Impact of a noise-polluted urban environment on the song frequencies of a cosmopolitan songbird, the Great Tit (*Parus major***), in Denmark**

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Low-frequency ambient noise is known to cause shifts in the song frequency of different species of songbirds, such as the Great Tit (*Parus major*). The present study was conducted to test the generality of these findings by measuring the distribution of energy across the spectrum of songs of the Great Tit. The studied individuals were either exposed to low-frequency ambient traffic noise in an urban environment (Copenhagen, Denmark) or not exposed to such an environment (the Strødam Reserve north of Copenhagen). A trend throughout all frequency-energy quartilesillustrated that the species sang at an elevated frequency in urban environments compared to rural ones, and that both the upperand lower-frequency-energy quartiles were signifcantly higher in the former.

1. Introduction

Urban encroachment on natural landscapes has been the source of both positive and negative effects on ecosystems surrounding populated areas (Marzluff *et al.* 2001, Francis *et al.* 2009, Francis *et al.* 2012). However urbanization produces a wide range of negative impacts, including habitat fragmentation, habitat loss, and various types of pollution. The above mentioned impacts of urbanization have many associated indirect consequences. One of the indirect effects of urban encroachment is the development of anthropogenic noise pollution associated with vehicle traffic, and other mechanical sources. Noise pollution has a far-reaching effect on a variety of both terrestrial and aquatic animals (Foote *et al.* 2004, Popper *et al.* 2002, Wright *et al.* 2007a, 2007b). However, only recent studies have considered the chronic exposure to such noise (Foote *et al.* 2004, Wright *et al.* 2007b, Francis *et al.* 2009, Francis *et al.* 2012). Noise exposure and the resulting stress have negative effects on the health, fitness, and ecological interactions of many different types of animals from humans to birds, and possibly even invertebrates (Wright *et al.* 2007b, Francis *et al.* 2009, Francis *et al.* 2012).

Until recently, low-frequency ambient noise produced in urban environments (for a power spectrum, see Bradbury & Vehrencamp 2011), was not known to have much of an effect on wildlife, especially territory-defending songbirds (Slabbekoorn & Smith 2002a, Slabbekoorn & Peet 2003, Slabbekoorn & Ripmeester 2008). However, it has recently been discovered that lowfrequency ambient noise associated with urban environments is correlated with an increase in the minimum frequency of songs in the Great Tit (*Parus major*; Slabbekoorn & Peet 2003). An increase in the minimum frequency could be a mechanism to compensate for masking effects from ambient noise. Masking has been shown to cause stress, and may reduce range size and clarity of acoustic communication in a variety of animals (Rheindt 2003, Brumm & Slabbekoorn 2005, Slabbekoorn & Ripmeester 2008, Wright *et al.* 2007a, Halfwerk *et al.* 2011a, 2011b).

Our study species, the Great Tit, is found in all the European countries, as well as in Asia and North Africa. This cosmopolitan species inhabits forests, shrublands, parks, and gardens. It primarily breeds in cavities, and readily breeds in artificial nest boxes (Gosler 1993). Song is used to defend a territory that can range from 0.2 to 4 ha, and is thought to signal male quality to females (Björklund *et al.* 1989). Great Tits can have up to eight song types depending on the individual, and songs consist of a repeated phrase composed of one to six elements (Gosler 1993). It has been suggested that habitat type and density of conspecifics can influence Great Tit song parameters, in large part because songs are learned from neighbors (Gosler 1993, Hunter & Krebs 1979, McGregor & Krebs 1982a). Songs differ between populations, to the extent that European Great Tits do not respond to Asian conspecifics (Gosler 1993). Those individuals that have similar, but not the same songs as the females' father, are preferentially chosen by females to males that sing an unfamiliar song type (Baker *et al.* 1987, McGregor & Krebs 1982b).

Song adaptation to urban environments by the Great Tit could have cascading effects on interand intra- specific interactions, could be a necessary adaptation to circumvent vocal masking by ambient noise to become a successful urban species, and/or possibly lead to a divergence between urban and rural populations due to assortative mating for preferred song types associated with specific habitat types (see Evans *et al.* 2009, Slabbekoorn & Smith 2002a) Slabbekoorn and Peet's (2003) finding that Great Tits sing at a higher pitch in urban environments might have been exceptional or specific only to the study population, but recent studies have supported these results (Baker 2006, Slabbekoorn & den Boer-Visser 2006, Mockford & Marshall 2009, Salaberria & Gil 2010, Hanna *et al.* 2011, Mockford *et al.* 2011). Whether the increase in lower song frequencies is a direct effect of background noise is still debated,

and other pathways to circumvent urban noise have been discussed. These include sound windows when background noises are of lesser interference (Bergens & Abs 1957, Fuller *et al.* 2007), or an elevation of song amplitude (Brumm 2004). The increase in frequency has also been suggested to be a side effect of an increase in amplitude (Nemeth & Brumm 2010) or an adaptation to the large reflecting surfaces characteristic of urban environments (Mockford *et al.* 2011).

