

INVITED REVIEW

Birdsong and anthropogenic noise: implications and applications for conservation

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Abstract

The dramatic increase in human activities all over the world has caused, on an evolutionary time scale, a sudden rise in especially low-pitched noise levels. Ambient noise may be detrimental to birds through direct stress, masking of predator arrival or associated alarm calls, and by interference of acoustic signals in general. Two of the most important functions of avian acoustic signals are territory defence and mate attraction. Both of these functions are hampered when signal efficiency is reduced through rising noise levels, resulting in direct negative fitness consequences. Many bird species are less abundant near highways and studies are becoming available on reduced reproductive success in noisy territories. Urbanization typically leads to homogenization of bird communities over large geographical ranges. We review current evidence for whether and how anthropogenic noise plays a role in these patterns of decline in diversity and density. We also provide details of a case study on great tits (*Parus major*), a successful urban species. Great tits show features that other species may lack and make them unsuitable for city life. We hypothesize that behavioural plasticity in singing behaviour may allow species more time to adapt to human-altered environments and we address the potential for microevolutionary changes and urban speciation in European blackbirds (*Turdus merula*). We conclude by providing an overview of mitigating measures available to abate noise levels that are degrading bird breeding areas. Bird conservationists probably gain most by realizing that birds and humans often benefit from the same or only slightly modified measures.

Keywords: adaptation, biodiversity, city life, conservation, ecological speciation, homogenization, traffic noise, urbanization

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Introduction

Urbanization concerns all environmental changes associated with urban development and is a global phenomenon affecting animals, including humans, as well as plants (Vitousek et al. 1997; Western 2001). Expectations are that in the next two decades an additional two billion people will need a place to live, and they will not live in the current cities but in newly developed urban areas (Meyer & Turner 1992; World Resources Institute 2004). Urbanization usually has a negative effect on rare species and favours others that become more and more common, which can be native generalist species, but often means non-native urban colonizers (Bolger et al. 1997; Sewell & Catterall 1998;

Lim & Sodhi 2004; Marzluff 2005). At a local scale, urbanization does not necessarily lead to a drop in species diversity because the heterogeneous urban habitat does provide quite a variety of niches. However, at a larger scale, urbanization leads to homogenization and a drop in diversity because the typical urban species turn out to be the same everywhere irrespective of the original fauna (Clergeau et al. 2006; McKinney 2006). For species that still occur within and outside of cities, it is known that urban challenges may be relatively stressful as reflected for example by a divergence in heterophil-leucocyte ratios (Ruiz et al. 2002) or increased baseline corticosterone levels in male birds of city environments (Bonier et al. 2007). Nevertheless, although many species disappear from urban areas because they depend on habitat features that do not exist anymore, others find a new niche among bricks and concrete and adapt to a life in the city (Luniak 2004).

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Cities differ from rural or forested areas in a number of ways (Warren *et al.* 2006; Slabbekoorn *et al.* 2007). Urban areas are usually warmer, have artificial lighting regimes, more chemical pollution, and have relatively little and often exotic vegetation in a landscape dominated by street pavement and concrete buildings. Furthermore, cities harbour a different suit of parasites (Gregoire *et al.* 2002) and predators including domestic cats (Woods *et al.* 2003; Lepczyk *et al.* 2004), and a different set of food sources (Horak & Lebreton 1998). For example, urban house sparrows are reported to have higher cholesterol levels compared to rural ones, and food samples indeed reveal higher fat and protein content in urban diets (Gavett & Wakeley 1986). Consequently, food preferences also affect which species are more likely to do well under the urban food conditions; omnivorous and frugivorous birds are typically more successful than insectivorous and carnivorous species (Clergeau *et al.* 1998; Lim & Sodhi 2004).

One of the most prominent novel urban conditions concerns the ambient noise and the acoustic space available for animals to use acoustic signals (Slabbekoorn & Peet 2003; Katti & Warren 2004). All habitats are noisy to some extent, but the usual urban cacophony produced by cars, mopeds and all sorts of machinery is evolutionarily speaking novel and dramatically different from most natural habitats. Urban noise is typically loud and low in pitch which also applies to anthropogenic noise in areas around highways, railway lines and airports – which together form an ever denser network penetrating deeply into rural and forested areas (Forman & Alexander 1998; Reijnen & Foppen 2006). Anthropogenic noise could be an important factor driving bird species out of cities and away from highways, even when other habitat requirements are still sufficient.

Many studies have reported lower species diversity and lower breeding densities of birds along highways (Van der Zande *et al.* 1980; Reijnen & Foppen 1991, 1994; Illner 1992; Kuitunen *et al.* 1998, 2003). The negative impact of roads on birds has been linked repeatedly with traffic load (Reijnen *et al.* 1995, 1997; Forman *et al.* 2002; Peris & Pescador 2004), showing that the impact is not due to the mere presence of a road. However, direct evidence for traffic noise being the dominant detrimental factor is still lacking and other potential factors are visual disturbance, chemical pollution, road-kills and soil vibration. An interesting study concerns an impact assessment along a German motorway, which revealed a song-frequency-dependent pattern in breeding density in two transects parallel to the road (Rheindt 2003). Bird species with relatively low mean song frequencies were less abundant near the road, while species singing with higher frequencies occurred in higher numbers near the noisy road than in the more quiet transect. Although the lack of replication and statistical significance were limitations to this study, this is the first

direct indication that low-frequency traffic noise may constrain breeding opportunities of birds.

