsible for 82% of publications), that larger birds are underrepresented due to the scarcity in those areas. However, if studies branched into further regions, mainly those in the southern hemisphere, it may be possible to not only gain representation of other species missed from the literature, but also those of varying size and vocal characteristics. Until this has been achieved, it will be difficult to accurately predict how these varying species will react to an environment of increasing noise and

development, as adaptation to novelty cannot be assumed to be the same across such a varied taxon.

## **Methodological Approaches**

### *Playback v Natural Experiment*

In early studies, the dominant approach to noise research was via natural experiment, with 71% of studies published in the 2000s using only naturally occurring sound (Table 3). In this case, a 'natural experiment' is one defined as using only sound which is currently produced in the environment, with researchers having little/no control over production. It can be argued that using natural experiments yields the most realistic results and most accurate representation of behaviours as they are currently. However, with restriction to only present noise levels, we cannot provide firm predictions as to behaviour in the presence of potential future noise levels. Using naturally occurring sound also restricts the studies to individuals currently in that area, which may already have developed some habituation to the noise (Chan, *et al.* 2010; Payne, *et al.* 2012) and may be impacted by confounding factors other than noise such as a visual disturbance (Blickley, *et al.* 2012).

The playback approach to noise research involves a recording of the focal stimulus being played to, or in the vicinity of, an individual to elicit a response. The use of playback events allows for noise exposure levels to be controlled and manipulated, enabling researchers to present their subjects with varying intensities of a novel stimulus, which may not be readily available in that environment. Noise playback can also be used to replicate studies in controlled settings, such as a laboratory. An important issue to address with playback studies however is the chance of unintentional pseudoreplication (McGregor, 2000; Deecke, 2006). Presenting only a single playback track to individuals and measuring behavioural response is not a true replication (McGregor, 2000; Deecke, 2006). Regardless of the number of noise levels the track is presented at, the replication is still not true, as birds may be responding to a specific noise sequence within the track itself (McGregor, 2000). Therefore, multiple exemplar playback tracks must be presented to individuals to count as true replicates (Deecke, 2006).

With the correct replications used, playback studies can ensure confounding factors often associated with anthropogenic noise are eliminated from impacting the study (Blickley,

*et al.* 2012). For example, with road noise experiments, noise playback can be used in an environment absent of road, but also absent of conflicting aspects such as visual disturbance from vehicles, pollution, ground vibration, air turbulence and edge-effects (Arévalo and Newhard, 2011; Blickley, *et al.* 2012; Crino, *et al.* 2013; Injaian, *et al.* 2018a). This allows the study to test for the effect of the noise alone (Blickley, *et al.* 2012). Effectively demonstrated by McClure, *et al.* (2013) and McClure, *et al.* (2017), both studies set up a 0.5km “phantom road” in a forested area using 15 speakers emitting 55-60dBA road noise (point count locations were 30-50m from the noise source). Both studies found that the noise from the phantom road caused reduced bird abundance and complete avoidance from some species (McClure, *et al.* 2013; McClure, *et al.* 2017). The latter study also found that the noise disturbance caused a shift in the age structure of surrounding individuals during periods when the noise was broadcast, causing greater levels of avoidance behaviour in younger individuals (McClure, *et al.* 2017). It was hypothesised that this level of avoidance in younger individuals may be due to their inexperience with efficient foraging rates, predator evasion and road noise, making them more susceptible to disturbances.

Although the popularity of playback experiments increased 2010-2019 (35%), the use of natural experiments was still unrivalled (Table 3). Overall, spanning the three decades, 60% of studies involved natural experiments, 34% playback, 4% used a combination of both approaches and 2% used theoretical work to formulate predictions (Table 3). Though some studies do benefit solely from the use of natural experiments, particularly when studying environmental noise, those investigating more specific noise stimuli sources (such as transport and industry) can often benefit from the added control of noise playback. Currently, 75% of environmental studies have used a natural experimental approach (with environmental studies forming 41% of the overall published noise literature on birds). Conversely, 55% of studies on transport noise and 75% of research on industrial noise have used natural experiments, potentially in the presence of confounding environmental variables. With the assumption that traffic levels will continue to rise with the human population and that developing nations are predicted to see the most dramatic changes in industrial development in coming years (Shannon, *et al.* 2016a), utilising more playback-central studies could prove invaluable. Investigating the response of naïve populations of birds to road and industry noise before they are present in the environment could provide the most accurate prediction of how species

may respond and adapt in the future. With those results, conservational management strategies can be implemented to lessen any foreseen negative impacts, and the transition into a noisier future can be thoroughly discussed.

Table 3 - An overview of study approaches used in published literature focused on the effects of anthropogenic noise on birds, spanning 1990-2019 ( $N=225$ ).

<b>Study Type</b>	1990-1999	2000-2009	2010-2019	1990-2019
Playback	25% <b>1</b>	29% <b>7</b>	35% <b>69</b>	34% <b>77</b>
Natural Exp.	25% <b>1</b>	71% <b>17</b>	59% <b>117</b>	60% <b>135</b>
Playback & Natural Exp.	50% <b>2</b>	0% <b>0</b>	3% <b>6</b>	4% <b>8</b>
Theoretical	0% <b>0</b>	0% <b>0</b>	3% <b>5</b>	2% <b>5</b>
<b>Study Location</b>	1990-1999	2000-2009	2010-2019	1990-2019
Field	75% <b>3</b>	87% <b>21</b>	87% <b>172</b>	87% <b>196</b>
Laboratory	25% <b>1</b>	13% <b>3</b>	10% <b>19</b>	10% <b>23</b>
Both	0% <b>0</b>	0% <b>0</b>	3% <b>6</b>	3% <b>6</b>
<b>Sound Level Presentation</b>	1990-1999	2000-2009	2010-2019	1990-2019
Binary	50% <b>2</b>	71% <b>5</b>	83% <b>62</b>	80% <b>69</b>
Dose	50% <b>2</b>	29% <b>2</b>	17% <b>13</b>	20% <b>17</b>

*Parentheses in bold show the sample size per timeframe.*

### *Field v Laboratory*

From the onset of anthropogenic noise studies on birds, field studies have been the most popular option. This is most likely due to the abundance and ready availability of birds in the environment, and the ease of studying them in their natural setting. The introduction of laws and protocols such as The Animals (Scientific Procedures) Act 1986, which encourage the reduction of aspects such as stress and unnatural confinement of as few individuals as possible, will also have contributed to the popularity of studying birds in-situ. Spanning the three decades, currently only 23 studies have been conducted solely in laboratory settings (10%), with 87% conducted in the field and 3% of studies using a combination of both approaches (Table 3). Though fieldwork is seen as the most natural method of studying wild individuals, studies can be affected by many confounding factors. Visual disturbance, edge effects, human presence, pollution, air turbulence and



vegetation preference in an area can all affect the outcomes of a field experiment if not accounted for (Arévalo and Newhard, 2011; Blickley, *et al.* 2012; Crino, *et al.* 2013; Injaian, *et al.* 2018a). Fieldwork studies also have a substantial potential for observer error; with the behaviours of individuals from large, wild populations easily missed when gathered in high densities (Bart and Schoultz, 1984). In contrast, laboratory settings can successfully control for many factors through design setup, and studies can be repeated with precision. However, the sterile, unnatural test environment may prove unrealistic and impact results inadvertently through increasing stress levels (Hawkins, *et al.* 2001).

The early popularity of using natural experiments will have contributed to favouring the fieldwork approach over the past decades. Without the use of playbacks via pre-recorded noise clips, studying individuals within the environment where the noise is naturally present is the only way to collect behavioural data. However, with advancing technologies allowing playback studies to be conducted more easily, future studies conducted in-situ can benefit from greater control and replication potential; once only achievable in a laboratory. Field playbacks are therefore now a very effective method of studying representative behaviours in a bird's natural surroundings whilst also allowing for the control of confounding environmental factors (Blickley, *et al.* 2012).

### *Binary v Dose-response*

Noise level presentation must also be considered. Since 1990, 80% of research published on the response of birds to anthropogenic noise has used a binary presentation of noise, i.e. presented a single noise level to individuals to measure whether a response was observed in noise versus control conditions (Table 3). Though this is an effective way of measuring the presence of a response, restricting the study to a single noise level would limit the conclusions which could be drawn. The single noise level would allow for a simple 'yes/no' response to be determined, but the intensity of the response and how this behaviour varied when exposed to other noise levels could not be determined. As the level of anthropogenic noise in the environment is not at a constant, known to vary spatially with proximity to the source and temporally with seasons and time of day (Blickley, *et al.* 2012), a dose-response approach may provide an insight of greater significance.

Restricted to only 20% of existing bird studies (Table 3), a dose-response approach requires the presentation of multiple noise levels, increasing in relatively equal increments, to allow for a direct comparison in behavioural responses. The dosage-response therefore provides insight as to whether birds demonstrate a threshold to noise at lower levels or if behavioural response to increasing noise levels is linear (Foote, *et al.* 2004). The earliest paper recorded on the dataset, Brown (1990), was also the first study of that decade to use a dosage presentation of noise to birds. The study was conducted in the field and used noise playback to replicate varying noise levels of aircraft to seabirds, ranging from 65-95dBA, played approximately 8m from the seabird colonies (Brown, 1990). The study used seven noise levels, increasing in 5dBA increments, and was able to show how the behaviour of a seabird colony increased in startle, alert, scanning and escape behaviour with the increase in noise exposure (Brown, 1990). The study showed that the colony demonstrated significantly greater levels of alert throughout all intensities of noise compared to the control (0dBA of broadcasted noise), and there was a strong correlation between the proportion of the colony's response and increasing noise level (Brown, 1990). Brown (1990) also showed however that the startle and escape behaviours were only demonstrated at the highest noise levels (90-95dBA), which may have been missed had only a single median noise level been investigated. With this study, Brown (1990) provided an excellent framework for future anthropogenic noise studies: eliminating a significant number of confounding factors in the study by using noise playback, testing for a dosage-response with varying noise levels and collecting realistic data by studying birds in-situ.

Since then, dosage-response research has branched into studying sources of anthropogenic noise such as road traffic, industry, environmental sounds and synthetic pink/white noise. A study by Senzaki, *et al.* (2016) focused on the ability of nocturnal predatory species (short-eared owls (*Asio flammeus*) and long-eared owls (*Asio otus*)) to successfully hunt alongside road noise. This particular study used five traffic noise playback levels of 40, 50, 60, 70 and 80dB to represent noise levels at varying distances from a roadside (Senzaki, *et al.* 2016). By using these varied noise levels, the study was able to replicate distances from a roadway in its absence; excluding the confounding factors associated with a physical road. By using a wide range of noise levels, the lowest being near that of the ambient background noise level (35dB), Senzaki, *et al.* (2016) were able to demonstrate that even owls hunting in low levels of road noise were still

susceptible to disturbance. Owls were impacted by noise levels as low as 40dB, representative of >120m from a road (Senzaki, *et al.* 2016).