The present study on frequency variation in the song of urban Danish Great Tits represents an important test of whether other areas within the species' range compliment previous results. Specifically, song frequencies of the focal species were compared between urban and rural areas. Based on the above-cited research, lower frequencies are expected in urban sites because of higher background noise.

2. Material and methods

2.1. Study sites

The city of Copenhagen, Denmark (55°40' N, 12°34'E) was used for the urban site, with five different sub-sites within the city used to make the recordings (Fig. 1). The sub-sites were parks consisting of mixed trees, shrubs and grass planes that were bordered on one or more sides by high to medium intensity of vehicle traffic (average number of vehicles per day for 2009 was $34,500 \pm 15,000$ SD median 30,000, range 19,900–52,600; Teknikog Miljøforvaltningen 2010). The Strødam Reserve (55°57'33" N, 12°16'44" E), located 36 km North of Copenhagen on the fringe of the large Grib Skov and the village of Gadevang, was used as the rural site (Fig. 1).

The reserve has one caretaker that lives fulltime on the property, but otherwise the reserve has limited access. The reserve consists of mixed forest and woodland with scattered bogs and ponds. The intensively-studied Great Tit population at this site breeds largely in nest boxes in the northern half (e.g., Otter *et al.* 1999, Peake *et al.* 2001, 2002, 2005, Blumenrath & Dabelsteen 2004). A road with diurnal commuter traffic is located on the border of the south end of the property. Therefore, all recordings (see below) were conducted

 Fig. 1. A map illustrating the rural and urban study sites where songs of Great Tits were recorded in Denmark.

within the northern half of the reserve where the traffic noise is negligible.

2.2. Experimental design

The sound recordings were made between April and May, 2009. The maximum recording distance from each singing bird was 10 m, but was less in most instances thus ensuring that both the lowest and highest song frequencies were above the background noise level. Each individual was recorded once, and only if it held a territory with a nest site and was over 50 m from the nearest displaying neighbor. The latter criteria was used to minimize the risk of pseudo-replication. Because population density may affect the level of agitation by conspecifics and may thus be a confounding factor (Nemeth & Brumm 2009, Hamao *et al.* 2011), all recordings were conducted after the dawn chorus (ca. 06:00 AM) to reduce the chance of increased song frequency because of agitation. For the same reason, most recordings considered individuals that were singing solo, i.e., not in a duel with conspecifics. An equal number of recordings were made at the urban and rural sites during congruent daylight hours and the recordings were distributed equally throughout the breeding season, because Great Tits increase their minimum song frequencies during the breeding season (Slabbekoorn & Ripmeester 2008). Each recording was obtained using a PortaDAT PDR1000 recorder and a Senneheiser MKH70 P48 directional microphone with a MZA 14 P48 preamplifier and a Rycote wind-buffer (frequency response of recording system: $140 - 22,000$ Hz \pm 3dB).

2.3. Song analysis

The song analysis was conducted using Avisoft-SASLab Pro2 (Avisoft Bioacoustics, Berlin, Germany), with the following settings: $FFT = 512$, Overlap = 0, Window = Hamming, Frame = 100 , and a resolution of 43Hz. From each recorded individual the three first complete phrases within a song containing all the elements from the phrase for a particular song type, and the background noise located immediately before, after, or between the first three phrases were analyzed to find the frequency-energy quartile breakdown and the peak frequency with maximum amplitude for each particular phrase. Therefore, four measures were applied: the lower (25%), mean (50%), and upper (75%) frequency-energy quartiles, and the peak frequency, for each separate phrase and the background noise from each recording. Before a song was analyzed it was band-pass filtered (FIR in Avisoft-SASLab Pro2) using default settings (number of taps 128, Hamming Window). The cut-off frequencies, as determined from spectrograms, were 2–300 Hz above and below the upper and lower frequencies of each particular song, respectively. The filtering removes the majority of background noise but does not affect the frequency range of song elements.

