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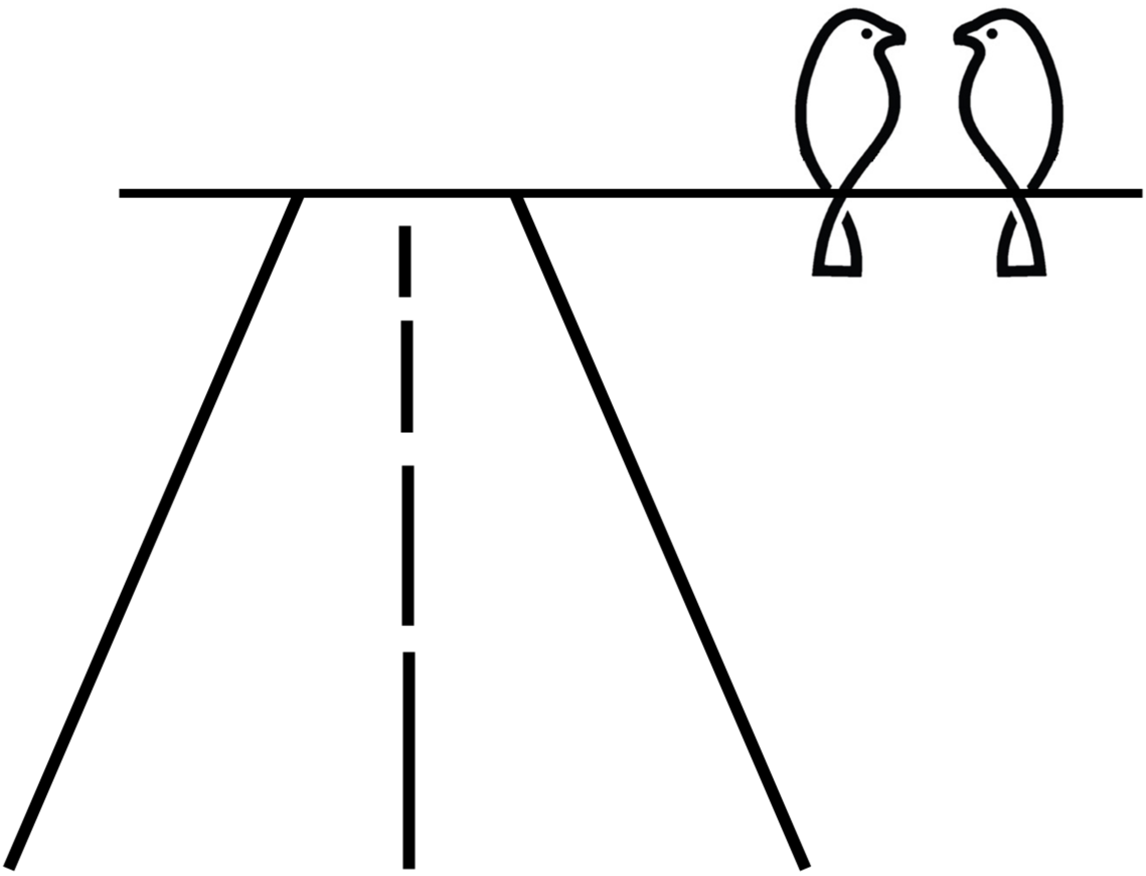
Chapter 6

Thesis Summary & General Discussion



The importance of studying the effects of noise on animals

Anthropogenic noise negatively affects wildlife in a wide range of taxonomic groups, from molluscs to mammals (Slabbekoorn et al., 2018a; Kunc & Schmidt, 2019). Especially for birds, a substantial number of observational studies have now shown negative associations between noise pollution and abundance and diversity along roadsides (Reijnen et al., 1996; Francis et al., 2009; Halfwerk et al., 2011). Birds might be more studied in general than other species, but as they rely on sound for communication, they may also be particularly susceptible to masking effects of noise. Consequently, researchers investigating birds' behavioural responses to high level noise to date have mostly focused on the immediate adjustment of vocal signalling behaviour. However, there is more than one mechanism by which birds might cope with increasing noise levels (reviewed by Potvin, 2017). They may show immediate behavioural reactions, such as spatial avoidance and/or vocal adjustment, but also more ontogenetic adjustments with long-term consequences like changes in sensory and personality traits (Dooling & Popper, 2007; Carrete & Tella, 2011).

