Bearing with noise: the effects of highway noise on behaviour and development in zebra finches

Liu, Q.

Citation

Version:	Publisher's Version
License:	
Downloaded from:	

Cover Page

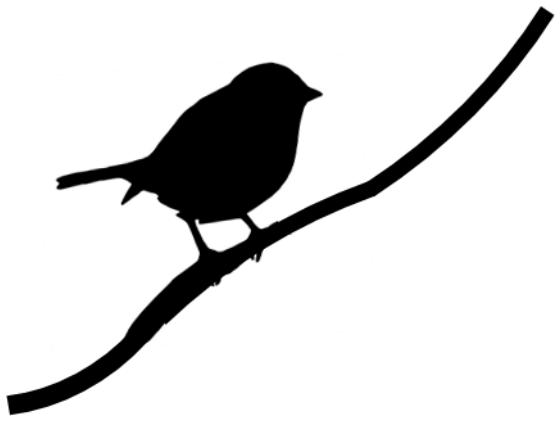# Universiteit Leiden

The handle https://hdl.handle.net/1887/3180750 holds various files of this Leiden University dissertation.
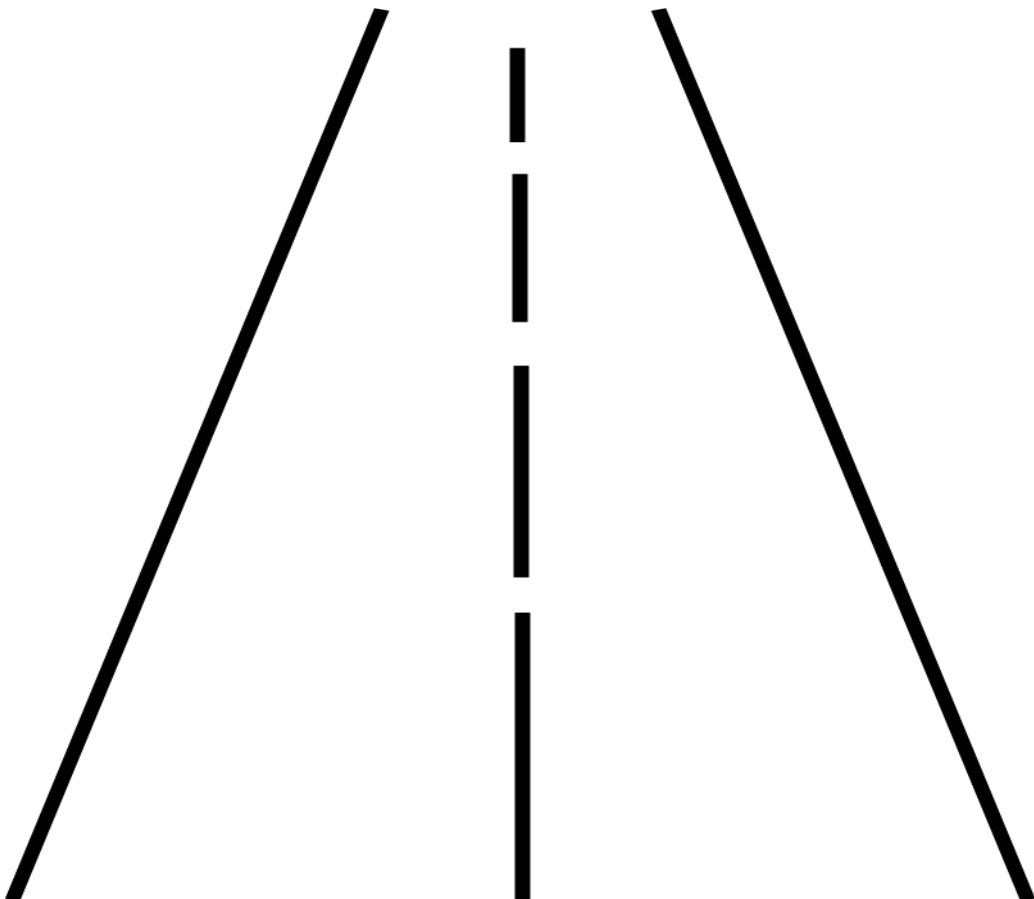
Author: Liu, Q.
Title: Bearing with noise: the effects of highway noise on behaviour and development in zebra finches
Issue Date: 2021-06-02

