

BIRD SONG: THE INTERPLAY BETWEEN URBAN NOISE AND SEXUAL SELECTION

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ABSTRACT

Ambient noise is present almost everywhere in the biosphere. Because background noise can potentially mask the acoustic signals that many animals use to communicate, many species may face a problem when trying to get their messages through noisy environments. Here I reviewed some of the strategies that birds use to deal with ambient noise, and related this information to the possible consequences that may result when birds use their songs in the context of sexual selection, a process that has been widely acknowledged as a main force shaping the evolution of bird songs. I suggest that, depending on the species-specific nature of the sexual selection process in relation to the sender songs, ambient noise may impair the probability of reproduction to different degrees in different species. For instance, species whose songs are effective at communicating in noisy environments, but at the same time render the sender a lowered probability of attracting a mate and defending a territory, may face a greater reduction in reproductive success than if the sender's songs fail in one aspect of sexual selection (e.g. female attraction), but not in the other (e.g. male-male competition). However, more studies are needed if we are to obtain a clearer picture of the possible outcome that may result from the interaction between ambient noise and sexual selection. Some questions that need answers are: to what extent ambient noise impairs the processes of sexual selection in nature? Are sub-oscines equally vulnerable than oscines?

Keywords: Bird song, sexual selection, noise, anthropogenic.

RESUMO

CANTO DE AVES: INTERAÇÃO ENTRE A POLUIÇÃO SONORA URBANA E SELEÇÃO SEXUAL. A poluição sonora urbana está presente em quase toda a biosfera. Uma vez que o ruído pode mascarar os sinais acústicos que muitos animais usam para a comunicação, várias espécies poderiam encontrar-se frente ao problema de enviar suas mensagens em um ambiente sonoramente poluído. Aqui faço uma revisão sobre algumas estratégias que as aves usam para enfrentar este problema e relaciono esta informação com as possíveis conseqüências que poderiam resultar quando as aves usam seus cantos no contexto da seleção sexual, um processo que tem sido amplamente reconhecido como uma força maior que modela a evolução do canto nas aves. Sugiro que, dependendo da natureza espécie - específica dos processos de seleção sexual em relação aos cantos do emissor, o ruído ambiental poderia estar afetando a possibilidade de reprodução em diferentes graus variáveis de acordo com as espécies. Por exemplo, aquelas espécies em que os cantos são efetivos para comunicar-se em ambientes barulhentos, porém ao mesmo tempo diminuem a probabilidade de o emissor atrair uma parceira e defender um território poderiam enfrentar uma redução maior no êxito reprodutivo que se o canto do emissor falha em relação a um aspecto de seleção sexual (ex., atração da fêmea), porém não em outro (ex., competição entre machos). São necessários outros estudos se quisermos obter uma imagem mais clara das possíveis conseqüências que poderiam resultar da interação entre a poluição sonora do ambiente e a seleção sexual. Algumas das perguntas que precisam ser respondidas são: Até que ponto a poluição sonora ambiental prejudica os processos de seleção sexual na natureza? Os suboscines são tão vulneráveis quanto os oscines?

Palavras-chave: Canto das aves, seleção sexual, poluição sonora, antropogênico.

RESUMEN

CANTO DE AVES: INTERACCIÓN ENTRE EL RUIDO URBANO Y SELECCIÓN SEXUAL. El ruido ambiental está presente casi en todos lugares en la biosfera. Debido a que el ruido puede potencialmente enmascarar las señales acústicas que muchos animales usan para comunicarse, varias especies podrían encontrarse con un problema al tratar de transmitir sus mensajes a través de ambientes ruidosos. Aquí hago una revisión de algunas de las estrategias que las aves usan para lidiar con el ruido ambiental y relaciono esta información con las posibles consecuencias que podrían resultar cuando las aves usan sus cantos en el contexto de selección sexual, un proceso que ha sido reconocido ampliamente como una fuerza mayor que moldea la evolución del canto en las aves. Sugiero que, dependiendo de la naturaleza especie-específica de los procesos de selección sexual en relación a los cantos del emisor, el ruido ambiental podría estar menoscabando las probabilidades de reproducción en diferentes grados en distintas especies. Por ejemplo, aquellas especies cuyos cantos son efectivos para comunicar en ambientes ruidosos, pero que al mismo tiempo disminuyen la probabilidad del emisor de atraer una pareja y defender un territorio, podrían enfrentar una reducción mayor en éxito reproductivo que si el canto del emisor falla en un aspecto de selección sexual (p. ej. atracción de la hembra), pero no en otro (p. ej. competencia entre machos). Más estudios son necesarios si queremos obtener una imagen más clara de las posibles consecuencias que podrían resultar de la interacción entre el ruido ambiental y la selección sexual. Algunas de las preguntas que necesitan respuestas son: ¿hasta qué punto el ruido ambiental perjudica los procesos de selección sexual en la naturaleza? ¿Son los sub-oscinos igual de vulnerables que los oscinos?

Palabras clave: Canto de aves, selección sexual, ruido, antropogénico.

