Tango to traffic : a field study into consequences of noisy urban conditions for acoustic courtship interactions in birds

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Chapter 8

Summary and general discussion

Urbanization and the associated rise in noise levels affect many animals in their struggle to survive and reproduce[1,2] . Animals have been found to respond to urban noise by changing their communication signals, or by avoiding noisy areas during breeding[1,3] . For instance, great tits in cities have faster songs that are also higher in frequency compared to their forest counterparts[4] and urban nightingales sing louder songs during noisy weekdays compared to quiet weekends[5] . However, the precise causes and consequences of these noise-dependent behavioral adjustments are far from being understood[6] .

This thesis addresses the impact of anthropogenic noise on avian communication and its reproductive consequences by using carefully conducted field experiments in combination with breeding data obtained from an area with varying noise levels (see for an overview Figure 1.1). The focus of the thesis is on communication between members of a breeding pair, looking at the impact of noise on the sender's side, the receiver's side and the interaction between these two. The sender's side is experimentally exposed to noise to assess the mechanism underlying noise-dependent frequency use. Furthermore, the receiver's side is experimentally exposed to noise to assess the impact of song frequency change on signal detection and signal attractiveness and to examine the role of females in providing noise-dependent feedback to singing males. Finally, the consequences of breeding in noise are addressed in a field study relating local noise levels to long-term breeding data and by providing noise-exposed nest boxes to birds during the period of nest-site choice.

Studying the mechanisms of noise-dependent frequency use

The impact of noise on animal communication systems depends on the overlap in acoustic energy, in time and frequency, between signal and noise (i.e. masking). To avoid urban noise interference, birds can change the frequency of their songs by upward shifting of song elements or their whole song, or by selective song type use when they possess a repertoire[7] . We exposed singing male great tits (*Parus major*) during the dawn chorus to artificial low- and high-frequency noise and found song type duration to be affected by the amount of noise masking (chapter 2). Males sang low song types for shorter duration in low-frequency noise compared to high song types and showed an opposite trend when confronted with high-frequency noise. Consequently, birds singing a relative low song type, switched earlier to another, on average higher song type, although this was not specifically the optimal song type for masking reduction.

As an additional control, we exposed singing males to a white noise treatment, with a flat amplitude level across all frequencies. We did not find birds to change their song frequencies consistently, but we did find an impact on song rate, mainly because some individuals ceased singing. This result suggests that there could be performance constraints on singing in noise, or point to the importance of acoustic feedback (see below).

Male great tits could have assessed the spectral overlap with their songs directly, or they could have monitored their own song output as a feedback mechanism to adjust song type bout duration (chapter 2). Monitoring of own signal-to-noise ratios may have caused great tits to increase song amplitude during noise exposure (a taxonomically widespread phenomenon, known as the Lombard effect), which could have increased song performance or energy demands and led to an early switch to another song type to reduce motor fatigue[8]. If such auditory feedback mechanism is masking-dependent, it could explain the increased use of high-frequency songs in urban noise (chapter 3). Singing males may also have relied on social feedback, from males during matched counter-singing contests, or from females during acoustic dawn chorus interactions (chapter 4 & 5). Feedback from noise-exposed females did not lead to a change in their mate's song frequency during the dawn chorus, but we did find males to sing from a closer perch in response to the experimental treatment (chapter 5).

Consequences of communicating in noisy urban environments

Urban noise causes males to use high-frequency songs, which probably increases signal detection, but may come at the cost of reduced attractiveness to females. Vocal performance can be related to male size or condition, and females could favor low songs, when the use of these songs reflects bigger, healthier or stronger males[9]. We studied great tit vocal performance during the dawn chorus ritual and found males to peak with their lowest songs at the height of female fertility. Furthermore, females with social mates singing relatively high-frequency songs from their repertoire turned out to be more involved with extra-pair copulations than those with social mates that hit their low notes more often (chapter 4). We did not find other song parameters to vary with fertility or paternity, except for the start of the dawn chorus, which increased progressively with laying stage. The moment of female nest box emergence also increased across egg-laying, but more interestingly, we found very early emergence to be related to extra-pair copulation engagement of females.