Not only have dosage noise amplitude levels played an important part in avian noise research, but also bandwidths. In the study by Mejia, *et al.* (2019), a “phantom natural gas field” (similar to the aforementioned “phantom road” experiment by McClure, *et al.* 2013 and McClure, *et al.* 2017) was set up by broadcasting broadband and narrowband synthetic gas compressor noise to wild song birds. It was found that during the playback of narrowband noise, the abundance of only Brewer’s sparrows (*Spizella breweri*) declined (Mejia, *et al.* 2019). In contrast, during the playback of broadband noise, the abundance of the overall songbird community declined (Mejia, *et al.* 2019). This result would suggest that with greater sound bandwidth and accompanying sound level, the negative impact on bird populations would be inflated; in-line with the authors’ prediction (Mejia, *et al.* 2019). Not only do the results from this study contribute to the current knowledge surrounding the impact of noise on birds, but also to an alternative large-scale approach to noise playback studies.

## Conclusion

It is clear from this review and others before it that the current state of knowledge on the effects of anthropogenic noise on birds has both expansive yet detailed coverage. Whilst behavioural studies are extremely popular, linking changes directly to fitness has proven challenging; often requiring longer, more controlled experiments. To continue to broaden our understanding of these effects and how they apply to the taxa in its entirety, more effort must be made to conduct studies across greater spatial and temporal scales with increased variety of focal species.

Expanding the study regions into those more poorly represented, such as South America, Australia, Asia and Africa, we could begin to formulate a conclusive view of how bird species across the world react to noise. Without this expansion, our views remain biased towards species historically exposed to comparatively high levels of noise in Europe and North America, and many species in less developed parts of the world will continue to go unstudied. Developing nations are predicted to see the most change in development, and currently possess an overwhelming level of biodiversity; species that are largely naïve to noise exposure. By expanding anthropogenic noise study areas, data collected could prove invaluable with regards to how species may react to noise levels in the future.

With this shift of interest, research should also focus on biological responses other than vocal behaviours, and greater attention paid to responses such as life history/reproduction, vigilance and surrounding ecosystem health. By increasing research into these particular responses, we will be provided insight into how noise exposure directly affects the health and survival of bird species. Future focus on the impacts of noise on vigilance, predation, feeding rates and brood success could highlight areas vital for future management. Though linking environmental impacts to fitness directly is challenging, identifying exactly where the challenges lie and how these issues may become more widespread in the future may be crucial for effective conservation efforts.

As there is a firm belief that noise sources such as transport will continue to increase in the future, it is vital that future studies present noise levels over realistic time-frames to properly represent exposure to long-term, chronic noise. Without doing so, studies are at risk of not being truly comparable, and incorrect conclusions being drawn from research. Steps must also be taken to ensure thorough recording of sound metrics used for

comparison and synthesis; documenting elements such as broadcast duration, received sound level and sound weighting. Without these improvements, future attempts to bridge underrepresented gaps in the literature may fail to yield valuable results and proper meta-analysis will be limited.

Progressing into underrepresented areas will also provide opportunity to study species outside of those most typical of current studies. Future research must aim to redirect focus towards less well-known orders, specifically moving away from passerine species, and focus particularly on those of greater body mass. Without this redirection, future research can only contribute to what is already known about popular focal orders, such as the Passeriformes, and cannot be regarded as applicable to all species.

Ensuring the correct research approach to provide results capable of enhancing current knowledge is vital. What is required currently is greater understanding of potential future noise levels and their impacts. Increasing field playback studies which present differing noise levels to individuals ensures results are accurate within the environment, confounding variables are accounted for and that a full range of noise levels have been tested. With dose-response studies represented by only 20% of current bird research, greater effort should be invested into pursuing studies which include a wide array of noise levels. This would provide a better representation of behaviours and reduce the likelihood of key responses being missed.

As the increase in anthropogenic noise is predicted only to rise globally alongside human population growth, ensuring the aforementioned gaps are bridged and suitable research approaches are taken will provide crucial information for dealing with the impact of future noise exposure. Because of the arms race between gathering knowledge on increasing noise levels whilst environmental noise increases, it is of the utmost importance that conservational efforts are in place before sound levels in the environment reach those deemed harmful to wildlife. The physical management of soundscapes and the mitigation of noise effects is now vital, and it is critical that progress towards implementing these plans and discovering their limitations is made in the near future.

## Chapter 2: Empirical Paper

### Abstract

The impact of anthropogenic noise on wildlife has received increasing research attention over the past two decades, with a significant focus dedicated to avian species. Surprisingly, one behavioural response that is comparatively understudied is the impact of noise on vigilance behaviour. In an increasingly noisy environment, the vital trade-off between vigilance and crucial behaviours such as foraging may become increasingly difficult to balance. With environmental noise levels predicted to rise globally, there is growing concern that species may no longer be able to maintain efficient vigilance and foraging rates amongst the disturbance, which will potentially impact individual and population-level fitness. In this study I investigated whether the foraging and vigilance behaviour in blue tits (*Cyanistes caeruleus*), great tits (*Parus major*) and coal tits (*Periparus ater*) was affected by increasing levels of traffic noise, and whether individuals demonstrated a tolerance to lower noise levels. I also investigated the impact of vegetation assemblage on the disturbance of individuals, testing whether access to cover influences the behavioural responses of birds to noise exposure. Data were collected on the behaviour of individual birds at in-situ feeders during periods of road noise playback at Treborth Botanic Garden, North Wales. Metrics studied during varied levels of noise exposure were: time individuals spent foraging or vigilant at the feeders, visit duration, visit frequency and peck rate. Results show that as traffic noise levels increased, particularly past 60 dBA, birds made shorter visits to the feeders and vigilance levels increased. Although the proportion of foraging behaviour did fall, it was largely maintained due to shortened visits prioritising food acquisition and spending less time at the feeder. Cover was not as influential as first predicted; only accounting for a weak effect on increased visit duration within a closed vegetation assemblage. Aspects of behaviour such as visit frequency and peck rate were largely driven by seasonality, with fewer visits but a higher peck rate as the study period progressed. It is likely that these results stemmed from an increased abundance of alternative food sources paired with increased feeding rate for breeding and offspring provision as the year progressed from winter to spring. As noise levels in excess of 60 dBA continually caused a reduction in time spent at the food source and heightened levels of vigilance, increasing noise levels of widespread road networks will likely continue to pose an issue to our native bird

species. As the presence of protective vegetation did not appear to significantly mediate the negative effects of increasing noise, it is likely that species will be pushed into more remote areas as the prevalence of anthropogenic noise increases in the environment.

## Introduction

Deemed a major source of anthropogenic noise globally, roads now stretch further than ever before, driven by the demand for access to increasingly remote areas and to successfully transport a growing human population. In the United States of America (USA) for example, 83% of land areas are reportedly located within 1km of a road (Barber, *et al.* 2010), with demand continuing to rise. By 2050, it is predicted that a further 2.5 billion people will live in urban areas (United Nations, 2019), forcing the global urbanisation rate (the proportion of the world's population living in urban areas) to reach 66% (Shi, *et al.* 2019). It is forecast that by 2050, there may be as many as 2 billion vehicles globally (Sitty and Taft, 2016), compared with the 1.4 billion we see today, continuing to apply pressure on building more widespread road networks to keep towns and cities connected. These expansive road networks not only threaten wildlife through the increased risk of direct road mortality, which alone causes ~80 million bird fatalities in the USA annually (Erickson, *et al.* 2005), but also via pollution, visual disturbance, wind turbulence, ground vibration, habitat degradation and edge-effects (Arévalo and Newhard, 2011; Blickley, *et al.* 2012; Crino, *et al.* 2013; Ciach and Fröhlich, 2017; Injaian, *et al.* 2018a). Vehicle noise is known to be particularly pervasive throughout many habitats, capable of affecting the most sensitive bird species over 1km away from a busy roadside (Forman and Alexander, 1998). As growing pressure is placed on species to adapt to living alongside this development and increasing levels of disturbance, it is vital to understand how the expansion of roadways may continue to impact wildlife in the future.

Anthropogenic noise pollution has received increased attention in recent years with regard to the impacts it has on surrounding wildlife, particularly bird species (Hatch and Wright, 2007; Nowacek, *et al.* 2007; Weilgart, 2007b; Wright, *et al.* 2007; Kight and Swaddle, 2011; Ortega, 2012; Shannon, *et al.* 2016a). Birds rely heavily on the acoustical environment to ensure the successful transmission and reception of vital vocal communication relating to territory defence (Kleist, *et al.* 2016), alarm calls (Templeton, *et al.* 2016), mate attraction (Halfwerk, *et al.* 2011a; Luther, *et al.* 2016), offspring cues (Leonard and Horn, 2012; Lucass, *et al.* 2016) and predator-prey interactions (McLaughlin and Kunc, 2013); all of which are vulnerable to the presence of introduced anthropogenic noise (Rheindt, 2003; Hu and Cardoso, 2009; Lowry, *et al.* 2012;



McLaughlin and Kunc, 2013). When communication is impacted by noise, spatial behaviour is also at risk of being affected (McLaughlin and Kunc, 2013). In the past, species exposed to anthropogenic noise have been driven away from historical nesting (Francis, *et al.* 2009), migratory stop-over (McClure, *et al.* 2013) and breeding grounds (Blickley, *et al.* 2012) to avoid competition with noise.

