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

AUMENTO DE LA FRECUENCIA DE CANTO EN RESPUESTA AL RUIDO URBANO EN EL CARBONERO COMÚN *PARUS MAJOR* REVELADO POR DATOS DEL MAPA DE RUIDO DE LA CIUDAD DE MADRID (ESPAÑA)

Concepción SALABERRIA* [1] and Diego GIL*

SUMMARY.—*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.*

Several studies have identified urban noise effects on animal communication. Birds adjust different characteristics of their songs to avoid the interference from background noise. We have studied whether song frequency characteristics of great tit song in the urban population of Madrid are related to local noise levels as measured by the city noise map. We recorded the songs of great tits in 22 different locations throughout parks and green areas of the city of Madrid, and analysed the relationship between song characteristics (minimum frequency, maximum frequency, band width, peak frequency per note and strophe length) and the amplitude of urban noise as reported in the noise map of the city available from the Environmental Department of the Madrid City Council. Great tits in noisier locations sang with a higher minimum frequency and narrower bandwidth than in quieter locations. None of the other song components measured (maximum frequency, peak frequency per note or strophe length) covaried with noise levels. An increase in minimum frequency in the song of the great tit is expected to facilitate detection and song perception by conspecifics over the strong levels of low-frequency urban noise. Such song plasticity may be one of the characteristics that allows this species to be a successful urban coloniser. Our data provides a replication of previous studies in the great tit and other species and underlines the usefulness of city noise maps as tools for conservation biology.

Key words: birdsong, habitat adaptation, maximum frequency, minimum frequency, *Parus major*, strophe length, urban noise.

RESUMEN.—*Aumento de la frecuencia de canto en respuesta al ruido urbano en el carbonero común* Parus major *revelado por datos del mapa de ruido de la ciudad de Madrid (España).*

Diversos estudios han identificado efectos del ruido urbano en la comunicación animal. Las aves modifican diferentes características de sus cantos para evitar interferencias con el ruido de fondo. Se ha analizado la influencia del ruido urbano en diferentes características del canto del carbonero común en la ciudad de Madrid. Se grabaron y analizaron cantos de carboneros comunes en 22 lugares distintos de

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*   Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), José Gutiérrez Abascal 2, E-28006 Madrid, Spain.

[1]   Corresponding author: baobabcps@hotmail.com

la ciudad de Madrid (frecuencia mínima, frecuencia máxima, ancho de banda, pico de frecuencia por nota y longitud de estrofa). Posteriormente se relacionaron dichos parámetros con los niveles de amplitud de ruido urbano obtenidos a partir del mapa de ruido de Madrid (datos del Departamento de Medio Ambiente del Ayuntamiento de Madrid). Los carboneros comunes en lugares más ruidosos cantaban con mayor frecuencia mínima y menor ancho de banda de canto que en lugares más silenciosos. Ninguno de los otros componentes del canto medidos (frecuencia máxima, pico de frecuencia por nota o longitud de estrofa) se relacionaron con los niveles de ruido. El aumento en la frecuencia mínima del canto de los carboneros comunes permitiría a estas aves ser mejor percibidas por sus congéneres en situaciones de niveles altos de ruido urbano. Esta plasticidad en el canto puede ser uno de los factores que contribuyen al éxito de colonización de las ciudades por esta especie. Los resultados corroboran estudios previos en otras ciudades europeas para el carbonero común y otras especies, y ponen de manifiesto la utilidad de los mapas de ruido urbano como herramientas de conservación.

*Palabras clav*e: adaptación acústica al hábitat, canto, frecuencia máxima, frecuencia mínima, longitud de estrofa, *Parus major*, ruido urbano.

INTRODUCTION

Natural selection favours vocalisations that transmit effectively in the habitat in which they are used, since acoustic communication requires a good propagation through the environment between the sender and the receiver (Morton, 1975; Wiley, 1991; Slabbekoorn, 2004). One important source of selection on vocalizations is the filtering effect of the background noise on communication. Selection is thus expected to favour the evolution of strategies that allow animals to cope with background noise.

