

Urban acoustic ecology: untangling the relative importance of phenotypic plasticity and developmental plasticity in response to anthropogenic noise

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Abstract

Urbanization provides unique selection criteria on native flora and fauna. One of the factors with large impact is anthropogenic noise, which typically consists of low-frequency notes and which can have a masking effect on acoustic signalling of many animals for who these signals play an important role in mate attraction a reproduction and hostility behaviour. To colonize a city successfully, species have to possess certain characteristics in phenotype or behaviour to overcome this noise. In this paper I investigate whether changes in call or song in response to anthropogenic noise are due to phenotypic plasticity, developmental plasticity or a combination. Untangling the relative importance of developmental plasticity versus phenotypic plasticity for a species' success in a given city will contribute to understanding how and why some species, but not others, are able to colonize and persist in urban environments There is a clear difference between taxa. Where most birds species respond to anthropogenic noise in a plastic, reversible way, frog and grasshopper species respond in a way that points to developmental plasticity. More species should be investigated to find out whether the found differences between taxa are consistent. Also, more research can be conducted on speciation and the influence of response to anthropogenic noise in this.

Introduction

In the future, more humans live in cities than outside them as a result of increased human population growth and migration from rural to urban areas (Ritchie & Roser, 2019). Urbanization involves an extreme change of land use, leading to a complete restructuring of vegetation and natural ecosystems. In addition to altered habitat structure, urbanization leads to reduced species diversity and elevated abundance of some species in urban environments. So not all species can live in a human dominated environment, but those that can, may thrive (Shochat et al., 2006).

Humans living in cities provide unique selection pressures upon local flora and fauna, including air and light pollution, but also in the form of noise (Slabbekoorn & Peet, 2003). Anthropogenic noise differs from natural background noise in various ways. It contains much more energy and has most of the energy concentrated at the low frequencies of the human hearing spectrum. Sound at low frequencies is perceived as sound at a lower pitch. Examples of low frequency sounds are traffic noise, industrial sounds from factories, and the level of human speech. Anthropogenic noise can have implications for previously undisturbed biotic communities even in the absence of pervasive physical urban landscape changes, for example, in cases where oil pipeline compressors or other industrial infrastructure passes through natural areas (Potvin, 2017).

Communication through sound is important to many animals and urban noise can interfere with these signals (Potvin, 2017). Acoustic interference, also known as masking, occurs when background noise reduces the active distance of a signal. Urban noise will interfere with low frequency signals of animals. In many species low-frequency signals typically represent hostile intentions, and are often

used in threatening displays towards rivals (Morton, 1977). A male who reduces energy in low-frequency notes, or excludes them, may suffer a decrease in signal efficacy, less effective territorial defence and can be perceived as less attractive by potential mates (Slabbekoorn & Smith, 2002).

Hence, to colonize and establish successfully in a city, species have to possess certain phenotypic characteristics (Rivkin et al., 2019), which can be a result of multiple evolutionary and non-evolutionary processes. The definitions of these processes used in this paper are given in box 1. Species may have evolved biological traits in their historic, non-urban environment that help them cope with an urban environment. For example, plants that naturally occur in a rocky habitat like coastal cliffs and may thrive in a city environment with loads of stone and vertical surfaces. Schilthuizen (2018) calls this 'pre-adaptation'.

Croci et al. (2008) investigated the differences in biological traits between birds that live in cities, so-called urban adapters, and birds that live outside cities, so-called urban avoiders. She found that on large spatial scales urbanization acts as a filter on traits. Urban avoiders allocate more energy to reproduction than urban adapters do, while urban adapters allocate more energy to survival. Urban adapters also seem to prefer forested habitats, are relatively sedentary, omnivorous, widely distributed, high altitude nesters, and have large wingspans. These traits match a city environment, where birds nest in forested areas e.g. parks or on rooftops. The difference between urban adapters and avoiders may originate from (pre-)adaptation, but other processes may also play a role. Firstly, individuals may acclimatize to an urban environment via developmental plasticity, i.e., via irreversible changes in morphological and physiological traits during development (box 1), which may increase survival chances in an urban environment. This process may possibly lead to adaptation to the new habitat over multiple generations. Secondly, individuals may show sufficient phenotypic plasticity, reversible changes in behaviour or physiology (box 1), enabling coping with living in an urban environment. Since level of plasticity will vary between and within species, some species or individuals will do better in urban environments than others.