It is not only the masking of important biological cues by anthropogenic noise which can interfere with the daily survival of wild bird species, but also the impact on vigilance behaviour. Within any environment, a trade-off between maintaining a high-energy intake whilst also spending ample time vigilant towards potential threats (e.g. predators or competitors) is crucial (Lima, 1987; Fransson and Weber, 1997; Cresswell, *et al.* 2003; Whittingham, *et al.* 2006; Watson, *et al.* 2007). As the impact of missed feeding opportunities can be tolerated by individuals for longer than the direct impact of predation, antipredator behaviours are prioritised, and can often monopolise large amounts of foraging-time (Powolny, *et al.* 2014). The 'risk-disturbance hypothesis' suggests that anthropogenic noise disturbance is perceived by birds similarly to the threat of predation (Frid and Dill, 2002; Barber, *et al.* 2010; Francis and Barber, 2013), and capable of increasing vigilance rates (Owens, *et al.* 2012; Shannon, *et al.* 2014; Meillère, *et al.* 2015; Shannon, *et al.* 2016b). A study by Quinn, *et al.* (2006) found that when in the presence of heightened background noise, foraging chaffinches (*Fringilla coelebs*) increased vigilant scanning time and decreased their inter-scan interval. Due to the requirement to shift from auditory to visual cues to detect approaching predators in an environment exposed to white noise. Quinn, *et al.* (2006) suggested that the need to repeatedly raise the head to scan visually caused a reduction in food-intake rate. In contrast, a study by Cresswell, *et al.* (2003) found that foraging chaffinches were good at predator detection due to the need to raise their heads when food-handling. Individuals with a high peck rate therefore spent large amounts of time food-handling head-up and had high levels of successful predator detection as a result, with foraging rate unaffected (Cresswell, *et al.* 2003). However, the chaffinches studied by Cresswell, *et al.* (2003) were not exposed to increased levels of background noise whilst foraging, and demonstrated the ability to simultaneously maintain food-intake rate and remain vigilant in an environment devoid of acoustic distraction. The study by Quinn, *et al.* (2006) demonstrates that an added element of noise disturbance can alter feeding rates substantially.

Coined by Chan, *et al.* (2010), the ‘distracted prey hypothesis’ states that any perceived stimulus has the ability to distract an individual’s finite attention span away from responding to threat (Dukas, 2004; Chan and Blumstein, 2011; Grade and Sieving, 2016). Whilst performing simultaneous tasks, foraging blue jays (*Cyanocitta cristata*) have been found to react more slowly to an object in their peripheral vision when focused on finding more cryptic prey (Dukas, 2004). Had this object been predatory, it is possible that the jays’ antipredator behaviour may have been delayed (Dukas, 2004). A similar result was found in a study involving Caribbean hermit crabs (*Coenobita clypeatus*), which repeatedly allowed a simulated predator to approach more closely before hiding during bouts of boat motor playback (Chan, *et al.* 2010). Due to the limitations of a finite attention span, food density/accessibility plays a key role in determining vigilance rates amongst foraging individuals (Powolny, *et al.* 2014), with less-fruitful foraging grounds requiring greater allocation of time spent searching and less on feeding and the detection of predators (Dukas, 2004; Chan, *et al.* 2010). In environments where these sparse conditions are paired with the presence of extraneous stimuli such as peripheral anthropogenic sound, it can be assumed that the further distraction will only contribute to inhibiting successful feeding.

Surprisingly, few current studies have focused on the impacts of noise on bird vigilance (Meillère, *et al.* 2015; Zhou, *et al.* 2019) and fewer on how this may affect other behaviours such as foraging (Quinn, *et al.* 2006). Vigilance behaviour is known to be largely determined by perceived predation risk, and can vary greatly with many environmental factors; such as predator type (Jones, *et al.* 2007; Jones, *et al.* 2009), predator detectability (Jones, *et al.* 2009; Powolny, *et al.* 2014), distance to refugia (Lima, 1987; Griesser and Nystrand, 2009) and surrounding vegetation composition (Lima, 1987; Griesser and Nystrand, 2009; Powolny, *et al.* 2014). The preference for vegetation composition in “risky” situations appears highly dependent on the predatory-evasion tactics used by species (Lima, 1987; Griesser and Nystrand, 2009). Those which utilise speed to out-pace a predator often forage further from highly protective vegetation, and increase vigilance behaviour with proximity to it; due to the vegetation providing cover for, and hampering detection of, ambush predators (Quinn and Cresswell, 2004; Griesser and Nystrand, 2009). In contrast, species which flee and hide from predators increase vigilance with distance from protective cover (Griesser and Nystrand, 2009). Furthermore, ground-foraging species which rely on crypsis to evade predation prefer

areas with taller vegetation, whereas those which flee prefer shorter (Whittingham, *et al.* 2006; Powolny, *et al.* 2014). These preferences can even differ between the sexes of a species, such as Eurasian skylarks (*Alauda arvensis*); with males leaving a fruitful “risky” area with tall vegetation as it inhibits predator evasion, whilst females choose to stay and exploit resources, relying on camouflage (Powolny, *et al.* 2014). It is therefore assumed that the presence of the preferred vegetation composition provides security to foraging individuals (Powolny, *et al.* 2014), and may go as far as to reduce individuals’ perceived level of risk and vigilance rates; though the relationship between vigilance rates and predation risk can prove challenging to explain (Lima, 1987). One such discrepancy is the preference of house sparrows (*Passer domesticus*) to feed close to cover, yet individuals in proximity to cover displayed greatest scanning time, suggesting greater perceived risk (Lima, 1987). Although past research has focused on the impacts of vegetation composition on vigilance rates in the presence of general predation risk, this relationship when birds are exposed to increased risk via heightened levels of anthropogenic noise in the same study has not been explored.

Noise research has progressed from behavioural observations during sound events (Ellis, *et al.* 1991; Delaney, *et al.* 1999), to correlative studies relating metrics of abundance and diversity to noise levels (Habib, *et al.* 2007; Francis, *et al.* 2009; Parris and Schneider, 2009), and finally onto the use of experimental playbacks to explicitly isolate the impacts of noise from other confounding variables in the environment (Blickley, *et al.* 2012; McClure, *et al.* 2013; Dorado-Correa, *et al.* 2018). The incorporation of a playback element into a study has allowed research to benefit from the ability to test noise levels which are not present within an environment; such as traffic noise studies in the absence of vehicles. It therefore allows for a study to isolate and focus on the impact of noise alone, excluding confounding factors which can impact a study if not accounted for; such as visual disturbance, edge-effects and pollution (Arévalo and Newhard, 2011; Blickley, *et al.* 2012; Crino, *et al.* 2013; Shannon, *et al.* 2014; Ciach and Fröhlich, 2017; Injaian, *et al.* 2018a). With playback studies capable of being executed in-situ, research is now no longer reliant on the artificial laboratory environment to conduct studies with the same amount of control and replicability (Hawkins, *et al.* 2001). Ultimately, this reduces the chance that studies will inadvertently be compromised by the stress levels of subjects exposed to artificial laboratory environments (Hawkins, *et al.* 2001), potentially increasing data reliability. Utilising multiple noise levels in a dose-response approach is also a valuable

way of testing the intensity of a behavioural response, compared to a binary approach testing simply whether or not a response is present (McLaughlin and Kunc, 2013; Senzaki, *et al.* 2016). The dose-response approach also allows for insight as to whether a tolerance to lower noise levels is demonstrated by individuals, or whether behaviour responds linearly with increasing noise (Foote, *et al.* 2004; McLaughlin and Kunc, 2013). Multiple exposure levels provide a realistic representation of the impact of noise within the environment, particularly as noise levels vary with distance from the source (Blickley, *et al.* 2012; Senzaki, *et al.* 2016).

In this study, I explored how traffic noise affects avian foraging and vigilance behaviour across various exposure levels, and whether these behavioural responses are further affected by the presence/absence of protective vegetation. The study focussed on the behaviour of three common passerine species from the Paridae family; blue tit (*Cyanistes caeruleus*), great tit (*Parus major*) and coal tit (*Periparus ater*). These three species were chosen due to their abundance, relatedness, variance in boldness, ease of identification from one another and presence across the urban-gradient. Reportedly used by their Paridae relatives in Eastern North American, these individuals were assumed to adopt a similar predator evasion technique of fleeing and seeking refuge in woody-cover, a tactic common to many passerines (Lima, 1993). The specific objectives of this study were to (1) discover whether birds vary their foraging and vigilance rates with increasing traffic noise, (2) whether birds demonstrate a tolerance to lower anthropogenic noise levels, or whether this disturbance increases linearly, (3) if the presence or absence of protective vegetation has an impact on the birds' foraging rates, and finally (4) how the impact of traffic noise varies between the three closely-related species.

## Methods

### *Study Site*

Playback experiments were conducted in Treborth Botanic Garden, a small botanical garden owned by Bangor University, located in Bangor, Wales. The 18ha garden lies on the shores of the Menai Strait and comprises 15ha native woodland, 2ha species rich unimproved grassland and 1ha managed orchard. Approximately one third of the woodland is a Site of Special Scientific Interest (SSSI), and the predominant canopy tree species are oak (*Quercus petraea*), beech (*Fagus sylvatica*) and turkey oak (*Quercus cerris*). The garden also contains many mature tree and shrub plantations of species such as lime (*Tilia x.europaea*) and scots pine (*Pinus sylvestris*), wildlife ponds, tropical greenhouses and an Ornamental Chinese Garden.

The garden has a single-track, 5-10mph road along one edge of the site, with travelling cars each producing noise of ~45 dBA when measured 5m from the centre of the road using a calibrated ATP ET-958 data logging sound level meter set to a-weighted decibels (dBA) (Appendix 3). Directly beyond the perimeter fence of the gardens runs the North Wales Coast Line train line and ~500m beyond that the A487, a single carriageway with a speed limit of 60mph (Appendix 3). Passing vehicles on the carriageway produce noise of around 75 dBA (~80 dBA when wet) 5m from the centre. It is therefore likely that birds which frequent the site have been exposed to relatively high anthropogenic noise levels from the surrounding area. Common passerine bird species at the site include blue tit (*Cyanistes caeruleus*), great tit (*Parus major*), coal tit (*Periparus ater*), European robin (*Erithacus rubecula*), chaffinch (*Fringilla coelebs*), nuthatch (*Sitta europaea*), dunnoek (*Prunella modularis*) and siskin (*Spinus spinus*).

### *Experimental Setup*

A two-week pre-experimental period was carried out from 14 January 2019. This involved six provisioned bird feeders stationed in areas deemed suitable for the study and allowing the birds to become familiar with the feeding areas before the noise experiments commenced. Feeders were mounted on poles at a height of 1.95m (measured from ground level to the top of the feeder) ensuring that feeder height was not a confounding factor, as blue tits are known to increase vigilance with proximity to the

ground (Lendrem, 1983). The metal tubular feeders were chosen due to their suitability for small passerine birds and unsuitability for feeding larger corvid and squirrel species which also frequent the site. The feeders were provisioned with a mix of peanut pieces and mealworm suet pellets; appropriate for the feeder style, high in nutrients needed for winter and easy for the target species to handle at the feeder. Three feeders were positioned in areas with open vegetation and three in closed vegetation (Appendix 4). The open vegetation habitats were areas in which the bird feeders were a mean distance of 6 m from the nearest tree, and closed habitats were those with trees at a mean distance of 1.7 m to the feeders. Each feeder had a mean distance of 25m between itself and the nearest neighbouring feeder. During this pilot phase, feeders were checked every other day to ensure all remained upright and contained sufficient bird food that was accessible from all feeding ports.

