



Urban bioacoustics: it's not just noise

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The acoustic environment has a major influence in shaping animal communication systems. Humans, particularly in cities, profoundly alter the acoustic structure of their environment. Recent articles have identified effects of noise on animal communication and behaviour. These studies, however, serve to highlight the surprising dearth of research on the behavioural responses of animals to altered acoustic environments. We argue that noise is not the only aspect of urban bioacoustics that researchers should explore. In addition to elevated noise levels, urban areas are characterized by a spatial heterogeneity in noise levels, predictable diurnal variation in noise levels and the existence of many vertical reflective surfaces. All of these characteristics have parallels in natural environments. We suggest that cities are a fruitful area for future research on the evolution of animal communication systems, with more general implications for conservation in human-altered environments.

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Research on acoustic communication in animals has provided some of the clearest demonstrations of the ways in which organisms adapt to their environments. Classic work by Morton (1975) and Wiley & Richards (1978, 1982) provided a theoretical framework for predicting the effects of habitat structure on acoustic signal structure and calling behaviour, and this has been supported by subsequent empirical work (e.g. Hunter & Krebs 1979; Morton 1987; Ryan et al. 1990). Most work to date has focused on natural environments such as forests, meadows and ponds. Increasing urbanization worldwide is creating novel environments that animals must either adapt to or abandon. Several recent studies provide the first examples of bird songs responding adaptively to noisy urban environments (Brumm & Todt 2002; Slabbekoorn & Peet 2003). Little work has been done, however, to characterize the overall acoustic environment of human-dominated ecosystems such as cities.

Although noise is the most noticeable element of the urban acoustic environment, it is not the only factor that distinguishes urban areas. Despite the heterogeneity of urban landscapes, human modifications of the environment in cities have some common characteristics likely to affect communication, such as elevated noise levels, abundant large flat surfaces and altered sound channels. These characteristics have parallels in natural systems, such as streams, canyons and windy environments. The long history of research on habitat acoustics in animal behaviour research provides a basis for making predictions about the effects that novel acoustic environments should have on signal design, signal detection and the timing of signalling.

We provide here both a review of existing literature and a conceptual overview of topics that are ripe for further research. Perhaps because noise pollution is an issue for human residents of urban areas, much existing behavioural research focuses on effects of noise. Thus, we devote the first portion of our review to addressing the effects of noise on animal communication systems, identifying critical areas in need of further research. We draw upon this literature as well as our own research in Phoenix, Arizona, U.S.A., to characterize the spatial distribution of

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noise in urban landscapes and examine the possible contribution of spatial variability of noise levels to acoustic divergence in animal signals.

In addition to the review, we present an examination of the ways that animal behaviour can benefit from incorporating ideas and information from the fields of architecture and urban design. These fields have amassed a substantial body of research on human-generated noise and on the acoustics of built environments. We provide two examples: diurnal variation in noise levels and the dawn chorus and the acoustics of urban 'canyons'. In each case, we generate predictions based on information from urban planners and engineers. Moreover, there are many parallel conditions in natural or less human-dominated systems that also remain relatively unexplored by researchers in animal behaviour. We call for future research to exploit these opportunities for addressing some of the processes of adaptation to rapidly changing environments and novel selection pressures.

Defining Urban

For ease of discussion, we define 'urban' to include any area of high-density human population and human-built structure. This definition intentionally encompasses a range of human-modified environments, including commercial/industrial, suburban and residential land uses (i.e. the portion of the urban-rural gradient often labelled urban-to-suburban; McDonnell & Pickett 1990; McIntyre et al. 2000; Kinzig & Grove 2001). This definition also includes such urban growth phenomena as sprawl and leapfrog development that are bringing high-density human settlement increasingly in contact with 'wild lands'. Roads and their concomitant elevated noise levels reach into these rural and wild land areas, subjecting them to similar alterations to their acoustics (Forman & Alexander 1998; Forman 2000). Thus, the phenomena that we address in this review are becoming increasingly common in areas not traditionally thought of as 'urban'.

EFFECTS OF HUMAN NOISE ON ANIMAL COMMUNICATION

The absolute noise levels achieved by human-operated machines are unrivalled in the natural world. Regular sources of urban noise include transportation noise (automobiles, trains, airplanes), industrial noise and air conditioning compressors and fans. Other, more intermittent noise sources include construction, car horns, car brakes, crowd noise and amplified performance noise. At high human population densities, as in urban areas, all of these noise sources are likely to be present, combining to generate a drastic increase in noise levels in urban areas relative to exurban areas. Elevated noise has received considerable attention from researchers interested in human well-being. Noise has been studied as a stressor with effects on human health (e.g. Passchier-Vermeer & Passchier 2000; Ouis 2001; Lercher et al. 2003), and there is substantial research on the physiological effects of noise, often using animal models (e.g. Kempf & Huppopp

1996; Maschke et al. 2000). Studies of noise effects on animal communication systems, however, are less common, and fall into two categories: effects of noise on signal design and effects of noise on animal distributions and reproductive success.

Noise and Signal Design

High levels of noise mask acoustic signals, potentially making it more difficult for animals to defend territories, attract mates or attend to other important communication signals such as begging, alarm or distress calls. Recent evidence also suggests that anthropogenic noise can suppress calling in some amphibians (Sun & Narins 2005). Two alterations of animal signals can mitigate the effects of masking noise: changes in amplitude and changes in frequency (Fig. 1). Each of these changes in signal design might occur as short-term phenotypically plastic responses, long-term phenotypically plastic responses (e.g. via song learning) or as evolutionary responses via natural selection.