INTRODUCTION

For obvious reasons most research on the effects of ambient noise on behavior and physiology has been carried out in humans (e.g. Hockey 1970, Evans et al, 2001, Melamed & Bruhis 1996, Stansfeld *et al.* 2005, Muzet 2007). On the other hand, and because ambient noise can disrupt acoustic communication, much research on non-humans has focused on animals that communicate using acoustic signals and on the effects of this form of pollution on these signals (e.g. frogs, Narins *et al.* 2004, Witte *et al.* 2005, Feng *et al.* 2006, Feng & Narins 2008; fishes, Scholik & Yan 2001; primates, Brumm *et al.* 2004). In this field much attention in the recent years has been given to birds (reviews in Brumm & Slabbekoorn 2005, Patricelli & Bickley 2006). In part, this is because biologists have long been interested in trying to understand the function and origin of birdsong diversity and ambient noise can be viewed as one factor influencing song variation. The evolution of birdsong, however, has been most studied invoking processes of sexual selection (i.e. mate choice and competition for a mate, Catchpole & Slater 2008), and it is clear that many important aspects of the life of birds, some of which are related to sexual selection, are mediated by acoustic signals. For instance, birds may use

vocalizations (i.e. calls or songs) to interact with their offspring (Kilner & Johnston 1997), maintain group cohesion (Ritchison 1983) and pair bonds (Swaddle & Page 2007), to attract a mate (review in Catchpole & Slater 2008), stimulate it for reproduction (Kroodsma 1976), and compete with other individuals of the same sex for a territory (review in Catchpole & Slater 2008), a prerequisite in many species before males can attract a mate. All these processes can have a direct or indirect effect on fitness and it thus becomes relevant to study the possible effects of disrupting factors (such as urban noise, see below) both on acoustic signals and on attributes of populations or communities (e.g. population density, diversity).

Ambient noise may disrupt acoustic communication, especially when its frequency overlaps that of the acoustic signal, and when the signal to noise ratio (SNR) is below the detection threshold of the receiver (Marten & Marler 1977). Therefore, urban noise may represent a relatively novel factor that birds may have to deal with if they are to communicate and reproduce. One strategy that birds may use to communicate in noisy locations is adjusting their vocalizations to different noise levels so as to make their signals stand out more, and thus ambient noise may potentially influence birdsong structure. Noise is generally understood as any sound that interferes with

the proper transmission of an acoustic signal, from sender to receiver (Brumm & Slabbekoorn 2005). If we bear this in mind, it will not be surprising to see that ambient noise is ubiquitous and also common in natural habitats (e.g. wind, waterfalls, sounds from other animals), and animals that use acoustic signals to communicate, and live in natural settings, may have had enough time for such sources of ambient noise to be considered as an important selective factor shaping the evolution of their vocalizations.

In this review, I first explore the different strategies that may help birds to deal with ambient noise in general and urban noise in particular, and give examples of how these strategies lead to different changes in song attributes. In the second part, I consider how these changes in song characteristics may interact with intra- and inter-sexual selection processes with potential fitness consequences.

THE STRATEGIES

Birds can change or adjust their vocalizations in relation to noise levels in different ways. Some of the most studied strategies that birds may use to avoid acoustic interference from noise are related to adjusting the frequency, temporal or amplitude related parameters of song. An additional strategy that birds may use to deal with noise, and that has received some attention, refers to shifting the timing of singing. These vocal adjustments can be “short term adaptations” or “long term adaptations” (Brumm & Slabbekoorn 2005). The first case refers to changes that are based on plasticity, whereby a singing bird is able to adjust its vocalization in response to current levels of noise. On the other hand, long term adaptations are related to evolutionary change whereby, in this case, noise is a selecting factor that leads some birds that sing in a particular way to be favored by selection while others are selected against. There is a third intermediate way in which birds can achieve vocal adjustments. That is, by means of song ontogeny and learning (Slabbekoorn & Peet 2003, Wood & Yezerinac 2006). For instance, if young birds learn only those songs that, in a noisy environment, can hear (e.g. high pitched songs, see below), they may end up singing only high pitched songs, even if the tutor sang also low pitched songs. This could result in a long term vocal adjustment based on song development. Although the term

“adaptation” is generally used to mean evolutionary change, in this work I will use it simply to refer both to short term and long term adjustments of vocalizations to different levels of noise.

ADJUSTMENTS IN FREQUENCY RELATED PARAMETERS

The first work reporting that birds could change the frequency of their songs in relation to different levels of ambient noise, in this case urban noise, was that of Slabbekoorn & Peet (2003). They studied a population of great tits (*Parus major*) in the Dutch city of Leiden, and found a positive correlation between the minimum frequency of their songs and the level of urban noise, meaning that those birds living in noisier places sang songs with a higher pitch than those birds in quieter areas. This result was later confirmed in a comparison among different populations (Slabbekoorn & den Boer-Visser (2006). These authors found that great tits in ten different capital cities across Europe sing higher pitched songs than their counterparts in nearby forests, which is consistent with the idea that great tits sing higher pitched songs in noisy locations as a way to evade noise masking. As the energy of urban noise is concentrated in low frequencies, singing higher pitched songs, well above this frequency, may aid birds to avoid noise masking.

This correlation between song frequency and noise level has also been found in song sparrows (*Melospiza melodia*, Wood & Yezerinac 2006), house finches (*Carpodacus mexicanus*, Fernández-Jurizic *et al.* 2005), and chaffinches (*Fringilla coelebs*, Brumm & Slater 2006). The correlation found in this last study, however, should be taken cautiously because it depended on a single bird that was considered as an outlier. Another important common result among all these studies is that, while birds were shown to sing songs with a higher minimum frequency in noisy environments, this correlation was not found for the maximum frequency of their songs. In laboratory experiments, Lohr *et al.* (2003) showed that sounds with greater bandwidth are more difficult to detect. Thus, increasing the minimum frequency, but not the maximum frequency, in noisy conditions may render songs more easily detected. These studies (Slabbekoorn & Peet 2003, Wood & Yezerinac 2006, Fernández-Jurizic *et al.* 2005, Brumm & Slater

