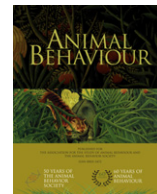


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Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds

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Urbanization leads to homogenization of avian communities through local extinction of rare bird species and increasing numbers of the same common urban bird species over large geographical areas. Successful city birds often persist through some sort of behavioural plasticity that helps them survive and reproduce close to humans, in built-up areas, with all the typical urban feasts and hazards. In this review, I address whether behavioural plasticity of the acoustic phenotype can be an additional factor in explaining which species end up as urban survivors. Anthropogenic noise has been shown to negatively affect avian distribution and reproduction, especially for species that rely on relatively low-frequency songs for mediating territorial conflicts and attracting partners for mating. Spectral differences between songs of city and forest populations of the same species and correlations between individual song frequency use and local noise levels suggest that many successful city species shift song frequency upward under noisy urban conditions. Experimental evidence has confirmed the ability of several species to show rapid spectral adjustments as well as perceptual benefits of singing at higher frequency in noisy habitats. However, empirical evidence of fitness benefits for birds showing the ability and tendency of noise-dependent spectral adjustment is still lacking. Furthermore, depending on the species and the underlying mechanism for spectral change, there may also be fitness costs through a compromise on signal function. These two aspects are only two of many remaining avenues for future studies. The acoustic phenotype of urban birds provides a great model system to study fundamental processes such as causes and consequences of environmentally induced signal changes, 'cultural assimilation', and the relationship between phenotypic and genotypic evolution. Furthermore, the current and expected rate of urbanization remains high at a global scale, which will lead to further spread in time and space of artificially elevated noise levels. This should guarantee the continued interest of scientists, politicians and conservationists for many years ahead.

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The world counts more than 7 billion people; a number that is still on the rise with a growing proportion living in urban instead of rural areas (United Nations 2012). The associated spread of urban areas around the world causes dramatic habitat alterations and introduces novel environmental conditions for animals within and surrounding new and expanding cities (Vitousek et al. 1997; Marzluff 2001; Faeth et al. 2005; Warren et al. 2006). Such human-induced rapid environmental changes typically lead to declines and local extinction of indigenous species. Birds have been investigated particularly well in this context. Some bird species may persist while others will newly arrive from urban habitat elsewhere (see Fig. 1). These processes cause urban areas to harbour very similar avian communities across vast geographical areas independent of

the original habitat type; a phenomenon labelled 'urban homogenization of the avifauna' (Clergeau et al. 2006; McKinney 2006; Devictor et al. 2007).

Species remaining or colonizing and sometimes thriving in urban areas have been referred to as human commensals, urban exploiters or synurbic species (Shochat et al. 2006; Francis & Chadwick 2012). Some typical example species that remain in European cities include great tits, *Parus major*, European blackbirds, *Turdus merula*, and wood pigeons, *Columba palumbus*, which often persist at elevated densities during increasing degrees of urbanization. House sparrows, *Passer domesticus*, European starlings, *Sturnus vulgaris*, and rock doves, *Columba livia*, are examples of species that colonize newly urbanized habitat from other built-up areas. Furthermore, there are also several corvid species that have been doing well in and around cities for a long time (Zmihorski et al. 2010), while several gull species have become common roof-nesters in many coastal cities relatively recently (e.g. Belant 1997; Soldatini et al. 2008).

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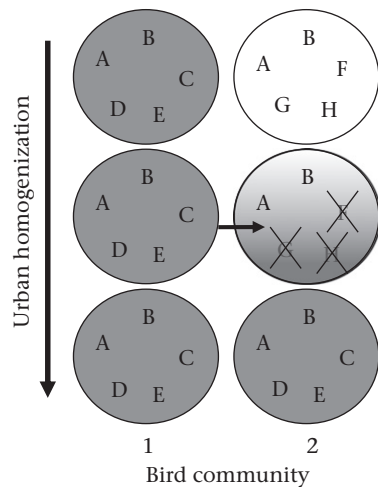


Figure 1. Schematic illustration of the phenomenon of urban homogenization by the convergence of two bird communities (numbered 1 and 2, on the left and right) with the passing of time (progressing in two steps from top to bottom). Each circle represents an area inhabited by a number of bird species represented by the letters A to H. Area 1 is an urban area with the same five bird species consistently present. Area 2 undergoes dramatic habitat alteration and changes from a particular natural habitat type into an urban habitat, with three species (F–H) that do not persist, but which are replaced by three species from urban area 1 (C–E). The diversity in terms of number of species within areas remains the same after the turnover (two areas \times five species), but declines overall (from eight to five species).

Several explanations exist for why some species cope well with urban conditions, while many others do not (McKinney 2002; Chace & Walsh 2006; Francis & Chadwick 2012). Urban success in birds has been related to species-typical features such as relatively large brain size, wide-ranging diet choice, high rate of feeding innovations, low fear of human proximity, broad environmental tolerance, opportunistic nest site selection (exploiting human architecture), high degree of sociality and sedentariness (e.g. Sol et al. 2002, 2005, 2013, this issue; Bonier et al. 2007; Kark et al. 2007; Croci et al. 2008; Møller 2009, 2010; Evans et al. 2011; Maklakov et al. 2011). These comparative studies are often not completely consistent in the set of traits investigated, and traits are typically not mutually exclusive and often complementary. However, all studies seem to converge on a combination of features that best explains high urban survival and reproductive success in cities. Notably, behavioural flexibility often plays a key role (see Sol et al. this issue).

A dominant environmental factor associated with urban areas and human activities in general concerns the artificial elevation of natural noise levels (Slabbekoorn & Ripmeester 2008; Barber et al. 2009; Nega et al. 2012; Francis & Blickley 2012). Examples of so-called anthropogenic noise sources include motorized traffic, industrial practices, construction work, and all sorts of noisy recreational activities. Although noise could involve disturbance and deterrence by fear, the potential impact on urban species communities of noise per se has not received specific attention in the comparative studies cited above. However, sound is very important to most bird species as especially acoustic communication may be critical for survival and reproductive success through its impact on territorial defence and mate attraction. Anthropogenic noise may mask important signals and therefore singing behaviour, and the relative plasticity of the acoustic phenotype may also be an important species-specific feature explaining why some species persist and others fail in the typically noisy urban environment (Slabbekoorn & Peet 2003; Hu & Cardoso 2009; Francis et al. 2011a; Ríos-Chelén et al. 2012).

In this review, I will address the question of whether spectral flexibility of the acoustic phenotype could be a factor in explaining

the success of birds in a noisy urbanizing world. First, I will review the evidence for an impact of noise on bird distributions and breeding success, exploring especially the insights gained on frequency-dependent noise impact and noise-dependent song frequency use on variation in bird abundance. Second, I will explain what we know about the role of behavioural plasticity in explaining the noise-dependent patterns of song frequency use within species. Third, I will address how phenotypic plasticity at the individual level can lead to so-called 'cultural assimilation' of typical urban song frequencies and drive cultural evolution at the population level. Doing so, I will integrate birdsong data with the general concept of phenotypic plasticity and argue that cultural assimilation can quickly induce phenotypic divergence and eventually also genotypic divergence. I will conclude with an evaluation of the current evidence for fitness benefits of shifting song frequencies upward under noisy urban conditions and explain how a spectral compromise on signal function can also bring about fitness costs.

EFFECTS ON DISTRIBUTION AND REPRODUCTION

Reduced density and diversity in breeding bird communities has been attributed to traffic noise levels in several so-called roadside or urban studies (e.g. Reijnen & Foppen 2006; Tratalos et al. 2007; Fahrig & Rytwinski 2009; Strohbach et al. 2009; Arevalo & Newhard 2011). However, the contribution of the artificially elevated noise levels to the negative effects on bird breeding can typically not be distinguished from confounding variables that also vary between natural habitat and roads or cities (e.g. nesting opportunities, predation risk or traffic collision rates). Nevertheless, there are also similar reports from Canada and New Mexico that can rule out an impact of such confounding variables: anthropogenic noise is also linked to lower bird numbers for several species in comparisons between quiet and noisy compressor stations of the oil and gas industry that are otherwise identical (Bayne et al. 2008; Francis et al. 2009, 2011a). Similar results were reported in an experimental exposure study with drilling and road noise impact on greater sage grouse, *Centrocercus urophasianus*. Long-term playback of continuous and intermittent noise during the breeding season had detrimental effects on bird attendance at leks (Blickley et al. 2012).

The individual birds or species that persist in noisy areas do not necessarily represent healthy populations or communities. Habib et al. (2007) showed that male ovenbirds, *Seiurus aurocapilla*, at noisy compressor stations were of relatively low quality, as the more experienced, older males occupied the quiet stations. Furthermore, taking both individual and territory quality into account, singing male ovenbirds at noisy sites were significantly less successful in attracting a partner than those at quiet sites. Presumably, either females rated noisy sites as lower-quality territories, or the songs of males at noisy sites attracted fewer females due to masking. Evidence for these same mechanisms has also been found for noise pollution by car traffic in Europe. Willow warblers, *Phylloscopus trochilus*, that occur at relatively low densities along Dutch highways were also reported to be a juvenile subset of the population of potentially breeding males (Reijnen & Foppen 1994). Also, more reed buntings, *Emberiza schoeniclus*, remained unpaired at noisy than at more quiet lake shores in Switzerland (Gross et al. 2010).

Another indication of postsettlement impact on reproductive success was reported in a correlative study on great tits (Halfwerk et al. 2011a). In this study, spatial variation in noise levels independent of the proximity to the highway revealed a negative correlation between traffic noise levels and clutch size and fledgling success. This correlation could be due to a physiological impact on chick development (Kight & Swaddle 2011), or to an impact of

masking communication among parents and offspring (Halfwerk et al. 2012a; Leonard & Horn 2012). A recent study by Schroeder et al. (2012) on house sparrows also showed a negative correlation between clutch size, body weight, and recruitment rate and exposure to generator noise close to the nestboxes in which the sparrows were breeding. The results of this study suggest a direct effect of noise on female feeding rate and chick development through masking of parent–offspring communication.