Amplitude shifts

One well-known response to elevated noise levels is the Lombard effect (Katti & Warren 2004; Fig. 1b), a reflexive increase in amplitude in order to maintain high signal-to-noise ratios (Lombard 1911). The Lombard effect was first described for humans, but has since been shown in laboratory studies in a wide variety of animal species, including blue-throated hummingbirds, *Lampornis clemenciae* (Pytte et al. 2003), zebra finches, *Taeniopygia guttata* (Cynx et al. 1998), budgerigars, *Melopsittacus undulatus* (Manabe et al. 1998) and marmosets, *Callithrix jacchus* (Brumm et al. 2004). Brumm (2004) conducted a careful field study of the Lombard effect in nightingales, *Luscinia megarhynchos*, exposed to traffic noise. Measuring amplitude of animal signals in the field is difficult to do accurately. Through repeated measures of song amplitude at known distances and simultaneous measures of ambient noise, Brumm found higher nightingale song amplitudes under higher levels of anthropogenic noise, controlling for body size, temperature, humidity and time of day. Several individuals were measured on both weekdays and weekends, and correspondingly lower song amplitudes were found on weekends when traffic noise levels were lower.

No studies to our knowledge have addressed whether animals show longer-term changes in signal amplitude in response to elevated noise levels. We found no systematic treatment of species differences in signal amplitude, although such differences clearly exist. There are many natural sources of noise, including streams, wind and other animals (e.g. insect choruses), providing opportunities for elevated noise levels to exert selection on animal signals in a wide variety of contexts (Dubois & Martens 1984; Slabbekoorn & Peet 2003; Brumm 2004). It seems clear that many birds and mammals are able to compensate for some of the masking effects of elevated noise through a short-term phenotypically plastic response (Cynx et al. 1998; Manabe et al. 1998; Brumm & Todt

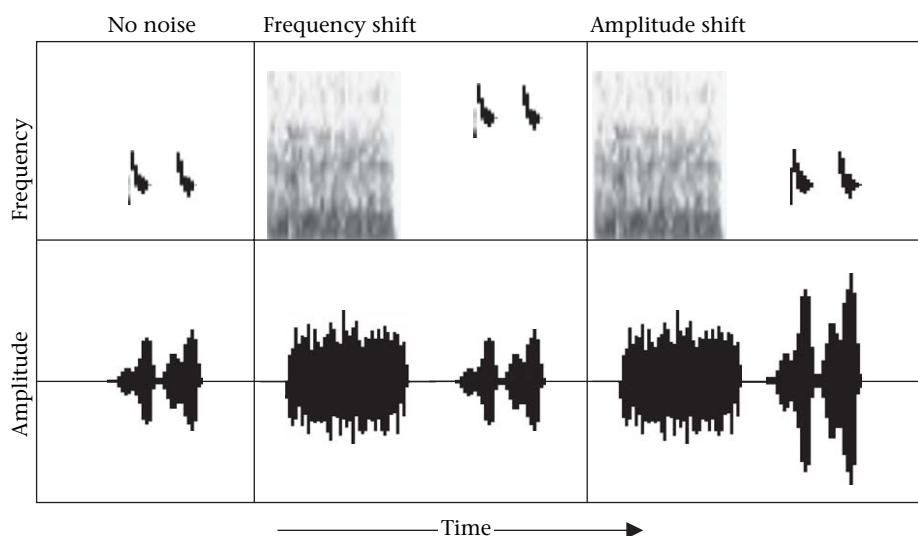


Figure 1. Faced with the problem of communicating through masking noise, animals have two main options for making their calls more audible: altering the frequency or altering the amplitude. Much of the noise generated by humans is concentrated at low frequencies. In that setting, animals may shift the frequency of calls upward to escape masking noise and/or increase the amplitude of their calls without altering their frequency. Reprinted with permission from Elsevier (Katti & Warren 2004).

2002; Kobayasi & Okanoya 2003; Pytte et al. 2003; Brumm et al. 2004). However, future studies should address whether elevated noise levels have long-term or evolutionary effects on animal signalling.

Frequency shifts

Many noise sources have energy concentrated in particular frequency bands. For example, anthropogenic noise sources are often concentrated at lower frequencies. Thus, frequency shifting presents another mechanism for avoiding masking noise (Katti & Warren 2004; Fig. 1c). Slabbekoorn & Peet (2003) found that human-generated sound energy was largely concentrated below 2000 Hz and that great tits, *Parus major*, in noisier portions of Leiden, Netherlands, produced songs with higher minimum frequencies than did those in less noisy portions of that city. These birds appeared to have shifted the frequency of their songs in response to this human-altered acoustic environment. Great tits are passerines and are capable of song learning. Thus, the authors acknowledged that the differences that they found might be either from learned changes in signal structure or evolved responses, although they argued that the former is a more likely explanation. Other parids such as chickadees are known to adjust song frequencies in winter flocks (Mammen & Nowicki 1981). Future studies could use technologies commonly used in studies of song learning, such as sound isolation chambers, to test whether low-frequency noise affects the frequency structure of learned bird song.

The generally low-frequency character of anthropogenic noise suggests that species using higher-frequency signals should be better able to tolerate this noise than those using lower-frequency signals. Only one researcher to date has tested this hypothesis and found a weak but significant relation between tolerance of proximity to roads and dominant frequency of the song (Rheindt 2003). Rheindt

compared the decline in abundance in proximity to roads with measures of dominant frequency and showed that species with higher abundances near roads (indicating greater tolerance to elevated noise levels) had significantly higher dominant frequencies than did species that were less abundant near roads. Rheindt ruled out two potential confounds: body size and detectability (because birds with lower-frequency song might be masked by the road noise). However, Rheindt's results rest upon low sample sizes: the study included only 12 species and is based upon differences in abundance between just two transects, which is effectively a sample size of one. This work should be repeated in other regions and with more robust replication.

Many species are physiologically constrained to produce low-frequency calls in the range of masking noise. Many bird and insect species either produce songs at higher frequencies or are capable of altering their signals to escape masking noise. However, many species of frogs and birds produce signals with most of their energy overlapping with the sound energy in anthropogenic noise. Unless these species find other mechanisms for adapting to noisy environments, such as shifting the timing of calling, their signals will experience small effective areas, potentially impairing their ability to communicate (Rabin & Greene 2002).