Chapter 1

General Introduction

Introduction

The past decades have seen a continuous rise in anthropogenic noise pollution. Worldwide, anthropogenic noise is affecting millions of people day and night (EEA, 2015; Wu et al., 2019) who suffer not only from short-term annoyance and sleep disturbance but also from long-term hypertension and cardiac disease (reviewed by Clark & Stansfeld, 2007). Traffic, especially road traffic, is a dominant source of anthropogenic noise (Barber et al., 2010; Mennitt et al., 2015) that reaches many animals: not only those living in urban areas, but also those in remote and protected areas, due to the ever increasing network of roads and highways (Barber et al., 2011; Buxton et al., 2017). This has raised concerns that animals are also being negatively affected by anthropogenic noise pollution (Kull & McGarrity, 2003; Wright et al., 2007; Slabbekoorn et al., 2010; Kunc & Schmidt, 2019). Birds are a taxonomic group in which noise pollution problems are especially well documented, perhaps because they are well visible and relatively easy to monitor, but they may also be particularly sensitive to anthropogenic noise (Dooling & Popper, 2007; Hutton & McGraw, 2016; Gilbert et al., 2017; Kleist et al., 2018).

Traffic noise can have a wide variety of effects on birds. Habitats near roads often have lower breeding bird densities (Reijnen et al., 1996; Bayne et al., 2008; Benítez-López et al., 2010) and different community structure compared to more quiet areas (Francis et al., 2009). Birds in noisy areas are also reported to be of lower body condition than conspecifics in more quiet areas (Phillips et al., 2018). Birds breeding in territories near noisy generators or along noisy highways are less likely to attract a mate (Habib et al., 2007), have a smaller clutch size (Halfwerk et al., 2011), and produce fewer fledglings (Kight et al., 2012) compared to conspecifics in relatively more quiet territories.

Next to differences in reproductive success, birds occupying noisy habitats also behave differently in comparison to conspecifics in more quiet areas. Birds near airports across the world have a clock-shifted dawn chorus beginning earlier than in control areas (Gil et al., 2015; Dominoni et al., 2016). Additional examples of noise-related changes in behaviour near airports are for example, European blackbirds (*Turdus merula*) singing less twitters in their songs (Sierro et al., 2017) and chiffchaffs (*Phylloscopus colybita*) reacting more aggressive to audio playbacks (Wolfenden et al., 2019). Similarly, great tits (*Parus major*) in urban areas start their dawn chorus earlier, but sing less later in the afternoon (Bermúdez-Cuamatzin et al., 2020). House finches (*Haemorhous mexicanus*) in noisy urban areas are less avoidant of novel noise stimuli than rural populations (Weaver et al., 2019). Birds typi-

cally sing louder (Brumm & Todt, 2002) and at a higher pitch (Slabbekoorn & Peet, 2003) when noise levels rise, a feature they share with many other animal species (Brumm & Zollinger, 2011). Many species also sing at higher sound frequencies when exposed to noise playbacks, as for example great tits (Slabbekoorn & Halfwerk, 2009), silvereyes (*Zosterops lateralis*, Potvin & Mulder, 2013) or house finches (*Carpodacus mexicanus*, Bermúdez-Cuamatzin et al., 2011). Black-capped chickadees (*Poecile atricapillus*) shifted their songs upwards in frequency only when they were familiar with noisy conditions (LaZerte et al., 2016). Urban but not rural white-crowned sparrows (*Zonotrichia leucophrys nuttalli*) similarly showed upward frequency shifts in their songs in response to noise playbacks (Gentry et al., 2017). While these examples show differences between birds in noisy versus quiet habitats, for many of the examples it is unclear whether differences in behaviour are examples of selection for particular genotypes or of short- or long-term behavioural plasticity and flexibility. The behavioural patterns could be a reaction to acute or chronic noise exposure or an ontogenetic result of a noisy rearing environment.