Anthropogenic noise is generally biased in energy towards lower frequencies, and more traffic noise typically means more bias towards low frequencies (Lohr et al. 2003; Slabbekoorn & Peet 2003). An important factor for the severity of masking acoustic signals is the overlap in frequency range between background noise and the important signal components of songs (Klump 1996; Brumm & Slabbekoorn 2005; Pohl et al. 2012). The more overlap, the more interference from masking is expected. As bird species tend to vary in their species-specific signals, with respect to the frequency bandwidth as well as the absolute minimum frequency, the negative impact of noise will not be the same for all and is expected to be worse for those species that rely on relatively low frequencies (Rheindt 2003; Slabbekoorn & Peet 2003).

The advantage of singing high in urban compared to forested areas was calculated by Nemeth & Brumm (2010), who used empirical data on signal amplitude, species-specific frequency ranges, discrimination thresholds, habitat-dependent attenuation rates and typical noise level and spectra to arrive at maximum communication distances. They used great tits and European blackbirds as example species. Their results show that under urban conditions the relatively high-pitched great tit songs reach over a larger distance than the relatively low-pitched blackbird songs and that the situation is reversed under forested conditions. The effect of intraspecific variation was also addressed: high-frequency song variants also do better than low-frequency song variants, for both species, in urban habitat but not in forest habitat (Slabbekoorn et al. 2012). Birds can also sing louder under noisy urban conditions (Brumm 2004; Brumm & Slabbekoorn 2005; Brumm & Zollinger 2011), and singing higher may be associated with singing louder (Nemeth & Brumm 2010; Verzijden et al. 2010; but also see Cardoso & Atwell 2011), which would lead to even stronger improvements in communication distance under noisy conditions (Nemeth & Brumm 2010; Nemeth et al. 2012; Slabbekoorn et al. 2012).

Overall, it is clear from the studies reviewed above that we now have sufficient empirical data to state that anthropogenic noise can negatively affect avian distribution and reproduction. Furthermore, singing high in noisy urban environments could lead to signal and fitness advantages, at least theoretically, based on the physical properties of sound transmission and perception.

FREQUENCY-DEPENDENT NOISE IMPACT

Several monitoring studies have reported that finding correlations between noise levels and bird distributions can depend on species-specific frequency use (Rheindt 2003; Herrera-Montes & Aide 2011). Goodwin & Shriver (2011) compared, for example, the number of individual breeding territories present in 15 relatively noisy forest plots and in 15 relatively quiet forest plots in northern Virginia, U.S.A. Two out of the eight species in the analyses showed a significantly negative correlation between noise level and occupancy rate, and those were the two species with the lowest frequency songs, the yellow-billed cuckoo, *Coccyzus americanus*, and the white-breasted nuthatch, *Sitta carolinensis*. Another monitoring study in New Mexico (one of those in which noisy and quiet gas extraction stations were exploited) also showed frequency-dependent correlations between noise level and nesting activity and abundance data, with low-frequency singers such as black-

headed grosbeak, *Phaeucticus melanocephalus*, western tanager, *Piranga ludoviciana*, and the mourning dove, *Zenaida macroura*, most negatively affected by noise (Francis et al. 2011a).

A recent study in urban parks of Spain and Portugal also reported a significant effect of city traffic noise on the distribution of 25 out of 91 bird species (Paton et al. 2012). They found that rare birds were associated with quieter park sites and that common species were especially present in noisier sites. As a consequence, noise level was not correlated with overall diversity, as common species appeared where rare species disappeared. This is in line with the phenomenon of urban homogenization of avian communities and suggests that noise impact could contribute to the phenomenon. Although this study did not explicitly address species-specific song frequency ranges, low-frequency users such as the European turtle dove, *Streptopelia turtur*, and the lesser spotted woodpecker, *Dendrocopos minor*, were among the most heavily affected species. However, the goldcrest, *Regulus regulus*, a species with songs of very high frequency, also became less common in noisier park sites.

Hu & Cardoso (2009) analysed the correlation between species-specific frequency use and urban occurrence more explicitly in a large comparative data set of archived recordings for European, North American and Australian bird species. They tested within-genera comparisons of 529 bird species from 103 genera and found that both passerine and nonpasserine species occurring in urban environments generally vocalized at higher dominant frequencies than strictly nonurban species. For passerine genera that sing at relatively low frequencies, urban species also had higher minimum song frequencies than nonurban congeners. These results are in line with the expectation that species using relatively high frequencies are better preadapted to inhabit urban environments where anthropogenic noise is especially masking of low frequencies (cf. Rheindt 2003; Slabbekoorn & Ripmeester 2008).

Overall, comparisons at the species level are not always consistent, probably because of other confounding variables that may also be important. We also need more well-replicated studies, but there is certainly already enough comparative data to suggest that singing at high frequencies may contribute to success in urban and other noisy areas.

THE URBAN PHENOTYPE WITHIN SPECIES

A link between species-specific frequency use and urban occurrence across species, and song frequency-dependent correlations between noise level and variation in bird abundance within species do not tell anything yet about a potential role for behavioural plasticity. However, behavioural plasticity could come into the picture if birds are capable of changing their song frequency use depending on the noise conditions of their habitat. If this were the case, song frequencies should also vary within species between relatively quiet and more noisy habitat. Such habitat-dependent spectral song features attributed to habitat-dependent variation in noise profiles have long been known and are reported repeatedly for natural habitat types (e.g. Morton 1975; Ryan & Brenowitz 1985; Martens & Guldig 1988; Slabbekoorn & Smith 2002a; Brumm & Slater 2006; Dingle et al. 2008; Kirschel et al. 2009). Work on great tits, rapidly followed-up by work on other species, has now provided similar patterns for urban habitat.

Slabbekoorn & den Boer-Visser (2006) revealed a highly consistent pattern in 10 city–forest pairs of great tit populations across Europe. Population averages of the minimum song frequency were consistently higher in noisy cities than in more quiet forest habitat nearby. Furthermore, in an earlier paper, Slabbekoorn & Peet (2003) found that individual averages of minimum frequency in songs of a single population of urban great tits were

correlated with local noise levels in the individual territories. Birds in relatively noisy territories sang with relatively high minimum frequencies. This correlative finding has now been replicated several times in this same species in Great Britain, Spain and Japan (Mockford & Marshall 2009; Salaberria & Gil 2010; Hamao et al. 2011) and in a growing number of other common urban species on almost all continents (e.g. European blackbirds in Europe: Nemeth & Brumm 2009; Ripmeester et al. 2010a; Chinese bulbuls, *Pycnonotus sinensis*, in Asia: Han et al. 2004; song sparrows, *Melospiza melodia*, in North America: Wood & Yezerinac 2006; rufous-collared sparrows, *Zonotrichia capensis*, in South America: Laiolo 2011; silvereyes, *Zosterops lateralis*, in Australia: Potvin et al. 2011).

An interesting study on urban white-crowned sparrows, *Zonotrichia leucophrys*, in San Francisco found no noise-dependent frequency shifts in space but did find noise-dependent frequency shifts in time (Luther & Baptista 2010; Luther & Derryberry 2012). City noise measurements confirmed a significant rise of decibel levels between assessments in 1972 and 2008, attributable to an increase in car traffic. Comparisons between historical birdsong recordings of 1969 and recent recordings in the same urban neighbourhoods in 2005 revealed significant upward shifts for minimum and dominant song frequencies. Although this comparison should be considered an unreplicated case study, because variables other than noise level may have changed over time, the findings are in line with the expectations for an effect of noise-dependent masking on song evolution. Playback results indicated that the differences between historical and recent recordings, including the spectral changes potentially driven by masking traffic noise, were biologically relevant. Songs sung 36 years ago triggered lower response levels than the songs sung just a few years ago (Luther & Derryberry 2012). These playback results are congruent with effects on response levels for current spatial variation among urban and forest populations of great tits (Mockford & Marshall 2009) and European blackbirds (Ripmeester et al. 2010b).

Parris & Schneider (2009) compared two Australian species and revealed that not all species show the now familiar pattern of noise-dependent spectral change. They found that the dominant frequency of the lowest note in the song of the grey shrike-thrush, *Colluricincla harmonica*, was positively correlated with noise levels in 58 different roadside sampling sites, but this was not the case in the grey fantail, *Rhipidura fuliginosa*. The latter uses an overall higher frequency bandwidth for its song, and the difference between these two species is therefore in line with a larger need for a shift in species with lower frequency ranges and consequently more overlap with traffic noise. Dowling et al. (2012) reported data in line with this on six bird species in 28 sites across an urban–rural gradient in North America; species with lower-frequency songs showed a larger noise-dependent upward shift. Furthermore, Hu & Cardoso (2010) analysed a set with 12 other Australian bird species, and their analysis suggested that only mid-frequency singers with minimum frequencies between 1 and 2 kHz showed noise-dependent spectral shifts, while species singing at high and very low spectral ranges did not.

Another case study on a species pair linked the presence of a noise-dependent spectral shift to distribution patterns for two North American (suboscine) bird species. Francis et al. (2011b) reported suggestive correlations between noise level, song frequency and occupancy rates at noisy and quiet gas extraction stations, again at their study site in New Mexico. The grey flycatcher, *Empidonax wrightii*, showed no noise-dependent song frequency shift, but occupancy declined for this species at noisy sites. In contrast, the ash-throated flycatcher, *Myiarchus cinerascens*, did reveal a noise-dependent rise in song frequency, and occupancy rate remained unaffected by noise for this species. This study

concerned just two species, but it emphasizes the possibility that behavioural flexibility in terms of frequency adjustments may well play a critical role in reducing noise impact on bird breeding distributions.