Other design features

Other features of signal design allow animals to mitigate the effects of masking noise (Aubin 2004; Sun & Narins 2005). For example, signals with narrower bandwidths (e.g. pure tones) are expected to be more detectable against background noise than are those with wider bandwidths (e.g. buzzes or trills). We found few studies in general addressing the design of signals in persistently noisy habitats. Some evidence suggests that birds living along streambanks produce signals dominated by pure tones

(e.g. American dipper, *Cinclus mexicanus*, in North America: Kingery 1996; torrent duck, *Merganetta armata*, in South America: Niethammer 1952; wallcreeper, *Tichodroma muraria*, and whistling thrush, *Myophonus caeruleus*, in Eurasia, Löhrl 1964; Dubois & Martens 1984). More compelling is evidence that three species of frog (*Rana rostandi*, *R. blandfordii* and *R. liebighii*) and one species of bird (*Phylloscopus magnirostris*) living alongside streams share a number of signal features that their close relatives do not (Dubois & Martens 1984). In addition, these frog and the bird species all produce short, narrow-band signals, in short sequences with long intervals between. Dubois & Martens speculated that the temporal features of the signals might also be important features for either contrast with the background noise or to aid in localization. Neither of these hypotheses was tested, nor did the authors make quantitative comparisons of frequency bandwidth between the species. Quantitative, phylogenetically controlled studies are needed to assess whether noisy environments affect signal design, but research to date suggests that animals with narrow frequency bandwidth signals may be able to communicate more effectively in noisy urban environments.

Several questions remain regarding the effects of elevated noise levels on signal design. First, are there thresholds of noise above which animals cannot compensate through the Lombard effect? That is, the absolute amplitude of some human-generated noise (e.g. industrial noise, airplanes) may be just too high. What are these thresholds? Do they differ between species? The masking noise levels used in several studies of the Lombard effect in birds were typically around 70 dB (Manabe et al. 1998; Kobayasi & Okanoya 2003; Pytte et al. 2003), and the maximum used in any study was 90 dB (Cynx et al. 1998). Zebra finches, *Taeniopygia guttata*, in a study using playbacks of masking noise at 60–90 dB, showed curvilinear responses to increasing levels of masking noise, suggesting that the birds may quickly reach a threshold above which they no longer show the Lombard effect (Cynx et al. 1998). The higher-amplitude song elements produced by nightingales increased little in response to increasing levels of masking noise, suggesting that nightingales may already be producing some portions of their songs at maximum levels, around 85 dB (Brumm & Todt 2002). Noise levels in airport flight paths reach 74 dB, and highway noise from 500 ft (152 m) away is around 70 dB, depending on the size and traffic speeds of the highway (Egan 1988). Thus, typical urban noise levels appear to fall in the decibel range that animals studied so far can accommodate via the Lombard effect, at least in the short term. We encourage animal communication researchers to include in their experiments noise-level treatments that match common urban noise sources.

Second, what are the costs of signalling under persistently noisy conditions, such as those found in cities and along roads? Using higher-amplitude signals should increase the energetic costs of signalling, although some studies suggest that singing in birds is not as energetically costly as might be expected (Brumm & Todt 2002). Under prolonged exposure to noise, energetic costs of signalling might lead to lower fitness for animals in noisy

environments. Studies of the Lombard effect have so far been confined to short-term studies, even when the focal species occupies persistently noisy environments such as streamsides (Pytte et al. 2003). Thus, we do not know whether animals can adapt to persistently noisy conditions by elevating the amplitude of their signals. In fact, avian reproductive success along highways shows reductions under noise levels of 42–48 dB, much lower than the noise levels used in studies of short-term Lombard effects (Forman & Alexander 1998). Understanding these long-term responses to noise has implications for communication under noisy conditions more generally, such as water noise alongside streams or the noise of animal choruses and flocks.

Third, what is the effect of noise on calling effort? Decreased time spent calling is generally expected to reduce opportunities for mating; thus, suppression of calling by anthropogenic noise should have negative effects on breeding success. One recent study suggests that noise from passing airplanes and motorcycles, as well as experimental playbacks of noise, suppresses calling in some species of amphibians, usually the dominant calling species (Sun & Narins 2005). However, the nondominant calling species, *Rana taipehensis*, increases calling during bouts of noise, possibly because of the lull in calling by other species (Sun & Narins 2005). This, to our knowledge, is the only experimental study of the effects of noise on calling behaviour. More work is called for in this area, but Sun & Narins' study suggests that noise may have complex direct and indirect effects on calling behaviour.

Cities and their rapid expansion provide a 'natural' laboratory for measuring effects of prolonged noise exposure. Commonly occurring species of birds that span the urban–rural gradient include mockingbirds, *Mimus polyglottus*, in many North American cities and the European blackbird, *Turdus merula*. Some species of frogs continue to breed along roadsides or in urban areas (Hermy & Cornelis 2000; Lesbarreres et al. 2003). Comparative studies could measure, among other things, calling amplitudes in these species in both urban and exurban areas. Researchers should also take advantage of natural experiments such as the relocation of an airport or the building of a new road to measure effects of both increasing and decreasing noise levels on calling amplitudes.

Noise Effects on Animal Distributions and Reproductive Success

Chief conservation concerns about anthropogenic noise are that it might limit the distributions of particular animal species that are intolerant of noise or negatively affect reproductive success in species forced to breed in noisy environments. Most research on negative effects of noise has focused on road noise (but see Leddy et al. 1999). Many bird species occur at lower densities closer to roads, and bird diversity is often lower in proximity to roads (Reijnen & Foppen 1994, 1995; Forman et al. 2002; Rheindt 2003; Peris & Pescador 2004). Both birds and frogs appear to have lower breeding success near roads (Reijnen & Foppen 1995; Forman & Alexander 1998;

Spellerberg 1998; Lesbarreres et al. 2003). Several authors have argued that, in addition to ecological impacts of roads, elevated noise levels along roads also impair the ability of animals to effectively communicate during breeding, thereby impacting reproductive success (Forman et al. 2002). Here, we ask what evidence there is that road noise negatively affects animals via effects on animal communication. Research in this area has focused almost exclusively on birds.

Four lines of evidence have been used to argue for negative effects of noise on animal communication systems.

