Chapter 1

General Introduction

Living on a noisy planet

Animals rely on sensory systems, such as vision, hearing or smell, to survive and reproduce[1], but this is becoming more and more difficult due to human activities[2-5]. Humans disturb the sensory environment with artificial lighting, noise production or chemical emission, thereby affecting biological processes at various spatial scales[6-9]. The anthropogenic disturbance of natural areas is expected to increase exponentially[2] and will affect biodiversity worldwide[6,10].

Anthropogenic noise is a well-known feature associated with human activities, which is especially prominent at urban habitats, such as in cities or in the proximity of highways. Anthropogenic noise affects animals through the disturbance and deterrence of individuals, or by masking of important acoustic signals and cues[2,5,11]. Acoustics play an important role in predator avoidance as well as prey detection and many species rely on acoustic signals to find mates or to fight their rivals[1]. Signal interference through masking noise may therefore have important fitness consequences and may determine whether species will remain in or near the urban habitat[12,13].

Studies on animal communication and anthropogenic noise have reported patterns at the level of the individual as well as the population, without paying much attention to the underlying mechanisms nor to the associated consequences[12]. Individual animals have for instance been found to adjust their signaling behavior in response to anthropogenic noise[14]. However, whether such response is sufficient to avoid a negative impact of noise, or whether there are associated fitness consequences, has, so far, been largely ignored[12,15]. Likewise, most studies focusing on an impact of noise on animal populations[e.g.16,17,18] lack the integration with studies on underlying mechanisms at the individual level[2]. Furthermore, most experimental data come from lab studies[14,19], whereas understanding how noise affects individuals, populations and ultimately communities requires field studies, taking natural behavior and ecological conditions into account.

Animal communication in noise

Acoustic communication involves signal exchange between senders and receivers. A sender produces a sound that will be transmitted through a particular environment before it is detected by a receiver[1]. The production, transmission as well as perception of sound all have their own specific limitations that warrant attention when trying to understand signal evolution under changing acoustic conditions. The production of acoustic characteristics can be constrained by morphological structures, or physiological demands. Very low-frequency or fast signals, for example, can be difficult to produce, whereas very loud signals may require a lot of energy[20]. The transmission properties of the habitat influence the distance over which individuals can communicate and may affect signal evolution[21,22]. For instance, in most habitats high-frequency sounds are more attenuated compared to low-frequency sounds, favoring selection of low-frequency long-range signals. Finally, the cognitive machinery of receivers is tuned to specific acoustic features that typically match signal characteristics while sounds outside the perceptual tuning range are less well perceived[23].

Communication ultimately requires extraction of the relevant signal components from the background noise by a receiver[14,24]. This ability depends on the signal-to-noise ratio at the position of the receiver and his *masked* auditory threshold. Acoustic energy is processed in particular frequency ranges and when the neuronal response evoked by a signal can not be discriminated from the response evoked by irrelevant sounds, such as noise, that share the same frequency range, the signal is said to be *masked*. A sender can anticipate a rise in noise level and the associated increase in masking thresholds of the receiver by increasing the amplitude of his signal[14]. When confronted with urban noise, with most acoustic energy typically biased towards lower frequencies, senders can also respond by raising the frequency of their vocalizations, thereby reducing the spectral overlap with noise, and hence the masking impact[14].

The increased noise levels associated with the urban habitat can mask particular signals at the side of the receiver, consequently forcing senders to vocalize louder or at higher frequencies[11,15]. However, the benefits of such signal adjustment may come at the costs of reduced transmission or production efficacy, or negative fitness consequences, such as increased predation risk or reduced attractiveness to females. Therefore, understanding the impact of communication in noise requires an integrative approach, looking at processes found at the level of senders, receivers and transmission properties of the habitat, and both on a short- and a long-term.

THESIS FOCUS

In this thesis, I concentrate on the question how anthropogenic noise affects communication and reproduction in the great tit (*Parus major*). The effects of typical anthropogenic noise profiles associated with urban habitats will be addressed and the term ‘urban noise’ will be used in case the source is not specified. Urban noise profiles show a bias in spectral energy towards the lower frequencies and can refer to the common ‘soundscape’ found in cities, as well as more specifically to sounds coming from heavy machinery, or busy highways. I will focus on song behavior of male great tits and relate noise-dependent changes of individuals to fitness consequences, which may ultimately affect interactions at the population and community level (Figure 1.1).