Solutions to high levels of background noise may involve evolutionary changes in signal characteristics that result in signal-to-noise ratios advantageous for a better perception. Differences in noise characteristics between habitats may thus cause differences in song structures between species (Morton, 1975; Sorjonen, 1986), between subspecies (Dingle *et al*., 2008) or even in different populations of the same species (Hunter and Krebs, 1979; Slabbekoorn and Smith, 2002). These changes involving natural selection or vocal learning mechanisms represent long-term adjustments to noise levels.

On the other hand, there are short-term adjustments involving changes of signal characteristics as a response to immediate variation in background noise levels (Brumm and Slabbekoorn, 2005). For instance, the Lombard effect (Lombard, 1911) is a mechanism common in several bird and some mammal species, including humans (Brumm and Slabbekoorn, 2005), in which the signaller increases the amplitude of its vocalizations in response to an increase in noise amplitude. In birds, this phenomenon has been demonstrated in nightingales *Luscinia megarhynchos* in an experiment in captivity (Brumm and Todt, 2002) and also in their natural environment (Brumm, 2004).

Other strategies include regulation of serial redundancy (Brumm and Slater, 2006). For example the king penguin (*Aptenodytes patagonicus*) increases the number of syllables in its calls when the background noise levels rise (Lengagne *et al*., 1999). By increasing the number of repetitions, signals would be less vulnerable to masking by noise. Another possibility is the modification of song spectral characteristics. Since background noise is typically distributed in a low frequency range, birds could increase the frequency of their songs, thus reducing overlap, and avoiding masking by noise. Evidence for such an effect is provided by data showing a positive corre-

lation between urban noise levels and minimum frequency in several species of passerines; (Slabbekoorn and Peet, 200 Fernández-Juricic *et al*., 2005; Wood and Yezerinac, 2006; Bermúdez *et al*., 2009).

Since anthropogenic noise is widespread, particularly in large cities (Warren *et al*., 2006), it is important to study the impact of this kind of pollution on birdsong, as song plays an important role in territory defence and mate attraction (Krebs, 1977; Lambrechts and Dhondt, 1986; Searcy and Andersson, 1986). Therefore, the masking effect of noise may have important fitness consequences and also determine patterns of population densities. The aim of our study was to examine the effect of the background noise on song characteristics in the great tit *Parus major* in its urban population of the city of Madrid. To this end, we recorded songs in different areas and related their spectral characteristics to noise levels as reported by the Madrid noise map. This study shows for the first time how a city noise map can be a useful tool to study the impact of noise impact on bird song.

METHODS

We recorded great tit song between the 29th February and the 28th May 2008, during morning hours from dawn until noon. We visited different locations in the city of Madrid, and recorded 22 different individuals, and obtained an average of 17.4 strophes per individual (SD = 11.4). Recordings were carried out only during working days, avoiding weekends when the traffic and environmental noise levels were lower in the morning hours. Since the birds were not individually marked, we made sure that different recordings were separated from each other by at least 100 m, to avoid recording the same bird twice. The whole area where the birds were recorded can be circumscribed by a circle with a radius of 3 km.

Song analysis

Great tits sing in bouts. A song bout is a group of repeated strophes of a given song type which is separated from another by a period of silence. A strophe is composed of phrases which are composed of a combination of different notes. Different song types were determined by their specific phrase composition (Lambrechts and Dhondt, 1987). We recorded between one and three song types per individual. In the analysis, every song type from a given individual was considered separately since intra-individual variation in song types is as great as inter-individual variation (Slabbekoorn and den Boer-Visser, 2006).

Song characteristics are known to change during a song bout. For example, the first note of the first phrase in a strophe is almost always shorter than the first notes in later phrases (Lambrechts and Dhondt, 1987). Similarly, pauses between notes increase in length between the beginning and the end of a long strophes, giving rise to the phenomenon called "drift" (Lemon, 1975; Lambrechts and Dhondt, 1986). In order to avoid biasing our measurements because of these changes, we analysed two strophes per song-type of a given individual, and two phrases per strophe to obtain more reliable measurements. Thus, from each individual song type, we analysed one strophe at the beginning and another at the end of the recording bout. The variables measured in each strophe were: maximum frequency (Hz), minimum frequency (Hz), frequency band width (represented as difference between maximum frequency and minimum frequency, Hz), peak frequency per note (measured as the mean of the peak frequencies of the notes in the phrase) and strophe length (s). These measurements were taken in two phrases per bout and the mean was calculated.