Few studies have tried to assess a negative impact of anthropogenic noise on birds while excluding other possibly contributing factors. A study in natural habitat of the Rocky Mountains, USA, showed a negative correlation between the number of species and anthropogenic noise levels (Stone 2000). Another recent study reported the first data on a decline in reproductive success due to anthropogenic noise without confounding parameters typically associated with highway or urban studies (Habib *et al.* 2007). The authors compared ovenbirds (*Seiurus aurocapilla*) in Canada, in two sets of territories of equal quality, except for either being located next to noise-generating compressor stations or next to noiseless well pads. Significantly more inexperienced first-year breeders were found at the noisy locations, while the pairing success at noisy territories showed a considerable decline, independent of the individual quality. This study unequivocally confirms a negative impact of human-generated ambient noise, but how does the sound affect the birds?

In this paper, we will address in what way birds may be affected by anthropogenic noise as well as how birds may counteract artificially altered noise conditions in their territories. We will discuss a case study of great tits (*Parus major*) which provides insight into how a successful urban species gets at least partly around the noise problem in cities across Europe. Subsequently, we will address to what extent urban habitat may drive divergence of urban populations and how sensible it is to make a case for ecological speciation in this context. The potential emergence of new urban species takes place over an evolutionary time scale and does not relate to conservation of today's biodiversity. Therefore, we will conclude with considering the available options to abate the negative impact of anthropogenic noise on current species at an ecological time scale.

Noise annoys

Extreme noise levels can result in temporary and permanent hearing loss (Ryals *et al.* 1999), but also the ubiquitous condition of more moderate noise levels may have adverse impacts. In humans, traffic noise at the front door of people's houses is a significant predictor of ischemic heart disease (a hospital-based case-control study with controls matched according to sex, age and hospital: Babisch *et al.* 2005), and repetitive exposure to aircraft noise has been shown to reduce performance at school (Stansfeld *et al.* 2005). Even relatively modest noise levels of train- and car traffic can already negatively affect cognitive development and reading skills (Lercher *et al.* 2003). Clearly, humans pay a price for

living in noisy cities or along roads with heavy traffic loads with respect to physical and psychological welfare (Miedema & Vos 1998; Nilsson & Berglund 2006). This may also be true for animals, including birds.

Measurements to assess direct and detrimental physical effects of anthropogenic noise on birds, such as an increased heart-beat (Helb & Hüppop 1991), are rare or nonexistent. Nevertheless, a wide variety of animal species has been reported to be affected by anthropogenic noise as indicated by behavioural changes (e.g. birds: Slabbekoorn & Peet 2003; Brumm 2004; whales: Foote *et al.* 2004; Miller *et al.* 2000; frogs: Sun & Narins 2005; ground squirrels: Rabin *et al.* 2006). One of the behavioural changes concerns an increase in vigilance behaviour at the expense of time spent feeding (Rabin *et al.* 2006). For example, chaffinches (*Fringilla coelebs*) spend less time with their head down, pecking at food, during artificially increased noise levels (Quinn *et al.* 2006). The nature of the behavioural change in this experiment suggests that these birds did not change general alertness due to a novel stimulus but have to rely more on visual scanning for predators when the detection of auditory cues is limited by masking noise. Predation risk in noisy conditions may therefore have negative consequences for food-intake rates and ultimately lead to lower survival and lower reproductive success.

Anthropogenic noise may not only hamper the detection of heterospecific predators but also the detection of conspecifics. Many animal species, and especially birds, depend heavily on acoustic signals for intraspecific communication (Catchpole & Slater 1995; Marler & Slabbekoorn 2004). Typically, males defend a territory for access to food, hiding places and nest sites. Singing and song features such as repertoire size or spectral and temporal details may have a direct impact on how well they are able to do so. Encoded in acoustic variation, birds may convey a message about their species identity, fighting ability and motivation to defend a resource (e.g. Ten Cate *et al.* 2002; Ripmeester *et al.* in press). Successful transmission of such a message may prevent competitors from approaching and may save energy, time and risks of injury. In addition, females also pay attention to these messages and are known to select their mates based on male song features (Riebel 2003). Therefore, whether songs are heard properly or not may have serious consequences for territory tenure and mate attraction (Klump 1996), potentially affecting individual fitness and population viability.