Natural noise can lead to an array of adaptations in acoustic signalling in animal populations (Brumm & Naguib, 2009). However, given the current speed of urbanisation and expansion of infrastructure, the numbers of anthropogenic noise sources like highways increase at a higher pace than populations previously not exposed to such noise can evolve. Consequently, birds have to rely on mechanisms acting within an individual's life time to cope with noisy conditions, such as spatial avoidance or habituation. The potential extent of behavioural plasticity and flexibility is discussed widely in this context but has seen little experimental testing, aside from studies on song adjustment (reviewed in Potvin 2017). It is important to understand the underlying mechanisms for a proper interpretation of the many observational field studies showing declining bird numbers near roads. If we can disentangle the effects of noise *per se* from other factors related to traffic (increased pollution, moving vehicles, habitat destruction and human presence), we may be better able to understand, predict and mitigate detrimental effects of anthropogenic noise.

It is often argued that animals habituate to noise, or that growing up in noise might change sensory thresholds. However, to my knowledge there have been no experimental studies to date that have addressed whether rearing noise levels lead to more noise tolerant phenotypes in birds. Gaining insight regarding these issues requires an experimental approach to disentangle noise impact from confounding factors, and exposing developing birds to long-term noise testing them at different stages towards and into adulthood.

On the impacts of traffic noise on zebra finch behaviour and development

Testing noise avoidance

In Chapter 2 of this thesis, I developed a method to test whether traffic noise (rather than a combination of all traffic and road associated factors) itself is avoided. By offering birds a choice between two identical aviaries with different levels of highway noise playbacks, I was able to 'ask' them whether they prefer a quiet over a noisy area. Previous studies, using experimental noise exposure, typically exposed birds to one type of noise and compared it to a non-exposed control group. An important methodological difference of the approach I chose was that I not only compared the birds' reactions to sound with a control group but also that I used two types of traffic noise. This method not only revealed that different levels of noise from the same site can be treated differently by the birds, but also provided an opportunity to disentangle the effects of traffic noise from the presence of any novel sound. In the tests, birds exhibited clear preferences, but they only preferentially moved to the quiet aviary during playback of traffic noise recorded at near distances, not during playbacks of noise recorded at far distances. When the near- and far-distance recordings were played back simultaneously, the birds likewise avoided the aviary where they would be exposed to near-distance traffic noise recordings and preferred staying in the aviary with playback of the far-distance recording. These results demonstrate that birds avoid traffic noise once it has a certain level and intensity, and given that the two aviaries were identical apart from the noise, the avoidance must have been caused by high levels of (traffic) noise *per se*. A neophobic response can also be excluded as explanation as the birds were not deterred by the far-distance traffic noise. It is important to point out that all experimental noise levels were recorded in open rural landscape near real highways, where wild and farm animals are continuously exposed to these sound levels. The non-avoided noise was recorded at 200 - 400 meters away from the highway at 55 dB(A), a level that is classified as noise pollution and annoys humans (Nugent et al., 2014). The avoided noise was much louder around 70 dB(A), but was recorded at a distance (5 - 15 meters from the highway) where birds can be observed albeit that their numbers are often reported to be lower near roads across many studies and habitats (Benítez-López et al., 2010). The experiments in Chapter 2 only tested short-term avoidance, but the results demonstrated that different levels of noise can affect spatial distribution of birds.