Overall, many correlative studies on individual birds of the same species provide evidence for a widespread link between ambient noise and song frequency use. This could mean that singing at high frequencies, or at least reducing the use of low frequencies that are masked more by traffic noise, may provide signalling and fitness benefits in noisy urban areas. This hypothesis could be tested through an analysis of the link between detrimental noise impact and noise-dependent spectral flexibility in species pairs, such as in the flycatcher study addressed above (Francis et al. 2011b), but then replicated at the species level.

THE EXPERIMENTAL APPROACH

Noise-associated variation among individuals of the same species in the context of evolutionarily recent phenomena such as noisy urban habitat and gas wells with noisy compressors, strongly suggests behavioural plasticity as the underlying mechanism for urban phenotypes of increased frequency (Slabbekoorn & Peet 2003; Patricelli & Blickley 2006). A recent comparative study in cities of Brazil and Mexico revealed again a strong correlation between song frequency and noise levels, but especially for oscine species that learn their song through social experience (Rios-Chelén et al. 2012). Furthermore, species with more divergent song frequencies among populations also showed tighter correlations, suggesting that learning ability and song plasticity are critical features in explaining noise-dependent spectral variation. However, only experimental data can provide solid evidence for the apparent noise-dependent plastic response and elucidate more about the temporal scale at which the noise-dependent patterns can emerge. Several studies have now experimentally exposed singing birds to elevated noise levels (Slabbekoorn 2012). These experimental studies have revealed individual capacities for rapid spectral changes, which are of the order of magnitude of observational studies (e.g. Gross et al. 2010; Verzijden et al. 2010; Hanna et al. 2011; Montague et al. 2012). Interestingly, the underlying mechanism explaining the experimentally induced spectral changes turns out to vary per species (Fig. 2).

Halfwerk & Slabbekoorn (2009) exposed great tits to city-like, low-frequency noise while they were singing in their natural territories. Males of this species have a repertoire of song types consisting of notes that vary considerably in frequency. There were no differences in frequency of the same song type before and during noise exposure, but there was significant variation in the persistence of using particular song types during and after the 4 min noise exposure depending on the spectral overlap between the signal and the noise. High-frequency song types were used for longer durations than low-frequency song types in the urban noise treatment. These results revealed that a temporal adjustment in song type switching behaviour can yield noise-dependent spectral variation and that it involves a phenomenon of individual flexibility that could explain patterns of noise-dependent song variation among individuals and among populations (Slabbekoorn & Peet 2003; Slabbekoorn & den Boer-Visser 2006, respectively).

Another experimental exposure study tested whether and how house finches, *Carpodacus mexicanus*, can modulate the minimum frequency of their songs in response to fluctuating noise levels (Bermudez-Cuamatzin et al. 2010). Males of this species sing stereotypic strings of different syllables, warbling up and down in frequency, with repeatedly identifiable individual syllable types. Bermudez-Cuamatzin et al. recorded songs of caged males, which were stimulated to sing by a nearby female in another cage,

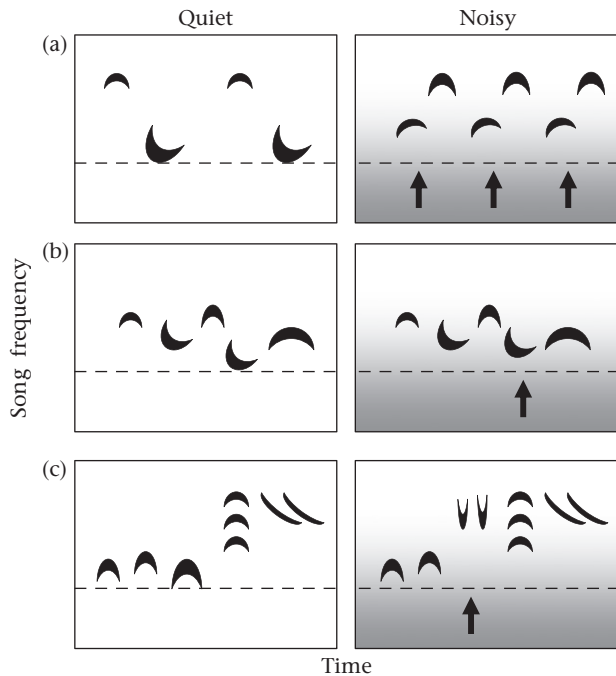


Figure 2. Examples of noise-dependent frequency use in schematic sonagrams illustrating three ways in which song changes can yield upward shifts in frequency. (a) Great tits under noisy urban conditions switch more quickly from repeating a relatively low-frequency song type (left) than from repeating a relatively high-frequency song type to repeating another song type from their repertoire (Halfwerk & Slabbekoorn 2009), which has a certain probability to be one of higher minimum frequency (right). (b) House finches under noisy urban conditions sing their lowest-frequency song elements at higher frequencies (right) compared to when they sing in more quiet conditions (left), which elevates the minimum frequency for the whole song (Bermudez-Cuamatzin et al. 2010). (c) European blackbirds in relatively quiet forest habitat sing songs with relatively long low-frequency motif parts (left), while in more noisy urban habitat they sing songs with relatively long high-frequency twitter parts (right). A larger twitter proportion under noisy conditions yields an upward spectral energy shift in urban songs (Ripmeester et al. 2010a, 2010b). Dashed lines indicate the minimum frequency of the songs on the left sung in relative quiet to make the upward shift under noisy conditions in the songs on the right visible. Positions in the songs where the upward spectral shift is visible are indicated by arrows. The fading gradient in grey indicates the sound energy distribution of anthropogenic noise.

during low and high noise levels. They found a significant noise-dependent increase in minimum song frequencies, like in great tits, but in this case due to the same low-frequency syllable types sung at different frequencies in different treatments. The results are congruent with their earlier observational findings in which they found a positive correlation between noise level and song frequencies of shared syllable types among individuals of the same song theme neighbourhood residing in more or less noisy territories (Bermudez-Cuamatzin et al. 2009).

These two experimental studies on great tits and house finches clearly show that individual birds, albeit in very different ways, have the capacity to change spectral song features within a matter of minutes. The two independent studies also both provide explicit links between individual flexibility and urban song variation in the observational data of earlier studies on the same model species. The almost immediate spectral changes could indeed explain noise-dependent variation among individuals and populations (cf. Slabbekoorn & Smith 2002b; Ripmeester et al. 2010a). However, this does not mean that we can exclude contributions of plasticity at other timescales. While the rapid noise-dependent changes by individuals can be regarded as context-dependent plasticity (cf. Snell-Rood this issue), the observed patterns of song variation in the field may also be affected by developmental plasticity and cultural evolution (cf. Hansen 1979; and see Slabbekoorn & Smith

2002b; Podos et al. 2004). In the next section, I will address the various levels at which behavioural plasticity may affect song variation in the field by using the great tit as a model species. Although the great tit is one of the best-studied species in terms of acoustics, be aware that much of the following will include speculation awaiting empirical tests.

PLASTICITY AND CULTURAL ASSIMILATION

The available data on great tits provide a start to get a better understanding of the phenomenon of high-frequency urban phenotypes in birdsong. Great tit males sing a repertoire of song types that is acquired from conspecific males heard during or after dispersal, predominantly early in life. Although it is unclear the extent to which they remain sensitive to acquisition and accurate imitation of newly heard song types later in life, they adjust acoustically to neighbours during territory establishment and when new males turn up later in subsequent years (McGregor & Krebs 1982, 1989). How often male great tits sing each of the different song types that are available within their more or less crystallized repertoires varies with social context (Franco & Slabbekoorn 2009) and the phase in the breeding cycle (Halfwerk et al. 2011b) (see Fig. 3a, b). Similarly, individual differences in song frequency use associated with ambient noise level could be attributable to temporal adjustment of song type switching (Halfwerk & Slabbekoorn 2009), leading to spectrally divergent use of similar

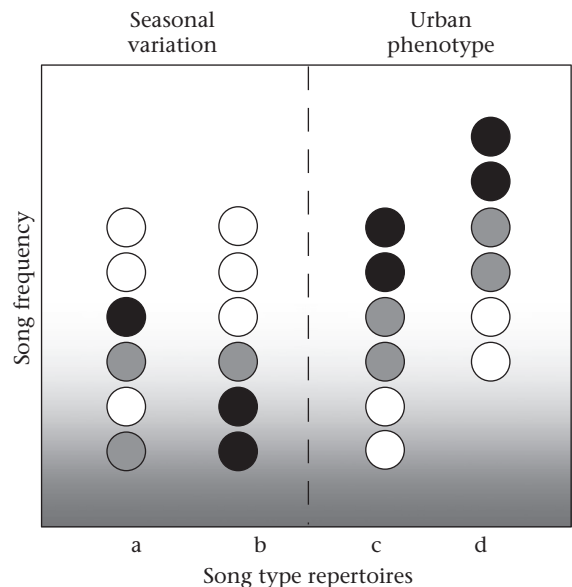


Figure 3. Schematic illustration of behavioural plasticity of the acoustic phenotype through variation in song repertoire use. Circles reflect song type repertoires of individual birds (a, b, c, d), each with six song types of varying frequency. The occurrence of each song type in each individual's repertoire is indicated by black (often), grey (occasionally) or white (rarely). The two examples on the left illustrate seasonal variation for the same individual; song types of the same frequency range are sung at different rates, leading to different weighted frequencies (Halfwerk et al. 2011b). Example (a) reflects the repertoire use well before or well after the egg-laying phase and (b) reflects the repertoire use right before egg laying during the fertile period. The two examples on the right illustrate variation for (c) an individual switching away from singing the lowest-frequency song types (Halfwerk & Slabbekoorn 2009) under noisy urban conditions and (d) another individual also predominantly singing its highest-frequency song types through continuous environmental induction by noise as well as by social feedback from neighbours. The individual in (d) also incorporated new song types beyond the traditional frequency range (speculating about a mechanism for changes in song over time). The fading gradient in grey represents again the sound energy distribution of anthropogenic noise. According to the hypothesized trade-off between being attractive or being heard well, male (b) would do well in terms of female fidelity, but badly in terms of masking. Male (c) and (d) would do badly in terms of female fidelity, but well in terms of masking avoidance.

repertoires (Fig. 3c). In this way, consistently induced singing of high-frequency song types under noisy urban conditions could lead to a situation in which only a subset of potential song types is predominantly heard in cities (i.e. due to context-dependent plasticity).