However, there are many signalling strategies available to birds to avoid or reduce masking by ambient noise (Brumm & Slabbekoorn 2005). Species-specific abilities in this respect may explain why some species resist urban noise conditions and others do not. A widespread strategy,

for example, concerns the Lombard effect: birds as well as humans raise their signal amplitude with noise level. Recently, urban nightingales (*Luscinia megarhynchos*) in the city of Berlin, Germany, were found to raise their song volume in response to traffic noise; as a result they appear to sing louder on weekday mornings than in weekends (Brumm 2004). Another way to adjust to fluctuating noise conditions concerns a temporal shift in singing activity. Several urban bird species are reported to start singing earlier during the day than their forest counterparts (Bergen & Abs 1997), but the potential relationship with avoiding traffic peaks has not been investigated in enough detail yet. However, European robins (*Erithacus rubecula*) sing both, during day and night time, and whether or not birds are active during the night was recently shown to be dependent on day-time noise levels in a study in the city of Sheffield, UK (Fuller *et al.* in press). There was less of an effect in this study of ambient light pollution, to which nocturnal singing in urban birds is frequently attributed. Although it is not clear yet whether nocturnally active robins reduce their day-time activity and whether they gain any fitness benefits by doing so, it seems plausible that this strategy may enable them to avoid masking noise and breed in noisy territories. In general, a division between species surviving in urban conditions and those fleeing the cities may very well depend on how effectively members of a species can adjust their signalling behaviour to the volume, temporal fluctuations or spectral characteristics of traffic noise.

Signalling flexibility in urban great tits

Over the last five years, we have studied patterns of song variation among individual great tits (*Parus major*) within an urban population in Leiden, The Netherlands, and among 20 different urban and forest populations across Europe. We first found in the single-population study that individual variation in the frequency range correlated to local urban noise levels (Slabbekoorn & Peet 2003). Birds of noisier territories sang with higher minimum frequencies, thereby avoiding masking by low-pitched traffic noise (Fig. 1). We speculated at the time that these results could mean that urban birds could have diverged from forest birds, and that flexibility through learning may be the behavioural mechanism underlying the correlation. Subsequently, we confirmed that urban birds across Europe have diverged from nearby forest birds in several parameters, among which the minimum frequency. A surprising 10 out of 10 independent city-forest comparisons revealed a consistent shift (Slabbekoorn & den Boer-Visser 2006).

The habitat-dependent acoustic shift in great tits could be an evolutionary or ontogenetic shift, or it could be based on the ability to adjust at an even shorter temporal

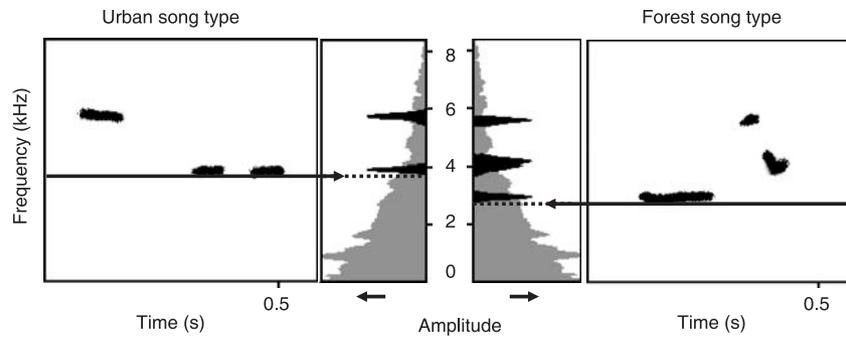


Fig. 1 Sonograms of a three-note song type recorded in an urban habitat, with a relatively high minimum frequency (3.8 kHz, left graph) and of a three-note song type recorded in a forest habitat with a relatively low minimum frequency (2.7 kHz, right graph). The centre panels illustrate the energy concentration of each of the spectral components present in the song, normalized at an equal amplitude and contrasted, at an arbitrary level, against the energy distribution of a typical anthropogenic sound spectrum of urban traffic noise. Noise levels gradually increase towards lower frequencies, and the figure illustrates that critical signal-to-noise ratios leading to perceptual problems are more likely for notes of low frequency. As a consequence, song types without relatively low notes will on average be heard better in noisy cities.

scale (Patricelli & Blickley 2006). It is known from long-term field observations that great tits are probably capable of postdispersal adjustment of song-type repertoires guided by vocal interactions with neighbours (McGregor & Krebs 1989). Noisy conditions may affect such social influences through selective copying or selective reinforcement: song types of neighbours that are not heard well may not be copied, and song types sung but hardly eliciting a response from neighbours may be dropped. Recently, we found that adult males are even more flexible than previously thought. We played back unfamiliar song types and assessed the repertoire of a series of males before and after playback (Franco & Slabbekoorn, unpublished). The song-type repertoire size remained relatively constant over the season, but the rates at which different song types were sung varied and the repertoire composition was sometimes modified dramatically within a week. This shows that great tits have a larger repertoire memorized than they actually sing at a time or that they can make up new song types late in life. Most importantly, this means they have remarkably flexible singing behaviour. They are capable of mobilizing a large set of song types to adjust to new neighbours or possibly to new noise conditions.