2.4. Statistical analysis

The statistical analysis was conducted using GraphPad InStat3 (GraphPad Software, Inc., San Diego, USA). The frequency measures for the first three phrases from each individual were averaged and used as statistical units. However, for the peak frequency, if one measurement differed appreciably from the other two measurements (i.e., if it mirrored a different frequency-energy quartile) then it was discarded from the average. Therefore, the statistical units for the song comparisons between the urban and rural sites were each individual's averaged frequency measures (urban *n* = 17 individuals, rural $n = 12$ individuals). Where background noise showed marked differences within a recording (such as cars stopped at traffic lights, compared to flowing traffic), the measurements from the differences were averaged. All statistical units were rounded to the nearest integer and tested for normality (Kolmogorov-Smirnov test) and variance homogeneity. If the requirements for parametric testing were fulfilled, an unpaired *t*-test was performed, and if not, a Mann-Whitney test was performed. All tests were two-tailed. Results are reported as mean \pm SD. Significance will be referred to in its statistical sense only, and was defined as $p \leq 0.05$.

Fig. 2. Song-frequency measures of the Great Tit in urban and rural sites. Mean values with standard deviations are shown.

3. Results

All the frequency-energy quartiles and the peak frequency of background noise were significantly lower in the urban than in the rural environment (Table 1). Half of the song measures varied significantly between the two enviroments. The lower (25%) and upper (75%) frequency-energy quartiles of the songs were significantly higher for the urban recordings, whereas the mean (50%) showed a non-significant increase in the urban sample, but the peak frequency did not vary significantly between the two environments (Table 1, Fig. 2). This indicates a shift in the urban birds towards higher song-frequency limits (upper and lower frequency energy quartiles) but not a higher frequency for the main energy of their songs as represented by the peak frequency.

4. Discussion

Only the first recorded song type per individual was used in the analysis, resulting in a random sampling effect. Frequency variation in the Great Tit song was greatly impacted by an urban setting, as the upper and lower frequency-energy quartiles were higher there than in the rural areas. However, the mean frequency-energy quartile and the peak

frequency were only marginally affected. These results partly corroborate those of Slabbekoorn and Peet (2003), who demonstrated that only the lower frequencies (range 2,820–3,770 Hz) were higher in urban settings. However, our results suggest that the lowest as well as the highest frequencies within a song were higher in urban birds (Fig. 2). Another study strongly supports a significant difference between frequencies for up to ten different species of forest and city birds (Slabbekoorn & Ripmeester 2008).

On the other hand, Baker (2006) found a nonsignificant correlation between mean frequency and ambient background noise in Australia. Significant difference in the peak frequency between urban and rural environments was not found in the present study, probably because this measure is not influenced by background noise or reflective surfaces (Blumenrath & Dabelsteen 2004). The peak frequency is undoubtedly essential for perceiving the timing patterns of singing, which is important for long-range communication (Otter *et al.* 1999, Peake *et al.* 2001, 2002, 2005). The present study showed that both Baker's (2006) and Slabbekoorn and Ripmeester's (2008) observed patterns could be represented by Danish Great Tits because there was a distinct tendency and partial significance across the frequency-energy quartiles, but no significant difference for the peak frequency.

Frequency	Urban	Rural	Statistics	df/n1.n2	P	
Background noise						
25% quartile	315 ± 75	482 ± 188	$t = 3.318$	27	0.0026	
50% quartile	779 ± 106	1.139 ± 626	$U = 48$	17.12	0.0161	
75% quartile	$1,464 \pm 157$	2.829 ± 1032	$t = 5.403$	27	< 0.0001	
Peak	133 ± 55	247 ± 138	$U = 48$	17.12	0.0161	
Song						
25% quartile	3.952 ± 354	3.687 ± 285	$U = 55$	17.12	0.038	
50% quartile	$4,311 \pm 309$	4.115 ± 283	$t = 1.742$	27	0.0928	
75% quartile	4.784 ± 534	4.407 ± 191	$t = 2.325$	27	0.0279	
Peak	$4,045 \pm 294$	4.072 ± 371	$U = 85$	17.12	0.4711	

Table 1. Frequency energy-quartile comparisons of the Great Tit song between urban and rural sites in Denmark. The numerical values for urban and rural sites are Hz ± SD. Test statistics refer to *t*- and Mann-Whitney *U* tests. n1 = number of urban individuals, n2 = Number of rural individuals.