(1) Bird densities are depressed beyond the view of roads (Reijnen & Foppen 1994, 1995; Reijnen et al. 1995, 1996). A series of studies in the Netherlands makes the case that the effects of road noise are detectable far beyond the distance at which roads are visible to birds. Noise levels in one study regularly exceeded 50 dB at 500 m from the road, but the sight distance to the road was only 25 m (Reijnen & Foppen 1994). Bird densities were significantly lower for more species at sites with higher noise loads when the authors controlled for traffic visibility, but there were no significant differences in densities when they varied traffic visibility and controlled for noise load (Reijnen et al. 1995). These studies eliminated one confounding effect of roads, the disturbance effect created by the motion of cars in traffic. The results suggest that noise impairs the effectiveness of male songs for attracting and keeping mates (Reijnen & Foppen 1994), but they cannot eliminate alternative explanations such as stress effects of noise (Kempf & Huppopp 1996; Maschke et al. 2000).

(2) Bird diversity is lower in noisier sites, independent of land use type (Stone 2000). Stone (2000) compared noise levels to bird diversity over a range of surrounding land use types (agricultural, residential, industrial, native grassland). Observers conducted bird counts along riparian zones surrounded by the different land use types and provided subjective assessments of noise level (high, medium, low). Stone compared bird diversity to estimated noise level for each land use type separately and found consistently lower diversity at noisier sites. The power of this test comes from both good replication and coverage of a wide variety of habitats. No other habitat measures were taken at the sites, however, so the possibility remains that other confounding variables accounted for the differences in diversity. For example, noise level could be correlated with habitat features such as greater impervious ground surface and lower vegetative cover, both of which are well known to predict avian diversity in developed areas (DeGraaf & Wentworth 1986; Blair 1996; Germaine et al. 1998; Marzluff 2001; McKinney 2002).

(3) Observations of birds foraging near roads, but not breeding there (Forman et al. 2002). Breeding birds use low-amplitude calls to communicate near their nests and to communicate with offspring. If birds are willing to forage but not to breed near roads, it might be because of interference of noise in these low-amplitude signals involved in reproduction. In other words, as Forman and colleagues suggested, parents simply cannot hear their offspring's begging calls in the presence of high levels of traffic noise. There is some evidence that disrupting these signals has

effects on reproductive success. Experimentally muting nestling birds so that they cannot produce begging calls leads to lower rates of food provisioning by parents (Glassey & Forbes 2002). Forman et al. (2002) argued that their observations refute two alternative hypotheses: (1) that birds opt not to breed near roads because there is insufficient habitat to support feeding of offspring, and (2) that birds avoid breeding on roadsides to avoid exposure to the stressful effects of traffic. This hypothesis does not eliminate the possibility that birds are more tolerant of stress while foraging than while nesting.

(4) Birds with higher-frequency songs have higher abundances near roads (Rheindt 2003). This is perhaps the most compelling evidence that noise affects animal distributions via direct effects on their ability to communicate. There is, however, only a single, poorly replicated study showing this pattern (Rheindt 2003; also see discussion of Frequency shifts, above).

Taken together, these four lines of evidence are suggestive, but they do not present irrefutable evidence for effects of anthropogenic noise per se on animal distributions and reproductive success. Playback experiments with noise are the most effective means of demonstrating the effects that all of the above authors hypothesize. The disruption of low-amplitude communication signals could easily be studied using playback experiments in controlled laboratory conditions. Field experiments could also test effects of noise playbacks near to and further from nesting birds. Not only could these experiments ask whether noise per se mediates the observed effects of roads on breeding success, but they would also test, more generally, the importance of these low-amplitude signals for breeding success in birds. Although these communication signals are assumed to be important for breeding success, this hypothesis has rarely been tested (Budden & Wright 2001; Glassey & Forbes 2002).

Noise and Acoustic Divergence

Some authors have argued that variation in anthropogenic noise levels could lead to acoustic divergence of urban and nonurban populations of the same species or even speciation (Slabbekoorn & Peet 2003). Urban landscapes have high spatial heterogeneity (Rebele 1994), and this also extends to acoustic space. The most pervasive source of noise in most cities is traffic. In general, the shape of the noise space in a city is expected to be highly variable, with bands of noise along major roads and polygons around airports and factories (Egan 1988), contrasting with quieter pockets in residential areas. Consistent spatial variation in noise over time provides the opportunity for acoustic and even evolutionary divergence among populations in and around cities.

There is a small body of evidence for effects of noise on intra- and interspecific variation in signal design (Ryan & Brenowitz 1985; Slabbekoorn & Smith 2002a). Differences in the minimum frequency of little green bulbul, *Andropadus virens*, song appear to be driven by differences between habitats in the level of low-frequency ambient noise (Slabbekoorn & Smith 2002b). These song differences are

correlated with morphological differences (Slabbekoorn & Smith 2002b), providing the opportunity for the habitat differences in song to lead to reproductive isolation (Slabbekoorn & Smith 2002a).

The smaller scale of spatial heterogeneity in cities seems to indicate a lower potential for reproductive isolation among divergent populations, but Leader et al. (2000, 2002) found microgeographical variation in songs of two sunbird, *Nectarinia osea*, populations within an Israeli city as well as acoustic discrimination between dialects, in part based on maximum frequency, despite the extremely short distances between the two populations. More recently, Leader et al. (2005) examined noise levels and acoustic transmissivity of the habitats occupied by birds singing the two dialects as well as apportionment of energy between low-frequency and high-frequency portions of the song. Noise levels were higher in the area with high-frequency dialects, but birds in the noisier habitat did not apportion greater energy to the high-frequency portions of their song. This result and the small sample size of the study (many birds, but only two dialects in two habitats) leave unclear whether variation in noise levels contributes to intraspecific acoustic divergence in urban populations.