In this paper I investigate if individuals cope with an urban habitat via developmental plasticity, phenotypic plasticity (especially behavioural plasticity), (pre-)adaptation or a combination of the three. I focus on acclimatization and adaptation to anthropogenic noise pollution in the acoustic signals themselves and timing of these signals, because acoustic communication may play a critical role in reproduction. Differences in how well species can cope with noise pollution may also be related to other causes. E.g. whether offspring acquires sound signals or song type via endogenous or exogenous learning origin, may have an influence on flexibility in response to noise. Also the influx

Box 1: Definitions

Pre-adaptation: Species have evolved in their historic environment certain traits that help them cope with a new environment as well.

Adaptation: The process of change by which a species becomes better adapted to its environment as a result of natural selection acting on heritable variation

Developmental plasticity: The ability of one genotype to produce more than one phenotype when exposed to different environments during development. This variation in phenotype is irreversible.

Phenotypic plasticity: The ability of an organism to react to an internal or external environmental input with a reversible change in form, state, movement, or rate of activity. E.g. the physiological preparation for the reproductive period.

Source: Science Direct

and efflux of genes in a population may play a role, because with high levels of influx, selection on adaptive genes becomes challenging. Untangling the relative importance of adaptation versus plasticity for a species' success in a given city will contribute to understanding how and why some species, but not others, are able to colonize and persist in urban environments (Rivkin et al., 2019).

Responses to overcome noise in urban areas

A response to overcome noise and prevent the masking of signals is increasing the vocal amplitude in response to an increase in background noise. This form of signal plasticity is called the Lombard effect. Humans do this by speaking louder in a noisy environment, like in a busy restaurant or café. Not only humans, but animals too may respond to noise according to the Lombard effect. E.g., bats that use echolocation responded to noise with an increase in call volume (Luo et al., 2015), while mallard ducklings (*Anas platyrhynchos*) increased the amplitude of their calls in noise, but did not change the duration of call syllables or their call rates (Dorado-Correa et al., 2018). The Lombard effect is not always sufficient to get signals through a noisy environment. Moreover, in some cases it is energetically too costly to raise the volume of the signal, as shown in frogs and birds (Parris et al., 2009).

Another solution to overcome urban noise is to raise the minimum frequency of the call or song. This is found in many bird species. Great tits (*Parus major*) sing with a higher minimum frequency at noisy locations to prevent their songs from being masked by the low-frequency noise of the city (Slabbekoorn & Peet, 2003). In song sparrows (*Melospiza melodia*) in North America, the minimum frequency of their song varied with urban noise (Wood & Yezerinac, 2006): song sparrows singing at noisier locations exhibited higher minimum frequency notes than song sparrow singing at less noisy areas.

Hu & Cardoso (2010) hypothesized that species vocalizing at lower frequencies should raise their frequency to a greater extent, because anthropogenic noise has the strongest masking effect on low frequency signals. They recorded 12 species in urban and nonurban environments investigated if the minimum frequency was increased in urban environments and whether the extent of increase in minimum frequency varied with the average frequency of the species. They found a clear curvilinear relationship between the extents that species raise their minimum frequency and the typical minimum frequency of the species (figure 1). Species with typical intermediate frequencies around 1 ~1.5 kHz raised the minimum frequency the most. Species with a high minimum frequency, which are likely less affected by urban noise, did not changed their vocalizations much. Surprisingly, species with a low minimum frequency song that do suffer from masking effects from urban noise, also did not changed their minimum frequency. Possible for them raising the minimum frequency of vocalizations is not an efficient way of overcoming masking by noise. Another explanation may be that the use of low frequencies is necessary for territory protection or hostility signals. If at a certain frequency range, noise levels are too loud for small adjustments in frequency to be efficient, other strategies for coping with noise may be used instead (Hu & Cardoso, 2010).