Individuals may not only sing high-frequency song types more often under noisy urban conditions, but urban and forest populations (cf. Slabbekoorn & den Boer-Visser 2006) may diverge further because an increasing number of individuals may include high-frequency song types in their repertoire. This impact of developmental plasticity may result from selective copying due to a numerical bias in song types heard during vocal interactions among conspecifics of the neighbourhood (Nordby et al. 2000; Beecher et al. 2007) or by the qualitative bias in song types heard well enough after being degraded by transmission and while being (partly) masked by ambient noise (Hansen 1979; Morton et al. 1986; Peters et al. 2012). Once more males share more high-frequency song types they will also use these more often in so-called matched countersinging (McGregor et al. 1992). Together, these processes could be referred to as cultural assimilation analogous to genetic assimilation in which a phenotypic character, initially popping up only in response to some environmental influence, becomes taken over by the genotype (or in this case becomes dominant in the local pool of song types), so that it starts to appear also in the absence of the environmental influence that had at first been necessary (Waddington 1961; West-Eberhard 2003).

The context-dependent plasticity and cultural assimilation discussed above can explain cultural evolution among populations (Slabbekoorn & Smith 2002b; Ripmeester et al. 2010a). Cultural assimilation, like genetic assimilation, should typically lead to contraction of realized variance (as a subset of all possible songs will become dominantly present at the expense of others), and could potentially lead to restrictions on plasticity. However, very much in the same way as described for the so-called Baldwin effect (Baldwin 1902), noise-dependent use and copying of learned song type repertoires could also drive variation beyond traditional limits (Wcislo 1989; West-Eberhard 2003). New song types likely emerge, also in great tits, through a process of copying errors, recombination and improvisation (e.g. Baptista 1977; Ince et al. 1980; Marler & Peters 1982; Payne 1996; Slabbekoorn et al. 2003). Therefore, frequency characteristics of new song types may have a probability to be extreme depending on the population-specific spectrum, which comprises the spectra of all individual birds singing the current song types in that population. Consequently, new extremes at the high-frequency end may be more likely to appear in cities, as the urban songs may involve a smaller subset of the total but also a subset closer to the upper frequency limits. Such new song types may readily become culturally assimilated under positive selection of noisy urban conditions and yield further divergence of urban populations beyond previous frequency range limits (see Fig. 3d).

The spectral plasticity of urban song through selective repertoire use and selective song learning might be a pre-existing trait evolved to adjust to previous environmental unpredictability (cf. Mery & Burns 2010; Frank 2011; Sih *this issue*). This may concern unpredictability in terms of male song neighbourhoods or female preferences (Nottebohm 1972; Payne 1982; Aoki 1989; but also see Lachlan & Slater 1999), or the natural heterogeneity in space and time of acoustic conditions for signal transmission and interference (Hansen 1979; Slabbekoorn & Smith 2002b; Peters et al. 2012). Accidental preadaptation or not, the spectral variation with varying urban noise conditions can be regarded as a typical reaction norm, and such plasticity may by itself not come without costs and constraints (see e.g. DeWitt et al. 1998), but should largely prevent habitat-dependent selection on genetically determined components of acoustic signal development (e.g. Pigliucci 2001; Lande 2009). Song types that may be useless and

thereby detrimental under some environmental condition will not yield a selective burden to the singer if they can be avoided at no expense by exchanging them flexibly with another, better song type. Nevertheless, phenotypic divergence in spectral measures beyond previous limits due to cultural evolution could be a case in which the environment affects which phenotypes are exposed to selection (West-Eberhard 1989; Price et al. 2003). Therefore, cultural evolution may also drive selection on the genetic basis for variation in the underlying cognitive, morphological or physiological capacities that allow birds to sing those new song types, including extreme frequencies or with extreme upward shifts. In this way genotypic changes may follow environmentally induced phenotypic changes (cf. West-Eberhard 2003; Ghalambor et al. 2007). Consequently, population divergence in realized variation due to the environmental selection in combination with behavioural plasticity may eventually lead to population divergence in potential variation (Slabbekoorn & Smith 2002b; Podos et al. 2004).

FITNESS AND PERCEPTUAL BENEFITS

The widespread occurrence of noise-dependent geographical distribution patterns among and within species could mean that singing higher may yield fitness benefits in noisy cities and, as explained above, behavioural plasticity may contribute to cultural and eventually genetic evolution of song frequency use in city birds. Such behavioural plasticity and contemporary evolution may in this way contribute to the chances of species survival in cases of rapid environmental change in new or altered habitat (Baldwin 1902; Robinson & Dukas 1999; Stockwell et al. 2003; Frank 2011). However, the empirical evidence for actual fitness benefits of individual city birds that sing higher compared to those that do not is still largely lacking, and there may be perceptual benefits as well as costs that need to be incorporated into calculations of adaptive value (Crispo et al. 2010; Nemeth et al. 2012; Snell-Rood 2012; Slabbekoorn et al. 2012).

Although not directly translatable to fitness, there is empirical evidence for perceptual advantages of singing relatively high under noisy urban conditions. Laboratory studies have shown that species are typically well adapted to extract conspecific sounds from a background of natural noise sources (e.g. Brémond 1978; Hulse 2002) as well as from a background of anthropogenic noise (Lohr et al. 2003; Pohl et al. 2009, 2012). Great tits show remarkable perceptual plasticity in how they use different signal features in different noise conditions. While discrimination among different song types in woodland noise is based on aspects of the whole song, including the high-frequency elements, discrimination in urban noise relies entirely on features of the high-frequency elements (Pohl et al. 2012). Nevertheless, signal perception in general is negatively affected by anthropogenic noise, especially by the higher noise energy levels at relatively low frequency (Lohr et al. 2003; Pohl et al. 2009, 2012). In line with the theoretical expectations, Pohl et al. (2012) provided a proof of principle for the perceptual advantage through masking avoidance for relatively high-frequency song variants. Songs artificially shifted to higher frequencies were easier to detect under urban noise conditions than the same songs shifted to lower frequencies, which was not the case under woodland noise conditions.

Very similar perceptual results were found for a study under more natural conditions in which incubating female great tits were triggered to emerge from their nestbox by playback of unmanipulated male songs (Halfwerk et al. 2011b). Females were tested with high-frequency and low-frequency song types from the repertoires of their own mates, with and without experimental exposure to typical traffic noise spectra. There was no significant noise-dependent decline in the response to the high-frequency song

types while the response to low-frequency song types dropped almost to zero during the noise treatment. Only during the exposure to low-frequency noise, and not under the natural ambient conditions of the forest, female great tits emerged significantly more often in response to playback of high-frequency song types than in response to playback of low-frequency song types.

The experimental evidence for a noise-induced reduction in signal efficiency dependent on the frequency of the song type (Halfwerk et al. 2011b) does not prove but does suggest that effects on reproductive success (Halfwerk et al. 2011a) could be attributed to a masking impact on parent–offspring communication (cf. Schroeder et al. 2012). Unfortunately, there were no data available on song repertoires for the long-term data set that could have revealed a frequency-dependent effect of male song on reproductive success (Halfwerk et al. 2011a). It was recently shown, however, in another hole-nesting species, the North American tree swallow, *Tachycineta bicolor*, that elevated noise levels can yield an increase in the number of missed detections by the nestling birds (Leonard & Horn 2012). This finding shows that begging behaviour can be less efficient in noisy than in quieter environments, but also less efficient for low-frequency songs than for high-frequency songs in noisy urban areas.

SPECTRAL COMPROMISE ON SIGNAL FUNCTION

Importantly, the perceptual advantage of singing high may have to be traded off by the male great tits against a functional advantage of singing low (Slabbekoorn & Ripmeester 2008; Gross et al. 2010). Halfwerk et al. (2011b) found that male great tits vary in weighted song frequency (i.e. taking into account both the composition of the repertoire and the rate at which each song type of varying frequency was actually sung). Male great tits varied in this frequency measure among individuals but also within individuals, with the lowest-frequency performance in the days of brood fertilization right before egg laying. Furthermore, it turned out that female fidelity was related to the male's spectral performance in these important days of the breeding cycle. Males with extrapair young in their nest had higher weighted frequencies and had not shifted to singing their lowest song types more often, as was done by the noncuckolded males.

Although we obviously still lack the complete picture of male reproductive success in great tits (Eens et al. 2012), the results of Halfwerk et al. (2011b) suggest a potential frequency-dependent reproductive drain for birds that sing high-frequency song types during elevated noise levels in urban areas (Halfwerk et al. 2012b). Birds under noisy conditions may be faced with a 'choice' between singing high and being heard well or singing low and being liked better (Slabbekoorn & Ripmeester 2008). This hypothesis requires further testing, and it would, for example, be nice to find out whether spectral measures signal any male quality trait in great tits (see e.g. ten Cate et al. 2002; Gil & Gahr 2002; Cardoso 2012; Linhart et al. 2012), or whether variation in female fidelity can be explained by transmission benefits of the low-frequency song types into nestboxes (Blumenrath et al. 2004; Halfwerk et al. 2012a). Nevertheless, the point is that we need to confirm not only that masking release leads to fitness benefits, but also that there are no extra costs to noise-dependent frequency use due to some sort of functional compromise. The potentially maladaptive side of spectral adjustments is likely to vary per species and with the underlying mechanism for spectral change (Fig. 2).