The singing behaviour and repertoire flexibility of great tits has likely evolved to fit their social system in the context of the original forest habitat. They may be just lucky in the sense that these features turn out to be very suitable for coping with dramatic and, evolutionarily speaking, sudden rises in anthropogenic noise levels. The ability to spectrally adjust their song after dispersal to the local circumstances of a breeding territory, and this potentially throughout life, may be key to urban success. At the same time, despite the fact that they remain in cities breeding at relatively high densities,

it is not certain that great tits are not at all negatively affected by anthropogenic noise (see Box 1). However, their acoustic counter-strategy seems at least sufficient for urban populations to survive under potentially sub-optimal conditions (also see Junker-Bornholdt *et al.* 1998). Our results from the single-population study have now been independently replicated in two other North American bird species that are also very successful in urban environments (house finch, *Carpodacus mexicanus*: Fernández-Juricic *et al.* 2005; song sparrow, *Melospiza melodia*: Wood & Yezerinac 2006). An earlier study on chaffinches did not find a correlation between traffic noise levels and call characteristics (Skiba 2000). Nevertheless, this species, which can be very common in cities, does show the same increase in minimum frequency of their songs with varying levels of natural river noise (Brumm & Slater 2006). We are now waiting for data showing that bird species which are less successful in noisy areas are lacking the ability of spectral adjustment through repertoire changes.

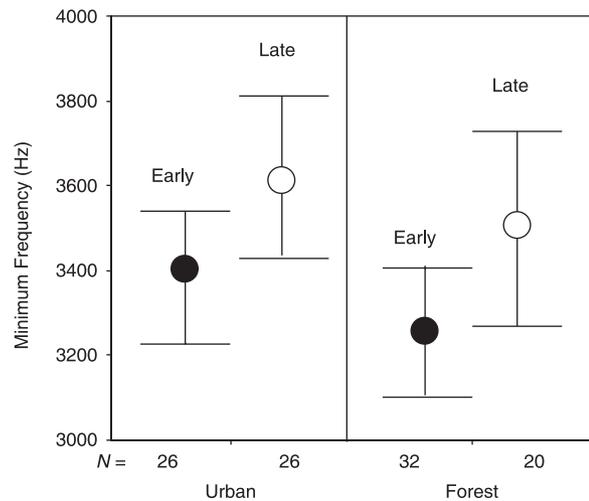
Divergent phenotypes in great tits: a case for urban speciation?

Behavioural plasticity may allow urban birds enough time to evolve and adapt to human-altered environments. Although it is possible, currently there is no evidence that the acoustic divergence between city and forest tits involves any microevolutionary changes and associated genetic differentiation. However, habitat-dependent divergence in a sexual trait like song in birds may play an important role in population divergence and ecological speciation (Slabbekoorn & Smith 2002a, b), and we may be able to consider urban speciation. Species with a distribution across ecological gradients may evolve different subpopulations in different habitats. These

Box 1 Is singing low important to great tits?

There is a general relationship in birds between body size and frequency of pitch: larger species typically sing lower. Small birds with small vocal organs may be lacking the power, the essential size of the vibrating source, or the suitable resonance features of the vocal tract, that allow the production of low-pitched sounds. This creates the possibility of using low frequencies as a way to signal condition or size to competitors and potential mates (Ten Cate *et al.* 2002). However, we do not know whether intraspecific variation in male body measures is related to the minimum frequency in great tits, nor do we know if female great tits prefer males singing low-pitched songs. If it were hard for great tits with a territory to sing low, you may expect that they sing songs relatively high in pitch when the motivation to sing is low. Such a situation occurs at the end of the breeding season, in both urban and forest habitat. Males still sing their stereotypic song types but the resources at stake in their territory have decreased in value until the start of the next breeding season. A decline in motivation to sing is clear from a decline in number of repeated songs (phrases) in a strophe, independent of habitat: in the city of Rotterdam from six to three phrases, and in the forest called the Liesbos from six to four phrases on average (ANOVA: $F_{2,100} = 27.4$, $P < 0.001$). Interestingly, controlling for habitat differences, we found that the minimum frequency increases dramatically when recordings from relatively early in the season (early April: 'Early') are compared to recordings from late in the season (late May: 'Late', ANOVA:

$F_{2,100} = 7.8$, $P < 0.01$). We therefore hypothesize that it may be an important signal of quality to have low-pitched notes in the song type repertoire, which may cause a trade-off especially for the urban birds in noisy territories. Low-frequency noise may constrain the capacity to signal individual qualities: urban birds may need to choose between being heard well or being rated high as a competitor or mate. High noise levels may increase the number of intruding competitors needing physical combat and may affect the number and quality of potential mates that are attracted. Consequently, although great tits are successful in cities, and even though they show a remarkable flexibility in spectral adjustment to local noise conditions, this does not mean that traffic noise interference is not harmful to individual birds.



subpopulations may show genetic divergence in fitness-related traits related to morphology, physiology, neurobiology or life-history. Congruent geographical patterns of variation in sexual and fitness-related traits may arise because varying environmental selection pressures in different habitats shape both types of traits. Congruent patterns may also emerge because acoustic changes are an inherent result of, for example, changes in bill morphology (Slabbekoorn & Smith 2000; Podos *et al.* 2004). As a consequence, under both conditions, songs may guide female birds to the locally adapted males, accelerating the process of reproductive divergence. The fact that many birds learn their songs from conspecifics adds a layer of complexity (Baker & Cunningham 1985; Slabbekoorn & Smith 2002b), as it will accelerate phenotypic divergence among populations but may actually constrain genetic differentiation (Ellers & Slabbekoorn 2003). Nevertheless, divergence in learned song will still

increase the rate and chance of speciation for a subset of evolutionary scenarios (Lachlan & Servedio 2004; Ellers *et al.* unpublished).