Habitat influences song morphology and transmission, and it has been suggested that surfaces associated with forested areas, such as tree trunks, degrade songs more quickly than reflective surfaces associated with urban areas, such as buildings (Dabelsteen *et al.* 1993, Mockford *et al.* 2011). Therefore, the possibility exists that structural differences in habitat could influence song structures and frequencies, which is supported by song types for Great Tits having been found to have more similar characteristics in regards to habitat type than for geographical proximity. (Hunter & Krebs 1979, Mockford *et al.* 2011). The possibility also exists that not all the background noise could be filtered out during the analysis, which could have affected the results by artificially reducing the lower frequency-energy quartile of the city-dwelling birds.

However, this would only increase the significance of the present results, especially concerning the lowest frequencies, as most background noise was substantially below the song-frequency measurements (Table 1). Nemeth and Brumm (2010) have found that birds increase their song amplitude in the presence of noise, and it is possible that the frequency of songs correlates positively with song amplitude (Nemeth *et al*. 2012). Fig. 2 shows that urban birds sing at a higher frequency over the full range of their songs. This result contrasts with the findings of Slabbekoorn and Smith (2002b) or Slabbekoorn and Peet (2003), who found that there was no overall shift in frequency, but only an increase in the minimum frequency. In Madrid,

Spain, urban-noise maps were used to predict frequency variation, but no overall shift in frequency could be demonstrated, illustrating that only the minimum frequencies were significantly effected (Salaberria & Gil 2010).

The present findings are ecologically highly relevant. If there is a strong divergence between songs because of habitat differences, such as background noise or reflective surfaces, behavior could be altered or even speciation could occur (Slabbekoorn & Smith 2002a, Baker 2006, Slabbekoorn & Ripmeester 2008, Mockford & Marshall 2009, Nemeth & Brumm 2010, Mockford *et al.* 2011). Low frequencies incorporated into songs and masked by ambient noise, or reflected by large buildings and streets (Mockford *et al.* 2011), could have a negative effect on the fitness and reproduction of the Great Tit by falsely indicating that a male is of lesser quality (Slabbekoorn & Ripmeester 2008, Halfwerk *et al.* 2011b). The possibility also exists that low frequencies could be an honest signal of large body size and high competitive ability, and masking by ambient noise or blurring by reflective surfaces would be a handicap to these individuals (Redpath & Appleby 2004). Another common urban species, the Common Blackbird (*Turdus merula*), has shown a divergence from its rural counterpart by breeding earlier and at higher densities, by selecting different habitats and by exhibiting genetic differences (Evans *et al.* 2009, Slabbekoorn & Ripmeester 2008).

In conclusion, the urban environment seems to

influence the song of Great Tits in Copenhagen in comparison to a rural site, which is manifested in differences in song frequencies. It has recently been suggested that birds exhibit plasticity in song frequency in the presence of low-frequency noise (Tumer & Brainard 2007, Halfwerk & Slabbekoorn 2009, Verzijden *et al.* 2010), and further efforts to determine the limits of this plasticity are warranted. The structure of cities, including highly reflective surfaces of buildings in comparison to absorptive woodlands, could affect the song transmission and receivability, but whether the effects of reflective surfaces are positive or negative is still debatable (Nemeth *et al.* 2006, Warren *et al.* 2006, Mockford *et al.* 2011). The implications of diverging songs between urban and rural areas could have profound effects on the evolution of cosmopolitan species. Assortative mating, because of song differences, could lead to shifts in population behavior and life histories, or even genetic divergence.

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Effekterna av en bullerförorenad stadsmiljö på sångfrekvenser hos talgoxar i Danmark

Lågfrekvent buller har visats orsaka förändringar i sångfrekvensen hos olika arter av sångfåglar, t.ex. hos talgoxe (*Parus major*). Denna studie genomfördes för att testa hur generella dessa fynd är. I studien mätte vi fördelningen av energi över hela spektrumet av sång hos sådana talgoxar som utsatts för lågfrekvent, omgivande trafikbuller (Köpenhamn, Danmark) jämfört med artfränder som inte utsatts för sådant buller (Strødamreservatet norr om Köpenhamn). Vi konstaterade att trenden i samtliga frekvenskvartiler var en förhöjd sångfrekvens hos talgoxar i urbana miljöer jämfört med de skogslevande fåglarna i kontrollgruppen. I både övre och undre kvartilen var sångfrekvensen signifikant högre i urbana områden.