URBAN ANGER

Another example of functional compromise may be the European blackbird, which also sings higher in noisy urban habitat than

in more quiet forest or rural areas (Nemeth & Brumm 2009; Ripmeester et al. 2010a, b; Mendes et al. 2011). This species has a very large repertoire of syllables that features a highly variable series of songs with so-called immediate variety (i.e. two subsequent songs are never the same; Dabelsteen 1984; Ripmeester et al. 2007). However, each song starts with a low-frequency motif followed by a twitter, which is of higher frequency and wider bandwidth. Urban males show an increase in the peak frequency of the low-frequency motif at the population level, but also show a shift to a proportionally longer, high-frequency twitter (Fig. 4). Although experimental exposure data is still lacking for this species, the flexible duration of the twitter relative to the duration of the whole song could be another example of a mechanism by which temporal song adjustment can lead to a noise-dependent spectral shift (Fig. 2c). The potential advantage of masking release, however, could yield a compromise on the song function of motivational signalling.

Spectral features have been found to vary with context in several species and can play a critical role in acoustic mediation of conflicts (e.g. DuBois et al. 2009; Searcy & Beecher 2009; Linhart et al. 2012). In European blackbirds, the relative duration of the two parts has been related to signalling aggression (Dabelsteen 1984; Dabelsteen & Pedersen 1990); more agitated birds sing longer twitters and playback of songs with relatively long twitter parts also trigger stronger responses than songs with relatively short twitter parts (but also see Ripmeester et al. 2007). Congruently, higher territorial densities, associated with a larger number of vocally interacting males per territory, have been found to correlate with an increase in duration of the twitter proportions (Ripmeester et al. 2010a; also see Hamao et al. 2011).

As territory densities are typically higher in urban than in forest populations of the European blackbirds, higher twitter proportions were expected in urban birds with more neighbours. However, on

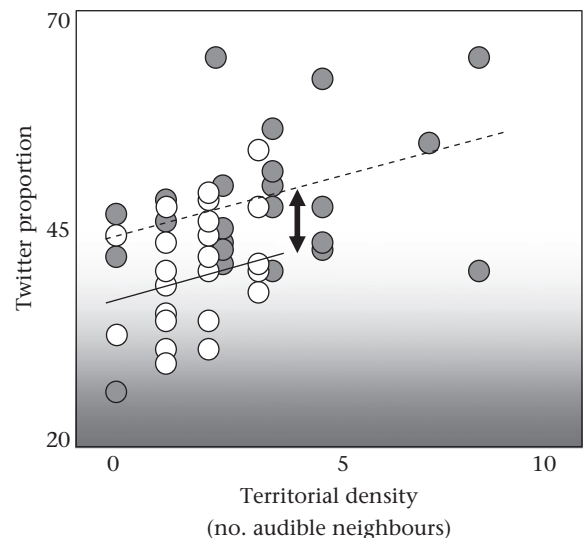


Figure 4. Variation in the proportion of the high-frequency twitter part in blackbird song in the noisy urban habitat of the city of Leiden (filled circles) and the nearby, relatively quiet forest habitat of Meijendel (open circles). The fading gradient in grey represents again the sound energy distribution of anthropogenic noise. The twitter proportion is positively correlated with territorial density in terms of the number of audible neighbouring competitors (dotted and solid lines show the regression lines for the urban and forest sites, respectively). The range of territorial density extends further upward with more audible neighbours for the urban habitat, and, on top of that, there is an additional shift towards a larger twitter part in the city independent of territory density (from Ripmeester et al. 2010a). This shift, indicated by the double arrow, is referred to in the text as potentially noise-induced, and culturally assimilated, 'urban anger'.

top of the density-related correlation, Ripmeester et al. (2010a) found songs of urban birds in the city of Leiden to exhibit an additional shift towards longer twitter parts compared to songs from a nearby forest for territories at equal densities (Fig. 4). The generality of this pattern needs to be tested by sampling a replicate set of other cities, but if this shift were to be explained by noise-dependent adjustment through environmental induction and cultural assimilation of relatively large twitter proportions, traffic noise may be responsible for some kind of 'urban anger' in the average song frequency use. Perceptual consequences in urban birds remain to be tested, but the urban anger may affect the efficiency of the flexible twitter proportion in mediating territorial interactions or attracting mates with potentially negative consequences for individual fitness. Consequently, singing high and being aggressive or bold could be good or bad for city life (cf. Møller 2010; Atwell et al. 2012; Sih 2012). There are also examples of other bird species, with a reported song frequency-noise level correlation (Wood & Yezerinac 2006; Slabbekoorn et al. 2007) that also appear more (Evans et al. 2010; Scales et al. 2011) or less aggressive (Newman et al. 2006) in urban than in nonurban populations. We obviously need more integrated studies for a better understanding of the potentially complex relationships among increased song frequency use, masking release, levels of aggression and urban success (see e.g. Bonier 2012; Fokidis & Deviche 2012).

CONCLUDING REMARKS

It has become clear that anthropogenic noise can negatively affect the distribution and reproduction of birds, and we have only started to get an idea about the complexity of noise impact on avian communities (Slabbekoorn & Halfwerk 2009; Francis et al. 2012). Furthermore, frequency-dependent patterns in urban bird distributions among species and frequency-dependent geographical variation at the population and individual level within species point to a masking-related impact from low-frequency noise. Rapid upward shifts in song frequency use during experimental exposure indicate that the apparently widespread urban phenotype with increased-frequency song is at least partly due to behavioural plasticity. The perceptual studies in the laboratory and the field on great tits confirm a differential impact of high- and low-frequency song types on communication to the female partner under noisy urban conditions. However, direct evidence of fitness benefits of spectral plasticity in city environments is not yet available for any bird species. Furthermore, there may also be costs involved because of spectral compromises on signal function, which will vary between species and the species-specific behavioural mechanisms underlying spectral change.

As in any field, there is also reason for methodological concern in noise-impact studies and I would like to call attention here to the scientific rigour that we should aim for in terms of experimental design and data interpretation (cf. Hurlbert 1984; Kroodsma 1989; Slabbekoorn & Bouton 2008). As stated before, many of the investigations into noise impact on birdsong concern correlational studies that inherently lack the capacity to prove causal relationships. Patterns are useful and may provide ideas and stimulate speculation. However, experimental investigations, which have started to appear in this field in the last few years, are required to prove underlying mechanisms or behavioural consequences that may affect fitness (e.g. Halfwerk & Slabbekoorn 2009; Blickley et al. 2012). Note that correlational data on noise impact collected in urban and rural areas are inherently confounded by many factors other than ambient noise that exist between these habitat types and their avian inhabitants. The studies on noisy and quiet gas extraction stations in Canada and New Mexico are excellent examples of how this problem can be circumvented (e.g. Bayne et al. 2008; Francis et al. 2009).

Another major concern is that many studies lack proper replication. Comparisons at the population or habitat level should not rely on the number of individuals sampled at one site in each category, but should be replicated with samples across multiple independent sites in both categories (cf. Slabbekoorn & den Boer-Visser 2006; Mockford & Marshall 2009). Without proper replication, we can only report suggestive data for a particular case, but we certainly do not prove the existence of the reported correlations as general patterns. Although this is true for any type of data, including morphology and physiology, it is especially true for birdsong. Given the dialectal character of learned song, acoustic differences between birds at any two sites are to be expected and should not be interpreted as evidence for being related to environmental acoustics without proper replication at the appropriate level.

Many case studies together may still contribute to the credibility of a hypothesis, but it is better to properly match the sampling design to the target question within any particular study planned for the future. And indeed, more studies are required, for example on fitness benefits and costs, which concerns only two of many avenues for future investigations. Urban birdsong has emerged over the last 10 years as an excellent model system to investigate, and speculate about, fundamental processes such as causes and consequences of environmentally induced signal changes, cultural assimilation, and the relationship between phenotypic and genotypic evolution. The model system is likely to continue to flourish as the field is still growing with respect to progress in methodology (e.g. Verzijden et al. 2010; Slabbekoorn 2012; Zollinger et al. 2012) as well as in the number of research groups interested, the taxonomic spread and the variety of disciplines involved (e.g. Barber et al. 2009; Slabbekoorn et al. 2010; Herrera-Montes & Aide 2011; Kight & Swaddle 2011; Pijanowski et al. 2011; Bonier 2012; Francis & Blickley 2012; Montague et al. 2012). I especially hope that the urban bird work continues to raise awareness and that more insights will generate applied value for noise management and mitigation in urban planning and avian conservation.

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References

- Aoki, K. 1989. A sexual-selection model for the evolution of imitative learning of song in polygynous birds. *American Naturalist*, **134**, 599–612.
- Arevalo, E. J. & Newhard, K. 2011. Traffic noise affects forest bird species in a protected tropical forest. *Revista de Biología Tropical*, **59**, 969–980.
- Atwell, J. W., Cardoso, G. C., Whittaker, D. J., Campbell-Nelson, S., Robertson, K. W. & Ketterson, E. D. 2012. Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. *Behavioral Ecology*, **23**, 960–969.
- Baldwin, J. M. 1902. *Development and Evolution*. New York: Macmillan.
- Baptista, L. F. 1977. Geographic variation in song and dialects of the Puget Sound white-crowned sparrow, *Zonotrichia leucophrys pugetensis*. *Condor*, **79**, 356–370.
- Barber, J. R., Crooks, K. R. & Fristrup, K. M. 2009. The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution*, **25**, 180–189.