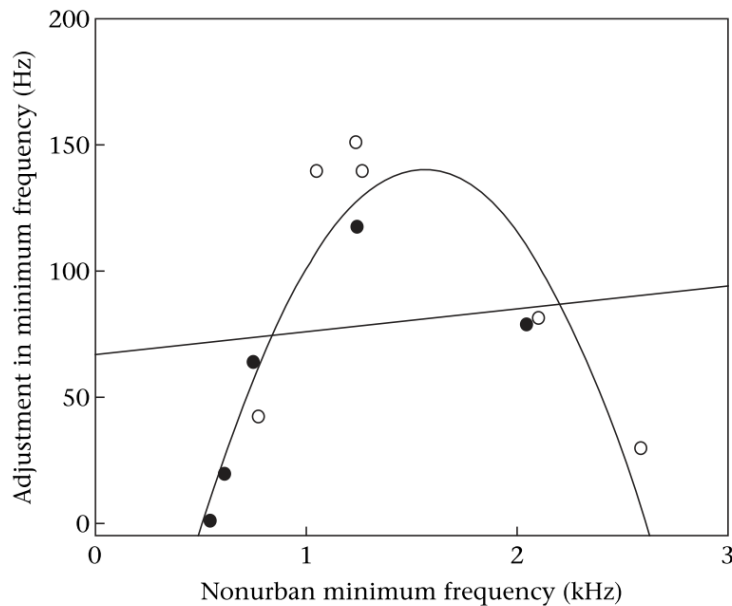


Figure 1. The adjustment in minimum frequency in relation to nonurban minimum frequency of the species. The best linear and curvilinear fits are shown. Solid and empty dots represent respectively species songs or calls studied (Hu & Cardoso, 2010).

There are predictable diurnal patterns in the levels of urban noise, with a significant reduction during the night, when human activity decreases. Therefore switching to nocturnal singing by birds that normally sing during the day only, may be an efficient way to minimize interference from ambient urban noise. However, such a response would be costly, because singing at night instead of resting, leads to a large increase in metabolic rate (Fuller et al., 2007). The advantage of nocturnal singing, which is audibility and thus increasing the chance of attracting a potential mate, and eventually reproduction, would have to outweigh the extra energetic expenses of nocturnal singing. In addition, the receiver of the call, in this case the female robin, has to be awake during the night as well. Indeed, urban European robins (*Erithacus rubecula*) living near a major airport were found to sing during the night instead of the day. In this way robins avoided the masking effect of the air traffic noise at the time it is the loudest. Nocturnal singing in urban birds is frequently attributed to ambient light pollution, and not to daytime noise (Miller, 2006), but it has been shown that the effect of daytime noise is much stronger than the effect of ambient light pollution on timing of singing (Fuller et al., 2007). This was shown in urban European blackbirds (*Turdus merula*). The higher the urban noise level, the earlier the blackbirds started singing, while ambient light did not affect timing of singing (Nordt & Klenke, 2013).

Developmental plasticity

Developmental plasticity refers to the capacity of a genotype to adopt different developmental trajectories in different environments (box 1). This differs from activational plasticity, where differential activation of an underlying network varies in different environments such that an individual may express various phenotypes throughout their lifetime (Snell-Rood, 2013). From now on, activational plasticity will be referred to as phenotypic plasticity, which will be discussed in the next chapter. In this chapter, developmental plasticity will be central as a mechanism in responding to urban noise.

Responses to urban noise, mainly in the form of road traffic noise, have been investigated in numerous species, but mostly in birds (Gil et al., 2015; Nordt & Klenke, 2013; Senzaki et al., 2016; Slabbekoorn & Peet, 2003; Slabbekoorn & Smith, 2002; Verzijden et al., 2010). Yet the responses to road noise of other acoustically communicating animals yield also very interesting information. For instance, frog calls are of endogenous origin and not as plastic as bird songs, so changes in frog calls are likely attributed to other causes than behavioural plasticity (Parris et al., 2009). Male frogs use calls to attract females for mating and to let other males know a territory is occupied. Females select males based on call properties, such as frequency, pitch, call length or call rate. In general, females prefer males that produce energetic costly calls, because this indicates that the male has energy reserves and is healthy and strong (Sullivan, 1992). In frogs, the energetic cost of calling increases exponentially with loudness or call amplitude (Parris et al., 2009).

Frogs are likely to experience masking from traffic noise when calling at breeding sites close to roads. The energy in traffic noise is concentrated in the lower part of the frequency spectrum, below 2 kHz (Parris et al., 2009), and thus higher pitched signals may suffer less acoustic interference from traffic noise than lower-pitched signals. But a higher pitch is less energetic costly, and thus male frogs are between a rock and a hard place: calling at higher pitch in traffic noise will increase audibility, but may be less attractive. This indicates that there may be a trade-off between audibility and attractiveness (Parris et al., 2009). As a result, frogs calling at an intermediate frequency may be favoured by selection, because they are audible and reasonably big, and thus still attractive to females. They are expected to reproduce more offspring as compared to large males with very attractive low pitched calls that are inaudible. If call pitch has a genetic base, the populations near a road will therefore likely produce mainly offspring with intermediate pitched calls. Now the question remains, will female preference evolve the same way? This may arise if female frogs living near roads that prefer higher pitched calls are more likely to find a mate and reproduce than females who prefer the energetic costly low pitch calls that are inaudible.