2006) were all correlative, and it is not clear whether the reported vocal adjustments are short term or long term changes. However, in the case of great tits (Slabbekoorn & Peet 2003), it is suggestive for a long term adaptation that some males at noisy places kept singing high pitched songs even during quiet periods. Given that all these four species are oscines, in which song ontogeny involves a learning process, it is possible that the observed vocal adjustments are the result of changes during song ontogeny (Slabbekoorn & Peet 2003). In another study, aimed at elucidating the influence of sound transmission on song structure in structurally different habitats, Slabbekoorn *et al.* (2007) compared the minimum frequency of dark-eyed juncos (*Junco hyemalis*) songs from an urban population and those from different forest populations. They found that the minimum frequency of songs recorded in the urban population was higher than those recorded in the forests populations. Assuming that the noise levels were higher in the urban habitat, this result is consistent with the idea that dark-eyed juncos sing at a higher pitch in noisy environment to escape noise masking. So far, the capability for a plastic and short term vocal adjustment to current noise intensities has been demonstrated for the Bengalese finch (*Lonchura striata var. domestica*, Tumer & Brainard 2007). In this laboratory study, Tumer and Brainard used a reinforcement contingency procedure by which Bengalese finches were conditioned to increase or decrease the fundamental frequency of single syllables within a song. These authors applied bursts of white noise to particular targeted syllables, and found that these syllables were the only ones whose frequency was modified within the song. Thus, this study shows a remarkable capacity of Bengalese finches to select only those syllables that are being masked by noise and modify their frequency. It is possible that other avian species may use similar “syllable pitch plasticity” capabilities to deal with ambient noise in natural settings. This remains an interesting possibility to be studied in the future.

ADJUSTMENTS IN AMPLITUDE RELATED PARAMETERS

Perhaps the most obvious way in which animals that use sounds to communicate can override the masking effects of noise is by vocalizing loudly (i.e.

with high amplitude). The Lombard effect, an increase in vocalization amplitude or intensity in response to background noise, has been most extensively studied in humans (e.g. Herbert *et al.* 1989, Scott & Lang 1992, Junqua 1993, Patel & Schell 2008), and has also been shown to occur in birds in laboratory and natural conditions (see below). Measuring amplitude in sound signals in the field is a complex task because amplitude level will depend on a number of factors. For instance, the registered amplitude level will vary with the relative position and angle of the microphone in relation to the source of sound (e.g. the beak of the bird) and with the distance of the source of sound to the microphone. It is, perhaps, because of these technical difficulties that measuring birdsong amplitude in the field was not reported until the pioneering work of Henrik Brumm at the beginning of this century (Brumm 2004). However, experiments to study the Lombard effect in birds, in more controlled laboratory conditions, were carried out earlier (e.g. with the budgerigar, *Melopsittacus undulatus*, Manabe *et al.* 1997; with the zebra finch, *Taeniopygia guttata*, Cynx *et al.* 1998; with the nightingale, Brumm & Todt 2002). These laboratory studies showed that birds, like humans, are capable of voluntary modification of the amplitude in their songs so as to make their vocalizations more audible in noisy conditions. The question then arises whether free living birds also make use of this capacity to avoid noise masking? The work by Brumm (2004) demonstrated that free living nightingales, living in Berlin, sing songs with higher amplitude in places with more urban noise than in quieter ones. By comparing the amplitude of songs in three birds on two different days (one at the weekend, the other a working day), he also showed that a particular individual is capable of adjusting the amplitude level of its songs according to different levels of noise on those different days, thus confirming the ability of single individuals to modulate the amplitude of their songs, a short term and plastic adaptation.

In this section it is worth noting the study by Wood & Yezerinac (2006) with song sparrows. They found, not only that the lowest frequency of song sparrows songs was higher with higher levels of urban noise, but also that there are modifications in the amplitude within the songs. In particular, they showed that song sparrows in noisy places produce songs with

a relatively higher energy (amplitude) level in the upper frequency range (4-9 kHz) of their songs than in the lower frequency range (1-4 kHz). However, the mechanism by which song sparrows achieve this, or whether this is a short term or long term adaptation, is still unclear.

ADJUSTMENTS IN TEMPORAL ATTRIBUTES OF SONG

The evidence for, and patterns of, temporal adjustments in songs in relation to urban noise is less clear than that found with frequency or amplitude related song parameters. Theoretically, birds should increase the length of their vocalizations (i.e. increase the number of syllables or elements), or sing with increased serial redundancy (i.e. sing the same song type several times before switching to another song type) in noisy environments, because this would increase the probability that the signal is detected (see Fernández-Juricic *et al.* 2005, Brumm & Slater 2006). This is exactly what Brumm & Slater (2006) found with a population of chaffinches (*Fringilla coelebs*) living in the wild. They showed that chaffinches living near natural sources of noise (i.e. waterfalls and torrents) sang longer bouts of the same song before switching to another type. This suggests that, in noisy environments, chaffinches sing the same song type more times than in quiet locations, because this increases the probability that the message will be detected by a potential receiver. In the other hand, and contrary to expectations, house finches sang shorter songs (i.e. songs with fewer syllables) in noisy environments (Fernández-Juricic *et al.* 2005). It is unclear why house finches sing shorter songs in noisy locations. One possibility is that, if house finches also sing higher amplitude songs with increasing levels of urban noise, they face a trade-off between song amplitude and number of notes per song to optimize the energy that will be used during the breeding season (Fernández-Juricic *et al.* 2005), or could also be a short-term interaction, so that performance constraints oblige the two to be negatively related. The study of Wood & Yezerinac (2006) with song sparrows, showed a non-significant tendency ($P = 0.13$) for songs to have fewer notes in noisy places than in quiet ones.