Males may only be able to rely on very low songs to secure female fidelity under poor light conditions, but these songs may suffer increased loss of detection in urban noise. We examined this apparent trade-off in signal efficiency experimentally by exposing females inside their nest boxes to artificial urban noise and found low-

TO BE LOVED OR TO BE HEARD IN A NOISY WORLD

Male Great Tits, as well as other male birds found in cities, are faced with a dilemma: how can they make sure they are heard above the noise of people and traffic? Results from earlier research suggested that they can achieve this by singing their songs at higher pitch. In chapter 4 we show that this is an effective approach for being heard better, but the downside could be that females find these songs less impressive, resulting in an modern trade-off between signal detection and signal attractiveness.

frequency songs to suffer reduced attractiveness, favoring high-frequency songs in noise (chapter 4). These results suggest that high-quality males have lost the potential to stand out acoustically in noisy urban environments by using low-frequency songs and that females, living under these conditions, may have shifted their preferences towards high-frequency songs, or towards songs reflecting other characteristics of quality-related vocal performance.

Anthropogenic noise can also affect interactions between members of a breeding pair, which may have consequences for reproductive investments by males and females[10] . We exposed females inside their nest box to artificial urban noise during the dawn chorus, while leaving the singing male unaffected, to test for an impact on intra-pair communication at the receiver side. We found females to respond later to male song in the noisy condition (chapter 5). Furthermore, we found males from the noise treatment group to sing closer to the nest box within several days of exposure, which led to higher song amplitudes at the position of the nest box. The increased song amplitudes restored the inside signal-to-noise ratios and consequently brought back communication to equal levels between treatment and control groups. These results show the importance of intra-pair communication and provide yet another strategy of noise-dependent signaling in birds. Males may change spatial singing to increase male-female efficiency in urban noise, although we have little insight into potentially negative consequences of this behavior, such as, a decrease of male-male communication or an increase in predation risk, associated with song post exposure.

Reproductive consequences of living in a noisy world

Noise can have a negative effect on reproductive success and ultimately cause bird breeding populations to decline. Noise can affect the individual directly by disturbance, deterrence, and masking or indirectly by changing interactions with conspecifics as well as heterospecifics[2,11] . We studied the impact of anthropogenic noise on avian reproductive success in a nest box population situated close to a highway with high traffic load (A2 in the Netherlands, between Utrecht and Arnhem). We monitored fluctuations in traffic noise throughout the great tit's breeding season and found a significant temporal and spectral overlap over a large spatial range (chapter 6). Noise levels were high when singing activity peaked and remained high throughout most of the day. Furthermore, noise levels changed with season as well as traffic load (noise levels were higher during weekdays compared to weekends). High frequencies attenuate faster compared to low frequencies, especially in forests[12] , but noise levels in the frequency range overlapping song of the great tit were nevertheless detectable throughout the whole population.

We related temporal, spatial and spectral noise patterns to available long-term breeding data. Traffic noise levels were negatively related to reproductive success through an independent impact on clutch size as well the number of produced fledglings (chapter 6). The impact was best explained by seasonal overlap between noise and the start of egg-laying, as well as by a spectral overlap between song and noise. The negative correlation could have been directly caused by an impact of noise on individual stress levels, or through the masking impact of noise on the communication between male and female, or between parent and offspring in great tits. Alternatively, the negative correlation could be caused by social-ecological factors related to interactions with individuals of own and different species.

Traffic noise fluctuations may result in a heterogenic breeding distribution through an effect on the interaction between individuals of different quality. For instance, high-quality birds who can produce large clutches could avoid noisy areas, which will subsequently be occupied by low-quality individuals, leading to a correlation between reproductive success and noise levels. Anthropogenic noise can also affect interactions between species, altering predator-prey interactions or heterospecific competition. We tested the latter possibility by providing noise-exposed nest boxes prior to nest site settlement in an area occupied by two competing species, the great tit and the blue tit, and found a species-specific nest box occupancy pattern (chapter 7). Great tits were more often found to breed in quiet control nest boxes, whereas blue tits settled more for noisy nest boxes, most likely because these boxes were released from competition with the larger, dominant great tits. These results show that noise affects breeding distribution of individual birds, which ultimately can alter processes at the community level.