To better understand and address how noise affects animals, several studies have started to address the mechanisms underlying the behavioural and physiological impact of noise and how it relates to specific noise properties. Pioneering experimental studies testing how birds adjust timing of their singing to avoid fluctuating short-term increases of noise did not find a consistent pattern across species. Eurasian wrens (*Troglodytes troglodytes*) did not temporally adjust their singing pattern to fluctuations in traffic noise, nor did they avoid singing during playbacks of broadband white-noise (Yang & Slabbekoorn, 2014), while chiffchaffs along train tracks interrupted their sequence of songs for a passing train (Slabbekoorn et al. unpublished data). The mechanism of physiological effects of long-term noise exposure on neuroendocrine system, metabolism, and development of the auditory system (reviewed by Kight & Swaddle, 2011) has also been studied. In house sparrows (*Passer domesticus*), feather corticosterone levels of juveniles before moulting (reflecting long-term corticosterone levels) were positively correlated with urbanization levels (Beaugeard et al., 2019), indicating that noisy urban environment may be a stressor to developing birds. Behaviourally, animals have been reported to respond to noise through changes in their spatial distribution, the use and structure of vocalizations, and in foraging patterns related to predation or anti-predatory behaviour (reviewed by Mellinger, 2016). Any of these effects, could play a role in generating associations found between traffic noise and reductions in bird density and diversity (reviewed by Newport et al., 2014).

The behavioural and physiological differences between bird populations in noisy and quiet areas could come about by a number of different and mutually non-exclusive processes acting at different life stages and at different time scales (Figure 1). Noise could elicit an imme-
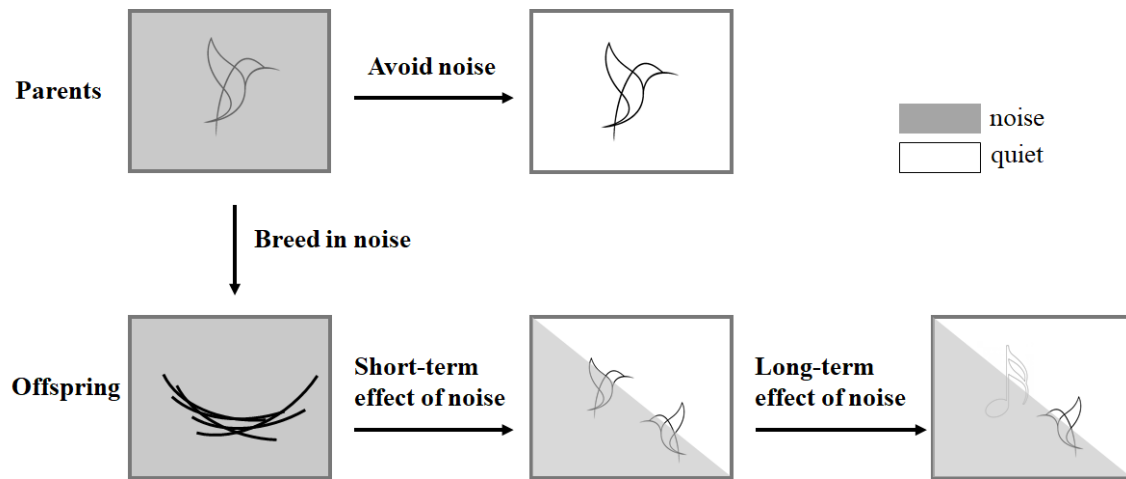
Figure 1: Different life stages and time scales at which traffic noise may affect bird behaviour. When exposed to traffic noise, birds may directly avoid noisy habitats. If birds do not avoid the noise and stay on to breed in high level traffic noise, direct or indirect effects on the parents could affect their behaviour towards their offspring. In addition, noise can also have direct short- and long-term effects on offspring phenotypes and behaviour.

diate response (e.g. avoidance) but also cause long-term effects (e.g. singing less complex song). The background noise of the rearing environment of birds may affect their responses to noise later in life. Investigating the mechanisms and processes underlying the possible explanations for noise-related patterns and identifying whether they are due to (self) selection or phenotypic plasticity can facilitate the understanding and possibly the mitigation of the effects of traffic noise on birds and their reduced numbers near roads. An important question the field has to address now experimentally is whether decreasing numbers near roads arise just from avoiding moving cars, chemical pollution, or poorer habitats or whether birds are also repelled by noise *per se*. Two studies tested this question in the field: Blickley et al. (2012) played back drilling and road noise at leks of greater sage-grouse (*Centrocercus urophasianus*) and found that there were fewer males attending the noisy leks compared to the control leks. McClure et al. (2013) used a speaker array playing back traffic noise to imitate a noisy road ('phantom highway') at an avian migratory stop-over site. On days with playback they observed fewer visiting individuals from multiple bird species. These results are in line with both deterring or masking effects of noise. In both these field tests, birds were tested in a context where they would seek out and be attracted by the presence of vocally active conspecifics. If the noise masked the vocalizations normally attracting the birds (Mönkkönen & Forsman, 2002; Schepers & Proppe, 2017) to mating and stop-over sites then they might have failed to locate the other birds, rather than having been deterred by noise. For now, these studies thus show that noise alters birds' spatial distribution but do not address the underlying mechanism.