In terms of gene flow, it may be improbable that urban habitat could generate phenotypically distinct and reproductively isolated subpopulations, as cities are typically scattered geographically and form a patchy network within a matrix of forested and agricultural area (Marzluff 2005). Habitat imprinting, on the other hand, may strongly influence dispersal patterns, and urban-borne birds may preferentially settle in urban territories (see e.g. Septon *et al.* 1995). In terms of consistent directional selection, despite considerable heterogeneity within urban habitat, some urban selection pressures are clearly distinct and dramatically different from those in more natural habitat. These consistent habitat-dependent selection pressures may have the potential for driving divergence of an urban phenotype despite ongoing gene flow.

We are not aware of any publications on gene flow, or dispersal, between urban and nonurban populations of great tits, but there are some studies on urban-related phenotypic divergence. Plastic environmental responses were found for carotenoid-derived plumage coloration, with urban birds being less yellow compared to forest birds (Horak & Lebreton 1998) and also for timing of reproduction and clutch size, with later and smaller broods in (sub)urban great tits compared to their forest counterparts (Riddington & Gosler 1995). Another study, not involving urban habitat, addressed the balance between the response to divergent selection pressures and levels of gene flow over a very short distance. A partial cross-fostering experiment with great tits of two qualitatively different parts of Wytham Woods in Oxfordshire, UK, allowed the separation of genetic and environmental sources of variation (Shapiro *et al.* 2006). Nestlings in the high-quality part of the forest were larger, heavier and in better condition than in the low-quality part irrespective of the part from which they originated. Interestingly, in addition, significant differences in condition and shape could be attributed to area of origin, suggesting genetic differentiation. The areas of varying quality in this comparison were only a few kilometres apart and interconnected by forest, which reveals the evolutionary potential of divergent selection in ecologically distinct habitat for driving populations apart. Another recent and small-scale study on great-tit populations also reported interesting findings with respect to the balance between divergent selection and gene flow. A biased influx of birds from the mainland to only one side of the Dutch island of Vlieland created a local abundance of breeding birds that were not locally adapted (Postma & van Noordwijk 2005).

Evidence for microevolutionary changes in urban habitat

The evidence for genetic differentiation related to anthropogenic selection pressures in cities is also still scarce when we look at bird species beyond great tits. A nice example of selection in an urban environment driving evolutionary change is found in an exceptional urban bird population on the campus of the University of California in San Diego, USA. Dark-eyed juncos (*Junco hyemalis*) have been breeding in this urban setting since the early 1980s (Yeh & Price 2004). The birds were presumably winter visitors that decided to stay instead of return to their natural breeding habitat: montane pine forest at least more than 70 km away (Nolan *et al.* 2002). Population comparisons and a common-garden experiment with hand-raised birds revealed that wing- and tail size, as well as a sexual trait (the amount of white in the tail) has diverged on campus beyond the extend attributable to phenotypic plasticity or drift (Rasner *et al.* 2004; Yeh 2004). However, there was only limited evidence for song divergence between this

small urban population of about 70 pairs and four forest populations (Slabbekoorn *et al.* 2007). Although there were strong indications for divergent selection pressures on acoustic signals related to sound transmission, sexual selection based on song may be relaxed, as suggested by a reduced response to playback of junco songs in the urban population (Newman *et al.* 2006). The urban juncos make a strong case for microevolutionary changes related to anthropogenic selection pressures, but they require more study and better replication to increase our insight into the role of song in urban speciation.

Another bird species for which there is growing evidence for urban-related population divergence is the European blackbird (*Turdus merula*), a very common city bird in most parts of Europe (Luniak *et al.* 1990). Urban blackbirds breed in higher densities and start breeding earlier in the year than their forest counterparts (Partecke 2003). A common garden experiment, with nestlings collected in the city of Munich and the nearby Lichtenauer Forest, revealed phenotypically plastic divergence but also suggested that some of the variation reflects genetic differentiation (Partecke *et al.* 2004, 2005, 2006a). The habitat-dependent difference in timing of reproduction corresponds to an earlier initiation of the development of the reproductive system in male and female urban birds (Partecke & Gwinner 2007). The prolonged breeding season allows urban individuals to have more breeding attempts per year than individuals from forests, who on the other hand have a larger clutch size and more fledglings per successful nest (Gregoire 2003). Urban blackbirds also live longer than forest birds (Luniak *et al.* 1990), have a smaller tendency to migrate (Stephan 1999; Partecke & Gwinner 2007) and have a lower acute corticosterone stress response (Partecke *et al.* 2006b). Finally, a pattern of habitat-dependent divergence starts to emerge from several studies at different geographical locations, with blackbirds from cities and forests being distinct from each other in several morphological measures (Lippens & van Hengel 1962; Partecke 2003; Ripmeester & Slabbekoorn, unpublished).