Predictable variation in noise levels

For variation in noise levels to lead to acoustic divergence, spatial variation in noise levels must be both predictable and consistent. Among urban planners and acoustic engineers, there is considerable interest in whether this is the case. Recent European Union standards of environmental quality (Wolde 2003) have prompted the development of noise maps for Paris (Butler 2004). These maps are publicly accessible (<http://www.paris.fr/FR/Environnement/bruit>), and they depict lower noise levels in the outer ring of Paris than in the central ring. A study in a small city in Ohio in the U.S. showed higher

noise levels in predominantly minority neighbourhoods (Forkenbrock & Schweitzer 1999). In Tokyo, noise attenuation increased (i.e. lower noise levels experienced by residents) with building density and average building height (Ishiyama et al. 1991). All three of these studies rely heavily on modelled noise levels based on traffic volume data rather than on field measurements of noise. The models used are derived from well accepted and validated acoustic and traffic models. The Paris noise maps have been validated by comparing field noise level measurements to the model predictions. However, it is important to get direct empirical measures of variation in noise levels, because there are many other sources of noise aside from traffic.

Preliminary data from our own field measurements in small parks in residential areas of Phoenix suggest that noise levels do vary predictably across the city. We measured noise levels in 16 neighbourhood parks of similar design. Mean noise levels consistently varied between sites more than within sites (MANOVA including site, date, time interval: $F_{1,15} = 10.59$, $P < 0.0001$). Furthermore, noise levels were strongly inversely predicted by distance from the urban centre (Fig. 2a) and by neighbourhood income level (2000 U.S. Census data; Fig. 2b). Of the two, income level was the stronger predictor of mean noise level in a multiple regression ($F_{1,1} = 6.99$, $P = 0.02$). Income, distance from urban centre, age of the neighbourhood and ethnic composition of the neighbourhood were all correlated in Phoenix as well as in many other U.S. cities (Kinzig et al. 2005). Higher-income neighbourhoods tend to be further from the urban core, newer and predominantly Caucasian, and these same neighbourhoods appear to be subject to lower noise levels (Fig. 2). By far, the most commonly reported source of noise by observers in Phoenix was traffic. At the sites with the highest noise levels, observers also identified airplanes and industrial plants as common noise sources. This observation suggests that the

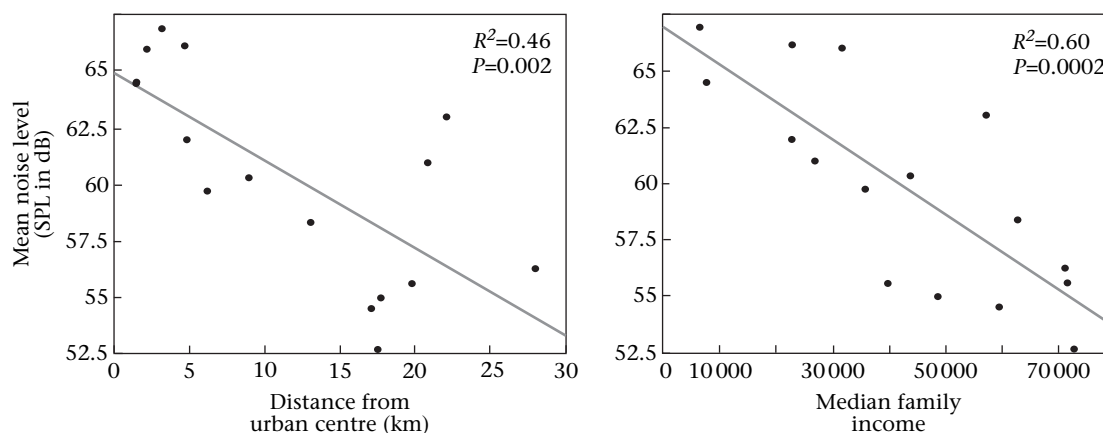


Figure 2. Spatial variation in noise level in Phoenix, Arizona. We measured noise levels in 16 neighbourhood parks of similar design varying in size from 1.7 to 5.6 ha (see method for site selection in Martin et al. 2004; Kinzig et al. 2005). Three groups of five observers (total of 15 people) visited each park once in the morning (0630–0830 hours) or the evening (1600–1900 hours) for a total of 45 measures per park during 1–30 June 2003. At each visit the five observers took simultaneous measures of sound pressure levels (SPL) using handheld SPL meters while standing at five separate locations: the centre of the park and the edges of the park facing outward in the four cardinal directions. Distance to urban centre is measured from the intersection of Central Avenue and Jefferson Street in Phoenix (Luck & Wu 2002). Income data is median family income for the surrounding census tract (2000 U.S. Census).

differences between sites in noise level are not solely because of their proximity to roads or differences in the behaviour of residents. Although bird species diversity varies considerably between these parks, a core set of species, including both native species (e.g. curve-billed thrashers, *Toxostoma curvirostre*, and cactus wrens, *Campylorhynchus bruneicapillus*) and nonnative species (e.g. European starlings, *Sturnus vulgaris*, and house sparrows, *Passer domesticus*), occurs at all 16 Phoenix parks (Kinzig et al. 2005). Thus, variation in noise levels in Phoenix has the potential to contribute to acoustic divergence between populations of resident urban bird species.

Despite the small body of literature on spatial variation in noise levels, our review suggests that acoustic divergence of bird song in cities is a fruitful area for future research. Noise levels appear to vary consistently within cities and on urban–rural gradients (Ishiyama et al. 1991; Forkenbrock & Schweitzer 1999; Fig. 2). Acoustic divergence occurs over short geographical distances within a city (Leader et al. 2000, 2002) and in response to habitat differences in noise levels (Slabbekoorn & Smith 2002b).

Understanding the effects of spatial variability in noise requires better maps of actual noise levels. This is a potential area for collaboration between biologists and acoustical engineers and architects. For example, noise contours around airports are regularly developed for city planners, and architects develop and test barriers to noise alongside highways (Egan 1988). Most of this monitoring of traffic noise is not conducted systematically at extensive scales, but traffic flow and volume is regularly monitored (Lomax et al. 2003). Urban planners in various European cities have begun using modelling approaches to circumvent the costs of monitoring traffic noise more directly (Butler 2004). Citywide maps of noise levels could be beneficial both for city planners interested in effects of traffic noise on humans and for biologists studying distributions of species.

OTHER ACOUSTIC FEATURES

Many other acoustic features of the urban environment may affect animal communication systems. We briefly highlight two areas: effects of rush hour traffic on the avian dawn chorus and acoustic phenomena in urban canyons. In neither case does existing research in animal behaviour specifically address urban populations. However, in each case, clear predictions arise from considering well-known phenomena in animal communication along with well-known urban phenomena.