References

- Baker, M. C., McGregor, P. K. & Krebs, J. R. 1987: Sexual response of female Great Tits to local and distant songs. — Ornis Scandinavica 18: 186–188.
- Baker, M. C. 2006: Differentiation of mating vocalizations in birds: acoustic features in mainland and island populations and evidence of habitat-dependent selection of songs. — Ethology 112: 757–771.
- Bergens, F. & Abs, M. 1997: Etho-ecological study of the singing activity of the Blue Tit (*Parus caeruleus*), Great Tit (*Parus major*) and Chaffinch (*Fringilla coelebs*). — Journal of Ornithology 138: 451–467.
- Björklund, M., Westman, B. & Allander, K. 1989: Song in Swedish Great Tits: intra- or intersexual communication. — Behaviour 111: 257–269.
- Blumenrath, S. H., & Dabelsteen, T. 2004: Degradation of Great Tit (Parus major) song before and after foliation: implications for vocal communication in a deciduous forest. — Behaviour 141: 935–958.
- Bradbury, J.W. & Vehrencamp, S.L. 2011. Principles of animal communication, $2nd$ ed., \sim Sinauer Associates Inc., Sunderland.
- 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 Behaviour 35: 151–209.
- Dabelsteen, T., Larsen, O. N. & Pedersen, S. B. 1993: Habitat-induced degradation of sound signals – quantifying the effects of communication sounds and bird location on blur ratio, excess attenuation, and signal-tonoise ration in Blackbird song. — Journal of the Acoustical Society of America 93: 2206–2220.
- Evans, K. L., Gaston K. L., Frantz, A. C., Simeoni, M., Sharp, S. P., McGowan, A., Dawson, D. A., Walasz, K., Partecke, J., Burke, T., & Hatchwell, B.J. 2009: Independent colonization of multiple urban centres by a formerly forest specialist bird species. — Proceedings of the Royal Society of London Ser. B 276: 2403– 2410.
- Foote, A. D., Osborne, R. W., & Hoelzel, A. R. 2004: Whale-call response to masking boat noise. — Nature 428: 910.
- Francis, C. D., Ortega, C. P., & Cruz, A. 2009: Noise pollution changes avian communities and species interactions. — Current Biology 19: 1415–1419.
- Francis, C. D, Kleist, N. J., Ortega, C. P. & Cruz, A. 2012: Noise pollution alters ecological services: enhanced pollination and disrupted seed dispersal. — Proceedings of the Royal Society of London Ser. B 279: 2727–2735
- Fuller, R. A, Warren, P. H., & Gaston, K. J. 2007: Daytime noise predicts nocturnal singing in urban robins. — Biology Letters 3: 368–370.
- Gosler, A. 1993: The Great Tit. Hamlyn, London. 128 pp.
- 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., Both, S., Buikxa, J., van der Velde, M., Komdeur, J., ten Cate, C. & Slabbekoorn, H. 2011b: Low frequency songs lose their potency in noisy urban conditions. — Proceedings of the National Academy of Sciences 108: 14549–14554.
- 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.
- Hanna, D., Blouin-Demers, G., Wilson, D.R. & Mennell, D.J. 2011. Anthropogenic noise affects song structure in red-winged blackbirds (*Agelaius phoeniceus*). — Journal of experimental Biology 214: 3549–3556.
- Hunter, M. L. & Krebs, J. R. 1979: Geographical variation in the song of the Great Tit (*Parus major*) in relation to ecological factors. — Journal of Animal Ecology 48: 759–785.
- Marzluff, J. M., Bowman, R. & Donnelly, R. (eds.) 2001: Avian Ecology and Conservation in an Urbanizing World. — Kluwer Academic Publishing Group, Dordrecht.
- McGregor, P. K. & Krebs, J. R. 1982a: 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. 1982b. Mating and song types in the Great Tit. — Nature 297: 60–61.
- Mockford, E. J. & Marshall, R. C. 2009: Effects of urban noise on the song and response behaviour in Great Tits. — Proceedings of the Royal Society of London Ser. B 276: 2979–2985.
- Mockford, E. J. Marshall, R. C. & Dabelsteen, T. 2011: Degradation of rural and urban Great Tit song: testing transmission efficiency. — PloS ONE 6: e28242
- Nemeth, E., & Brumm, H. 2009: Blackbirds sing higherpitched 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., Dabelsteen, T., Pedersen, S. B. & Winkler, H. 2006: Rainforests as concert halls for birds: Are reverberations improving sound transmission of long song elements? — Journal of the Acoustical Society of America 119: 620–626.
- Nemeth, E., Zollinger, S. A., & Brumm, H. 2012: Effect sizes and the integrative understanding of urban bird song: a reply to Slabbekoorn *et al.* — American Naturalist 180: 146–152.
- Otter, K., McGregor, P. K., Terry, A. M. R., Burford, F. R.