Some invertebrate species like the grasshopper (*Chorthippus biguttulus*) also produce low frequency calls, which fall into the same part of the spectrum as the low frequency ambient noise (Lampe et al., 2012). In this species, male courtship signals serve to attract potential mating partners, similar to frogs. Thus, successful transmission of signals in noisy habitats are crucial for reproductive success of the males (Lampe et al., 2014). It has been shown that male grasshoppers exposed to road noise during their nymph stadium produced as adults, signal with higher frequency components than males reared under quiet conditions (figure 2) (Lampe et al., 2014). Also, individuals taken from both noisy and quiet places, did not respond the in similar noise conditions in captivity. This indicates that

the signal adjustment of grasshoppers to anthropogenic noise is caused by developmental plasticity and not by phenotypic plasticity, as seen in birds.

Developmental plasticity may play an important role in song trait modifications in response to anthropogenic noise. Furthermore it can be suggested that multiple roadside populations may have diverged in parallel, possibly in response to selection for minimizing signal masking by road noise (Lampe et al., 2014).

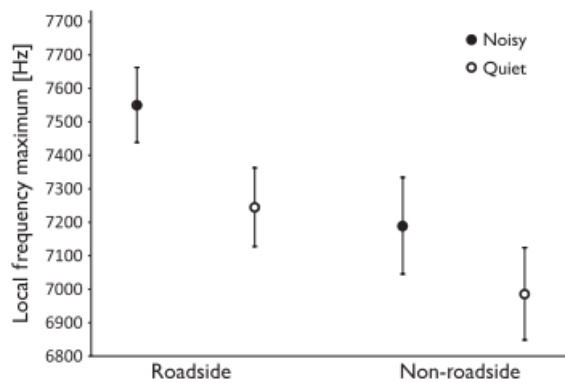


Figure 2. Predicted local frequency maxima (Hz) of calls of grasshoppers near a roadside or a non-road side from populations raised in a noisy (closed symbols) or a quiet environment (open symbols) (Lampe et al., 2014).

Phenotypic plasticity

Phenotypic plasticity allows animals to adapt to various life history stages via reversible changes in physiology and behaviour (Snell-Rood, 2013), e.g., from reproduction into wintering and vice versa. Because I consider responses in call and song to anthropogenic noise, I focus here on a specific form of phenotypic plasticity: behavioural plasticity. This concerns individuals that are able to modify their behaviour in response to environmental cues.

Birds are known to use behavioural plasticity to adjust their call amplitude, pitch and timing of calls to overcome the masking effects of anthropogenic noise (Dorado-Correa et al., 2018; Gil et al., 2015; Slabbekoorn & Peet, 2003). The observed changes varied between individuals and were, very important, reversible. An example of this behavioural plasticity is a study on two chiffchaff (*Phylloscopus collybita*) populations living near a highway and in a less noisy environment (Verzijden et al., 2010). The sound of the highway was recorded and blasted on a boombox to investigate the effect of traffic noise on the chiffchaff population living in a less noisy environment. The 'silent' chiffchaffs that had never heard the highway sound, promptly started to sing higher. This showed that the altering of the song was not inherited, because the chiffchaffs from the silent location never experienced the noise levels of the population living near the highway, but nonetheless could change their behaviour (Verzijden et al., 2010).

Other species than birds species show the ability to temporarily change their signalling behaviour in response to urban noise too. An example of this phenotypic plasticity and its reversibility is found in an endangered frog species (*Hyperolius pickersgilli*), living near a major airport in South Africa. *H. pickersgilli* males were found to make changes in both temporal and spectral properties of their call when an airplane flew over. Males called significantly more during and after an airplane flyby in relation to the call rate before the noise stimulus, but resumed normal call rhythms when measurements were taken 15 min after overflight. (Kruger & Du Preez, 2016). The reversibility of the response of the *H. pickersgilli* to noise shows that this is indeed a case of phenotypic plasticity instead of developmental (and irreversible) plasticity, as was seen before in tree frogs (Parris et al., 2009).