Dawn Chorus and Traffic Noise

Many animals engaging in long-range communication take advantage of sound channels for maximal sound transmission (Wiley & Richards 1978). The spectral properties of human-generated noise enable great tits in Leiden to use a sound channel not occupied by humans (i.e. frequencies above the level of masking noise; Slabbekoorn & Peet 2003). One well-known sound channel is the temporal window around dawn (Wiley & Richards 1978, 1982;

Brown & Handford 2003). In birds, a peak in singing activity occurs around dawn (dawn chorus; Staicer et al. 1996; Dabelsteen & Mathevon 2002; Brown & Handford 2003). Although a variety of processes, including residual energy from overnight fat stores, may account for the peak of singing activity at dawn (Hutchinson 2002; Thomas & Cuthill 2002), acoustical experiments suggest that the dawn chorus is at least facilitated by the favourable conditions for sound transmission that occur around dawn. Sound transmits further and more reliably at dawn than at midday because of lower wind noise, lower wind turbulence and fewer atmospheric fluctuations (Henwood & Fabrick 1979; Brenowitz 1982; Dabelsteen & Mathevon 2002; Brown & Handford 2003).

Temporal variation in noise levels associated with human activity produces the potential for negative effects of traffic on the dawn chorus. Morning rush hour, the peak in traffic flow associated with urban commuters, has the potential to overlap with the avian dawn chorus. In most cities in the U.S., rush hour consistently occurs between 0600 and 0900 hours (Lomax et al. 2003). Solar patterns vary seasonally, so the timing of rush hour relative to sunrise will also vary seasonally (Fig. 3a). As a case study, we examined Baltimore, Maryland, U.S.A., a temperate city. During much of the breeding season in Baltimore, there is as much as half an hour during which the dawn chorus can occur before the onset of rush hour (Fig. 3a). In March and April, however, when most bird territory establishment and mate selection is occurring, sunrise overlaps considerably with the rush-hour period (Fig. 3a). In other cities, the extent of overlap between rush hour and the dawn chorus is not as extreme. In the U.S., overlap increases with decreasing latitude but also varies with use of Daylight Savings Time (Fig. 3b). In areas with high traffic, these traffic patterns could generate selection for birds to shift the onset of the dawn chorus.

This analysis leads to two testable predictions: (1) traffic noise will affect birds singing in dawn choruses more at lower latitudes; (2) birds should shift their temporal pattern of singing in response to traffic noise.

Is there evidence that birds could alter the timing of the dawn chorus? Many species can alter their temporal pattern of vocal communication to avoid masking interference from other species (Ficken et al. 1974; Greenfield 1988; Paez et al. 1993; Sun & Narins 2005). To our knowledge, only one study addresses changes in temporal patterns of signalling in response to anthropogenic noise levels. Bergen & Abs (1997) measured song rates for three species of birds in an inner-city park in Dortmund, Germany and in a forest patch on the fringe of the city. All three species began singing significantly earlier in the urban park than in the nonurban forest patch. Bergen & Abs suggested an alternative explanation for the differences between their two study sites, that higher light levels in the city may contribute to altering the timing of singing, if light levels act as a proximate cue for the onset of the dawn chorus. Nevertheless, the study provides an intriguing demonstration that the timing of the dawn chorus can vary significantly over short geographical distances.

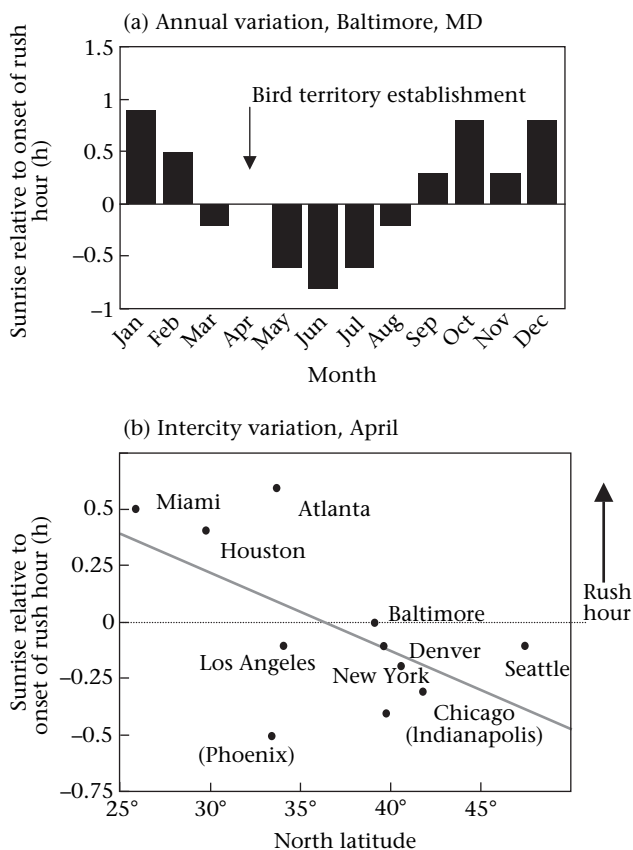


Figure 3. Relative timing of dawn and rush hour, assuming 0600 hours for the onset of rush hour (Lomax et al. 2003). Overlap between dawn and rush hour should impact avian dawn chorus. (a) Annual variation in the timing of sunrise within a single city, Baltimore, Maryland, U.S.A. During the breeding season (May–July), dawn occurs considerably earlier than the onset of rush hour. (b) Variation among U.S. cities in April, a month in which breeding birds are establishing territories in most of the cities depicted. Cities at lower latitudes tend to have greater overlap between rush hour and dawn chorus. Cities in parentheses do not use Daylight Savings Time.

There are additional sources of diurnal variation in noise with the potential to affect signalling at other times of the day. Airplane noise might instead produce a relatively even effect, with periodic noise occurring intermittently throughout the day. In many cities, truck traffic is confined to nighttime, potentially affecting the timing of calling by nocturnal animals. Effects of continuous sources of noise should be compared to effects of intermittent noise sources, such as trains.