Likewise, observations of reduced breeding outcomes near roads are not conclusive with respect to the underlying processes leading to these outcomes. Both observational and experimental approaches in the laboratory and the field have aimed to gain an understanding from different perspectives. Several studies have provided experimental evidence for noise interfering with acoustic communication within breeding pairs (zebra finches, Villain et al., 2016) and between parents and offspring (tree swallows *Tachycineta bicolor*, McIntyre et al., 2014; Leonard et al., 2015; blue tits *Cyanistes caeruleus*, Lucass et al., 2016). Noise playbacks can also directly affect the behaviour of the breeding parents. Female house sparrows fed their young with less food in noisier areas (Schroeder et al., 2012) and when experimentally exposed to noise during breeding, females had longer flush distance (Meillère et al., 2015). However, these impacts on parental behaviour seem to depend on various factors including the traits of the parents (sex and personality traits, Naguib et al., 2013) and even in the same species, the impacts of noise on parental behaviour are not always consistent (feeding rate, Injaian et al., 2018b, 2018a). Complementary study is required to see if traffic noise causes the changes in parental behaviour.

Changes in parental behaviour could potentially explain the observed differences in reproductive outcomes, but noise can also directly affect offspring if the chronic noise constitutes a stressor. Offspring reared in noisy conditions were affected morphologically (lighter mass, Potvin & MacDougall-Shackleton, 2015; Zollinger et al., 2020), and physiologically (lower metabolic rate, Brischoux et al., 2017 and faster telomere attrition, Salmón et al., 2016; Dorado-Correa et al., 2018; Injaian et al., 2019; Grunst et al., 2020). A number of studies investigated whether chronic noise exposure during development would affect the HPA-axis programming and physiological stress responses in several bird species (white-crowned sparrows, Crino et al., 2013; house sparrows, Angelier et al., 2016; tree swallows, Injaian et al., 2019; Japanese quails *Coturnix japonica*, Flores et al., 2020; zebra finches *Taeniopygia guttata*, Zollinger et al., 2020) but these studies have not shown a clear consistent pattern yet and also varied considerably in methodology. Perinatal exposure of repeated bouts of 5 minute traffic noise was associated with increased baseline corticosterone in tree swallows (Injaian et al., 2019) but in another study, white-crowned sparrow chicks continuously exposed to short recordings of passing traffic for five days after hatching, had decreased baseline corticosterone (Crino et al., 2013). House sparrow nestlings exposed to repeated short highway recordings for six hours per day (Angelier et al., 2016) had no altered baseline corticosterone levels at the age of nine days. There was likewise no effect of daily, eight hours playbacks of sound clips of downtown, highway and subway noise to Japanese quail chicks during the first eight days posthatching (Flores et al., 2020).

From the studies above, the interactions between type and duration of noise exposure and physiology cannot be fully characterised yet, and future studies will have to disentangle the effects from different noise treatments and species differences. It is worth noting though, that most of the studies to date either used artificial noise stimuli or repeated, short clips of traffic noise, that do not fully capture the dynamics of a busy road. Studies with realistic traffic noise stimuli can help validate the aforementioned results. For now several of these studies demonstrated an effect on physiological parameters known to covary with behaviour: developmental plasticity of the HPA axis reactivity is associated with behavioural differences in many birds (Schoech et al., 2011), but the long-term effects of experimental noise exposure to date have mostly focussed on physiology rather than behaviour (Injaian et al., 2020).

Little is known on how growing up in noisy conditions affects adult behaviour (other than song), but there are now a number of studies that suggest long-term effects in several songbird species. Chronic exposure of simulated traffic noise in captive adult Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*) made both bird species stay closer to conspecifics and have longer latencies to approach a novel food container (Owens et al., 2012). Moseley et al. (2018) presented white-crowned sparrow nestlings with tutor songs categorized as being of relatively high or low frequency, determined by how much the song was masked by low frequency city-like noises. When song was simultaneously played back with noise, the tutees showed a bias in copying the high frequency songs, which were less masked by noise. However, a similar study in great tits, exposing nestlings to broad bandwidth noise, masking either high (3 - 6 kHz) or low (0 - 3 kHz) frequencies of great tit songs, did not find any effect of traffic noise on song learning (Zollinger et al., 2017). These studies indicate that more studies are required on whether and how adult phenotypes are affected by noisy rearing conditions.