Slabbekoorn *et al.* (2007), compared different

song attributes of dark-eyed juncos (*J. hyemalis*) among different forest populations and an urban one, and found no significant differences in song length in these populations. Slabbekoorn & den Boer-Visser (2006) studied in more detail the effects of urban noise on great tit songs, but this time comparing different populations. They compared the songs of birds from ten different European capitals with songs recorded in nearby forests close to these cities, and found that great tits in cities sing rare song types consisting of one, five or more notes, whereas great tits in forests sing more song types (the so-called common song types) composed of 2, 3 or 4 notes. Songs from city birds were shorter and involved shorter inter-song intervals than those from forest birds. Additionally, urban songs had shorter first notes than forest songs, resulting in that these songs were produced in a hurried-fashion. Slabbekoorn & den Boer-Visser (2006) suggest that this temporal shift in the first note may be in part related to different structures in habitat, where more open habitats (like urban areas), relative to more close habitats (like forests), favor the use of acoustic signals produced as repetition of short elements (Slabbekoorn & den Boer-Visser 2006). Clearly, more studies are needed to assess whether changing temporal features of songs is a general strategy that birds use to cope with noise.

From all these studies, and regardless of whether this refers to a short term or a long term adaptation, it seems that a variety of songbirds may increase the amplitude and minimum frequency of their songs to cope with ambient noise. On the other hand, studies addressing changes in song temporal parameters in relation to noise intensity have yielded different results, some of which may be confused with other factors that may as well influence song structure, such as different habitat structures (i.e. open and closed habitats).

SHIFTS IN TIMING

Another way in which animals may cope with ambient noise is by avoiding signaling during the time at which noise is more prevalent. This phenomenon has been addressed both considering natural and anthropogenic sources of noise, and for intraspecific and interspecific interactions (Cody & Brown 1969, Ficken *et al.* 1974, Popp *et al.* 1985,

Waserman 1977, Brumm 2006, Fuller *et al.* 2007). For instance, Ficken *et al.* (1974) found an interesting temporal singing pattern between two different bird species, the red-eyed vireo (*Vireo olivaceus*) and the least flycatcher (*Empidonax minimus*), both of which sing within the same frequency range. Ficken and her collaborators showed that flycatchers tend not to start singing if a vireo is already singing, while the opposite pattern was not so strong. They also showed that the least flycatcher, but not the vireo, tended to “insert” its songs between different songs of the other species. Thus, it seems that the flycatcher plays a more active role in avoiding acoustic interference by vireo songs, rather than vice versa. This can be explained if the length of the songs is considered. The songs of the red-eyed vireo are longer than those of the least flycatcher. Therefore, there is a higher probability that, if the two species sing at the same time, the entire song of a flycatcher will be masked by the song of a vireo, while only a fraction of the vireo song would be masked by the flycatcher song (Ficken *et al.* 1974). Experiments to study shifts in timing to avoid temporal overlap between acoustic signals from different individuals have also been conducted (Popp *et al.* 1985, Brumm 2006). For instance, the study by Brumm addressed the responses of nightingales (*Luscinia megarhynchos*) to song playback of six different species that breed in sympatry with nightingales, and found that this species avoids temporally overlapping its songs with those of the other species, by singing during the silent intervals between the heterospecific songs.

In this section it is worth noting a study by Planqué & Slabbekoorn (2008). They studied 20 different bird species in a neotropical rain forest (in Peru) and considered two different strategies that birds may use to cope with noise: avoiding temporal overlap and avoiding frequency overlap. As neotropical forests have high biodiversity, this also means that these habitats are very noisy and acoustically complex, with much of the noise coming from different bird species. Thus, these authors predicted that birds should exhibit temporal and frequency avoidance between members of different species. Furthermore, as the acoustic space is limited, they predicted a negative relationship between temporal and spectral overlap; that is, species that show a high degree of temporal overlap should show a low degree of frequency

overlap, and vice versa. The results showed that some species may avoid temporal overlap with other species, especially if they sing within the most used frequency range of the bird community, but they did not find a general negative trend between frequency overlap and temporal overlap.

From all these studies cited above, it becomes apparent that many bird species have adopted a “shift in timing” strategy to avoid temporal overlap between their acoustic signal and those of other individuals. All these studies consider a short temporal scale, whereby birds take advantage of small time-windows of silence to sing their own songs. An effect of ambient noise on a larger temporal scale is also possible, as demonstrated by Fuller *et al.* (2007). These authors studied a population of European robins (*Erithacus rubecula*), and demonstrated that robins living in areas with high levels of anthropogenic noise during the day sing at night. Furthermore, they showed that the effect of noise was more important than the possible effect of the high ambient light in urban areas at night. Their results suggest that robins have adopted a major change in the time they sing (i.e. a change from singing during the day to singing at night) to overcome the acoustic interference of urban noise.

THE INTERPLAY BETWEEN AMBIENT NOISE AND SEXUAL SELECTION

As stated in the introduction, it has been realized that sexual selection has played an important role in shaping the structure of bird song (review in Catchpole & Slater 2008). It has been suggested that long and complex songs may have evolved via inter-sexual selection (i.e. female mate choice), while short and more simple songs may have done so via intra-sexual selection (i.e. male-male competition) (Catchpole 1982). Ambient noise may disrupt vocal communication and impair the process of sexual selection. If birds change their songs to cope with background noise, and if these changed songs are less preferred by females or are less effective for obtaining or maintaining a territory, the reproductive success of birds may be negatively affected. Traffic noise has been argued to probably be the most important cause for a reduction in densities of bird species near roads and high ways (Reijnen &

Foppen 1994, Reijnen *et al.* 1995). However, to the best of my knowledge, there are as yet no studies directly addressing how urban noise may impair the process of sexual selection in nature. Laboratory evidence indicates that white noise can erode female preferences in the zebra finches (Swaddle & Page 2007); that is, females showed a decreased preference for their mate in noisy conditions. Swaddle & Page (2007) argue that this could have occurred because white noise may have masked or distorted the contact calls of the (male) mate, or because the female could no longer recognize her mate.