Urban Canyons and Flutter Echo

Much information on acoustics of buildings in the architectural literature has not been integrated into studies of animal behaviour (Egan 1988). The most obvious characteristic of human-built structures is the presence of multiple, often parallel, sound-reflective surfaces, or urban canyons. High reflectance can allow sound to ricochet and linger, potentially impeding communication through

constructive interference. Humans and many nonhuman animals have perceptual mechanisms that can suppress echoes that would otherwise degrade their ability to localize or perceive signals (Snedden & Greenfield 1998; Litovsky et al. 1999; Bosch & Marquez 2002; Dent & Dooling 2004). Despite these perceptual accommodations, reverberations in rooms and urban canyons often render human speech unintelligible (Egan 1988), and reverberations in natural environments can degrade transmission of animal signals (Wiley & Richards 1982). A particular case of reverberation from built surfaces, known as flutter echo, is generated by the rapid ricocheting of sound waves back and forth between two parallel walls (or in a room) (Fig. 4b, c). We discuss here several ways that reflections in urban canyons, particularly the phenomenon of flutter echo, might affect animal communication and signal design.

Flutter echo in urban canyons should have two major effects. First, noise levels attenuate (lose amplitude) more slowly in canyons (Kang 2000; Lu & Li 2002). Thus, masking noise levels should be higher along roads surrounded by urban canyons than along more open roads (Kang 2001; Lu & Li 2002). Second, animal signals produced in canyons may be degraded by flutter echo. Receivers will hear not just the direct sound wave, but also the many reflected waves arriving at different times.

Suppression or detection of echoes as distinct sounds depends on their arrival times at the receiver relative to the original signal on its direct pathway (ΔT = delay in arrival time). The perception thresholds in arrival time delays appear to be similar across taxa (Snedden & Greenfield 1998; Litovsky et al. 1999; Dent & Dooling 2004). Reflections may be either summed with the original signal ($\Delta T < 0.4$ – 0.5 ms), suppressed in favour of the original signal (0.5 – 1.0 ms $< \Delta T < 8$ – 10 ms), or perceived as distinct echoes ($\Delta T > 8$ – 10 ms). The earliest arriving reflections can enhance the perceived loudness of the sound being created and mask or relocate the perceived source of a sound in humans and many nonhuman animals (Gardner 1968; Mills 1972; Dent & Dooling 2004). For arrival time delays in the middle range (0.5 – 10 ms), the reflections or echoes are suppressed, in favour of the signal on its direct path, which arrives first. This phenomenon is known as the precedence effect (Litovsky et al. 1999). Precedence effects and summing localization have been demonstrated in many nonhuman animals (Snedden & Greenfield 1998; Litovsky et al. 1999; Naguib & Wiley 2001; Bosch & Marquez 2002), and thresholds for summing in several bird species appear to be similar to those found in humans (Dent & Dooling 2004). Yet, given the short time intervals involved, reflections in urban canyons should rarely arrive in such close succession to the direct path signal as to invoke either summing localization or precedence effects. Instead, it is more likely that canyon reflections, even in relatively small canyons such as walled streets, will arrive beyond the receiver's echo threshold ($\Delta T > 8$ – 10 ms).

Reflections that arrive beyond the echo threshold are perceived as distinct sound images and typically do not interfere with sound localization (Dent & Dooling 2004). In addition, echoes approaching from the contralateral

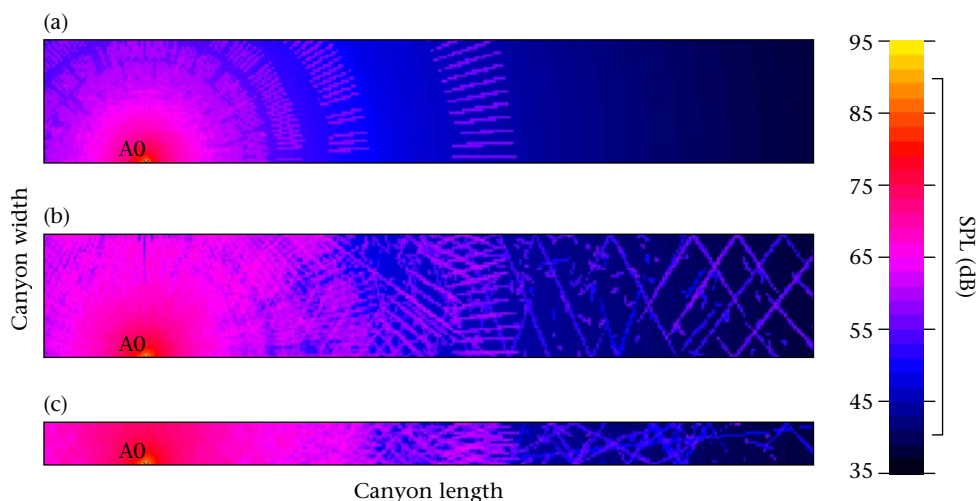


Figure 4. Wave reflections in: (a) an open field; (b) a small canyon $16 \times 300 \times 16$ m ($w \times l \times h$); and (c) a large canyon $48 \times 300 \times 48$ m. In (b) and (c), the source was 0.25 m from one wall, one-fourth of the way up the wall (4 and 16 m off the ground, respectively) and 40 m from one end of the canyon. Models were conceived in Catt-Acoustics (Gothenburg, Sweden) room acoustics ray tracing software, assuming that each canyon had brick walls and a concrete floor. The height of the receiver mapping plane was 1 m below the source. The source was omnidirectional at 90 db at each octave. For this study, 10 000 rays/octave were propagated for 1 s. All sound pressure level (SPL) measurements were taken at 2000 Hz.

side of the receiver, relative to the signaller, should be detected at much lower amplitude (Romer et al. 2002). This phenomenon of contralateral inhibition is thought by some to be a mechanism underlying the precedence effect (see above) (Romer et al. 2002). Nevertheless, the rapidity and high quantity of reflections present in flutter echo can still degrade the quality of a direct path signal. First, only some of the echoes in a canyon will arrive at the contralateral side of the receiver, particularly if a receiver is orienting lengthwise along the canyon. Second, reverberations can interfere by masking or blending signal elements (Wiley & Richards 1982; Slabbekoorn et al. 2002).