In the future, the method adopted in Chapter 2 could be used to test additional levels of traffic noise to investigate whether noise avoidance behaviour is triggered by any noise above a threshold noise level or whether noise avoidance proportionally increases with noise levels, meaning the birds would show stronger avoidance towards louder noise. Besides the intensity of the noise, its characteristics, i.e. its spectral content could also play an important role in deterrence as different bird species differ in how sensitive their hearing is in specific frequency bands (Dooling, 1992). Using the two-choice tests I established in Chapter 2, future experiments could help to identify the dosage and noise characteristics affecting noise avoidance behaviour in different species. For now, the results from Chapter 2 identified one avoided and one non-avoided type of traffic noise for our laboratory population of zebra finches. Having thus identified a level at which these birds avoided space exposed to traffic noise in favor of more quiet space when given a choice, allowed me to ask whether breeding in avoided versus non-avoided levels of traffic noise would affect the birds' breeding decisions and breeding success.

Testing effects of noise on parental behaviour and breeding success

In the experiment described in Chapter 3, the same birds that had been tested for noise avoidance (Chapter 2), were now given the opportunity to breed while exposed to noise to test the potential effects of traffic noise on parental care, breeding success and offspring mass. In a cross-over design, all breeding pairs were given two breeding opportunities where they were exposed to continuous traffic noise recorded at the same site as (and including) the 30-min stimuli used in the experiment in Chapter 2. Pairs were exposed once to playbacks of the avoided (near-distance) and once to the non-avoided (far-distance) traffic noise. In the (previously avoided) near-distance high level traffic noise, breeding pairs spent more time attending the nests than when exposed to the lower level, far-distance traffic noise. The results not only showed that traffic noise can affect nest attendance and feeding rate, but also provided additional validation of the noise avoidance test: the previously avoided noise levels that were recorded near highways were also the levels that affected subjects' behaviour during breeding. However, the noise exposure did not affect the number of eggs or hatchlings parents produced. Future work will have to investigate whether the higher nest attendance resulted from impaired intra-pair communication and nest relief, or whether it was a compensatory strategy by the parents to overcome detrimental masking effects on intra-pair communication or to respond to potentially increased nutritional needs by the chicks. The latter could arise from higher begging rates (Leonard et al., 2015) and/or changed corticosterone levels that have been observed in several other studies that exposed nestlings to noise (Crino et al., 2011; Kleist et al., 2018; Injaian et al., 2019).

Does growing up in noise alter birds' reactions to noise?

In the breeding experiment described in chapter 3, parents successfully raised chicks under two levels of traffic noise. This allowed me to test whether birds that had grown up in noise would be more tolerant to noise. Using the same experimental setup that was used to test noise avoidance in their parents (that had been raised without noise playbacks), the offspring from both treatments were now tested in the same way and with the same stimuli as previously used to test their parents. During the spatial preference tests, the subadult birds of both treatments did not show a preference for quiet space: they used both aviaries regardless of the noise playbacks and showed no evidence of noise avoidance. In contrast, birds of the same age reared in the same size cage in another breeding room without any noise playback did avoid the near-distance traffic noise by moving into the quiet aviary. However, when the experimental birds were tested for a second time, now as young adults and after having lived in quiet laboratory conditions for two months, noise reared birds from both treatments now avoided near-distance traffic noise. This change towards noise avoidance after experiencing a quiet environment is particularly interesting as it shows growing up in noise is not necessarily leading to increased tolerance towards noise in the long term.

Are there long-term effects of rearing noise on adult behaviour?

Noise avoidance behaviour is of course but one way the rearing environment could affect the birds. Following the experimentally noise-exposed birds into adulthood, I then addressed the question of potential long-term effects on adult behaviour in Chapter 5. I focussed on two candidate behaviours that often show individual differences and have been linked to behavioural syndromes in birds and that are often listed as being different between urban (noisy) and rural (quiet) populations, namely singing effort (Sierro et al., 2017; Bermúdez-Cuamatzin et al., 2020) and exploration (Lowry et al., 2013). Singing effort was chosen to establish the connection between this laboratory study to field experiments and observational studies that found birds' singing effort to be affected in noisy areas or by noise playbacks. Explorative behaviour is typically measured as how many objects are found or how many features visited in a novel environment. This type of exploration test has been used and validated in the zebra finch (McCowan et al., 2015; Wuerz & Krüger, 2015) and the measurement from this type of test has also been shown to be a trait with phenotypic plasticity in zebra finches (David et al., 2011; Krause & Naguib, 2011). A number of studies in different species have found associations between individual variation in exploration tendency and vocalization (Garamszegi et al., 2008; Amy et al., 2010; Naguib et al., 2010, 2016; Guillette & Sturdy, 2011). To test the birds' exploration, I developed a system where they could voluntarily enter and explore a novel environment. This new system avoids the potential impacts of catching and handling subjects before an exploration test. Comparing the offspring from the two different noise treatments, showed no systematic differences between the groups in either test: male offspring did not differ in their 24 hr singing efforts assessed in a standardised testing situation in a recording chamber, and offspring of both sexes did not differ in their behaviour in the voluntary exploration test. It is worth to point out that the birds reared in noise were only tested in a quiet test environment, so it remains to be tested how these birds would behave in noisy conditions or whether other behaviours would be affected by noisy rearing conditions.