European blackbirds may become the first bird species for which there is evidence for urban habitat-related divergence in both, fitness-related traits (as described above) and acoustic traits (Ripmeester & Slabbekoorn, unpublished). We are in the process of testing with playback recordings whether urban songs trigger stronger responses in city birds than in forest birds and vice versa. At the moment, we do not know yet whether congruent habitat-dependent divergence in song and morphology promotes the process of urban speciation. There is also no information available yet about habitat-guided dispersal, although a first study on divergence in neutral markers between the urban and forest birds of the common garden experiment in Germany could not confirm such a

phenomenon (Partecke *et al.* 2006a). It is clear, however, that the aspects of coding and neutral genetic divergence between urban and forest blackbirds warrant further investigation and several complementary studies are on the way.

Considerations on making bird breeding habitat more quiet

It is possible to make bird breeding habitat close to, or surrounded by, anthropogenic noise sources more quiet. We can build noise barriers, make depressed highways or underground tunnels (e.g. Maekawa 1977), or introduce porous road surfaces, speed limitations and restrictions on allowable noise emissions for road traffic related to engine features, break systems and tire types (e.g. Sandberg 1991). There are many examples of successful implementation of these techniques, typically to reduce noise exposure to humans. This means that the main threshold for applications to the benefit of wildlife will likely be the financial costs. However, when considering expensive mitigating measures, it is very important to realize that birds and humans often benefit from the same, or only slightly modified, measures. Urban birds live and breed near human residences, and birds of more natural areas inhabit space often used for recreational activities. The importance to human health and well-being can be used as additional arguments for installing measures to improve bird-breeding areas. In cases where noise barriers are already in place to the benefit of humans, small cost-effective modifications (e.g. increased height, added absorbent) could be a successful strategy (see Box 2).

Urban planners are increasingly aware of the need to consider noise pollution in constructing cities and residential neighbourhoods from a human perspective (Grimm *et al.* 2000; Yli-Pelkonen & Niemelä 2005; Bucur 2006; Nilsson & Berglund 2006). For example, the idea of urban canyons has received considerable attention: the use of relatively continuous rows of office buildings or apartment flats separating noisy human activities from living space in which noise is not appreciated (de Ruiter 2004). This living space may concern pedestrian areas, urban parks and private gardens, all areas in which urban birds would also benefit from reduced noise levels. The strategy of urban canyons also entails concentration of noise sources: canalization of traffic in a limited number of busy through-roads. This will limit the number of canyons to be constructed and make plans economically more feasible (Thorsson & Ögren 2005). Similarly, it is more realistic to concentrate on a restricted set of specified areas which are shielded from noise, instead of trying to reduce noise levels in all public areas (Kihlman & Kropp 2001; Thorsson *et al.* 2004). Urban canyons and 'quiet zones' provide people living in noisy cities with access to

at least some quiet areas nearby, which may be a last resort for noise-sensitive bird species at the same time. In the best scenario, bird-breeding data and species-conservation values would be incorporated in the process of selecting the areas to be relieved from urban racket.

More and more tools have been developed to assist policy makers to predict and extrapolate noise levels spatially, based on traffic flow, vehicle types and distance to the road (e.g. Horoshenkov *et al.* 1999; Li *et al.* 2002; de Coensel *et al.* 2005). Spatial extrapolation has also been applied to reveal the impact of traffic noise on bird habitat by using road effect-distances based on general dB-threshold values that are just acceptable for birds, and which depend on habitat type and target species (Reijnen *et al.* 1997). For example, roads with 50 000 vehicles a day result in effect-distances from 75 to 930 meters for grassland species and from 60 to 810 meters for woodland species, as was shown by a meta-analysis combining nine studies (Reijnen & Foppen 2006). Highways may negatively affect bird-breeding habitat in a variety of ways, as stated earlier (e.g. collision, chemical pollution). However, visual disturbance and noise are the primary factors that reach furthest in open habitat, while noise is the single most important factor impacting forested habitat beyond 50 meters from the road (Reijnen & Foppen 2006).