- Bayne, E. M., Habib, L. & Boutin, S. 2008. Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal Forest. *Conservation Biology*, **22**, 1186–1193.
- Beecher, M. D., Burt, J. M., O'Loghlen, A. L., Templeton, C. N. & Campbell, S. E. 2007. Bird song learning in an eavesdropping context. *Animal Behaviour*, **73**, 929–935.
- Belant, J. L. 1997. Gulls in urban environments: landscape-level management to reduce conflict. *Landscape and Urban Planning*, **38**, 245–258.
- Bermudez-Cuamatzin, E., Ríos-Chelén, A. A., Gil, D. & García, C. M. 2009. Strategies of song adaptation to urban noise in the house finch: syllable pitch plasticity or differential syllable use? *Behaviour*, **146**, 1269–1286.
- Bermudez-Cuamatzin, E., Ríos-Chelén, A. A., Gil, D. & García, C. M. 2010. Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird. *Biology Letters*, **7**, 36–38.
- Blickley, J. L., Blackwood, D. & Patricelli, G. L. 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. *Conservation Biology*, **26**, 461–471.
- Blumenrath, S. H., Dabelsteen, T. & Pedersen, S. B. 2004. Being inside nest boxes: does it complicate the receiving conditions for great tit *Parus major* females? *Bioacoustics*, **14**, 209–223.
- Bonier, F. 2012. Hormones in the city: endocrine ecology of urban birds. *Hormones and Behaviour*, **61**, 763–772.
- Bonier, F., Martin, P. & Wingfield, J. C. 2007. Urban birds have broader environmental tolerance. *Biology Letters*, **3**, 670–673.
- Brémond, J. C. 1978. Acoustic competition between the song of the wren (*Troglodytes troglodytes*) and the songs of other species. *Behaviour*, **65**, 89–97.
- Brumm, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. *Journal of Animal Ecology*, **73**, 434–440.
- Brumm, H. & Slabbekoorn, H. 2005. Acoustic communication in noise. *Advances in the Study of Behavior*, **35**, 151–209.
- Brumm, H. & Slater, P. J. B. 2006. Ambient noise, motor fatigue, and serial redundancy in chaffinch song. *Behavioral Ecology and Sociobiology*, **60**, 475–481.
- Brumm, H. & Zollinger, S. A. 2011. The evolution of the Lombard effect: 100 years of psychoacoustic research. *Behaviour*, **148**, 1173–1198.
- Cardoso, G. C. 2012. Paradoxical calls: the opposite signaling role of sound frequency across bird species. *Behavioral Ecology*, **23**, 237–241. <http://dx.doi.org/10.1093/beheco/arr202>.
- Cardoso, G. C. & Atwell, J. W. 2011. On the relation between loudness and the increased song frequency of urban birds. *Animal Behaviour*, **82**, 831–836.
- Chace, J. F. & Walsh, J. J. 2006. Urban effects on native avifauna: a review. *Landscape and Urban Planning*, **74**, 46–69.
- Clergeau, P., Croci, S., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L. & Dinetti, M. 2006. Avifauna homogenization by urbanization: analysis at different European latitudes. *Biological Conservation*, **127**, 336–344.
- Crispo, E., Di Battista, J. D., Correa, C., Thibert-Plante, X., McKellar, A. E., Schwartz, A. K., Berner, D., De Leon, L. F. & Hendry, A. P. 2010. The evolution of phenotypic plasticity in response to anthropogenic disturbance. *Evolutionary Ecology Research*, **12**, 47–66.
- Croci, S., Butet, A. & Clergeau, P. 2008. Does urbanization filter birds on the basis of their biological traits? *Condor*, **110**, 223–240.
- Dabelsteen, T. 1984. An analysis of the full song of the blackbird *Turdus merula* with respect to message coding and adaptations for acoustic communication. *Ornis Scandinavica*, **15**, 227–239.
- Dabelsteen, T. & Pedersen, S. B. 1990. Song and information about aggressive responses of blackbirds, *Turdus merula*: evidence from interactive playback experiments with territory owners. *Animal Behaviour*, **40**, 1158–1168.
- Devictor, V., Julliard, R., Couvet, D., Lee, A. & Jiguet, F. 2007. Functional homogenization effect of urbanization on bird communities. *Conservation Biology*, **21**, 741–751.
- DeWitt, T. J., Sih, A. & Wilson, D. S. 1998. Costs and limits to benefits as constraints on the evolution of phenotypic plasticity. *Trends in Ecology & Evolution*, **13**, 77–81.
- Dingle, C., Halfwerk, W. & Slabbekoorn, H. 2008. Habitat-dependent song divergence at subspecies level in the grey-breasted wood-wren. *Journal of Evolutionary Biology*, **21**, 1079–1089.
- Dowling, J. L., Luther, D. A. & Marra, P. P. 2012. Comparative effects of urban development and anthropogenic noise on bird songs. *Behavioral Ecology*, **23**, 201–209.
- DuBois, A. L., Nowicki, S. & Searcy, W. A. 2009. Swamp sparrows modulate vocal performance in an aggressive context. *Biology Letters*, **5**, 163–165.
- Eens, M., Rivera-Gutierrez, H. F. & Pinxten, R. 2012. Are low-frequency songs sexually selected, and do they lose their potency in male–female interactions under noisy conditions? *Proceedings of the National Academy of Sciences, U.S.A.*, **109**, e208. <http://dx.doi.org/10.1073/pnas.1119570109>.
- Evans, J., Boudreau, K. & Hyman, J. 2010. Behavioural syndromes in urban and rural populations of song sparrows. *Ethology*, **116**, 588–595.
- Evans, K. L., Chamberlain, D. E., Hatchwell, B. J., Gregory, R. D. & Gaston, K. J. 2011. What makes an urban bird? *Global Change Biology*, **17**, 32–44.
- Faeth, S. H., Warren, P. S., Shochat, E. & Marussich, W. A. 2005. Trophic dynamics in urban communities. *Bioscience*, **55**, 399–407.
- Fahrig, L. & Rytwinski, T. 2009. Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and Society*, **14**, 21.
- Fokidis, H. B. & Deviche, P. 2012. Brain arginine vasotocin immunoreactivity differs between urban and desert curve-billed thrashers, *Toxostoma curvirostre*: relationships with territoriality and stress physiology. *Brain, Behavior and Evolution*, **79**, 84–97.
- Francis, C. D. & Blickley, J. L. 2012. Introduction: research and perspectives on the study of anthropogenic noise and birds. *Ornithological Monographs*, **74**, 1–5.
- Francis, C. D., Ortega, C. P. & Cruz, A. 2009. Cumulative consequences of noise pollution: noise changes avian communities and species interactions. *Current Biology*, **19**, 1415–1419.
- Francis, C. D., Ortega, C. P. & Cruz, A. 2011a. Noise pollution filters bird communities based on vocal frequency. *PLoS One*, **6**, e27052.
- Francis, C. D., Ortega, C. P. & Cruz, A. 2011b. Vocal frequency change reflects different responses to anthropogenic noise in two subspecies tyrant flycatchers. *Proceedings of the Royal Society B*, **278**, 2025–2031.
- Francis, C. D., Keist, N. J., Ortega, C. P. & Cruz, A. 2012. Noise pollution alters ecological services: enhanced pollination and disrupted seed dispersal. *Proceedings of the Royal Society B*, **279**, 2727–2735.
- Francis, R. A. & Chadwick, M. A. 2012. What makes a species synurbic? *Applied Geography*, **32**, 514–521.
- Franco, P. & Slabbekoorn, H. 2009. Repertoire size and composition in great tits: a flexibility test using playbacks. *Animal Behaviour*, **77**, 261–269.
- Frank, S. A. 2011. Natural selection. II. Developmental variability and evolutionary rate. *Journal of Evolutionary Biology*, **24**, 2310–2320.
- Ghalambor, C. K., McKay, J. K., Carroll, S. P. & Reznick, D. N. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology*, **21**, 394–407.
- Gil, D. & Gahr, M. 2002. The honesty of bird song: multiple constraints for multiple traits. *Trends in Ecology & Evolution*, **17**, 133–141.
- Goodwin, S. E. & Shriver, W. G. 2011. Effects of traffic noise on occupancy patterns of forest birds. *Conservation Biology*, **25**, 406–411.
- Gross, K., Pasinelli, G. & Kunc, H. P. 2010. Behavioral plasticity allows short-term adjustment to a novel environment. *American Naturalist*, **176**, 456–464.
- Habib, L., Bayne, E. M. & Boutin, S. 2007. Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*. *Journal of Applied Ecology*, **44**, 176–184.
- Halfwerk, W. & Slabbekoorn, H. 2009. A behavioural mechanism explaining noise-dependent frequency use in urban birdsong. *Animal Behaviour*, **78**, 1301–1307.
- Halfwerk, W., Holleman, L. J. M., Lessells, C. M. & Slabbekoorn, H. 2011a. Negative impact of traffic noise on avian reproductive success. *Journal of Applied Ecology*, **48**, 210–219.
- Halfwerk, W., Bot, S., Buikx, J., van der Velde, M., Komdeur, J., ten Cate, C. & Slabbekoorn, H. 2011b. Low songs lose potency in urban noise conditions. *Proceedings of the National Academy of Sciences, U.S.A.*, **108**, 14549–14554.
- Halfwerk, W., Bot, S. & Slabbekoorn, H. 2012a. Male great tit song perch selection in response to noise-dependent female feedback. *Functional Ecology*, **26**, 1339–1347.
- Halfwerk, W., Bot, S., Buikx, J., van der Velde, M., Komdeur, J., ten Cate, C. & Slabbekoorn, H. 2012b. Reply to Eens et al.: urban noise can alter sexual selection on bird song. *Proceedings of the National Academy of Sciences, U.S.A.*, **109**, e209. <http://dx.doi.org/10.1073/pnas.1120485109>.
- Hamao, S., Watanabe, M. & Mori, Y. 2011. Urban noise and male density affect songs in the great tit *Parus major*. *Ethology Ecology & Evolution*, **23**, 111–119.
- Han, Y., Jiang, S. & Ding, P. 2004. Effects of ambient noise on the vocal frequency of Chinese bulbuls, *Pycnonotus sinensis* in Lin'an and Fuyang City. *Zoological Research*, **25**, 122–126.
- Hanna, D., Blouin-Demers, G., Wilson, D. R. & Mennill, D. J. 2011. Anthropogenic noise affects song structure in red-winged blackbirds (*Agelaius phoeniceus*). *Journal of Experimental Biology*, **214**, 3549–3556.
- Hansen, P. 1979. Vocal learning: its role in adapting sound structures to long-distance propagation, and a hypothesis on its evolution. *Animal Behaviour*, **27**, 1270–1271.
- Herrera-Montes, M. I. & Aide, T. M. 2011. Impacts of traffic noise on anuran and bird communities. *Urban Ecosystems*, **14**, 415–427.
- Hu, Y. & Cardoso, G. C. 2009. Are bird species that vocalize at higher frequencies preadapted to inhabit noisy urban areas? *Behavioral Ecology*, **20**, 1268–1273.
- Hu, Y. & Cardoso, G. C. 2010. Which birds adjust the frequency of vocalizations in urban noise? *Animal Behaviour*, **79**, 863–867.
- Hulse, S. H. 2002. Auditory scene analysis in animal communication. *Advances in the Study of Behavior*, **31**, 163–200.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–211.
- Ince, S. A., Slater, P. J. B. & Weismann, C. 1980. Changes with time in the songs of a population of chaffinches. *Condor*, **82**, 285–290.
- Kark, S., Iwanuk, A., Schalimtzek, A. & Banker, E. 2007. Living in the city: can anyone become an 'urban exploiter'? *Journal of Biogeography*, **34**, 638–651.
- Kight, C. R. & Swaddle, J. P. 2011. How and why environmental noise impacts animals: an integrative, mechanistic review. *Ecology Letters*, **14**, 1052–1061.
- Kirschel, A. N. G., Blumstein, D. T., Cohen, R. E., Buermann, W., Smith, T. B. & Slabbekoorn, H. 2009. Birdsong tuned to the environment: green hylia song varies with elevation, tree cover, and noise. *Behavioral Ecology*, **20**, 1089–1095.
- Klump, G. M. 1996. Bird communication in the noisy world. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 321–338. Ithaca, New York: Cornell University Press.
- Kroodsma, D. E. 1989. Suggested experimental designs for song playbacks. *Animal Behaviour*, **37**, 600–609.
- Lachlan, R. F. & Slater, P. J. B. 1999. The maintenance of vocal learning by gene–culture interaction: the cultural trap hypothesis. *Proceedings of the Royal Society B*, **266**, 701–706.
- Laiolo, P. 2011. The rufous-collared sparrow *Zonotrichia capensis* utters higher frequency songs in urban habitats. *Revista Catalana d'Ornitologia*, **27**, 25–30.