By far the largest number of developmental studies on effects of noise on adult phenotypes have been conducted in the zebra finch. This is probably due to widely accessible laboratory populations of zebra finches and because the zebra finch is a very suitable model to study behavioural development. Zebra finches breed easily in captivity and mature in about 100 days only, much faster than most songbirds. In combination with the extensive knowledge on their behaviour and development (Zann, 1996; Griffith & Buchanan, 2010), this species is suitable to study the short- and long-term behavioural effects of being exposed to noisy conditions during development. From the experiments to date (Table 1), we know from work on hearing physiology that song development in zebra finches can be delayed by overexposure with extremely loud noise, but actual hearing damage occurs only at extreme high amplitudes (120 dB SPL, 2-6 kHz, Ryals et al., 1999). Using much lower levels of compiled urban noise, Potvin et al. (2016) found that zebra finches, raised in noise levels similar to condi-

Table 1: Recent experimental noise exposure studies in zebra finches.

Research focus	Noise type	Noise level	Exposure period[1]	Measurement[2]	reference
Single playback studies					
Foraging	Broadband noise + colony vocalisation	70 dBA	2 h	Vigilance* and foraging*.	Evans et al. (2018)
Communication	Repeated short wind noise	59 – 64 dBA	Overnight (~ 16 hours)	Structure of duets*, calls*, pair spatial proximity during the duets*	Villain et al. (2018)
Pair preference	White noise	90, 75 and 45 dBC	40 min	Time spent near mate*	Swaddle & Page (2007)
Continuous playback studies					
Nestling growth and physiology	Repeated short traffic noise	Day: 65 – 85 dBA; Night: 45 – 75 dBA	Perinatal - 16 dph	Baseline corticosterone levels in parents*, granulocyte/lymphocyte ratio, embryo mortality, offspring survival at 120 days, offspring mass*,	Zollinger et al. (2020)
Telomere attrition	Same as Zollinger et al. (2020)		Perinatal - 18 dph or 18 – 120 dph	Telomere attrition rate*	Dorado-Correa et al. (2018)
Reproduction, parental corticosterone	Urban noise edited with vehicle sound	40 – 80 dBA, avg 65 dBA	0 – 100 dph	# offspring, embryo mortality*, offspring mass*, baseline corticosterone levels in parents.	Potvin et al. (2015a)
Adult song	The fathers in Potvin et al. (2015a)			Baseline corticosterone, song similarity, frequency*, duration and notes per song	Potvin et al. (2015b)
Offspring physiology, song and brain development	The offspring in Potvin et al. (2015a)			Song similarity*, song structure*, song similarity to tutor*, baseline corticosterone, telencephalon, RA, hvc* and area X*	Potvin et al. (2018)
Song learning	Pink noise	75 dBA	0 - 200 dph	Min, max and peak* frequency, song similarity	Funabiki & Konishi (2003)
Song learning	White noise	110 dBA	35 – 129 dph	Reproduction of tutor syllables*, song temporal pattern* and syllable sequences*	Funabiki & Konishi (2003)
Song learning	White noise	110 dBA	35 – 137 dph	Song learning after sensitive phase*	Funabiki & Funabiki (2009)

1 period is expressed in days post hatching (dph): 0 dph = hatching date. 2 statistical significance is indicated by *

7

tions close to a busy urban road, still learned their tutor songs, but with lowered song sequential similarity to their tutors (of sample size <= 6). Several studies looked at other physiological effects and found accelerated telomere attrition rate and decreased mass in noise exposed juveniles showing that noise can contribute to differences in condition (Dorado-Correa et al., 2018; Zollinger et al., 2020). To fully understand how traffic affects birds, it seems paramount to also investigate how noise affects their behavioural phenotypes.

It is clear from the reviewed observational and experimental studies that traffic noise has many effects on bird behaviour and physiology. However, most experimental noise exposure studies either tested birds of unknown rearing background (in the wild) or, when exposing them to noise in the laboratory, birds that had grown up at low ambient noise levels. There is thus still a substantial gap between the observations that bird numbers are dwindling along roads and potential behavioural drivers of this phenomenon. Are birds disappearing because they show aversion to noise, noise related habitat quality change, or because noise induced short- and/or long-term behavioural effects reduce their fitness? How important are rearing noise levels in shaping reactions of adult birds to noise? There is increasing documentation that growing up in noise can affect growth and physiology in birds, but are there long-term behavioural consequences of such physiological changes in young birds that manifest only in adult birds?