The importance of temporal and spectral overlap

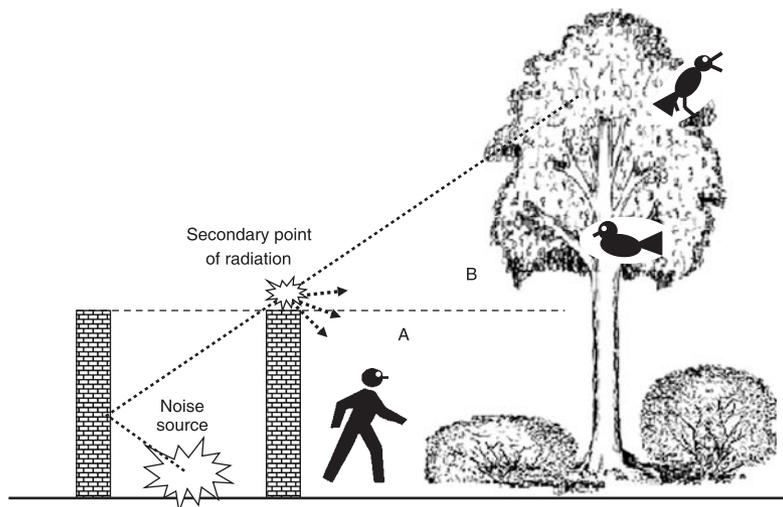
Birds often have a diurnal cycle of vocal activity which matches periods of optimal sound transmission early in the day (Staicer *et al.* 1996; Brown & Handford 2003). Diurnal fluctuations in anthropogenic noise levels are also highly stereotypic with, not surprisingly, noise peaks during the morning and evening rush hour (Jabben *et al.* 2001). Interestingly, traffic jams during these periods may bring down noise levels because of lower driving speeds. Most importantly, however, this means that dawn chorus and rush hour can co-occur at optimal times for sound transmission depending on latitude and season (see Warren *et al.* 2006). Good signalling periods are thus disproportionately affected due to temporal overlap with traffic activity.

The fact that there are often periods during the day in which anthropogenic noise is most detrimental due to concentration of bird singing activity and optimal noise-transmission conditions seems 'bad luck' but also provides the opportunity to ecologically sensible noise control. Reducing traffic flow for short but crucial periods of time, for example, on roads through nature reserves, will raise habitat quality for breeding birds with limited impact on human activities. Similarly, on a slightly larger temporal scale, traffic limitations through sensitive areas during the critical period in spring, when males vocally attract females, could also significantly improve habitat

Box 2 Noise barriers for birds

Raising a barrier between the noise source and bird breeding habitat can lead to a significant reduction in detrimental noise levels. Vegetation is only of limited use, although the effectiveness will increase with stem and leaf density and width of the zone (e.g. Cook & van Haverbeke 1972; Bucur 2006). A solid barrier as close as possible to the noise source will be most effective (Maekawa 1977; Ishizuka & Fujiwara 2004). Adding an overhang on the road side or increasing the height of a barrier which is already in place to benefit pedestrians at ground level (A), could be a very cost-effective measure to the benefit of flying and tree-dwelling birds at a higher level (B). It is usually also easier to filter out the bird-relevant frequency components of traffic or industrial noise than to block the lower frequencies. Construction details and barrier shape especially can have a big impact in the frequency range between 2.0 and 8.0 kHz. For example, sound-pressure levels at the barrier's edge (= secondary point of radiation) can be significantly decreased by installing a soft, absorbent material on top. This will lead to a decrease in the noise level behind the barrier, especially in the field below the barrier height (A). Specific shapes of the barrier top with multiple diffracting edges may add to this effect. For example, T-shaped noise barriers with soft material on top only have to be three meters high to be as effective

as a 10-metre high rigid-edged plain barrier (Ishizuka & Fujiwara 2004). This effect steadily gets stronger with frequencies above 250 Hz, also for the sound field above barrier height (B), which concerns the habitat layer typically most important for acoustic signalling in many bird species (Slabbekoorn 2004). Noise barriers at both sides of a road shield areas in both directions, but multiple reflections and scattering effects between the barriers will reduce the shielding capacity. Noise levels become higher especially above the barrier compared to a single barrier situation (Maekawa 1977). Buildings by the side of a busy road typically also increase noise levels within the street or urban canyon (Oldham & Radwan 1994; Heutschi 1995). Both inside and outside urban areas, the problem can be brought down by noise abatement schemes using a more absorbent ground surface and intermittent or continuous absorbers on the walls of buildings or noise barriers (Horoshenkov *et al.* 1999). Placing noise barriers at an angle will also reduce the impact of reflections by beaming them more upward into the sky or downward back towards the tarmac. Finally, the choice of construction material or absorbent matter may make noise barriers also bird-friendly in nonacoustic ways. Combination barriers incorporating trees or shrub layers can reduce the negative impact of an artificial, visual barrier in the landscape, and potentially provide nesting and foraging opportunities.



quality. These critical periods can be quite brief, as in some migratory species, for example, where males arrive at the breeding grounds just before the females. For such species, male singing effort peaks upon arrival and may already decline after one or two weeks.

In addition to seasonal and diurnal fluctuations in bird singing activity and noise levels, more short-term fluctuations may also warrant some attention. Fluctuating noise levels in terms of overall amplitude are usually more annoying to humans than relatively continuous noise levels,

especially when areas are relatively quiet overall with sudden unpredictable noise peaks (de Coensel *et al.* 2005). For birds, mean noise levels may similarly not describe the potential for auditory masking or stress levels adequately. Therefore, analyses of sound-level fluctuations in time can add a relevant descriptor capturing more of the dynamics of noise interference.