An alternative explanation other than phenotypic plasticity for the observed change in minimum song frequency in birds could be that individuals with genetically predetermined song spectra end up in matching territories with regard to noise spectra by trial and error (McGregor & Krebs, 1989). However this was proven wrong in Slabbekoorn & Peet's study on great tits (2003), who are known to learn their song. Major adjustments to this song occur in their breeding territory during interaction with neighbours. Thus, it is more likely that great tits learn to use a restricted range of their spectral capacity in response to local noise conditions: the adjusting of the song to the territory instead of territory to song. (Slabbekoorn & Peet, 2003)

Discussion

In existing literature, results on birds are consistent and vocal responses to noise are attributed to phenotypic plasticity. This is different in research on grasshoppers and frogs, where changes in response to noise are attributed to developmental plasticity.

Responding to noise in ways to overcome the masking effects leads to successful delivery of signals and therefore developmental and behavioural plasticity in call and song behaviour can lead to a successful establishment of a species in cities. In research on this subject, only one of two kinds of plasticity seems to play a role in being successful in an urban habitat. But, not in all taxa, behavioural plasticity is the mechanism underlying successful transmission of song or calls in urban environments. Some species are simply pre-adapted because their natural non-urban habitats possess the same characteristics as their new, urban habitat. Other species have a wide range of possible phenotypic changes due to developmental plasticity of the phenotypes. These changes are, in contrast to behavioural plasticity, not reversible. Grasshoppers from noisy environments that were put in a quiet environment didn't respond backwards (Lampe et al., 2014), while birds that were taken from a noisy environment and put into a quiet environment, did respond backwards (Verzijden et al., 2010). Differences in response between taxa can be explained by the way songs and calls are acquired. Most bird species, for example great tits (*Parus major*), learn their song, meaning the resulting song properties are highly influenced by the parental birds and the environment (Slabbekoorn & Peet, 2003). Species like the grasshopper, have innate calls and are less influenced by the environment in the individual's lifetime. But, adjustments can be a result of selection on individuals that have a call that is not in the same range as the noise, resulting in adaptation and divergence of populations.

Birds are highly plastic and thus capable of responding to temporal fluctuations in human noise patterns. This is very interesting because a bird population in an urban habitat, may genetically not be that different from bird populations of the same species that live in a nonurban habitat. Real evolution in the sense of divergence and speciation may not be the case with all bird species that thrive in cities. The question arises, how then does urbanization affect natural selection when it comes to anthropogenic noise pollution?

The unique characteristics of human-built environments confer a conflicting set of benefits and challenges that make it difficult to determine whether urban habitats are advantageous or constitute demographic sinks. If urban populations are sink populations, the gene pool is not big enough to sustain itself, so individuals from outside the population migrate to the sink population to add to the gene pool. This may be the cause of slowing of the evolution of 'urban' genes (Evans et al., 2018).

The conclusion is that a combination of plasticity and adaptation can lead to a successful establishment of a species in a city. The rate of plasticity can differ per individual and per species. Individuals that are more plastic are better equipped to colonize new environments like cities. If this is the case, then it can be argued that urban environments select for species with high plastic abilities. Although it can be debated if urban environments actually lead to divergence and creation of new species. This has to do with the high rate of influx and efflux of genes. Menno Schilthuizen on the other hand, wants to speak of a new urban species in the case of the blackbird (*Turdus merula*). In his book he calls this new species: '*Turdus urbanicus*' (Schilthuizen, 2018), because blackbirds from different cities are genetically more similar to each other than one blackbird from a rural population and another blackbird from an urban population. Blackbirds have colonized different cities in different countries, so one could say that every city has its own species of urban blackbirds. However, urbanization causes comparable selection pressures, resulting in urban blackbirds being more

genetically similar than the rural forest blackbirds they originate from. Also, the breeding season of urban blackbirds starts almost two months earlier than the breeding season of rural blackbirds, resulting in asynchronous life cycles and thus less and less genetic exchange. This genetic divergence can also be attributed to differences in song, which can lead to a fast divergence of species because of its important role in species recognition and reproduction.

Future research should focus on the question whether the differences found between taxa are consistent, because the number of species investigated for their acoustic signalling in response to noise are limited. Also, the impact of anthropogenic noise on other animals that are highly dependent on acoustic communication can be investigated. It would be interesting to look at sea creatures like whales and the effect of anthropogenic noise from ships and oil drilling stations. There is some research on whale migration and the influence of drilling sounds, but not on possible adaptations or changes in behaviour in response to the noise. Also, reproductive success and genetic exchange between rural and urban populations can be investigated to determine if urban populations are in fact source or sink populations. It will be difficult to attribute changes to either plasticity or evolution if not taken into account various other factors that play a role in adaptation and speciation.

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