In this introduction, I mostly used traffic noise as a generic term. However, noise effects depend on dosage and type of noise (Dooling, 2011). Stimuli to date have been diverse and only few studies have used external validation of experimented stimuli. Moreover, almost all experimental noise exposure studies used high levels of exposure as treatment and no-playback as a control condition. Without comparison of different types of noise, effects of a traffic noise playback might not be specific to traffic noise but to any noisy or even any novel sound. Identifying aversive and non-aversive levels of sounds and comparing the birds treated with aversive to non-aversive playback might avoid confounding effects from the mere presence of any type of anthropogenic sound (rather than its intensity). In this thesis, I addressed some of these open questions in a series of experiments with zebra finches.

Outline of the Thesis

To test what levels of highway traffic noise triggered noise avoidance in adult zebra finches, I developed a method to test spatial preferences in relation to noise levels in a two-way

choice test (**Chapter 2**). Experimental exposure studies in birds either used edited sound stimuli (high stimulus control) or original recordings from highways (high external validity) but rarely, if ever first established at which levels sounds would be aversive. I therefore developed a behavioural test to assess deterrence effects of different intensities of traffic noise. I first made 24-hour field recordings of two Dutch highways from near and far distances. Based on these recordings, 'far' and 'near' distance noise profiles were characterised and parts of the recording were used for behavioural testing. Birds were tested in flocks of four, and could freely choose between two aviaries (offering choices between near- and far-distance traffic noise or quiet, i.e. no playback). If traffic noise *per se* is sufficient to deter birds, the tested birds should always prefer the quiet aviary over the one with noise playback. If the properties of the noise affect the avoidance behaviour, the birds should show different levels of avoidance of the two types of traffic noise.

Based on the insights of the noise avoidance test, a breeding experiment was designed to test whether breeding in behaviourally avoided sound would affect reproduction (**Chapter 3**). The noise avoidance test in Chapter 2 demonstrated that birds' avoidance behaviour was affected differently by different types of highway noise. Breeding pairs were given two opportunities to breed: once being continuously exposed to near-distance traffic noise (avoided) and once being exposed to far-distance traffic noise (not avoided). This cross-over design using two types of sound avoids interpretation problems that can arise when using a 'no-playback' control where differences between groups might be caused by the difference between sound and no sound rather than being specific to the properties of traffic noise. If the behavioural avoidance in the spatial preference test is a good measure to assess which noise levels are aversive to the birds, then parental behaviour and reproduction should differ in breeding events with actively avoided noise versus noise that had not been actively avoided.

Rearing birds with different noise exposure also allowed testing whether rearing levels of traffic noise would affect birds' tolerance to noise (**Chapter 4**). Habituation or sensory adaptation are discussed widely as possible coping mechanisms during sustained noise exposure. To date, studies testing birds' behavioural responses to noise have either tested young birds in the nest or adult birds with unknown rearing background, but not whether rearing in noisy conditions leads to higher noise tolerance levels. Using the same experimental set-up used for testing the parents (**Chapter 2**), the offspring generation was tested for noise avoidance tendency at 65 days (with an additional same-age control group raised without any noise) and at 120 days post hatching. If being reared/housed in noise prior to testing affects noise

tolerance, the offspring should have behaved differently from the control group as subadults and should have behaved differently from their (not noise reared) parents as adults.

Once the offspring were adults, I also investigated whether there were long-term behavioural effects of traffic noise exposure during development (**Chapter 5**). Observational data in several bird species show individuals residing in noisy/urban areas to be bolder and to sing differently than individuals from quiet/rural areas. This has been hypothesised to be a phenotypic effect of chronic high noise levels on stress physiology and acoustic signals. While effects of traffic noise on song learning have now been tested in several species, effects on singing effort remain unclear. I therefore tested if rearing noise conditions affect singing effort and whether singing effort is correlated to explorative behaviour. If singing effort and exploration are affected by rearing noise conditions, the birds from different rearing noise backgrounds should have been different in these behaviours.

In the final **Chapter 6,** I briefly summarised the results of Chapter 2-5. I discussed the main conclusions and insights then on how to proceed with investigating the effects of traffic noise on animals.