### *Noise Stimulus*

Playbacks of traffic noise were modified from a 1 hour 8 minute recording of motorway road noise (see Shannon et al. 2014 for details). The original track was divided into 130, 30 second clips, removing any portion of the original track which included anything other than road noise. The 30 second clips were then assigned a number, and 24 were selected via a random number generator to create each 12 minute track using the sound software Audacity 2.3.0. This was repeated until 15 unique traffic sequences were produced and no sound distortion could be heard at the boundaries of each 30 second interval. Tracks were 12 minutes long to allow a 2 minute fade-in period at the beginning of each playback, and a 10 minute period of observation.

### *Playback Procedure*

150 playback experiments were conducted 28 January – 9 April 2019. Feeders were visited daily to conduct the playbacks and refill food. The playbacks were broadcast 15m from the feeders using a MiPRO MA707 portable loudspeaker at received levels of 0, 55, 60, 65 and 70 dBA. Note that 0 dBA of received playback noise refers to observations being taken in ambient noise levels, with 0 dBA of added noise from the traffic noise recording. The 0 dBA playbacks were treated as sham procedure trials, with the

experimental set-up procedures remaining exactly as they would if an experimental noise level (55, 60, 65, 70 dBA) were to be played from the speaker. A-weighting was selected for this study as this electronic filter has a frequency-response widely regarded as best suited to frequencies detected by human and avian hearing (Dooling and Popper 2007; Injaian, *et al.* 2018b). Noise levels were chosen based on an ambient background noise level of ~40 dBA at the site and so as not to exceed the ~75 dBA produced by a single carriageway road nearby. The playback exemplars were stratified to ensure all were played at each of the five specified sound levels in both the open and closed habitats, with systematically randomised presentation order. This gave a total of 150 playback events. No more than five playbacks were conducted per day, and each feeder had at least 24 hours between successive playbacks.

Prior to each playback, the observer recorded ambient sound level and checked the playback noise levels at the bird feeder (the received level) using a calibrated ATP ET-958 data logging sound level meter set to a-weighted decibels (dBA). The surrounding light level was measured via a URCERI MT-912 light meter (lux) and wind speed (km/h) measured with a ClimeMET CM2030 hand-held wind meter. Date, time, temperature (°C) and weather were also recorded. Playbacks were not conducted in the rain or in wind which exceeded 11 km/h to reduce the auditory effects from the wind and damage to electrical equipment. The observer entered a camouflaged bird hide positioned 15m from the feeder after completing experimental checks. No behavioural observations were taken or playbacks initiated until 10 minutes after the observer had entered the hide, allowing the birds to settle. Following the settling period, playbacks were faded-in to the desired level of either 0, 55, 60, 65 or 70 dBA over 2 minutes. Video recording of the feeder was carried out for 10 minutes using a Canon EOS 100D digital SLR camera and Canon EF 70-300mm telephoto lens mounted on a tripod. The camera was stationed with the observer in the hide during each playback, and the camouflage lens hood protruded from the door to avoid obstruction. The lens was at maximum zoom so that the feeder filled the frame, ensuring fine-scale behaviours could be recorded accurately.

## *Data Analysis*

Video footage was analysed using the Behavioural Observation Research Interactive Software (BORIS) 7.8.2 (Friard and Gamba, 2016). Ethogram behaviours were coded to a keyboard shortcut and were categorised as ‘foraging’, ‘vigilance’ and ‘other’. ‘Foraging’ behaviours were classified as a ‘peck’, a point event with no duration in which the beak comes into contact with the food source, and “head-down”, a state event recording duration that the head of the individual is below body level and engaged in feeding. ‘Vigilance’ behaviour was classed as “head-up”, another state event recording the duration the individual’s head was above body level observing surroundings. Being ‘out-of-sight’ and an individual’s ‘arrival’ to the feeder was classed as ‘other’ behaviour; both were state events whereby duration was recorded, allowing for the total duration of each visit to be measured and an accurate time budget to be generated. Subject keyboard shortcuts were also added to ensure each visit could be assigned to a species; subjects were ‘blue tit’, ‘great tit’, ‘coal tit’ and ‘other passerine’. As the birds could not be identified at an individual-level and likely make repeat visits, each visit by a bird to the feeder was classed as an independent ‘event’, with data analysed at playback-level to provide a more standardised replicate. The behaviour of birds which visited the feeder during the playback interval was recorded via continuous sampling and included the behaviours from all individuals during the 10-minute playback.

The data were analysed using R (RStudio 1.1.423) (RStudio Team, 2020). Collinearity between explanatory variables was tested, with no values  $>0.6 R^2$ . Due to the range differences between continuous variables, Julian day, temperature, received level and wind were all standardised to the same scale for easier comparison. The ‘AICcmodavg’ 2.3-0 package (Mazerolle, 2020) was used for model selection whilst the ‘reshape2’ 1.4.4 package (Wickham, 2007) allowed for the transformation of data between wide and long formats. Visit duration, number of visits and time spent head-up and head-down data were rounded up to whole integers and analysed using generalised linear mixed-effect models (GLMM). GLMMs for visit duration and number of visits were analysed using Poisson error structure. Head-up and head-down duration data were combined using the ‘cbind’ function, allowing the proportion of time foraging and vigilant to be directly compared using binomial error structure. Peck rate values were not rounded to integers due to the nature of the data and so were analysed using a Gaussian linear mixed-effects



(LME) model via the 'nlme' 3.1-147 (Pinheiro, *et al.* 2020) and 'lme4' 1.1-23 (Bates, *et al.* 2015) packages. The 'AICcmodavg' package was used to provide AICc scores for ranking 16 candidate model weights on the response variables. Candidate models included explanatory variables predicted to be most influential on visit duration, number of visits, time spent head-up/head-down and peck rate: Julian day, temperature, wind speed, habitat type, received noise level and species. One model per each response variable acted as the control devoid of any explanatory variables, six models tested a single explanatory variable, five models tested the joint impact of two variables and four models tested the impact of three variables on the response variable. In all candidate models, feeder number was entered as a random effect as multiple recordings were taken at each feeder location. Model averaging provided  $\beta$  estimates, and models that accounted for >95% of the cumulative model weight were deemed as most influential on the response variables. Explanatory variables within these top models which had confidence intervals that did not overlap zero were deemed strongest.

## Results

### *Feeder Visit Duration*

Received noise level and habitat type had the greatest impact on feeder visit duration and the proportion of time individuals spent foraging or vigilant. A single model accounted for 100% of the AICc weight for the visit duration GLMM, with received noise level, habitat type and species being most influential (Table 4).

Table 4 - Top models for blue, great and coal tit a) visit duration, b) proportion of foraging/vigilant behaviour, c) peck rate and d) number of visits accounting for  $\geq 0.95$  of the AICc weight.

		<b>K</b>	<b><math>\Delta</math>AICc</b>	<b>AICc weight</b>
a) Visit duration *				
	Habitat type + received level + species	6	0.00	1.00
b) Proportion of foraging/vigilant behaviour *				
	Julian day + received level	4	0.00	0.72
	Julian day + received level + habitat type	5	1.87	0.28
c) Peck rate $\blacktriangle$				
	Julian day + temperature	5	0.00	0.92
	Julian day + received level	5	6.89	0.03
d) Number of visits *				
	Julian day + temperature	4	0.00	1.00

\* Generalised linear mixed-effect models,  $\blacktriangle$  Linear mixed-effect models.

All models include feeder location as a random effect. *K* indicates the number of parameters.

The significant negative impact of received noise level showed that as received noise increased, visit duration declined (parameter  $\beta$  estimates:  $-0.13 \pm 0.01$  [CI:  $-0.14$  to  $-0.12$ ]). Habitat type had a weak effect on visit duration (parameter  $\beta$  estimates:  $-0.2 \pm 0.15$  [CI:  $-0.5$  to  $0.09$ ]), resulting in marginally longer visit durations overall in the closed habitat. The amount of time spent at the feeders decreased gradually from 55 dBA with increasing received noise level in the open habitat, however visit duration times were maintained for longer in the closed habitats before a more sudden drop-off (from 90 seconds in 60 dBA to 55 seconds in 65 dBA) (Fig. 3).

Species was another important predictor variable affecting visit duration, with the amount of time spent at feeders decreasing with increased received noise level across the three tit species (Fig. 4). When compared to blue tit visit durations, coal tit visit durations were markedly different (parameter  $\beta$  estimates:  $-0.39 \pm 0.02$  [CI:  $-0.43$  to  $-0.36$ ]), spending less time at the feeder across all noise levels. The length of great tit visit durations varied only slightly to those of the blue tits (parameter  $\beta$  estimates:  $-0.05 \pm 0.02$  [CI:  $-0.08$  to  $-0.02$ ]), with great tits spending marginally less time at the feeders. At 60 dBA, coal tits spent only marginally longer at the feeder than the blue and great tits were at 70 dBA.

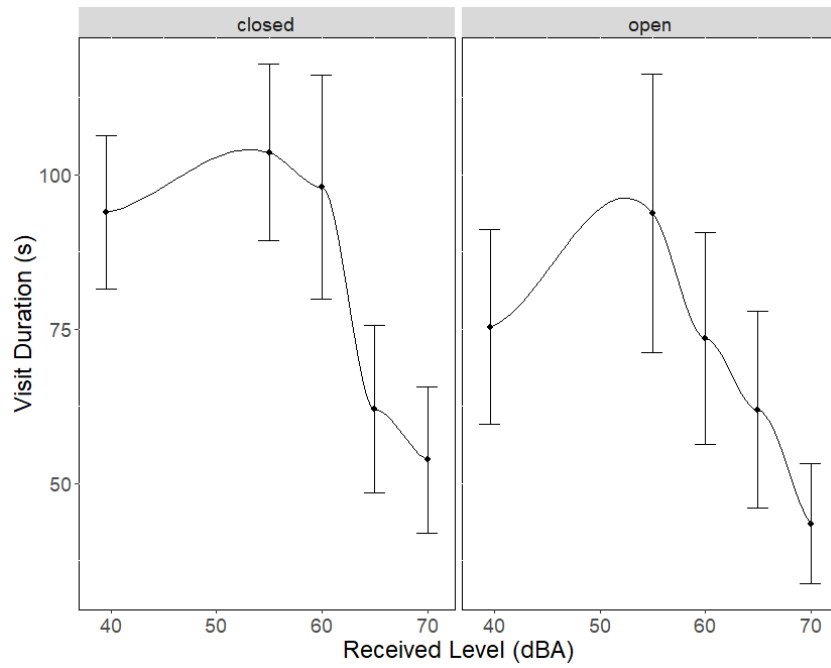


Figure 3 - the mean ( $\pm$ standard error) duration of feeder visits (s) in response to the received sound level (dBA) in both closed and open habitats.