The study system

The great tit is an ideal species to study acoustic communication in anthropogenic noise for several reasons. Great tits can be found in high numbers in relatively quiet forests as well as in anthropogenic noise impacted areas, such as cities and along highways[25-27], and can therefore be used as a model species to study the mechanisms related to communication and fitness that may have caused other species to disappear. The great tit also functions as key species in many studies regarding behavior, ecology and breeding performance, because of its preference for artificial nest boxes over natural cavities[28]. Song of the great tit has been related to the acoustic properties of the habitat[26,29] as well as to fitness[30,31], which allows us to translate an impact of noise on communication to an impact on lifetime reproductive success.

Great tit song variation has been related to variation in urban noise. Great tits produce higher songs in cities compared to nearby forests[32,33] and use higher frequency song types in noisy territories[26,34]. However, causes of this noise-dependent song frequency use were unknown prior to the studies reported in this thesis. Furthermore, we lack knowledge on consequences in terms of morphological or energy constraints. Sound propagation cannot be directly affected by urban noise, but other acoustic properties associated with urban environments, such as increased reverberation and attenuation may limit the use of high frequency songs in response to low-frequency noise[12,35,36]. The consequences of noise-dependent frequency use are likely to play their biggest role at the perceptual side. We know from lab studies that the auditory sensitivity of tits does not vary much over a large frequency range, which indicates that signal detection depends primarily on the amount of spectral overlap with the background noise[37]. However, we do not know how noise affects discrimination of songs by great tits and whether noise affects female assessment of signal attractiveness, as found for example for frogs[38]. Furthermore, although we expect the use of high-frequency songs to be favored through increased signal detection under urban noise conditions, we do not know how a noise-dependent signal change will affect female behavior.

Aim of the thesis

I will address how urban noise affects the sender's side through an impact on song production mechanisms. How do great tits change their song frequencies in response to noise? And how does this affect signal transmission? Next, I will focus on noise affecting females, one of the main receivers of male bird song. Do females provide feedback on acoustic performance to males? And how do noise-dependent signal strategies affect song attractiveness to females, or other types of receivers? A trade-off between signal detection and signal efficacy may translate into an impact of noise on reproductive success, which will be studied in the final part of the thesis. How does noise affect individual reproductive success? And can individual response to anthropogenic noise affect interactions within ecological communities?

Outline of the thesis

The thesis consists of eight chapters. This introduction chapter is followed by four data papers, two commentaries supplemented with extra discussion, or data, and concluded by a general discussion chapter.

Chapter 2: describes a noise exposure experiment with singing male great tits during the dawn chorus to test their ability to avoid masking by altering their singing behavior (Figure 1.1A).

Chapter 3: is a commentary paper on the mechanisms related to noise-dependent frequency use and the associated benefits in terms of signal transmission.

Chapter 4: examines the importance of song frequency in male-female communication and tests the consequences of noise-dependent frequency change in a noise exposure experiment with female great tits (Figure 1.1B).

Chapter 5: looks at noise-dependent female feedback and its role in affecting male song behavior, by exposing females inside their nest box to artificial urban noise, while leaving the singing male unaffected (Figure 1.1C).

Chapter 6: is a descriptive study in which fluctuations in traffic noise levels are related to long-term breeding data on great tits and discusses the mechanism underlying noise-dependent reproductive success (Figure 1.1D).

Chapter 7: discusses the impact of anthropogenic noise on bird breeding communities, with an additional case-study on a noise-dependent nest-site choice experiment (Figure 1.1E).

Chapter 8: summarizes results from previous chapters and suggests future directions.