L., Peak, T. M. & Dabelsteen, T. 1999: Do female Great Tits *(Parus major*) assess males by eavesdropping? A field study using interactive song playback. — Proceedings of the Royal Society of London Ser. B 266: 1305–1309.

- Peake, T. M., Terry, A. M. R., McGregor, P. K. & Dabelsteen, T. 2001: Male Great Tits eavesdrop on simulated male-to-male vocal interactions. — Proceedings of the Royal Society of London Ser. B 268: 1183– 1187.
- Peake, T. M., Terry, A. M. R., McGregor, P. K. & Dabelsteen, T. 2002: Do Great Tits assess rivals by combining direct experience with information gathered by eavesdropping? — Proceedings of the Royal Society of London Ser. B 269: 1925–1929.
- Peake, T. M., Matessi, G., McGregor, P. K. & Dabelsteen, T. 2005: Song type matching, song type switch and eavesdropping in male Great Tits. — Animal Behaviour 69: 1063–1068.
- Popper, A. N. 2002: Impact of anthropogenic sounds on fishes. — Journal of the Acoustical Society of America 112: 2431.
- Redpath, S. & Appleby, B. 2004: The hooting of Tawny Owls: structure and function. — In Nature's Music – the science of birdsong (eds. Marler, P. & Slabbekoorn, H.): 64. Elsevier Academic Press, San Diego.
- Rheindt, F. E. 2003: The impact of roads on birds: does song frequency play a role in determining susceptibility to noise pollution? — Journal of Ornithology, 144, 295–306.
- 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.
- Slabbekoorn, H. & den Boer-Visser, A. 2006. Cities change the songs of birds. — Current Biology 16: 2326–2331.
- 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: Bird song, ecology and speciation. — Philosophical Transactions of the Royal Society of London Ser. B 357: 493–503.
- Slabbekoorn, H., & Smith T. B. 2002b: Habitat-dependent song divergence in the Little Greenbul: an analysis of environmental selection pressures on acoustic signals. — Evolution, 56, 1849–1858.
- Teknik- og Miljøforvaltningen. 2010: Trafiktal og andre faerdselsundersøgelser 2005–2009. — Teknik- og Miljøforvaltningen Center for Trafik, København. 43pp. (In Danish)
- Tumer, E.C. & Brainard, M. S. 2007: Performance variability enables adaptive plasticity of "crystallized" adult birdsong. — Nature 450: 1240–1244.
- Verzijden, M. N., Ripmeester E. A. P., Ohms, V. R., Snel-

derwaard, P. & Slabbekoorn, H. 2010: Immediate spectral flexibility in singing Chiffchaffs during experimental exposure to highway noise. — Journal of Experimental Biology, 213, 2575–2581.

- Warren, P. S., Katti, M., Ermann, M., & Brazel, A. 2006: Urban bioacoustics: it's not just noise. — Animal Behaviour 71: 491–502.
- Wright, A. J., Soto, N. A., Baldwin, A. L., Bateson, M., Beale, C. M., Clark, C., Deak, T., Edwards, E. F., Fernandez, A., Godinho, A., Hatch, L. T., Kakuschke, A., Lasseau, D., Martineau, D., Romero, L. M., Weilgart, L. S., Wintle, B. A., Notarbartolo-di-Sciara, G., &

Martin, V. 2007a: Do marine mammals experience stress related to anthropogenic noise? — International Journal of Comparative Psychology 20: 274–316.

Wright, A. J., Soto, N. A., Baldwin, A. L., Bateson, M., Beale, C. M., Clark, C., Deak, T., Edwards, E. F., Fernandez, A., Godinho, A., Hatch, L. T., Kakuschke, A., Lasseau, D., Martineau, D., Romero, L. M., Weilgart, L. S., Wintle, B. A., Notarbartolo-di-Sciara, G., & Martin, V. 2007b: Anthropogenic noise as a stressor in animals: a multidisciplinary perspective. — International Journal of Comparative Psychology 20: 250– 273.