Songs were recorded with a directional microphone (Sennheiser K6, with a ME67 module), and a solid-state digital recorder

(Edirol R-09). Recordings were sampled at
a rate of 22 kHz, and transferred into a com-
puter, where they were analysed with the
Avisoft SASLabPro software.

Noise analysis

Mean noise levels (dB Lden) were obtained
from the noise map of the city of Madrid, pro-
duced by the Environment Department of the
Madrid City Council and publicly available at:
http://www.munimadrid.es/portal/site/munima
drid/menuitem.4acc01ad7bf0b0aa7d245f019
fc08a0c/?vgnextoid=60334177a511b110Vgn
VCM2000000c205a0aRCRD&vgnextchanne
l=4b3a171c30036010VgnVCM100000dc0ca
8c0RCRD. Lden (day-evening-night level) is a
descriptor of noise level based on energy equi-
valent noise level (Leq) which is commonly
used in order to determine noise exposure by
humans. A detailed description about this in-
dicator is available at: http://eurlex.europa.eu/
LexUriServ/LexUriServ.do?uri=OJ:L:2002:1
89:0012:0025:ES:PDF. The acoustic charac-
teristics used in generating this map were ob-
tained through field measurements and from
software-based calculations of the propagation
of the sound. Direct field measurements were
taken from moving vehicles that measure sound
at different points in the city in 2006 and from
30 fixed stations which have been measuring
noise levels for the last ten years. The preci-
se location of the 22 singing individuals was
plotted on a 1:12,000map. Amplitude levels per
territory ranged between 60 and 75 decibels.

Statistics

To analyse the effect of the noise on the
different characteristics of the song, we built
random mixed models in SAS (Proc Mixed),
in which data for each individual song type
was nested within individuals, which was
entered as a random factor.

RESULTS

As expected, we found that great tits at
noisy locations sing with a higher minimum
frequency and smaller frequency bandwidth
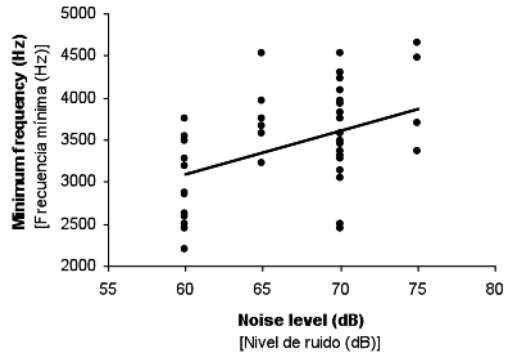than birds in quiet locations (table 1; figure 1;
figure 2).

FIG. 1.—Relationship between song minimum
frequency and ambient noise in a great tit urban
population.
*[Correlación entre la frecuencia mínima de can-
to y ruido ambiental en una población urbana de
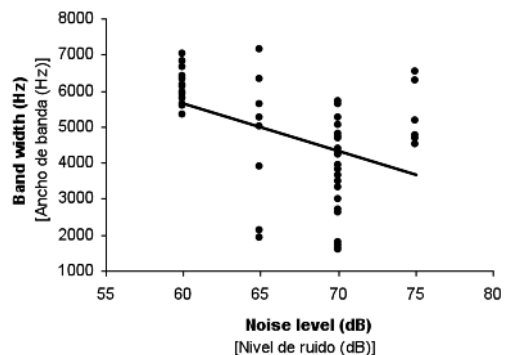carbonero común.]*

FIG. 2.—Relationship between song frequency
bandwidth and ambient noise in a great tit urban
population.
*[Correlación entre el ancho de banda y ruido am-
biental en una población urbana de carbonero
común.]*

TABLE 1

Summary of mixed model analysing the effect of noise levels on song characteristics (maximum frequency, minimum frequency, frequency bandwidth, strophe length and peak frequency per note). Individual was included as a random factor. Degrees of freedom were calculated by means of the Satterthwaite method.
[Resumen del modelo mixto que analiza el efecto del nivel del ruido en las características de canto (frecuencia máxima, frecuencia mínima, ancho de banda, longitud de estrofa y pico de frecuencia por nota). El individuo se consideró en el modelo como factor aleatorio. Los grados de libertad fueron calculados por medio del método Satterthwaite.]