Implications for other species

The great tit is one of the most abundant species throughout Europe and has been shown to breed readily in cities as well as in the proximity of busy highways. Clearly, great tit populations are not under threat of extinction through a negative impact of noise. However, several issues addressed in this thesis may be valuable to predict an impact of noise for other species, whether or not they are locally or globally threatened at the moment. Furthermore, even great tits show reduced breeding output in relation to noise (chapter 6), and their behavior is affected at low levels of song masking (less than 6 dB, chapter 5) which shows that having some prerequisites to adapt may not be sufficient to cope completely with high levels of anthropogenic noise.

A first step to make predictions about noise impacts on other species would be to determine the set of characteristics important in adaptation to anthropogenic noise, using great tits as a yardstick, and to assess which species lack one or more of these characteristics. Focusing on the topics addressed in this thesis, it seems that, 1) singing low-frequency songs, 2) lacking signal flexibility, 3) relying on long-distance communication, are key ingredients for susceptibility to noise masking. The latter issue may be especially important for conservation as threatened species are typically found at relatively low-densities. Those species that have to communicate over very large distances with sound will be disproportional affected by anthropogenic noise.

A second step would be to determine the distance from a source over which noise can affect species, incorporating insights from the first step. In this thesis, great tit reproductive behavior was found to be most affected by noise in the 2-kHz range, overlapping the lower part of this species song (chapter 6). At our highway site, noise in the 2-kHz range could be detected at distances of 400 – 800 m from the centre of the highway (chapter 6), which may correspond to the upper limit at which both behavior and reproduction of great tits are affected. Species that use similar frequency range for communication as great tits are will probably be affected over a similar distance, whereas species that are affected by noise in a lower frequency range are likely to be affected over larger distances.

Potentially affected species

Vocalizing at low frequencies has been found to be an important predictor of an impact of anthropogenic noise[13,14]. Among birds that show reduced numbers close to noisy structures, such as highways or gas compressor stations are various species of grosbeak, nuthatch, cuckoo, owl, pigeon, oriole and sage-grouse[11,15-18], all of which vocalize at low frequencies (majority of their song < 2 kHz). Several of these taxa contain globally threatened species in areas with high anthropogenic activity (grouse, owls, pigeons) and it is likely that these species are severely affected by anthropogenic noise over much larger distances than great tits[19], especially when noise is not obstructed by vegetation, or when a noise source is located opposite the predominant wind direction (chapter 6).
Other characteristics of acoustic behavior that may determine whether species will be affected by anthropogenic noise are signal plasticity or other constraints on signal change. Taxonomic groups that contain currently threatened species, such as tyrant flycatchers, vireos, pipits and wood- and leaf-warblers have been found to show reduced breeding numbers in areas with high levels of low-frequency anthropogenic noise, despite their relatively high frequency songs. The effect may be related to a lack in frequency plasticity (tyrant-flycatchers;[20]), or constraints on song attractiveness through sexual selection and extra-pair paternity (wood-and leaf-warblers;[21,22-24]).

Finally, migratory bird species may be more affected by noise compared to resident species for several reasons. Migratory birds typically have to broadcast their song over a range as wide as possible to attract overflying females[21] and any reduction in signal detection may negatively affect pairing success[15]. Migratory species are also more time constraint to attract mates, especially in forests, as breeding has to coincide with the pronounced peak in food availability in these habitats and because migratory birds have already difficulties catching up with phenologic shifts due to climate change[22,23]. Migratory species of forested habitats have been shown to be affected by anthropogenic noise[15,17], including several species which have shown strong population declines over the last two decades throughout Europe, including the Netherlands[23], and including a non-songbird species, the common cuckoo (*Cuculus canorus*), that probably lacks sufficient acoustic plasticity and also vocalizes at very low frequencies.