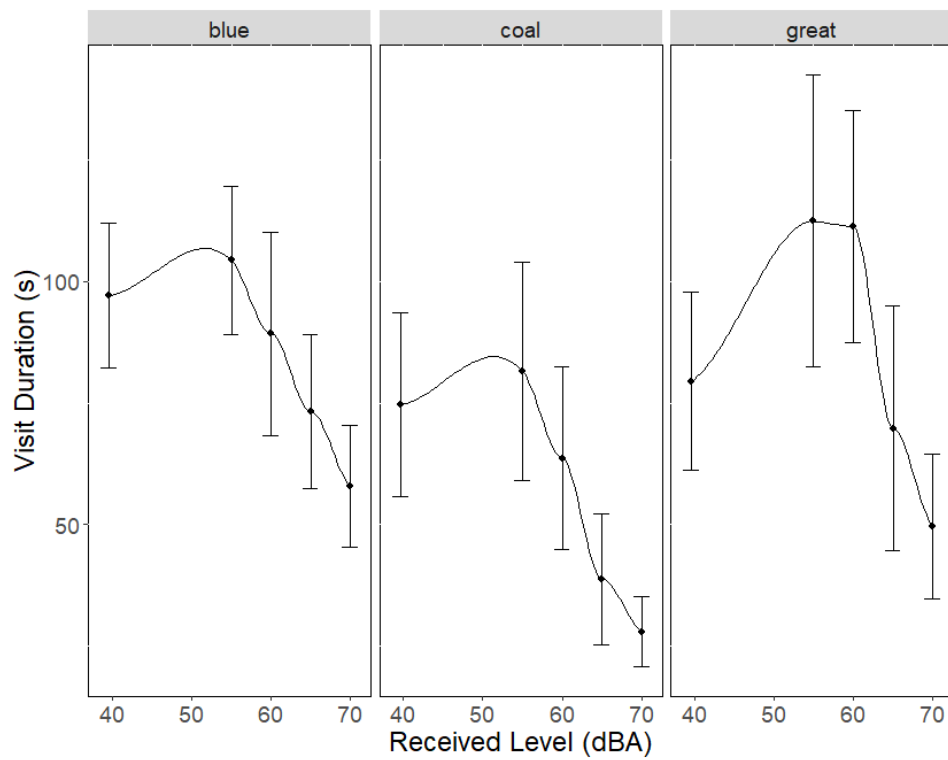


Figure 4 - the mean ( $\pm$ standard error) duration of feeder visits (s) in response to the received sound level (dBA) across the three focal tit species.

### *Proportion of Time Spent Foraging/Vigilant*

Two models accounted for 100% of the AICc weight for the proportion of time spent foraging or vigilant GLMM (Table 4).

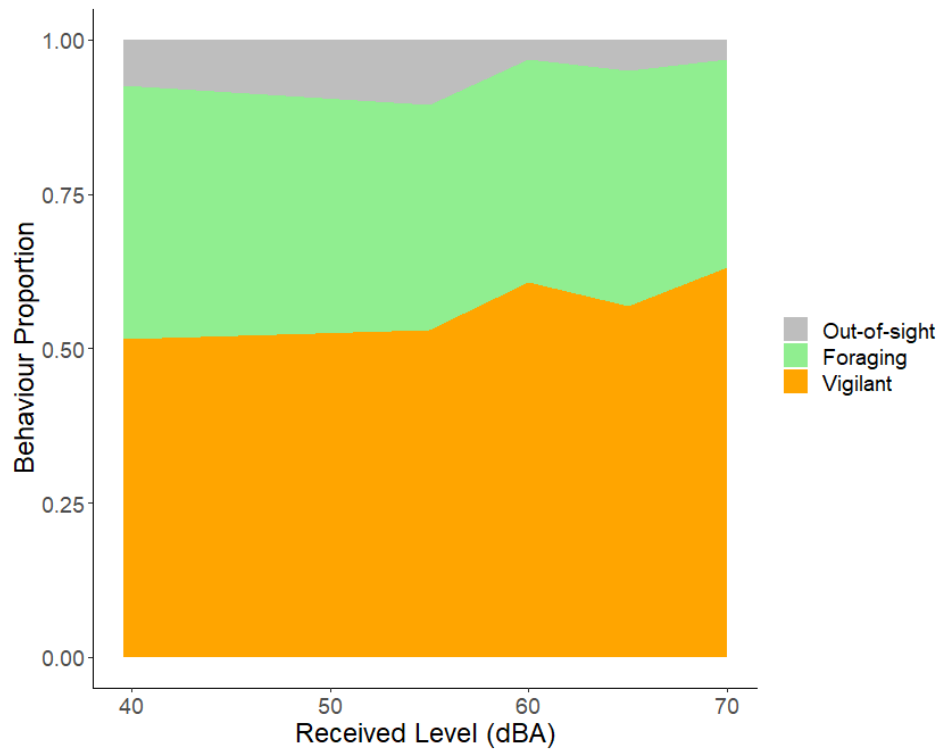


Figure 5 - the mean proportion of time birds were out-of-sight, foraging or vigilant in response to received noise level (dBA).

The impact of increasing received noise had a negative impact on the proportion of time birds spent head-down (hereafter referred to as 'foraging') and head-up (hereafter referred to as 'vigilant') (parameter  $\beta$  estimates:  $-0.1 \pm 0.02$  [CI:  $-0.13$  to  $-0.07$ ]) (Fig. 5). As noise at the received level increased, the proportion of time birds spent vigilant increased, particularly in conditions exceeding 60 dBA. When comparing these data with the impact of noise level on visit duration (Figs. 3 & 4), visits become shorter in greater noise levels with more time dedicated to vigilance behaviour. As a result of the increase in vigilance behaviour and reduction in visit duration, the proportion of foraging behaviour decreases, but only slightly. In contrast, foraging time increased with Julian day and time vigilant decreased (parameter  $\beta$  estimates:  $0.13 \pm 0.02$  [CI:  $0.09$  to  $0.16$ ]). Interestingly, closed habitats did not affect the proportion of time individuals spent

vigilant as strongly as first predicted (parameter  $\beta$  estimates:  $0.03 \pm 0.06$  [CI:  $-0.09$  to  $0.15$ ]).

### Peck Rate

Two models accounted for 95% of the AICc weight for the peck rate (pecks/s) LME (Table 4). Peck rate was highly influenced by seasonality, increasing linearly with both Julian day (parameter  $\beta$  estimates:  $0.11 \pm 0.03$  [CI: 0.04 to 0.18]) and temperature (parameter  $\beta$  estimates:  $0.1 \pm 0.03$  [CI: 0.04 to 0.16]) (Fig. 6).

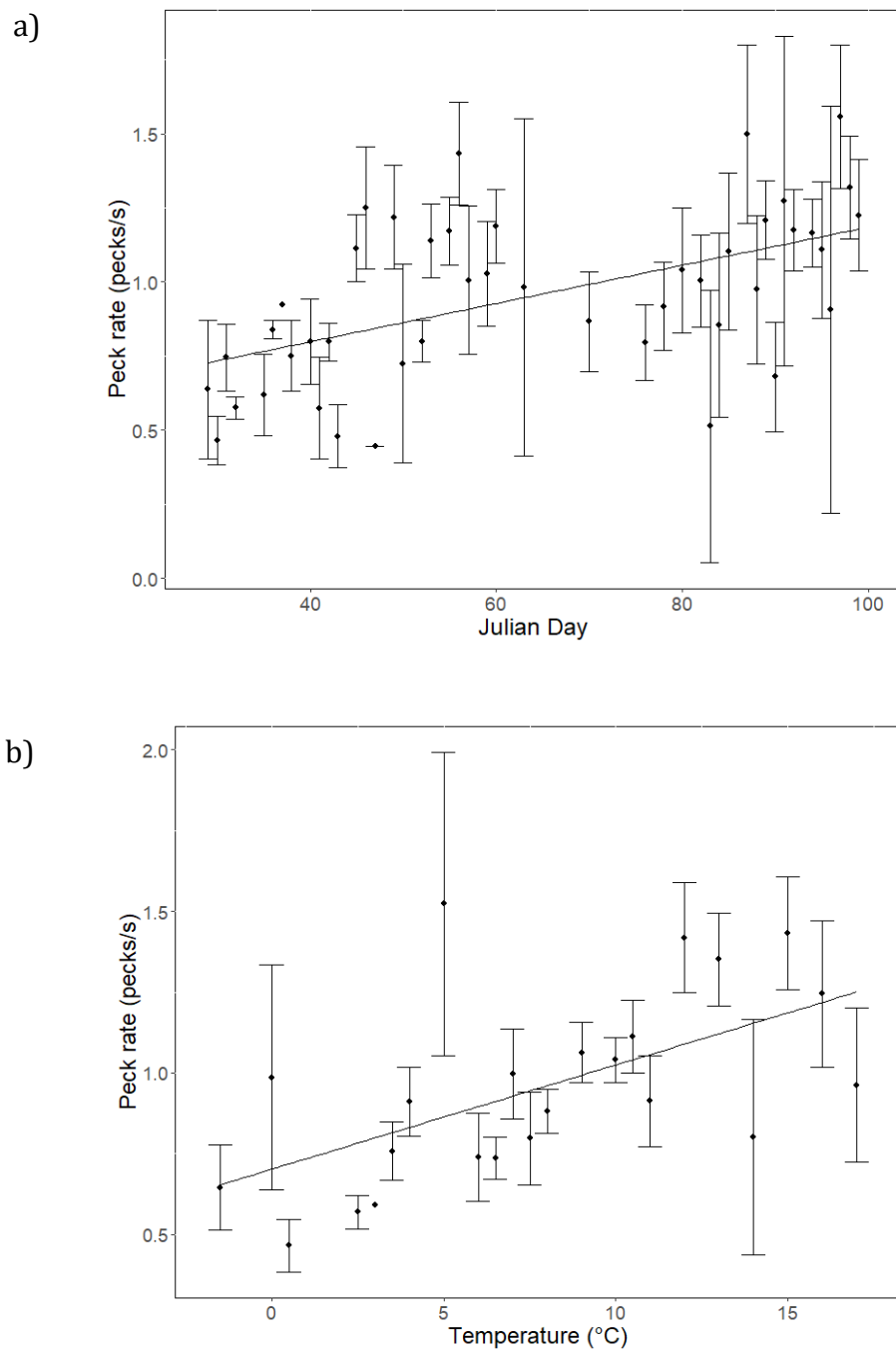


Figure 6 - the mean ( $\pm$ standard error) of peck rate (pecks/s) in response to a) Julian day and b) temperature (°C)

### *Number of Feeder Visits*

A single model accounted for 100% of the AICc weight for number of feeder visits (GLMM) (Table 4). Julian day and temperature were highly influential on the number of visits made by individuals, with visit frequency decreasing linearly with increasing Julian day (parameter  $\beta$  estimates:  $-0.43 \pm 0.03$  [CI:  $-0.48$  to  $-0.37$ ]) and temperature (parameter  $\beta$  estimates:  $-0.14 \pm 0.02$  [CI:  $-0.19$  to  $-0.09$ ]) (Fig. 7). When comparing these results with those for peck rate in Figure 6, it can be seen that although feeding rate at the feeders drastically increased with seasonality, the number of visits to the feeder falls.