Animal signals are commonly produced as sequences of sounds, either repeated or variable. These successive sounds are increasingly likely to overlap with reflections of previous sounds as reverberation times increase. Reverberations have the strongest effects on signals with rapid amplitude modulation, often called trills, and those with rapid and repetitive changes in frequency, or rapid frequency modulation (Wiley & Richards 1982). The effect of flutter echo on animal communication signals should therefore be similar to effects of reverberations in forest environments (Wiley & Richards 1982). The chief difference being that reflections from the strongly reflective surfaces of built structures will generally retain a greater portion of the original sound energy, producing a stronger degrading effect than reflections from vegetation, which tends to be more absorbent.

Signals with narrow frequency bandwidths (e.g. pure tones) can sometimes benefit from reverberations, sound waves scattered by intervening vegetation or other structures (Slabbekoorn et al. 2002). For these pure tone signals, the reflected sound waves effectively make the signal higher in amplitude and longer (Slabbekoorn et al. 2002). Canyon birds with pure tone signals might make similar use of the reflections generated by flutter echo.

Flutter echo is enhanced by the wall separation, the height of canyon walls, and the smoothness of the reflective surfaces (Kang 2001; Iu & Li 2002; Fig. 4). That is, taller, narrower canyons produce a more pronounced flutter echo effect. Wider canyons result in longer delay times between the direct wave and the arrival of the reflected waves. Thus, the reflected waves are less likely to interfere with the direct pathway wave. Architectural acousticians have developed tools to plot sound waves and their reflections in canyons (rooms) of different dimensions and of different materials (Fig. 4) as well as to model signal properties after transmission through different canyon environments.

This leads to two testable predictions: (1) narrow canyons should show longer signal decay times but greater signal degradation due to flutter echo; (2) areas with higher densities of urban canyons will amplify traffic noise.

Urban-dwelling species with populations in canyon environments provide opportunities for comparative study. The peregrines of North America are the most conspicuous example, nesting in the large-scale high-rise apartment and business districts. In addition, the archetypal canyon bird species, the canyon wren, *Catherpes mexicanus*, is also a common resident of Mexican towns where walled gardens and streets constitute smaller-scale urban canyons (Howell & Webb 1995). Similarly, row house neighbourhoods in Baltimore, Maryland and other cities provide urban canyon environments with substantial breeding populations of native bird and mammal species (S. T. A. Pickett, J. M. Grove, P. M. Groffman, L. W. Band, C. G. Boone, G. S. Brush, W. R. Burch, Jr, M. L. Cadenasso, J. Hom, J. C. Jenkins, N. Law, C. H. Nilon, R. V. Pouyat, K. Szlavecz, P. S. Warren & M. A. Wilson, unpublished data). Geckos, lizards that use acoustic signals, also occupy similar rocky niches in both urban and nonurban

environments. The role of canyon acoustics in the communication systems has not been studied even in natural canyon systems. Since urban canyons are in many respects more accessible than natural ones, this provides an opportunity for urban research to model animal communication systems more generally.

Flutter echo in urban canyons is only one of the potential implications of architectural acoustics for urban animal communication systems. We note, however, that even the extensive body of work on urban acoustics does not yet provide explicit models or even 'rules-of-thumb' for many of the situations encountered in built environments. We strongly encourage future research to focus on sound transmission through areas with varying densities and configurations of built structures.

CONCLUSIONS

Our review found a small body of literature on the effects of urban acoustic environments on animal signalling behaviour. Animals may behaviourally alter signal characteristics such as minimum frequency (Slabbekoorn & Peet 2003) or amplitude (Brumm & Todt 2002); they might also shift the timing of signal to avoid masking noise (Bergen & Abs 1997). Animals lacking learning or other forms of phenotypic plasticity and that are forced to respond via natural selection to altered environments may be unable to adapt to the rapidly changing conditions generated by urbanization (Rabin & Greene 2002). However, there is a growing body of literature demonstrating rapid evolutionary change in animals occupying human-altered landscapes (St Louis & Barlow 1988; St Louis & Barlow 1991; Badyaev et al. 2000). Animal behaviourists have much to contribute towards understanding which species will be able to adapt to these novel environments and which will be forced to abandon them.

Many questions remain unanswered. For example, which species can compensate for the extremely elevated noise levels found in cities? What are the effects of prolonged signalling at high amplitudes on animal fitness? It is becoming well accepted that roads with higher traffic loads have negative impacts on reproductive success. It is still not clear, however, whether this effect is due to effects of noise per se or whether noise affects animal fitness indirectly by impairing the ability of animals to communicate effectively.

We highlight three relatively new areas for future research: spatial distribution of noise and acoustic divergence in animal signals, temporal variability in noise levels and effects on timing of animal signalling (e.g. dawn chorus), and the acoustics of canyons. For all of these topics, there are parallel phenomena found in natural systems, providing opportunities to make direct comparisons between signalling behaviour of the same species in both their native habitat and nearby urban habitat. Some phenomena, such as canyon acoustics, have yet to be fully explored in natural systems. Future work in this area can, therefore, contribute powerfully to the study of animal communication generally as well as to

conservation and management of urban wildlife. Many of the tools to address these questions, such as playbacks of anthropogenic noise, are already in use by biological researchers, but others will require or will benefit from interdisciplinary collaboration with acoustical engineers and architects. Figure 4 provides an example of the contribution of architectural acousticians to modelling acoustic transmission in built environments. Other opportunities for collaboration include quantifying spectral properties of anthropogenic noise, spatial mapping of noise contours in field settings and temporal mapping of noise.

Finally, animals that live in urban environments must communicate in all the usual ways to obtain mates, defend territories, or maintain flock dynamics, so understanding how they adapt their communication systems (and the constraints upon adaptation) to the acoustic features of these environments is a promising area of research. Increasing our understanding of these adaptations and constraints has the potential to generate new insights into the biology of communicating in general. We hope that this review will serve as a call to action, bringing more animal behaviour researchers into our ever-expanding urban areas.

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