Synthesis

The results from the series of experiments reported in Chapters 2–5 provide new insights on potential impacts of noise on birds but also raise some new questions. I have demonstrated that traffic noise *per se* can contribute to spatial avoidance in birds and cause variation in parental behaviour, and that there can be changes in noise avoidance behaviour in the course of a life time. In the subsequent paragraphs, I will interpret my findings in the context of the existing literature and discuss potential broader implications of these findings and try to develop a framework that can be used to study the behavioural effects of traffic noise exposure.

The role of traffic noise in reducing avian populations near roads

Regardless of the increasing number of studies showing associations between increased noise pollution and decreasing wildlife near roads, it has been difficult to establish a causal link between these two. This is because roads are not only very noisy but also associated with additional potentially aversive factors for wildlife such as the presence of vehicles, chemical pollution and general habitat destruction. This makes experimental studies under controlled laboratory conditions valuable to test the effects of traffic noise itself while holding other factors constant. I used such an experimental approach in the research presented in this thesis. This allowed me to collect experimental data that are in line with the hypothesis that traffic noise *per se* is contributing to the spatial distribution pattern of birds along roads (Benítez-López et al., 2010). I also documented that the mere presence of high intensity traffic noise changed the duration of parental nest attendance and the pattern of feeding rate, adding to the parental behaviours that can be affected by noise (Leonard & Horn, 2012; Leonard et al., 2015). These results provide evidence for two proximate mechanisms through which traffic noise (even without the added potentially detrimental effects of traffic in general) can affect avian communities: noise itself might be sufficient in deterring birds from noisy but otherwise suitable habitat and might also affect their behaviour during breeding.

I did not find an effect of the experimental traffic noise exposure on the number of eggs or hatchlings, nor on growth or on the tested behaviour in the adult offspring. A possible explanation would be that noise primarily exacerbates other challenges that can affect offspring quality (i.e. food accessibility) which may not be seen under the benign laboratory conditions. It is also possible that the current noise exposure scheme was not at a level to affect the offspring. The traffic noise was played back at levels that were the same as at the recording sites, which in case of the near-distance noise was just 5-15 meters away from the highways, and projecting realistically high level traffic noise. It is difficult to extrapolate from an absence of an effect in the benign environment in the lab to an absence of an effect in the field, as the same levels might affect breeding pairs more in the field than in the lab. However, it is also possible that breeding near roads does not necessarily reduce reproductive outcome. Instead the major contributor to avian declines along roads, might not be negative effects on breeding but active avoidance of too noisy areas and not settling to breed. This interpretation can only be speculation at this stage, as one cannot generalise from one series of experiments in the laboratory involving only one species to all bird species in all habitats. The type of experiments presented here should therefore be replicated in other species in the future to better under what causes the observed reproductive reduction in the field (Halfwerk et al., 2011; Schroeder et al., 2012).

Can birds adjust to noise?