Variables	F	DF	Estimate (SE)	p
Maximum frequency *[Frecuencia máxima]*	2.21	1.24	–81.57 (54.91)	0.15
Minimum frequency *[Frecuencia mínima]*	7.1	1.24	52.07 (19.54)	0.01
Bandwidth *[Ancho de banda]*	6.18	1.24	–133.63 (53.75)	0.02
Strophe length *[Longitud estrofa]*	0.65	1.24	–0.02 (0.02)	0.43
Peak frequency per note *[Pico de frecuencia por nota]*	0.45	1.24	0.02 (0.03)	0.51

None of the other song components measured (maximum frequency, peak frequency per note or strophe length) showed a significant relationship with noise levels (table 1). The effect of individual is highly significant ($p < 0.001$) in all the cases, showing that acoustic characteristics of the different song types are highly repeatable within individuals despite possible drift phenomena.

DISCUSSION

Our results confirm previous studies of great tits (Slabbekoorn and Peet, 2003; Slabbekoorn and den Boer-Visser, 2006) conducted in several European cities in which a positive relationship between the minimum frequency of song and the amplitude of background noise was observed.

Furthermore, since habitat noise characteristics have been obtained from long term noise map data, our results suggest that song frequency adjustments induce stable and long-term differences between different areas. Previous studies also carried out in cities in song sparrows *Melospiza melodia* (Wood and Yezerinac, 2006), house finches *Carpodacus mexicanus* (Fernández-Juricic *et al.*, 2005; Bermúdez *et al.*, 2009) and blackbirds *Turdus merula* (Nemeth and Brumm, 2009), also corroborate the same trend. A similar shift has been observed in the vocalizations of birds living in habitats with high levels of

non-anthropogenic noise (Slabbekoorn and Smith, 2002; Brumm and Slater, 2006). This general trend thus suggests that birds show frequency adjustments in response to high levels of low frequency noise. This adjustment would lead to a reduction in note band-width caused by an increase in minimum song frequency and a non-significant trend for a decrease in maximum frequency. A decrease in song band-width could also be adaptive in noise conditions because sounds with large band-widths have been shown to be more difficult to detect from noise (Lohr *et al.*, 2003). Thus, signals with narrow band-widths, such as pure tones, are more easily detectable against background noise than are those with wider band-widths. Some evidence suggests that birds living along streams, where noise levels are very high and continuous, also produce signals dominated by pure tones (Dubois and Martens, 1984).

Alternative explanations to our findings may be related to differences between populations in physiology or morphology. This is because morphological traits may constraint song production or certain frequencies. For instance, several studies show that body size and beak gape and shape are related to acoustic frequencies (Wallschlager, 1980; Westneat *et al.*, *1993*; Podos *et al.*, 2004). For example, a study with different species of woodcreepers (*Dendrocolaptinae*) shows that the acoustic frequencies contained in their songs are negatively related to beak length across species (Palacios and Tubaro, 2000). However, we think it improbable that this may apply to our study, since the birds we recorded were in close proximity to each other, and morphological differences in beak size are not expected to develop on such a local scale. Additionally, eventual differences in hormone levels between city and urban birds could be a confounding effect, because testosterone levels may affect song frequencies (Nemeth and Brumm 2009). However, since our data involves comparisons within the city, we also

think it unlikely that great differences in hormone levels could be expected within such short distance.

We also analysed whether peak frequency changed with noise since previous studies have revealed changes in the relative amplitude of different frequency components in relation to background noise (Rabin *et al.*, 2003; Wood and Yezerinac, 2006), but we found no relationship with noise levels in our study. Similarly, we did not find changes in the temporal structure of vocalizations (strophe length) with regard to noise levels, although several studies have found such relationships. For example, a study of great tit song, which compared populations between cities and forests, showed that urban songs were shorter and faster than those sang in forests (Slabbekoorn and den Boer-Visser, 2006). Fernández-Juricic *et al.* (2005) also found a significant reduction in the number of notes in house finch songs in noisy areas. Since urban noise is predominantly characterized by low frequencies (Warren *et al.*, 2006), it is thus to be expected that the song of birds living in urban environments would be mainly modified in its low frequency, thus avoiding to be masked by the prevailing noise spectrum.