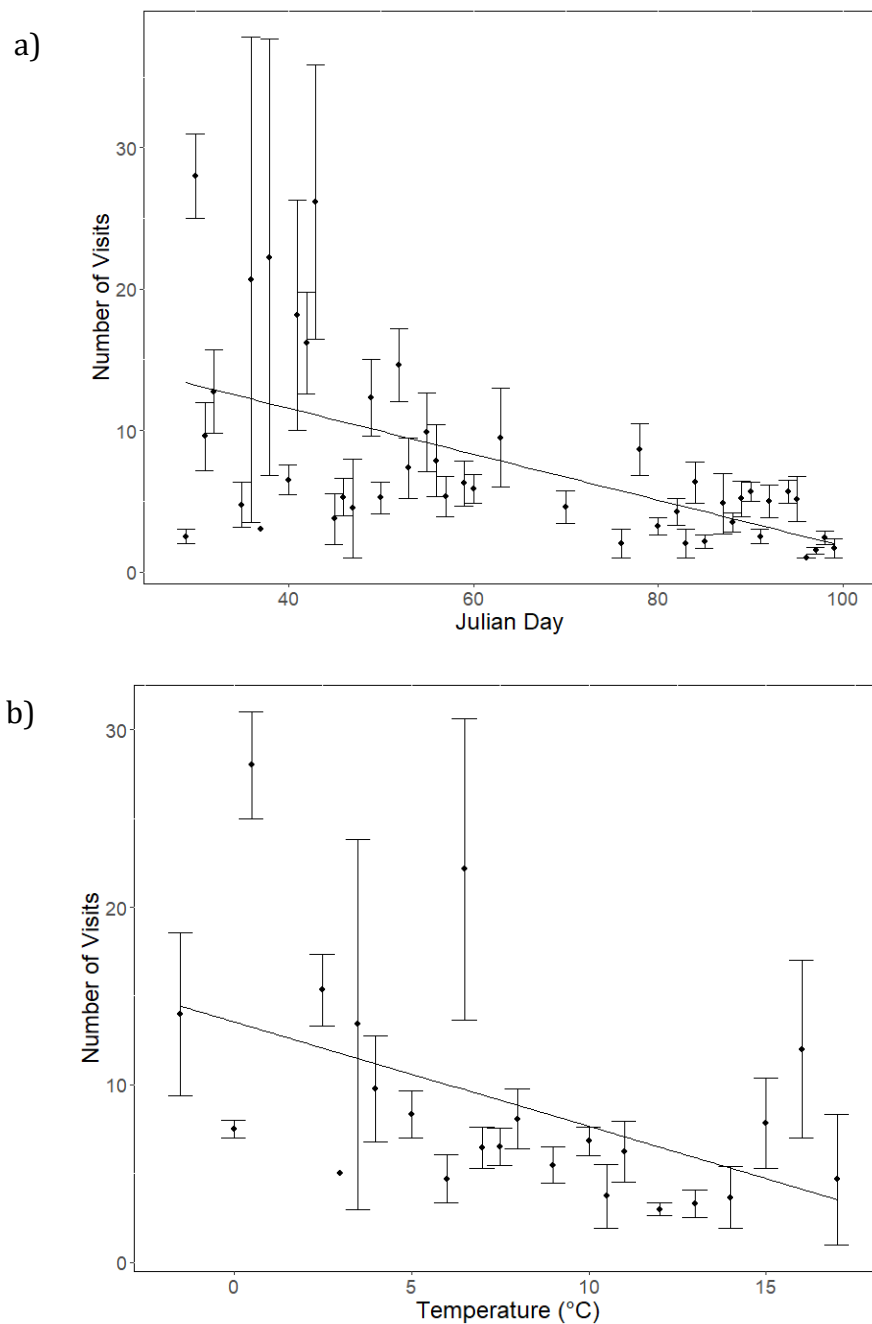


Figure 7 - the mean ( $\pm$ standard error) of the number of feeder visits in response to a) Julian day and b) temperature ( $^{\circ}$ C)



## Discussion

In this study, I provide novel evidence of a noise level tolerance demonstrated by three members of the Paridae family. The data collected in this study are among the first to investigate how foraging and vigilance behaviours are affected across a range of anthropogenic noise levels and how this may be further influenced by surrounding vegetation composition. Across all variables investigated, noise  $\geq 60$  dBA repeatedly caused the greatest disruption to behaviour. The duration individuals spent at the feeders dropped considerably once playback noise reached  $\geq 60$  dBA in both habitats, and continued to decline as noise levels increased. The proportion of time individuals spent vigilant also increased at 60 dBA, with foraging time falling accordingly. Noise did not impact peck rate and the feeder visit frequency as initially predicted, with these variables seen to be most greatly influenced by seasonality.

Visit duration declined in both habitat assemblages as noise level increased, particularly as noise levels hit and exceeded 60 dBA. The potential tolerance at 60 dBA coincides with the average great tit song amplitude in an area of high noise (Slabbekoorn and Peet, 2003). Great tit calls can vary from 42 dB in quiet residential areas to 63 dB in areas of high traffic noise (Slabbekoorn and Peet, 2003). Due to their relatedness and similar morphology, it is likely that the call amplitudes are similar for the blue and coal tits also. It is therefore possible that the birds were relatively unaffected by the lower environmental sounds ( $\sim 40$  dBA of ambient sound), but began altering their foraging visits as noise levels hit and exceeded their peak call volume due to potential masking effects. In turn, this causes a behavioural shift to favouring visual scanning of the surroundings (Brown, 1990; Quinn, *et al.* 2006; Klett-Mingo, *et al.* 2016) and cause the overall risk of feeding to increase (Quinn, *et al.* 2006; Klett-Mingo, *et al.* 2016). By increasing vigilance during periods of noise in which conspecific and predatory audio cues would likely go unheard, individuals are able to continue to inhabit an area; though likely at a fitness cost due to the reduced time spent foraging (Dukas, 2004; Chan, *et al.* 2010; Klett-Mingo, *et al.* 2016). By utilising shorter feeder visits, a greater proportion of visit time could be dedicated to food acquisition in a risky environment. Sacrificing vigilance behaviour at the food source would allow for food items to be handled and consumed away from the feeder in quieter, more secure areas where audial antipredator

cues could again be relied upon. This was demonstrated by individuals within this study, with a significant decrease in visit durations as noise level increased.

Interestingly, across all response variables investigated, vegetation composition did not prove as influential as first hypothesised. Habitat type only features in the models exploring feeder visit duration; though only demonstrated a weak effect, with confidence intervals overlapping zero. The data appeared to show a maintenance of visit durations in the closed habitat, with individuals remaining at the feeder for longer during all experimental playback noise levels (55-70 dBA), potentially allowing for greater opportunity to exploit resources. Visit duration at 60 dBA differed only marginally to that at 55 dBA in the closed habitat despite a noise increase of 5 dBA, whereas there was a marked decrease in duration in the open habitat. An increase in 3 dB equates to a doubling in sound energy (Dooling and Popper, 2007) whilst a 10 dB increase results in a sound perceived as twice as loud (for a 1kHz tone in humans) (Stevens, 1955). A substantial drop in visit duration did occur in the closed habitat as noise increased from 60 to 65 dBA; a sound level known to exceed maximum great tit call volumes (Slabbekoorn and Peet, 2003). At this noise level it appeared that prior visit durations could not be maintained, and individuals chose to make shorter visits. Due to the successful maintenance of longer visit durations in the closed habitat, it could be hypothesised that the presence of protective vegetation caused birds to feel less vulnerable at the feeder during periods of increased anthropogenic noise. These findings are largely speculative however due to the weak effect of habitat type on results and would need extensive future research.

Species type was an important influence on feeder visit duration. Blue tit visits were most abundant within the study (838 feeder visits), and so were used as the baseline for behaviour comparisons; with 713 coal tit visits and 379 great tit visits. As individual birds were unmarked, and could not be recognised within this study, it is difficult to estimate the number of birds which participated. Overall, 1,930 feeder visits were made by the three focal species throughout the study period, though some of which will inevitably be repeat visits by the same individuals. The sample size however was considerable, reducing risk of pseudoreplication, and data were analysed at playback-level; interpreting each feeder visit as an independent 'event'. The difference between blue and great tit visit durations were only marginal, whereas the difference between blue and coal

tits was quite pronounced. Both the blue and coal tits' visit durations decreased linearly with increasing noise; though coal tits repeatedly spent less time at the feeder across every playback noise level. Great tits spent comparable amounts of time at the feeder at each noise level to blue tits, with one marked difference. Great tits appeared unaffected by the playback noise increase from 55 to 60 dBA, with very little change in visit behaviour. As noise continued to increase past 60 dBA however, great tit visit duration dropped accordingly. Interestingly, no other parameters investigated in this study were strongly affected by species; such as peck rate or visit frequency. During field observations, it was noticed that there was a clear species hierarchy regarding displacing individuals from the feeder. With limited food ports, birds had to compete for position at the feeders, with arriving individuals often displacing those already feeding. As all individuals included in the study were wild, free to approach and leave the feeder at any time, this competition continued throughout playback events. Though separate species often fed from the feeders without conflict, it is worth noting that the blue and great tits were particularly dominant over resources in lower noise levels, and could have impacted the species visit durations data. With this in mind, the data do provide an accurate representation of naturally-occurring species interactions during anthropogenic noise, and should not be dismissed. Previously, a study comparing the adaptability of great, blue and marsh tits (*Poecile palustris*) found that great tits were the most successful urban dweller, capable of exploiting man-made food sources and nesting materials (Sasvári, 1979). Blue tits were also found capable of adapting to urban areas, though limited nesting to parks and large gardens, whereas the marsh tit rarely nested in cities at all (Sasvári, 1979). The plasticity and adaptability of some species can allow individuals to remain in an area and exploit resources more successfully in greater levels of disturbance whilst others are displaced, despite their relatedness. Over time, exposure to urban noise conditions has been seen to cause a reduction in species richness (Slabbekoorn and den Boer-Visser, 2006; Mena and Garcia, 2018). With acoustic conditions favouring those most adaptable, once diverse avian community compositions become increasingly homogenous and shy species are outcompeted and displaced to quieter habitats (Slabbekoorn and den Boer-Visser, 2006; Mena and Garcia, 2018).