If different strategies to deal with noise mean that this type of pollution hampers the process of sexual selection, this may be more evident in species that, as part of those strategies, change the structure of their songs (i.e. frequency or temporal parameters). In this section I briefly review the evidence of sexual selection processes operating in those few species that have been shown to change the structure of their songs in relation to ambient noise. However, as more information is needed to obtain insight into how ambient noise may affect the processes of sexual selection, part of this section is necessarily speculative. I end up citing studies from other species that may give a general panorama of the possible problems that birds may face while trying to attract a mate or compete with other males for a territory in noisy environments.

PARTICULAR CASES

THE GREAT TIT

Krebs *et al.* (1978) studied the function of the song repertoire (number of different types of songs) in great tits in UK. They removed from their territories male great tits and replaced them with loudspeakers. Some of these speakers broadcast many different song types (a large repertoire), while others broadcast only a small repertoire. They clearly showed that new males occupied the territories “defended” by small repertoires well before those in which the large repertoires were broadcast. This suggests that great tits singing large song repertoires may be more efficient at obtaining and defending a territory, a prerequisite for many passerines before they can attract a female and reproduce. So far, there are no studies reporting a relationship between song repertoire size in relation

to ambient noise levels in the great tit or any other avian species. However, Slabbekoorn & den Boer-Visser (2006) reported that songs in cities were shorter in duration, with the first note being shorter, and involved smaller intersong intervals than those songs recorded in forests. This resulted in city songs being produced at a faster rate (i.e. “hurried” songs). This is especially relevant if we consider that, by means of a playback experiment, McGregor & Horn (1992) showed that great tit songs may contain important information for male-male interactions in a temporal song parameter. They obtained evidence that the strophe length of great tit’s songs can contain information on the strength of response a male is able to give during male-male interactions. Thus, the information content of the acoustic signal could be modified if great tits sing shorter songs in noisy environments.

On the other hand, and although great tit song has also been related to the female fertile period (i.e. males sing more as egg laying approaches) (Mace 1987), no study has addressed female preference among song variants where the pitch or the length of temporal song parameters have been manipulated. This remains an interesting possibility for future research.

THE SONG SPARROW

The data for song sparrows are contradictory. On the one hand, Searcy (1984) found that female song sparrows in the laboratory are more sexually aroused by large song repertoires, but at the same time he found no evidence of a relationship between song repertoire size and mating success in nature. He concluded that song repertoire size has no important influence on female mating preferences in this species. Regarding the function of territory defense, Nowicki *et al.* (2002) showed that territorial song sparrows respond to simulated intrusions in a playback experiment, showing that this species uses song in the context of territory defense. However, it is not known whether females and males are sensitive to subtle variations in song attributes that vary with ambient noise (e.g. the pitch of songs), and thus no evidence can be invoked to propose whether song sparrows coping with background noise may be impairing their ability to efficiently repel other males from their territories.

THE CHAFFINCH

A clearer picture of how variation of chaffinch songs in the temporal domain can influence male-male and male-female interactions results from the studies of Riebel & Slater (1998) and Leitão & Riebel (2003). Chaffinch song is composed of two structurally different parts: a series of repeated notes (the trill) followed by a sequence of complex, and often non repeated, elements (Leitão & Riebel 2003). Riebel & Slater (1998) and Leitão & Riebel (2003) found that females prefer songs with relatively longer flourishes, while males are more aroused by songs with relatively shorter flourishes. This suggests a possible conflicting function in the context of sexual selection, whereby songs with longer flourishes may be used to attract mates and songs with shorter flourishes may be more effective during male-male interactions. Unfortunately, the study by Brumm & Slater (2006) of chaffinches singing in noisy conditions did not address whether there might be a difference in the relative durations of the trill and flourish. No data are available on the possible male or female chaffinch responses to songs differing in pitch either.

THE HOUSE FINCH

A laboratory experiment has given clear evidence that female house finches prefer long songs over short songs (Nolan & Hill 2004). Furthermore, in a field study, Mennill *et al.* (2006) found that the mates of house finches singing longer songs initiated their first clutch earlier. Thus, both studies combined give strong evidence that females prefer males that sing longer songs. Fernández-Juricic *et al.* (2005) showed that house finches singing in noisy locations sang shorter songs. Therefore, the house finch is probably the only example from which there is sufficient data to make clear predictions on how the influence of noise on song may have consequences for sexual selection. In this case, it is possible that males singing in very noisy locations are less preferred than males in relatively quiet places, unless female preferences have coevolved in the same direction as male songs, a possibility that has not yet been studied. There are no available data regarding the responses of female house finches to songs differing in pitch. Finally, house finches are non-territorial birds, and therefore

male-male interactions probably play a less important role in shaping the evolution of songs in this species.

From this section it is clear that more data on female and male responses to different song variants (especially where frequency and temporal song parameters are manipulated), is urgently needed if we are to have a clearer picture on how ambient noise may hamper female mate choice and male-male competition.