Future directions

Urbanization is expected to increase in the coming decades and it is unlikely that the world will get quieter soon. More traffic will also move into natural areas, leading to a global increase in anthropogenic noise levels, despite the current trend towards electric or hybrid transport engines. The need to understand the nature and magnitude of potential problems for animals, in air and underwater, will therefore only grow in the near future. The current thesis provides some initial answers and describes new approaches to address the most urgent questions with respect to its impact on birds. However, it also shows that studying the consequences of communicating under noisy urban conditions requires more detailed knowledge on causes related to noise-dependent signal strategies, in particular on the mechanism underlying the use of high-frequency songs in response to low-frequency noise. Furthermore, more work on signal evolution and sexual selection is needed, as well as on long-term fitness consequences of living under noisy conditions.

The role of social feedback in noise-dependent frequency use may be assessed in a playback experiment with singing males, mimicking matching contests with high and low song types, either in quiet and noisy areas, or by using artificial urban noise. Additionally, an interactive experiment with playback of calls from within the nest box towards males, in the absence of females (temporarily removed), would be an ideal approach to study the role of feedback-dependent singing behavior. Whether song type switching by male great tits is related to song amplitude and motor fatigue may be studied in a respiratory chamber[24], but it would be better to do this in the field, during the peak in territory defense and female fertility, as assessment of song performance constraints requires highly motivated birds. Although challenging, heart rate telemetry, which has been successfully applied in a similar-sized passerine, may be used in combination with urban noise exposure to singing great tits[25] . Furthermore, masking-dependent motor fatigue may also occur in species that do not display their songs with eventual variety and these species may be exposed with low-frequency, as well as high-frequency noise to test whether song frequencies change immediately with a rise in amplitude, or after some time, as suggested for noise-exposed great tits.

The consequences in terms of sexual selection pressures on particular song characteristics may be studied by comparing female preference or male aggression in birds from noisy urban, as well as quiet forest populations. A playback experiment using songs with varying levels of vocal performance, such as song frequency, song consistency, or singing speed,[26-28] , may be designed to test the role of noise in sensory drive. Furthermore, the extra-pair paternity rates may be correlated to song behavior and local noise levels to gain insight into the process of signal evolution in rapidly changing environments.

Finally, long-term experimental noise exposure to males in the field is required to get a full understanding of the consequences of singing high songs, by looking at production constraints, as well as a potential reduction of signal strength in territory defense or female attraction. Similarly, both members of a breeding pair would have to be exposed at different periods of the breeding cycle, to understand the mechanisms underlying the impact of anthropogenic noise on avian reproductive success. The female may be exposed inside the nest box, while the male is simultaneously exposed to noise in the proximity of the nest box. However, such an experiment may only start when females have chosen a particular nest site, whereas an impact of noise may arise prior to this, for instance during pair formation, a process for which surprisingly little is known in great tits. To assess fitness consequences of noise therefore requires a solid experimental approach throughout the breeding season and ultimately throughout an individual's life and may perhaps be achieved by equipping bird's with headphones, a procedure which has already been used in the lab[29] and which, in time, may be applied in the field as well.

Concluding remark

The alteration of natural areas into urban habitat at an unprecedented global scale may be viewed as a natural experiment that will generate new insights on environmental causes for evolutionary change. However, understanding the individual components of these processes ultimately requires a true experimental approach, excluding confounding variables, such as the ones described in this thesis. These experiments preferably mimic the ecological setting in which animals and their behaviors have evolved, which can often only be achieved in the field, although manipulation of the sensory environment can be methodologically challenging. Finally, we can observe animals in our own backyard and as more and more people will live in similar urban habitat it is likely that studies on urban ecology and evolution will continue to grasp public attention, but they should also raise awareness of the consequences of human behavior.

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Jac P. Thijsse had meer dan een eeuw geleden al oog voor veranderingen in het gedrag van merels in de stad Amsterdam:

“Zijn zang is maar zoo zoo. Doch buiten zijn er ook merels, die slecht zingen. Ik twijfel er evenwel niet aan, of deze stadsvogels zullen in den loop der tijden alle anders gaan zingen en zich anders gaan gedragen, dan vogels van het vrije veld. De stadsornithologen zullen hierover binnenkort interessante dingen te vertellen hebben.”

Uit ‘*Het intieme leven der vogels*’, 1906.