Traffic-noise fluctuations in terms of frequency are chaotic, but most of the common anthropogenic noise sources show a general decrease in amplitude from low to high frequencies. Bird species in many taxa, such as doves, owls, corvids, woodpeckers, herons and rails use frequencies well below 1.0 kHz. Whether or not species in these groups occur in urban areas or along highways (and some are typically abundant within these habitat types) is probably largely determined by other factors than the impact of noise interference. However, declining signalling efficiency may influence the balance between costs and benefits of city life, especially for those species relying on vocalizations for long-distance communication. Not many noncorvid songbirds use frequencies below 2.0 kHz. The majority of these species uses a bandwidth of 3.0–6.0 kHz, starting at 2.0 or 3.0 kHz and often going up to around 8.0 kHz. The few songbirds that do use very low frequencies down to 1.0 kHz, typically use wideband songs with a bandwidth of about 6.0–9.0 kHz (examples are: European blackbird; nightingale; house sparrow, *Passer domesticus*; European starling, *Sturnus vulgaris*; house martin, *Delichon urbica*), and may therefore be less vulnerable to noise pollution (although we do not know yet whether this is true). Few songbird species rely just on relatively low frequencies, but species that do, like the oriole (*Oriolus oriolus*), the great reed warbler (*Acrocephalus arundinaceus*) and the mistle thrush (*Turdus viscivorus*), may for this reason be relatively sensitive to the masking effect of traffic noise.

A study on distribution and breeding success of great reed warblers in a wetland area in the central part of The Netherlands provides interesting support for the suspected sensitivity to noise in this species (Foppen & Deuzeman 2007). A reed bed in the Vossemeer was known to be inhabited by about 5–10 pairs of reed warblers up until the early 1990s. This reed bed has not changed much since, but it is now situated right beside a road (Vossemeerdijk) with a few thousand cars passing by per day. In the last 15 years, typically only one or two territories each spring have been occupied by singing reed warblers. However, in two years (2003 and 2004) the road was closed to traffic for a substantial time during spring due to road works. The absence of the usual traffic was correlated with an increase from two in 2002 to seven territories in 2003. The return of the noise source was correlated with a decline from five in 2004 back to one territory in 2005. These fluctuations over the course of four seasons consti-

tute only anecdotal evidence, but they do suggest that the vulnerability to a masking of the low-pitched song by traffic noise may have contributed to the overall decline in reed warbler territories in this area since the early 1990s.

Although low-frequency bird songs are most affected by typical anthropogenic noise, it is not true that higher frequencies are free of the impact of anthropogenic noise interference. Masking depends on the amplitude of the acoustic signal relative to the amplitude of the ambient noise within the same frequency range (Lohr *et al.* 2003; Brumm & Slabbekoorn 2005), both measured at the receiver. So, the impact on detection and recognition of acoustic detail can still be serious and deleterious for faint high-pitched notes. Also, high-pitched songs heard at a large distance from the singer, with the receiver potentially being closer to the noise source, may be hampered by the high component of traffic noise which has most energy at low frequencies.

Conclusions

It is becoming more and more clear that the omnipresence of anthropogenic sounds is not only detrimental to human health and well-being, but can also negatively affect birds. Efforts to bring down anthropogenic noise levels to the benefit of bird-breeding areas will almost certainly encounter financial trade-offs. Mitigating measures are typically expensive or counteract economic values, for instance by slowing down, or putting restrictions on, traffic flow. When considering or arguing for expensive noise-reducing actions, it is very important to realize that birds and humans often benefit from the same or only slightly modified measures.

It is obvious from the remarks above on song spectra that we need a thorough comparative study to assess noise sensitivity of bird communities, or at least of those species of high conservation value. Although it may be true in general that making habitat more quiet will improve breeding conditions for many species, we still lack much essential data to guide conservation efforts with adequate detail. Optimally, such data would come from a comparative study that includes experimental assessment of developmental flexibility, tolerance to spectral range reduction and an assessment of the fitness consequences of masking (cf. Habib *et al.* 2007). Data on urban survivors, such as the great tit (Slabbekoorn & Peet 2003; Slabbekoorn & den Boer-Visser 2006), as well as urban 'losers' will be valuable to generate the insight needed to come up with ecologically solid recommendations.

Behavioural flexibility, such as song plasticity in postdispersal adjustment to neighbours under local noise conditions, may allow some species more time to adapt to human-altered environments. Consequently, thriving urban populations may be diverging from their

forest counterparts in several traits and may be on a track towards becoming even more successful and potentially an independent urban species. However, this may be true for a 'lucky' few, since many species will not be able to go down this fortunate path. Hopefully in the near future, we will be able to explain which species are negatively affected by anthropogenic noise and why. For those situations for which there is the political will and the financial support to reduce detrimental noise exposure, we hope our considerations on making bird breeding habitat more quiet will prove to be useful.

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