- Lande, R. 2009. Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *Journal of Evolutionary Biology*, **22**, 1435–1446.
- Leonard, M. L. & Horn, A. G. 2012. Ambient noise increases missed detections in nestling birds. *Biology Letters*, **8**, 530–532.
- Linhart, P., Slabbekoorn, H. & Fuchs, R. 2012. The communicative significance of song frequency and song length in territorial chaffinches. *Behavioral Ecology*, **23**, 1338–1347. <http://dx.doi.org/10.1093/beheco/ars127>.
- Lohr, B., Wright, T. F. & Dooling, R. J. 2003. Detection and discrimination of natural calls in masking noise by birds: estimating the active space signal. *Animal Behaviour*, **65**, 763–777.
- Luther, D. & Baptista, L. 2010. Urban noise and the cultural evolution of bird songs. *Proceedings of the Royal Society B*, **277**, 469–473.
- Luther, D. & Derryberry, E. P. 2012. Birdsongs keep pace with city life: changes in song over time in an urban songbird affect communication. *Animal Behaviour*, **83**, 1059–1066.
- McGregor, P. K. & Krebs, J. R. 1982. Song types in a population of great tits (*Parus major*): their distribution, abundance and acquisition by individuals. *Behaviour*, **79**, 126–152.
- McGregor, P. K. & Krebs, J. R. 1989. Song learning in adult great tits (*Parus major*): effects of neighbours. *Behaviour*, **108**, 139–159.
- McGregor, P. K., Dabelsteen, T., Shepherd, M. & Pedersen, S. B. 1992. The signal value of matched singing in great tits: evidence from interactive playback experiments. *Animal Behaviour*, **43**, 987–998.
- McKinney, M. L. 2002. Urbanization, biodiversity, and conservation. *Bioscience*, **52**, 883–890.
- McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation*, **127**, 247–260.
- Maklakov, A. A., Immler, S., Gonzalez-Voyer, A., Ronn, J. & Kolm, N. 2011. Brains and the city: big-brained passerine birds succeed in urban environments. *Biology Letters*, **7**, 730–732.
- Marler, P. & Peters, S. 1982. Developmental overproduction and selective attrition: new processes in the epigenesis of birdsong. *Developmental Psychobiology*, **15**, 369–378.
- Martens, J. & Geduldig, G. 1988. Acoustic adaptations of birds living close to Himalayan torrents. In: *Current Topics in Avian Biology: Proceedings of the International Centennial Meeting of the Deutsche Ornithologen Gesellschaft, Bonn 1988* (Ed. by R. van Elzen), pp. 123–131. Bonn: Verlag der Deutschen Ornithologen Gesellschaft.
- Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. In: *Avian Ecology and Conservation in an Urbanizing World* (Ed. by J. M. Marzluff), pp. 19–48. Norwell, Massachusetts: Kluwer Academic.
- Mendes, S., Colino-Rabanal, V. J. & Peris, S. J. 2011. Bird song variations along an urban gradient: the case of the European blackbird (*Turdus merula*). *Landscape and Urban Planning*, **99**, 51–57.
- Mery, F. & Burns, J. G. 2010. Behavioural plasticity: an interaction between evolution and experience. *Evolutionary Ecology*, **24**, 571–583.
- Mockford, E. J. & Marshall, R. C. 2009. Effects of urban noise on song and response behaviour in great tits. *Proceedings of the Royal Society B*, **276**, 2979–2985.
- Møller, A. P. 2009. Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia*, **159**, 849–858.
- Møller, A. P. 2010. Interspecific variation in fear responses predicts urbanization in birds. *Behavioral Ecology*, **21**, 365–371.
- Montague, M. J., Danek-Gontard, M. & Kunc, H. P. 2012. Phenotypic plasticity affects the response of a sexually selected trait to anthropogenic noise. *Behavioral Ecology*, published online 1 November 2012. <http://dx.doi.org/10.1093/beheco/ars169>.
- Morton, E. S. 1975. Ecological sources of selection on avian sounds. *American Naturalist*, **109**, 17–34.
- Morton, E. S., Gish, S. L. & van der Voort, M. 1986. On the learning of degraded and undegraded songs in the Carolina wren. *Animal Behaviour*, **34**, 815–820.
- Nega, T., Smith, C., Bethune, J. & Fu, W. H. 2012. An analysis of landscape penetration by road infrastructure and traffic noise. *Computers, Environment and Urban Systems*, **36**, 245.
- Nemeth, E. & Brumm, H. 2009. Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization? *Animal Behaviour*, **78**, 637–641.
- Nemeth, E. & Brumm, H. 2010. Birds and anthropogenic noise: are urban songs adaptive? *American Naturalist*, **176**, 465–475.
- Nemeth, E., Zollinger, S. A. & Brumm, H. 2012. Effect sizes and the integrative understanding of urban bird song. *American Naturalist*, **180**, 146–152.
- Newman, N. M., Yeh, P. J. & Price, T. D. 2006. Reduced territorial responses in dark-eyed juncos following population establishment in a climatically mild environment. *Animal Behaviour*, **71**, 893–899.
- Nordby, J. C., Campbell, S. E., Burt, J. M. & Beecher, M. D. 2000. Social influences during song development in the song sparrow: a laboratory experiment simulating field conditions. *Animal Behaviour*, **59**, 1187–1197.
- Nottebohm, F. 1972. The origins of vocal learning. *American Naturalist*, **106**, 116–140.
- Parris, K. M. & Schneider, A. 2009. Impacts of traffic noise and traffic volume on birds of roadside habitats. *Ecology and Society*, **14** (1), 29. <http://www.ecologyandsociety.org/vol14/iss1/art29/>.
- Paton, D., Romero, F., Cuenca, J. & Escudero, J. C. 2012. Tolerance to noise in 91 bird species from 27 urban gardens of Iberian Peninsula. *Landscape and Urban Planning*, **104**, 1–8.
- Patricelli, G. L. & Blickley, J. L. 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. *Auk*, **123**, 639–649.
- Payne, R. B. 1982. Ecological consequences of song matching: breeding success and intraspecific song mimicry in indigo buntings. *Ecology*, **63**, 401–411.
- Payne, R. B. 1996. Song traditions in indigo buntings: origin, improvisation, dispersal, and extinction in cultural evolution. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 198–220. Ithaca, New York: Comstock.
- Peters, S., Derryberry, E. P. & Nowicki, S. 2012. Songbirds learn songs least degraded by environmental transmission. *Biology Letters*, **8**, 736–739.
- Pigliucci, M. 2001. *Phenotypic Plasticity*. Baltimore, Maryland: John Hopkins University Press.
- Pijanowski, B. C., Farina, A., Gage, S. H., Dumyahn, S. L. & Krause, B. L. 2011. What is soundscape ecology? An introduction and overview of an emerging new science. *Landscape Ecology*, **26**, 1213–1232.
- Podós, J., Huber, S. K. & Taft, B. 2004. Bird song: the interface of evolution and mechanism. *Annual Review of Ecology, Evolution and Systematics*, **35**, 55–87.
- Pohl, N. U., Slabbekoorn, H., Klump, G. M. & Langemann, U. 2009. Effects of signal features and environmental noise on signal detection in the great tit, *Parus major*. *Animal Behaviour*, **78**, 1293–1300.
- Pohl, N. U., Leadbeater, E., Slabbekoorn, H., Klump, G. M. & Langemann, U. 2012. Great tits in urban noise benefit from high frequencies in song detection and discrimination. *Animal Behaviour*, **83**, 711–721.
- Potvin, D. A., Parris, K. M. & Mulder, R. A. 2011. Geographically pervasive effects of urban noise on frequency and syllable rate of songs and calls in silvereyes (*Zosterops lateralis*). *Proceedings of the Royal Society B*, **278**, 2464–2469.
- Price, T. D., Qvarnström, A. & Irwin, D. E. 2003. The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society B*, **270**, 1433–1440.
- Reijnen, R. & Foppen, R. 1994. The effects of car traffic on breeding birds in populations in woodland. 1. Evidence of reduced habitat quality for willow warblers (*Phylloscopus trochilus*) breeding close to a highway. *Journal of Applied Ecology*, **31**, 85–94.
- Reijnen, R. & Foppen, R. 2006. Impact of road traffic on breeding bird populations. In: *The Ecology of Transportation: Managing Mobility for the Environment* (Ed. by J. Davenport & J. L. Davenport), pp. 255–274. Heidelberg: Springer-Verlag.
- Rheindt, F. E. 2003. The impact of roads on birds: does song frequency play a role in determining susceptibility to noise pollution? *Journal für Ornithologie*, **144**, 295–306.
- Ríos-Chelén, A. A., Salaberria, C., Barbosa, I., Macías García, C. & Gil, D. 2012. The learning advantage: bird species that learn their song show a tighter adjustment of song to noisy environments than those that do not learn. *Journal of Evolutionary Biology*, **25**, 2171–2180. <http://dx.doi.org/10.1111/j.1420-9101.2012.02597.x>.
- Ripmeester, E. A. P., de Vries, A. M. & Slabbekoorn, H. 2007. Do blackbirds signal motivation to fight with their song? *Ecology*, **113**, 1021–1028.
- Ripmeester, E. A. P., Kok, J., van Rijssel, J. & Slabbekoorn, H. 2010a. Habitat-related birdsong divergence: an integrated study on the influence of territory density and ambient noise. *Behavioral Ecology and Sociobiology*, **64**, 409–418.
- Ripmeester, E. A. P., Mulder, M. & Slabbekoorn, H. 2010b. Habitat-dependent acoustic divergence affects playback response in urban and forest populations of the European blackbird. *Behavioral Ecology*, **21**, 876–883.
- Robinson, B. W. & Dukas, R. 1999. The influence of phenotypic modifications on evolution: the Baldwin effect and modern perspectives. *Oikos*, **85**, 582–589.
- Ryan, M. J. & Brenowitz, E. A. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. *American Naturalist*, **126**, 87–100.
- Salaberria, C. & Gil, D. 2010. Increase in song frequency in response to urban noise in the great tit *Parus major* as shown by data from the Madrid (Spain) city noise map. *Ardeola*, **57**, 3–11.
- Scales, J., Hyman, J. & Hughes, M. 2011. Behavioral syndromes break down in urban song sparrow populations. *Ethology*, **117**, 887–895.
- Schroeder, J., Nakagawa, S., Cleasby, I. R. & Burke, T. 2012. Passerine birds breeding under chronic noise experience reduced fitness. *PLoS One*, **7**, e39200. <http://dx.doi.org/10.1371/journal.pone.0039200>.
- Searcy, W. A. & Beecher, M. D. 2009. Song as an aggressive signal in songbirds. *Animal Behaviour*, **78**, 1281–1292.
- Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E. & Hope, D. 2006. From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution*, **21**, 186–191.
- Sih, A. 2012. Ecological implications of behavioural syndromes. *Ecology Letters*, **15**, 278–289.
- Sih, A. 2012. Understanding variation in behavioral responses to human-induced rapid environmental change: a conceptual overview. *Animal Behaviour*, this issue.
- Slabbekoorn, H. 2012. Measuring behavioural changes to assess anthropogenic noise impact on singing birds. In: *Proceedings of Measuring Behavior 2012, Utrecht, The Netherlands* (Ed. by A. J. Spink), pp. 158–162. Wageningen: Noldus Information Technology.
- Slabbekoorn, H. & den Boer-Visser, A. 2006. Cities change the songs of birds. *Current Biology*, **16**, 2326–2331.
- Slabbekoorn, H. & Bouton, N. 2008. Soundscape orientation: a new field in need of sound investigation. *Animal Behaviour*, **76**, e5–e8.
- Slabbekoorn, H. & Halfwerk, W. 2009. Noise annoys at community level. *Current Biology*, **19**, R693–R695.
- Slabbekoorn, H. & Peet, M. 2003. Birds sing at a higher pitch in urban noise. *Nature*, **424**, 267.