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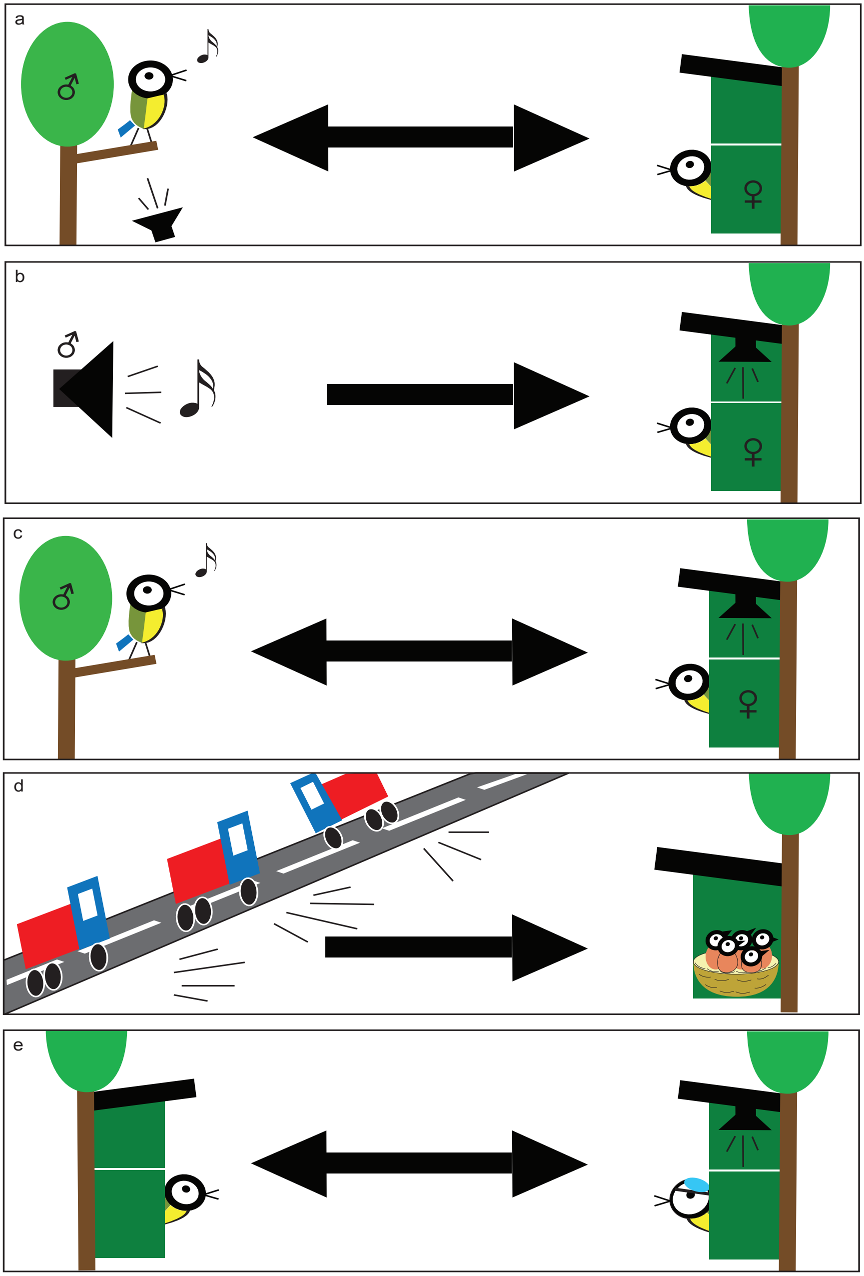

Figure 1.1. Schematic representation of the impact of traffic noise on avian communication as studied in the current thesis. An impact has been investigated **A**) at the sender side by experimental exposure of the natural dawn chorus song behaviour (chapter 2), **B**) at the receiver side by testing female responsiveness to playback with and without experimental noise exposure inside the nest boxes (chapter 4), and **C**) for effects on the interaction between senders and receivers (chapter 5). We also studied **D**) the impact on reproductive success by correlating spatial patterns of noise variation to a long-term data-set on breeding performance (chapter 6), and **E**) the impact at the community level by investigating noise-dependent competition between great tits and blue tits again with experimental noise exposure inside nest boxes and control boxes prior to settlement and occupation of nest boxes (chapter 7).

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