Different possible adjustments to traffic noise exposure may help birds cope with the sounds of busy highways. If noise tolerance is a trait with phenotypic plasticity (i.e. the developmental process whereby the same genotype develops into different phenotypes as the result of different genotype-environment interactions), then we would expect to see systematic differences of noise tolerance relating to rearing conditions (Stamps, 2003; Uller, 2008; Snell-Rood, 2013). If behavioural flexibility (i.e. the ability to react differently to the same stimuli in different contexts, at a different age or in a different state, or due to experience related behavioural adjustment) is of more importance in guiding birds' responses, then we would see more influence of recent and current rather than past environmental factors. Mapping the time scale and (ir)-reversibility of noise tolerance could contribute to our understanding of how individual fitness would be affected by noisy environments when avoidance is not an option (reviewed in Potvin, 2017).

There are some insights that arise from the observations during the experiments described in this thesis regarding behavioural changes determined by noise exposure. In Chapter 3, I reported data that showed that breeding zebra finches changed aspects of their parenting behaviour when exposed to aversive noise. However, this did not affect their reproductive outcome, suggesting that behavioural flexibility may help exposed birds to adjust to noise. One possible explanation is that the changed parental care may mitigate potentially negative physiological effects of traffic noise on the chicks (Potvin & MacDougall-Shackleton, 2015; Dorado-Correa et al., 2018; Injaian et al., 2019; Zollinger et al., 2020). The observation that the effect of noise exposure on feeding rate was exacerbated by brood size is in line with this interpretation. Overall, it seems that birds under benign lab conditions (sufficient food, no predators) could sufficiently adjust to a noisy environment in two subsequent breeding events but clearly were more affected when additionally challenged by larger brood sizes. This raises the question of how easily parents could accommodate additional challenges from noise in the context of possibly a more challenging environment in the wild and will need to be further researched.

The results of the noise avoidance experiments in Chapter 4 showed that birds exposed to noise during development, other than control birds, did not avoid noise as juveniles which is in line with both developmental plasticity or flexibility in noise avoidance. However, when tested as adults using the same stimuli, they clearly avoided the noise which contradicts the idea that the birds developed into more noise-tolerant phenotypes. The experiment was not set up to identify the underlying mechanisms of the change towards more avoidance, but it might be worth to discuss which short- and long-term processes of behavioural adjustment seem best in line with these results.

While developmental behavioural plasticity emphasizes different developmental pathways and resulting phenotypes arising from environment-gene interactions, behavioural flexibility (also referred as activational behavioural plasticity), on the other hand, emphasizes the importance of more recent or current environmental factors on behaviour, as it is defined as the ability of an individual to directly respond and adjust its behaviour to environmental stimuli throughout life (Coppens et al., 2010). The behaviour exhibited by the birds shows some key features of behavioural flexibility. The exposure to noise up until the test at day 65 led to a lack of noise avoidance behaviour in the experimental birds. After the first test and up until the second test, noise exposure ceased and was absent as environmental input, and in the second test, birds now spatially avoided the playbacks of the noise stimuli. As noise has been found to delay sensory development (Chang & Merzenich, 2003; Funabiki & Konishi, 2003) or cause to shift sensory thresholds (birds: Dooling & Popper, 2007; fish: Nedelec et al., 2014; rodents: Manohar et al., 2017), the difference in the first test could have been caused by noise exposure altering developmental trajectories. Permanent or even temporary auditory threshold shifts are less likely to explain the results, as the exposure noise levels during the breeding were far below the levels to cause hearing damage, permanent or temporary threshold shifts (at least in adult zebra finches, see Dooling & Popper, 2007).

A recent study comparing bird song amplitudes in urban areas several seasons before and then during the 2020 Covid-19 pandemic lockdown found that birds sang at a lower amplitude during the relatively quiet lockdown than before (Derryberry et al., 2020). These observations support the idea that even for birds having grown up in noisy areas, noise related behavioural changes can be a direct response to current noise levels and relatively quickly reversed, instead of a product of altered developmental trajectories. The results in Chapter 5 provided no evidence for different noise exposure levels during development leading to different phenotypes but only tested a limited set of behaviours. The birds raised with different types of noise did not differ in exploration, a trait that can covary with developmental stress in zebra finches (Martins et al., 2007; Spencer & Verhulst, 2007; Emmerson & Spencer, 2017). This suggests that either traffic noise was not a strong developmental stressor or that both groups were equally stressed (albeit at different levels of noise exposure) and that they, therefore, showed no behavioural differences as adults. Future studies exposing noise-reared birds also to noise in adulthood and then testing their noise avoidance tendency would provide insights into which of these processes are underlying the changes in noise avoidance behaviour. For now, the results in Chapter 3 and 4, showing zebra finches changing behaviours with noise exposure, highlight the importance of distinguishing effects of recent and current exposure to noise in behavioural studies (Gil et al., 2015; Sierro et al., 2017; Weaver et al., 2019; Bermúdez-Cuamatzin et al., 2020). While this shows that some adjustment is possible, the underlying mechanisms and time scales of such adjustment need to be better understood.