STUDIES IN OTHER SPECIES

Studies in coal tits (*Parus ater*, Adhikerana & Slater 1993) and vermilion flycatchers (*Pyrocephalus rubinus*, Ríos-Chelén & Macías Garcia 2007) show that longer songs are perceived by males as more threatening signals. Similarly, Balsby & Dabelsteen (2001) demonstrated that whitethroats (*Sylvia communis*) respond more strongly to small repertoires that have been artificially elongated in the time domain than to small repertoires of “normal” length, suggesting that song length carries information on the level of arousal of the emitter. On the other hand, there are species that use shorter songs for male-male communication. For example, Hoelzel (1986) and Galeotti *et al.* (1997) found that the robin (*Erithacus rubecula*) and the European starling (*Sturnus vulgaris*) respectively, sing short songs in aggressive intra-sexual and competitive contexts. A similar case can be made in the context of inter-sexual selection. There is evidence that long songs or long song bouts are preferred over shorter ones by females. This has been shown not only for the house finch (Nolan & Hill 2004, discussed above), but also for other bird species like the white-crowned sparrow (*Zonotrichia leucophrys*, Wasserman & Cigliano 1991) and the European starling (*S. vulgaris*, Eens *et al.* 1991). If the bird species mentioned in this paragraph sing shorter songs in noisy environments, as has been shown for the great tit (Slabbekoorn & den Boer-Visser 2006) and the house finch (Fernández-Juricic *et al.* 2005), the possibility exists that ambient noise may impair their capacity to defend a territory, especially in those species where longer songs are more threatening signals, or to effectively attract or stimulate a female. Those species that use shorter songs during contests between males may suffer less from the influence of background noise in those male-male interactions, but

may, on the other hand, face a increased probability of failing to attract or stimulate a female.

In relation to frequency parameters, Dabelsteen & Pedersen (1993) and Cardoso *et al.* (2007) have shown, for blackbirds (*Turdus merula*) and serins (*Serinus serinus*) respectively, that females prefer high pitched songs over low pitched ones. On the other hand, female canaries (*Serinus canaria*) were more sexually stimulated by songs in which the frequency of the “sexy” phrase was unaltered or lowered than by songs in which the frequency of this phrase was raised (Pasteau *et al.* 2007). Regarding song frequency and male-male competition, it has been shown, in an inter-specific study, that song frequency negatively relates to body weight in passerine birds (Wallschläger 1980), which is relevant in the context of male-male competition because heavier individuals may be bigger and stronger (ten Cate *et al.* 2002). Indeed, different song attributes may signal different aspects of male competitive potential (Galeotti *et al.* 1997) and in many different animals larger individuals produce lower frequency sounds (ten Cate *et al.* 2002). Thus, the frequency of songs could convey information on the singer’s ability to fight (review in ten Cate *et al.* 2002). It becomes clear that if birds sing at a high pitch to avoid noise masking, they may be transmitting the wrong message to other male competitors; that is one that does not reflect the male’s real ability to fight. This could result in escalated fights that, in turn, translate into lower reproductive success. This possible cost could be overcome to some extent if females (e.g. blackbirds and serins) prefer to mate with those males singing higher pitched songs, or could be increased if females (e.g. canaries) discard those males as potential mates.

CONCLUSIONS

Most studies aimed at understanding how birds cope with ambient noise have been carried out in oscine birds. Sub-oscines birds, a group of passerines in which learning does not seem to play a role in song development (Kroodsma 1982, but see Kroodsma 2004), have been unstudied. Given that in this group of birds song production is thought to be more determined by an endogenous mechanism, they can be expected to produce relatively less variable and plastic songs than oscines. This raises the question of whether sub-oscines are capable of some of the

strategies observed in oscines when dealing with noise (e.g. sifts in frequency). If they are not, what other strategies have they developed to deal with this kind of pollution? Are they more vulnerable than oscines in noisy environments? These are important questions that need answers if we are to have a more general panorama of the challenges that acoustic pollution impose to passerines.

Additional questions that probably will be studied in the next years have to do with the mechanisms of local adaptation to noise and some of its consequences. Are the strategies that birds use to get their signals through noisy environments short-term or long-term adaptations? Can ambient noise have an influence on population differentiation, and eventually on speciation? To what extent is ambient noise impairing the probabilities of attracting a mate or defending a territory in nature?

The extent to which bird species may be being affected by ambient noise may depend in part on how they use their songs in the contexts of inter- and intra-sexual selection. More studies are needed to have a clearer picture of the outcome that may result from the interaction between ambient noise and sexual selection processes. Those birds that are being affected both in the contexts of intra-sexual competition and mate choice may suffer a greater cost than those that perform poorly in one aspect of sexual selection but have an advantage in the other. Bird species could be facing different reproductive constraints depending on how the interplay between sexual selection and ambient noise they experience.

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REFERENCES

- ADHIKERANA, A.S. & SLATER, P.J.B. 1993. Singing interactions in coal tits, *Parus ater*: an experimental approach. *Animal Behaviour*, 46: 1205-1211.
- BALSBY, T.J.S. & LABELSTEEN, T. 2001. The meaning of song repertoire size and song length to male whitethroats *Sylvia communis*. *Behavioural Processes*, 56: 75-84.
- BRUMM, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. *Journal of Animal Ecology*, 73: 434-440.