- Slabbekoorn, H. & Ripmeester, E. A. P. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. *Molecular Ecology*, **17**, 72–83.
- Slabbekoorn, H. & Smith, T. B. 2002a. Habitat-dependent song divergence in the little greenbul: an analysis of environmental selection pressures on acoustic signals. *Evolution*, **56**, 1849–1858.
- Slabbekoorn, H. & Smith, T. B. 2002b. Bird song, ecology, and speciation. *Philosophical Transactions of the Royal Society London, Series B*, **357**, 493–503.
- Slabbekoorn, H., Jesse, A. & Bell, D. A. 2003. Microgeographic song variation in island populations of the white-crowned sparrow (*Zonotrichia leucophrys nutalli*): innovation through recombination. *Behaviour*, **140**, 947–963.
- Slabbekoorn, H., Yeh, P. & Hunt, K. 2007. Sound transmission and birdsong divergence: a comparison of urban and forest acoustics. *Condor*, **109**, 67–78.
- Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C. & Popper, A. N. 2010. A noisy spring: the impact of globally rising underwater sound levels on fish. *Trends in Ecology & Evolution*, **25**, 419–427.
- Slabbekoorn, H., Yang, X.-J. & Halfwerk, W. 2012. Birds and anthropogenic noise: singing higher may matter (a comment on Nemeth and Brumm, 'Birds and anthropogenic noise: are urban songs adaptive?'). *American Naturalist*, **180**, 142–145.
- Snell-Rood, E. C. 2012. Selective processes in development: implications for the costs and benefits of phenotypic plasticity. *Integrative and Comparative Biology*, **52**, 31–42.
- Snell-Rood, E. C. Evolutionary causes and consequences of behavioural plasticity: an introduction. *Animal Behaviour*, this issue.
- Sol, D., Timmermans, S. & Lefebvre, L. 2002. Behavioural flexibility and invasion success in birds. *Animal Behaviour*, **63**, 495–502.
- Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P. & Lefebvre, L. 2005. Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences, U.S.A.*, **102**, 5460–5465.
- Sol, D., Lapiedra, O. & González-Lagos, C. Behavioural adjustments for a life in the city. *Animal Behaviour*, this issue.
- Soldatini, C., Albores-Barajas, Y. V., Mainardi, D. & Monaghan, P. 2008. Roof nesting by gulls for better or worse? *Italian Journal of Zoology*, **75**, 295–303.
- Stockwell, C. A., Hendry, A. P. & Kinnison, M. T. 2003. Contemporary evolution meets conservation biology. *Trends in Ecology & Evolution*, **18**, 94–101.
- Strohbach, M. W., Haase, D. & Kabisch, N. 2009. Birds and the city: urban biodiversity, land use, and socioeconomics. *Ecology and Society*, **14**, 31.
- ten Cate, C., Slabbekoorn, H. & Ballintijn, M. R. 2002. Birdsong and male–male competition: causes and consequences of vocal variability in the collared dove (*Streptopelia decaocto*). *Advances in the Study of Behavior*, **31**, 31–75.
- Tratalos, J., Fuller, R. A., Evans, K. L., Davies, R. G., Newson, S. E., Greenwood, J. J. D. & Gaston, K. J. 2007. Bird densities are associated with household densities. *Global Change Biology*, **13**, 1685–1695.
- United Nations 2012. *World Urbanization Prospects, the 2011 Revision*. New York: United Nations Department of Economic and Social Affairs, Population Division.
- Verzijden, M. N., Ripmeester, E. A. P., Ohms, V. R., Snelderwaard, P. & Slabbekoorn, H. 2010. Immediate spectral flexibility in singing chiffchaffs during experimental exposure to highway noise. *Journal of Experimental Biology*, **213**, 2575–2581.
- Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. 1997. Human domination of Earth's ecosystems. *Science*, **277**, 494–499.
- Waddington, K. D. 1961. Genetic assimilation. *Advances in Genetics*, **10**, 257–290.
- Warren, P. S., Katti, M., Ermann, M. & Brazel, A. 2006. Urban bioacoustics: it's not just noise. *Animal Behaviour*, **71**, 491–502.
- Wcislo, W. T. 1989. Behavioural environments and evolutionary change. *Annual Review of Ecology and Systematics*, **20**, 137–169.
- West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics*, **20**, 249–278.
- West-Eberhard, M. J. 2003. *Developmental Plasticity and Evolution*. New York: Oxford University Press.
- Wood, W. E. & Yezerinac, S. M. 2006. Song sparrow (*Melospiza melodia*) song varies with urban noise. *Auk*, **123**, 650–659.
- Zmihorski, M., Halba, R. & Mazgajski, T. D. 2010. Long-term spatio-temporal dynamics of corvids wintering in urban parks of Warsaw, Poland. *Ornis Fennica*, **87**, 61–68.
- Zollinger, S. A., Podos, J., Nemeth, E., Goller, F. & Brumm, H. 2012. On the relationship between, and measurement of, amplitude and frequency in birdsong. *Animal Behaviour*, **84**, e1–e9.