How far can we extrapolate the effects of traffic noise to anthropogenic noise in general?

Highway traffic noise shares many characteristics with other types of anthropogenic noise like aircraft, urban and industry related sounds. Most anthropogenic noise (partly) overlaps with bird (and other animals') vocalisations, persists for a long period, and shows dynamic fluctuations (Barber et al., 2010). These similarities raise the question as to how the effects of traffic noise on birds reported in this thesis may, to some extent, apply to other types of noise (drilling noise, Habib et al., 2007; compressor noise, Bayne et al., 2008). For this it is also important to appreciate the many pronounced differences between different types of noise. Urban noise and aircraft noise near airports, for example, show larger circadian fluctuations than the relatively consistent highway traffic noise in busy areas (Slabbekoorn, 2013). The unique features of different types of noise may affect birds differently. For example, the observed circadian shifts of vocalization patterns seen in birds in noisy areas like cities and airports (Gil et al., 2015; Sierro et al., 2017; Bermúdez-Cuamatzin et al., 2020) can be caused by the distinct patterns of urban and aircraft noises due to the fluctuations in human activities. This highlights the importance of considering the characteristics of different types of noise when trying to assess its impact, as demonstrated in a number of recent marine noise exposure studies (Shafiei Sabet et al., 2015; Kok et al., 2018; Isojunno et al., 2020).

Anthropogenic noise can affect animals of a wide range of taxa

This study has found that traffic noise deters birds, alters birds' behaviour in the short term, and affects their breeding behaviour. However, birds are not the only animals that can be affected by anthropogenic noise. Invertebrates (Morley et al., 2014), fish (Slabbekoorn et al., 2010), amphibians and reptiles (Simmons & Narins, 2018) and mammals (Weilgart, 2007; Slabbekoorn et al., 2018b) can also be affected by anthropogenic noise. The negative effects of anthropogenic noise on wildlife have increasingly come to the attention of a wide audience over the past decades (Shannon et al., 2016; Slabbekoorn et al. 2018) and this field is witnessing a rapid increase in research effort trying to characterise the relationships between different types of noise exposure and their respective impacts (Morley et al., 2014; Kunc et al., 2016; Bunkley et al., 2017). A recent meta-analysis across multiple taxonomic groups confirms that noise is a form of very wide-spread pollution that affects wildlife from molluscs to mammals (Kunc & Schmidt, 2019). This stresses the necessity to study animals' responses to anthropogenic noise and the mechanisms underlying these responses (or lack of them) to confirm, comprehend, and perhaps, mitigate the detrimental effects of noise on wildlife.

Conclusions

With the experimental work described in this thesis, I set out to investigate the mechanisms underlying the effects of traffic noise on birds, conducted a series of experiments exposing birds to ecologically meaningful stimuli and testing birds of different experimental rearing noise backgrounds. I have provided evidence that traffic noise, even in the absence of traffic, can deter birds from using a particular space and that these behaviourally avoided levels of noise affect parental behaviour in situations where the birds cannot avoid it. Comparing different experimental groups at different ages for noise avoidance behaviour demonstrated substantial behavioural changes in noise avoidance behaviour of birds, which were influenced by their rearing and current noise experiences. These results contribute to our understanding of how avian individuals behaviourally respond to anthropogenic noise exposure and how these responses are shaped by the acoustic characteristics of their rearing environment, which in turn may help to better understand causalities between observed bird distribution patterns near roads and the associated levels of traffic noise.