There are several possible paths by which the observed shift in frequency may have arisen. These adjustments may imply long term adjustments, brought about by either evolutionary or ontogenic changes in signal characteristics, or may result from short-term adjustments, that is to say, immediate individual adjustments of signal traits in response to current variation in background noise which are considered as follows.

Long-term genetic selection. Selection for optimal sound transmission has been found to lead to differences in song structures between populations of the same species (Hunter and Krebs, 1979; Slabbekoorn and Smith, 2002). Although adaptive population differentiation is expected to be rare over small scales where gene flow is not limited (Endler, 1977), some

increasing evidence suggests that such processes may occur in populations at close distances. A partial cross-fostering experiment with great tits, of two qualitatively different areas separated only by a few kilometers, showed significant genetic differences in morphological variation (Shapiro *et al*., 2006). Thus it is plausible that the constant noise in a given frequency range and present during significant time may act as a selection pressure upon the evolution of song frequency in a given habitat. According to this, different subpopulations of great tits may in principle exist in our study area. However, this is unlikely because of the short distance between noisy and less noisy areas that we found in our study (all recordings were made within a circle with a 3 km radius).

Long-term ontogenetic changes. Habitat-dependent signal differences could also be the result of lifetime plasticity instead of adaptation through evolutionary time. This plasticity could result from ontogenetic changes based on individual learning processes. The great tit is an open-ended song learning species, which may continue to acquire and modify songs throughout their adult life (McGregor and Krebs, 1989). Great tits have a small repertoire of about two to seven song types in which syllables differ in frequency (Lambrechts and Dhondt, 1986). Birds would reduce the masking effects of habitat-specific noise through differential learning, a kind of environmental filter by which songs with syllables better coupled to noisy environments would have a higher probability of being heard and therefore learnt by birds in noisy environments (Hansen, 1979). Therefore, those songs that cannot be well heard would not be learnt (selective copying) or those songs that do no receive any answer from their neighbours may be dropped from the repertoire (selective reinforcement) (Slabbekoorn and den Boer-Visser, 2006). In two studies realized in great tits (Slabbekoorn and Peet, 2003; Slabbekoorn and den Boer-Visser, 2006), selective learning is considered the most probable mechanism to explain the differences of song in relation to different noise levels. In both studies, quiet and noisy areas are clearly separated. However, as previously pointed out, the different zones of our study are very close to each other, therefore the same individual would have to sing in two very close zones and with a very different noise levels. In this case, it does not seem very plausible to attribute the song differences in our study to differential learning processes.

Short-term adjustments. Another possibility is that habitat-dependent signal differences could be the result of individual plasticity in real time (short-term adjustments) (Brumm and Slabbekoorn, 2005). This would require individuals to adjust the characteristics of their songs in real time. This possibility seems the most plausible explanation for the mechanism that has acted in the studied population. Two different alternatives are possible here: (i) birds may sing those songs of their repertoires which have syllables of high frequency in noisy areas and would use songs with syllables of low frequency when they are in quieter zones (Halfwerk and Slabbekoorn, in press). (ii) Birds could sing the same song in both quiet and noisy places, but varying the frequency of syllables in function of the existing noise. For instance, in the house finch, birds have been shown to vary the frequency of individual syllables in relation to noise levels (Bermúdez-Cuamatzin *et al*., 2009).

Short-term responses do not require learning, though the usage of this mechanism of adjustment will be constrained by an individual's ability to detect masking and make subsequent changes when vocalizing (Patricelli and Blickley, 2006).

There are therefore several mechanisms, long or short term, by which the variations that we found in great tit song in relation to urban noise may be explained. The mechanisms are not mutually exclusive and can reinforce each

other. Studies that track individuals throughout their lifetime in urban environments with and without noise are needed to know the mechanisms that are acting. Song plays an important role in territory defence and sexual selection (Krebs, 1977; Lambrechts and Dhondt, 1986; Searcy and Andersson, 1986). Specific studies with great tit have shown that different features of song are related to territorial defence (Krebs, 1977) and the survival and reproductive success of this species (McGregor *et al.*, 1981; Lambrechts and Dhondt, 1986). Understanding the mechanisms that bring about this phenomenon would be important to predict the mechanisms in conservation because species-specific song plasticity can influence the individual fitness and the likelihood of populations surviving in highly urbanized ecological conditions. Our study shows that city noise maps can be a useful tool for analysing these types of adaptations.

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