Another parameter impacted by received noise level was the proportion of time individuals dedicated to foraging and vigilance behaviours whilst at the feeder. As noise level increased, individuals increased the proportion of time spent vigilant, and as a result

the proportion of time foraging declined; though not as sharply as anticipated. Again, as noise exceeded 60 dBA, a change in behaviour occurred, and individuals showed particularly heightened levels of vigilance. Comparing these results with the impact of received noise level on visit duration, it is clear that as the received level of noise reached and increased beyond 60 dBA, feeder visits became shorter with an increasing proportion dedicated to vigilance. It appeared that the birds' behaviour could be explained by the risk-disturbance hypothesis, distracted prey hypothesis and through the avoidance of masking. With greater levels of risk, it has been observed that individuals experience higher levels of the corticosterone stress hormone and are more likely to flee at non-lethal threat (Payne, *et al.* 2012; Injaian, *et al.* 2018a). Disturbances which result in greater energy expenditure therefore increase an individual's energy budget and ultimately food demand (Riddington, *et al.* 1996). In areas of high, continuous road noise, this disturbance could lead to a severe reduction in dedicated foraging bouts; which paired with unfavourable weather conditions or areas of low resource density could further exacerbate chance of starvation (Powolny, *et al.* 2014). Great tits have previously demonstrated a reduction in foraging and increase in vigilance rates during peak noise of aircraft take-off and landing, likely to compensate for masked predator and alarm-call detection in noisy conditions and increased risk (Klett-Mingo, *et al.* 2016). Though aircraft take-off and landing events are often frequent near airports, there is still the opportunity for relief from the noise between plane arrivals and departures. Road noise however is renowned for being continuous and widespread, and without relief from its disturbance it is possible individuals feeding nearby will amass fitness costs over time.

Territorial individuals in particular are often limited spatially, with quieter, high-quality territories aggressively defended by particularly dominant individuals (Reijnen and Foppen, 1994). This can force subordinate individuals into poorer-quality areas, such as those impacted by noise pollution near roads, airports or industrial sites where foraging behaviours are often more disrupted (Reijnen and Foppen, 1994). Male willow warblers (*Phylloscopus trochilus*) inhabiting areas near busy roadways were found to be a juvenile subset of breeding individuals, largely absent of older breeding males who defended higher-quality habitat (Reijnen and Foppen, 1994). Habib, *et al.* (2007) also found that male ovenbirds (*Seiurus aurocapilla*) which inhabited territory near loud compressor stations were of relatively poor quality and less successful in mate attraction due to call masking. It is therefore likely that these outranked individuals were in poorer body

condition and successfully sired fewer offspring due to exposure to greater environmental stressors, preventing successful communication and ample foraging time (Phillips, *et al.* 2018). If pervasive anthropogenic noise sources continue to spread as they are predicted, it is possible that more areas could be subjected to degradation through excess noise, and high-quality habitats will become increasingly isolated. These rare pockets of prime habitat will therefore be dominated by highest-quality individuals, and substandard territories will become the norm. It is very likely that individuals may continue to inhabit those poorer-quality areas, showing little sign of disturbance, however individuals' condition and breeding success is likely to reflect that of their environment (Carney and Sydeman, 1999; Beale and Monaghan, 2004; Phillips, *et al.* 2018). In time, greater proportions of bird communities could be affected by the wider-ranging disturbance and struggle to sustain viable populations.

Surprisingly, vegetation composition did not influence foraging and vigilance behaviour as strongly as predicted. It was hypothesised that in the closed habitats, birds would maintain a greater proportion of foraging behaviour due to the security provided by the protective vegetation. However, due to the weak impact of the variable (with confidence intervals overlapping zero), it can be assumed this is not the case. Individuals remained just as alert to threat in the closed habitat as the open, and foraging behaviour was still monopolised by vigilant anti-predator behaviour in greater noise levels (Powolny, *et al.* 2014). Though protective vegetation provides cover for individuals from aerial predators, it would also obscure the visual detection of predators; such as the Eurasian sparrowhawk (*Accipiter nisus*), a common tit predator. Many existing studies have reported increased vigilance and reduced foraging behaviour in obstructed habitats (Lima, 1987; Quinn and Cresswell, 2004; Whittingham, *et al.* 2004; Whittingham, *et al.* 2006; Griesser and Nystrand, 2009), however due to the species' predator evasion tactic of fleeing and seeking cover (Lima, 1993), feeding within cover was predicted to have a positive effect on foraging time (Griesser and Nystrand, 2009). Although this study intended to test the security provided by the vegetation, a possible reason for the outcome is that the obscured view from the feeder meant individuals were unable to scan the area for predation risk, and so the perceived level of risk was similar to that in the exposed open habitat. Interestingly, individuals did remain at the feeder for considerably longer in the closed habitat during ambient sound conditions (during control playbacks), but when noise was introduced, the time individuals spent at the feeder became similar

in both vegetation assemblages. This result goes against the prediction that the closed vegetation would offer security to foraging individuals in increased noise conditions (Powolny, *et al.* 2014), and may stress the importance of unobstructed areas for scanning and reliance on visual cues in even moderate levels of anthropogenic noise.

The proportion of time spent vigilant or foraging was also impacted by Julian day. As the study progressed from January to April, vigilant behaviour decreased and foraging behaviour increased significantly. As individuals progressed through the year, it is likely that they became more confident and less vigilant in their environment due to having successfully established territories; particularly under the assumption that territory defence often takes priority over resource exploitation (Schoener, 1983; Ydenberg and Krebs, 1987). The strong effect of seasonality was also evident on peck rate and the number of feeder visits. As seasonality progressed from winter into spring, peck rate increased rapidly, whilst the number of feeder visits fell just as sharply. This period during the year would have coincided with individuals entering breeding season (April-May), and it is likely that peck rate increased to maximise food intake in preparation for the onset of mate attraction, breeding, nesting and parental care (Staine and Burger, 1994; Barba, *et al.* 2017). The marked drop in feeder visit frequency was likely due to other food sources becoming available with the change in season (Ydenberg and Krebs, 1987; Cowie and Hinsley, 1988; Illera and Atienza, 1995); such as tree buds, berries and invertebrates (Ydenberg and Krebs, 1987; Illera and Atienza, 1995). Individuals would therefore be less reliant on the supplementary food from the feeders during warmer seasons, and chose to exploit other food sources in the area (Ydenberg and Krebs, 1987; Illera and Atienza, 1995). To provide a more inclusive overview of the effects of noise on peck rate and number of feeder visits, conducting the study over a full year would be valuable; as this would account for any seasonal variance.

## Conclusion

This study has highlighted the potential impact of increasing anthropogenic noise levels on the disturbance of three of our native bird species. It was clear that not only is the presence of anthropogenic noise capable of pronounced behavioural disturbance, but that increasing noise intensity exacerbates responses further. Greatest noise levels continued to reduce visit durations and foraging bouts, whilst the time individuals spent scanning for threat also continued to increase. It appeared that individuals were most affected by traffic noise  $\geq 60$  dBA, repeatedly causing shortened visits and increased vigilance rates. With shorter visits to feeding areas, food frequently being handled and consumed away from the source and overall heightened vigilance levels, areas of anthropogenic noise  $\geq 60$  dBA could cause heightened stress and poor condition of individuals. If individuals remain in these areas of high disturbance, it is possible that they could suffer from poor condition, reduced mate attraction and poor breeding success over time.

Although the presence of protective vegetation was hypothesised to mitigate the disturbance caused by anthropogenic noise, the results of its success were confounding. Visit duration was seen to be greatest in the closed vegetation during ambient sound conditions, but individuals remained just as vigilant in both habitats when subjected to noise. The similarity in vigilance rates may be due to comparable levels of perceived risk by individuals; predation from being spotted at a distance in the open habitat but risk of an ambush attack in the closed. Further research into this area to investigate vegetation preferences during foraging bouts in noisy conditions may yield valuable results to aid landscape management efforts in the future.

The coal tit, the shyest of the three species, was seen to be most affected during all levels of disturbance, with bolder species able to secure and retain a feeding position more efficiently during greater risk. This study aspect would benefit from greater future research focus as shy individuals may be those lost from an area first due to displacement by other, more adaptable, species. If resources are limited, such as optimal territory, they will be quickly dominated by more bold species. Testing the effects of anthropogenic noise on species which are solely found in quiet, rural areas could further stress the importance of reducing the spread of anthropogenic noise across our landscape. As these

species have already been pushed into more remote areas of the countryside, further expansion of our road networks may leave nowhere to retreat.