- BRUMM, H. 2006. Signalling through acoustic windows: nightingales avoid interspecific competition by short-term adjustment of song timing. *Journal of Comparative Physiology A*, 192: 1279-1285.
- 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. & TODT, D. 2002. Noise-dependent song amplitude regulation in a territorial songbird. *Animal Behaviour*, 63: 891-897.
- BRUMM, H.; VOSS, K.; KÖLLMER I. & TODT, D. 2004. Acoustic communication in noise: regulation of call characteristics in a New World monkey. *The Journal of Experimental Biology*, 207: 443-448.
- CARDOSO, G.; GAMA, M.P. & DEPRAZ, V. 2007. Female and male serins (*Serinus serinus*) respond differently to derived song traits. *Behavioral Ecology and Sociobiology*, 61: 1425-1436.
- CATCHPOLE, C.K. 1982. The evolution of bird sounds in relation to mating and spacing behavior. Pp. 297-319 In: D.E. Kroodsma, E.H. Miller & H. Ouellet (eds.). *Acoustic communication in birds* (v.1). Academic Press. 371p.
- CATCHPOLE, C.K. & SLATER P.J.B. 2008. *Bird song: biological themes and variations*. Cambridge University Press. 348p.
- CODY, M.L. & BROWN, J.H. 1969. Song asynchrony in neighbouring bird species. *Nature*, 222: 778-780.
- CYNX, J.; LEWIS, R.; TAVEL, B. & TSE, H. 1998. Amplitude regulation of vocalizations in noise by a songbird, *Taeniopygia guttata*. *Animal Behaviour*, 56: 107-113.
- DABELSTEEN, T. & PEDERSEN, S.B. 1993. Song-based species discrimination and behavior assessment by female blackbirds, *Turdus merula*. *Animal Behaviour*, 45: 759-771
- EENS, M.; PINXTEN, R. & VERHEYEN, R.F. 1991. Male song as a cue for mate choice in the European starling. *Behaviour*, 116: 210-238.
- EVANS, G.W.; LERCHER, P.; MEIS, M.; ISING, H. & KOFLER, W.W. 2001. Community noise exposure and stress in children. *Journal of the Acoustical Society of America*, 109: 1023-1027.
- FENG, A.S. & NARINS, P.M. 2008. Ultrasonic communication in concave-eared torrent frogs (*Amolops tormotus*). *Journal of Comparative Physiology A*, 194: 159-167.
- FENG, A.S.; NARINS, P.M.; XU, C.-H.; LIN, W.-Y.; YU, Z.-L.; QIU, Q.; XU, Z.-M. & SHEN, J.-X. 2006. Ultrasonic communication in frogs. *Nature*, 440: 333-336.
- FERNÁNDEZ-JURICIC, E.; POSTON, R.; DE COLLIBUS, K.; MORGAN, T.; BASTAIN, B.; ARTIN C.; JONES, K. & TREMINIO, T. 2005. Microhabitat selection and singing behavior patterns of male house finches (*Carpodacus mexicanus*) in urban parks in a heavily urbanized landscape in the western U.S. *Urban Habitats*, 3: 49-69.
- FICKEN, R.W.; FICKEN, M.S. & HAILMAN, J.P. 1974. Temporal pattern shifts to avoid acoustic interference in singing birds. *Science*, 183: 762-763.
- FULLER, R.A.; WARREN, P.H. & GASTON, K.J. 2007. Daytime noise predicts nocturnal singing in urban robins. *Biology Letters*, 3: 368-370.
- GALEOTTI, P.; SAINO, N.; SACCHI, R. & MØLLER, A.P. 1997. Song correlates with social context, testosterone and body condition in male barn swallows. *Animal Behaviour*, 53: 687-700.
- HERBERT, L.P.Jr.; SIEGEL, G.M. & FOX, P.W. 1989. Inhibiting the Lombard effect. *The Journal of the Acoustical Society of America*, 85: 894-900.
- HOCKEY, G.R.J. 1970. Effect of loud noise on attentional selectivity. *The Quarterly Journal of Experimental Psychology*, 22: 28-36.
- HOELZEL, A.R. 1986. Song characteristics and responses to playback of male and female robins *Erithacus rubecula*. *Ibis*, 128: 113-127.
- JUNQUA, J.C. 1993. The Lombard reflex and its role on human listeners and automatic speech recognizers. *The Journal of the Acoustical Society of America*, 93: 510-524.
- KILNER, R. & JOHNSTON, R.A. 1997. Begging the question: are offspring solicitation behaviours signals of need? *Trends in Ecology and Evolution*, 12: 11-15.
- KREBS, J.R.; ASHCROFT, R. & WEBBER, M. 1978. Song repertoires and territory defense on the great tit. *Nature*, 271: 539-542.
- KROODSMA, D.E. 1976. Reproductive development in a female songbird: differential stimulation by quality of male songs. *Science*, 192: 574-575.
- KROODSMA, D.E. 1982. Learning and the ontogeny of sound signals in birds. Pp. 1-23. In: D.E. Kroodsma, E.H. Miller & H. Ouellet (eds.). *Acoustic communication in birds* (v.2). Academic Press. 389p.