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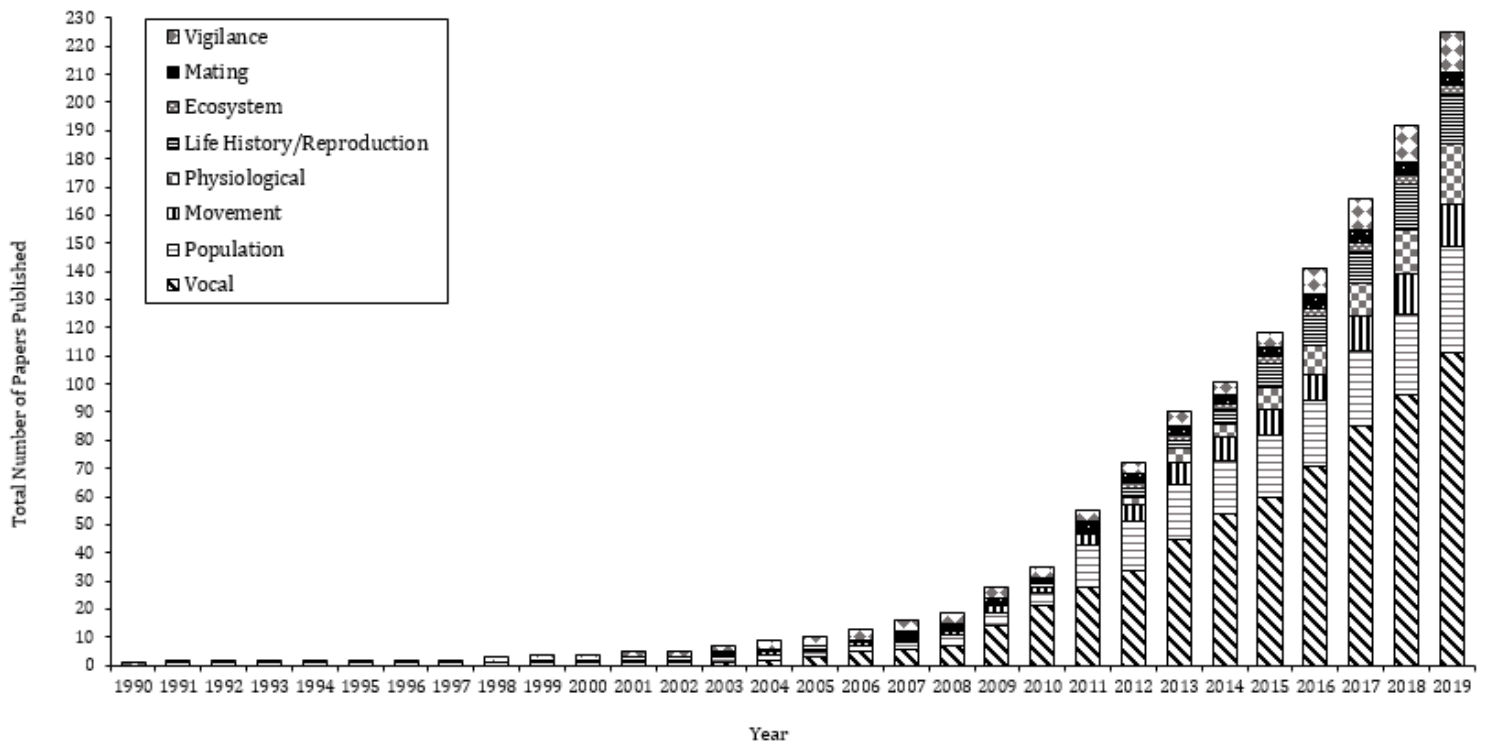
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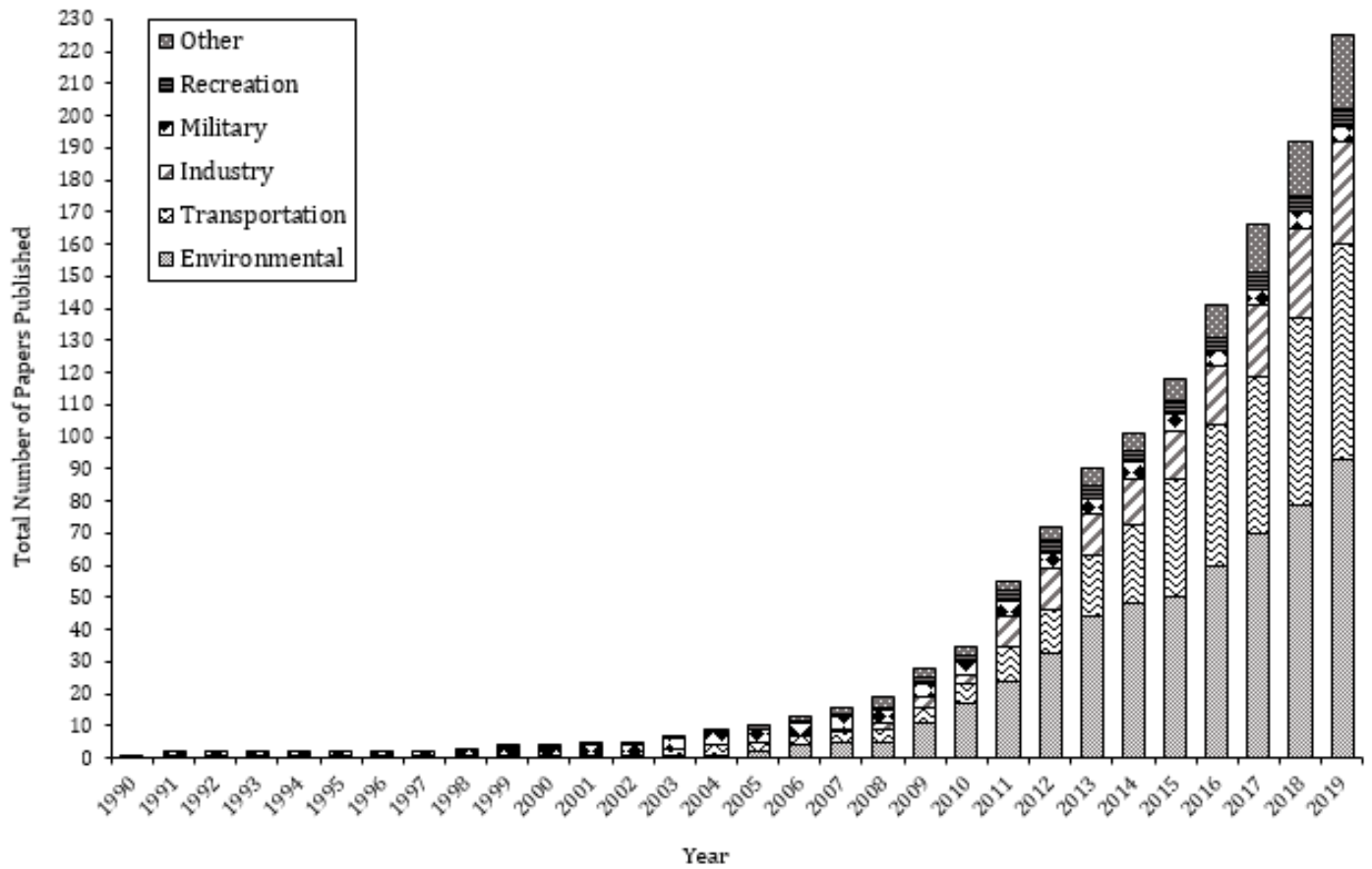
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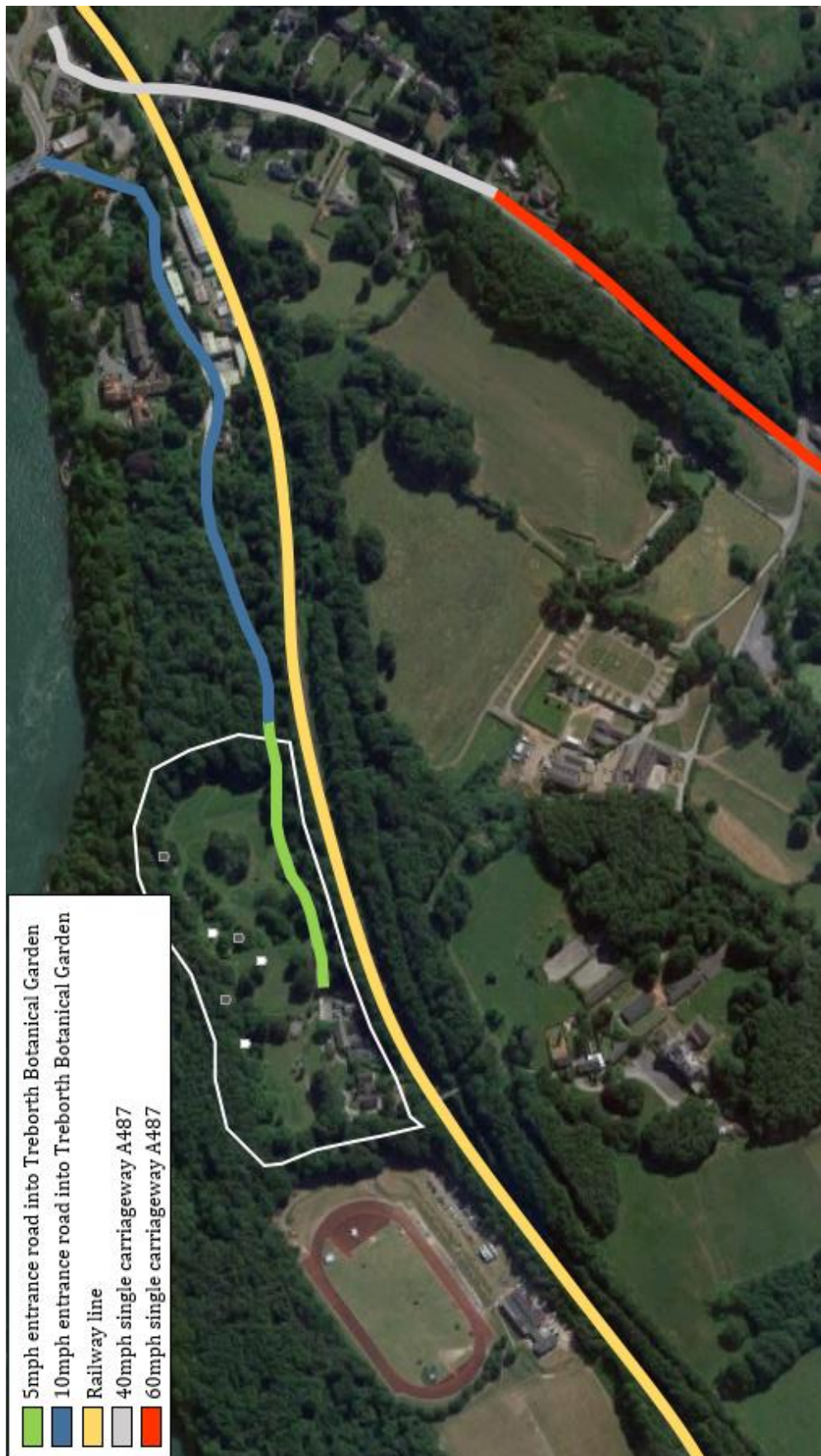
**Appendix 1 – Total number of papers published on the effects of anthropogenic noise on birds 1990-2019, categorised by biological response measured ( $N= 225$ ).**



**Appendix 2 - Total number of papers published on the effects of anthropogenic noise on birds 1990-2019, categorised by noise source studied ( $N=225$ ).**



### Appendix 3 – Study Site Map





#### Appendix 4 – Schematic of Feeder Locations within the Study Site