- KROODSMA, D.E. 2004. The diversity and plasticity of birdsong. Pp. 108-131. *In*: P. Marler & H. Slabbekoorn (eds), *Nature's music. The science of birdsong*. Elsevier Academic Press. 513p.
- LEITÃO, A. & RIEBEL, K. 2003. Are good ornaments bad armaments? *Animal Behaviour*, 66: 161-167.
- LOHR, B.; WRIGHT, T.F. & DOOLING, R.J. 2003. Detection and discrimination of natural calls in masking noise by birds: Estimating the active space of a signal. *Animal Behaviour*, 65: 763-777.
- MACE, R. 1987. The dawn chorus in the great tit *Parus major* is directly related to female fertility. *Nature*, 330: 745-746.
- McGREGOR, P.K. & HORN, A.G. 1992. Strophe length and response to playback in great tits. *Animal Behaviour*, 43: 667-676.
- MANABE, K; SADR, E.I. & DOOLING, R.J. 1998. Control of vocal intensity in budgerigars (*Melopsittacus undulatus*): Differential reinforcement of vocal intensity and the Lombard effect. *The Journal of the Acoustical Society of America*, 103: 1190-1198.
- MARTEN, K. & MARLER, P. 1977. Sound transmission and its significance for animal vocalization. *Behavioral Ecology and Sociobiology*, 2: 271-290.
- MELAMED, S. & BRUHIS, S. 1996. The effects of chronic industrial noise exposure on urinary cortisol, fatigue, and irritability: a controlled field experiment. *Journal of Occupational and Environmental Medicine*, 38: 252-256.
- MENNILL, D.J.; BADYAEV, A.V.; JONART, L.M. & HILL, G.E. 2006. Male house finches with elaborate songs have higher reproductive performance. *Ethology*, 112: 174-180.
- MUZET, A. 2007. Environmental noise, sleep and health. *Sleep Medicine Reviews*, 11: 135-142.
- NARINS, P.M.; FENG, A.S.; LIN, W.; SCHNITZLER, H-U; DENZINGER, A.; SUTHERS, R.A. & XU, C. 2004. Old World frog and bird vocalizations contain prominent ultrasonic harmonics. *The Journal of the Acoustical Society of America*, 115: 910-913.
- NOLAN, P.M. & HILL, G.E. 2004. Female choice for song characteristics in the house finch. *Animal Behaviour*, 67: 403-410.
- NOWICKI, S.; SEARCY, W.A.; KRUEGER, T. & HUGHES, M. 2002. Individual variation in response to simulated territorial challenge among territory-holding song sparrows. *Journal of Avian Biology*, 33: 253-259.
- PASTEAU, M.; NAGLE, L. & KREUTZER, M. 2007. Influences of learning and predispositions on frequency level preferences on female canaries (*Serinus canaria*). *Behaviour*, 144: 1103-1118.
- PATEL, R. & SCHELL, K.W. 2008. The Influence of Linguistic Content on the Lombard Effect. *Journal of Speech, Language, and Hearing Research*, 51: 209-220.
- PATRICELLI, G.L. & BLICKLEY, J.L. 2006. Avian communication in urban noise: cases and consequences of vocal adjustment. *Auk*, 123: 639-649.
- PLANQUÉ, R. & SLABBEKOORN, H. 2008. Spectral Overlap in Songs and Temporal Avoidance in a Peruvian Bird Assemblage. *Ethology*, 114: 262-271.
- POPP, J.W.; FICKEN, R.W. & REINARTZ, J.A. 1985: Short-term temporal avoidance of interspecific acoustic interference among forest birds. *Auk*, 102: 744-748.
- REIJNEN, R. & FOPPEN, R. 1994. The effects of car traffic on breeding bird populations in woodland. I. 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.; TER BRAAK, C. & THISSEN, J. 1995. The Effects of Car Traffic on Breeding Bird Populations in Woodland. III. Reduction of Density in Relation to the Proximity of Main Roads. *Journal of Applied Ecology*, 32: 187-202.
- RIEBEL, K. & SLATER, P.J.B. 1998. Testing female chaffinch song preferences by operant conditioning. *Animal Behaviour*, 56: 1443-1453.
- RÍOS-CHELÉN, A.A. & MACÍAS GARCIA, C. 2007. Responses of a sub-oscine bird during playback: Effects of different song variants and breeding period. *Behavioural Processes*, 74: 319-325.
- RITCHISON G. 1983. The function of singing in female black-headed grosbeaks (*Pheucticus melanocephalus*): family-group maintenance, *Auk*, 100: 105-116.
- SEARCY, W.A. 1984. Song repertoire size and female preferences in song sparrows. *Behavioral Ecology and Sociobiology*, 14: 281-286.
- SCHOLIK, A.R. & YAN H.Y. 2001. Effects of underwater noise on auditory sensitivity of a cyprinid fish. *Hearing Research*, 152: 17-24.
- SCOTT, G.A. & LANG A.E. 1992. Can the Lombard effect be used to improve low voice intensity in Parkinson's disease? *International Journal of Language & Communication Disorders*, 27: 121-127.

- 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: 267-267.
- SLABBEKOORN, H.; YEH, P. & HUNT, K. 2007. Sound transmission and song divergence: a comparison of urban and forest acoustics. *Condor*, 109: 67-78.
- STANSFELD, S.A.; BERGLUND, B.; CLARK, C.; LOPEZ-BARRIO, I.; FISCHER, P.; ÖHRSTRÖM, E.; HAINES, M.M.; HEAD, J.; HYGGE, S.; van KAMP, I. & BERRY, B.F. 2005. Aircraft and road traffic noise and children's cognition and health: a cross-national study. *The Lancet*, 365: 1942-1949.
- SWADDLE, J.P. & PAGEL, C. 2007. High levels of environmental noise erode pair preferences in zebra finches: implications for noise pollution. *Animal Behaviour*, 74: 363-368.
- TEN CATE, C.; SLABBEKOORN, H. & BALLINTIJS, 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.
- TUMER, E.C. & BRAINARD, M.S. 2007. Performance variability enables adaptive plasticity of 'crystallized' adult birdsong. *Nature*, 450: 1240-1244
- WALLSCHLÄGER, D. 1980. Correlation of song frequency and body weight in passerine birds. *Cellular and Molecular Life Sciences*, 36: 412-412.
- WASSERMAN, F.E. 1977. Intraspecific acoustical interference in the white-throated sparrow *Zonotrichia albicollis*. *Animal Behaviour*, 25: 949-952.
- WASSERMAN, F.E. & CIGLIANO, J.A. 1991. Song output and stimulation of the female in white-throated sparrows. *Behavioral Ecology and Sociobiology*, 29: 55-59.
- WITTE, K.; FARRIS, H.E.; RYAN, M.J. & WILCZYNSKI, W. 2005. How cricket frog females deal with a noisy world: habitat-related differences in auditory tuning. *Behavioral Ecology*, 16: 571-579.
- WOOD, W.E. & YEZERINAC, S.M. 2006. Song sparrow (*Melospiza melodia*) song varies with urban noise. *Auk*, 123: 650-659.

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