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CONSECUENCIAS DEL RUIDO AMBIENTAL EN LA COMUNICACIÓN ACÚSTICA DEL GORRIÓN MEXICANO (*Carpodacus mexicanus*)

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Consecuencias del ruido ambiental en la comunicación acústica del gorrión mexicano (*Carpodacus mexicanus*)

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Resumen

Este trabajo aporta evidencia de que el ruido antropogénico generado en zonas urbanas tiene un efecto sobre las señales acústicas del gorrión mexicano (*Carpodacus mexicanus*). En primera instancia, demostré de manera correlativa y experimental que machos de gorrión mexicano son capaces de ajustar de manera plástica en tiempo real la frecuencia mínima de sus cantos con base en el nivel de ruido urbano que experimentan, lo cual probablemente ayuda a que las señales no se enmascaren con las frecuencias bajas del ruido urbano. Estos estudios fueron de los primeros en reportar este tipo de plasticidad en paseriformes. También encontré que este pájaro emplea las mismas sílabas pero emitidas a una frecuencia mínima mayor cuando canta en lugares ruidosos. En un segundo estudio encontré experimentalmente que el incremento en la frecuencia mínima de los cantos en presencia de ruido urbano se logra en mayor medida por el ajuste de la frecuencia de las sílabas de menor frecuencia del canto, y que éste tiende a acortarse en condiciones de ruido elevado. Cuando las aves en vez de ajustar la frecuencia de las sílabas, las sustituyen por otras de frecuencia mayor, su longitud es incrementada en comparación con las mismas sílabas proferidas en condiciones de menos ruido. Todo ello muestra que esta especie tienen a su disposición diferentes estrategias tanto espectrales como temporales para lidiar con el ruido urbano. También revelé que en respuesta al ruido, esta especie ajusta de manera plástica tanto la frecuencia pico de los llamados, como la máxima, así como el número de armónicos que contienen. Estos ajustes podrían también facilitar la transmisión de las vocalizaciones cuando las profieren en medio de ruido urbano.

Evalué experimentalmente las respuestas de las hembras frente a cantos ajustados o no ajustados al ruido, y presentados en presencia o ausencia de ruido. Las hembras parecieron mostrar más interés -evidenciado por la frecuencia de aproximaciones a la bocina- en los cantos cuando éstos se reproducían en presencia de ruido que cuando se les presentaban contra un trasfondo de silencio. Es posible que esto obedezca a que el ruido obligue a las hembras a acercarse a la fuente del estímulo para poder percibirlo/evaluarlo adecuadamente. En mi experimento las hembras pasaron más tiempo orientadas a cantos no ajustados cuando se presentaban contra un fondo ruidoso. Parecería que estos cantos naturales son atractivos y que a pesar del ruido que agregamos experimentalmente, fueron adecuadamente percibidos por las hembras que, sin embargo, no se interesaron en los cantos ajustados. Sorprendentemente, las hembras mostraron más interés en los cantos ajustados cuando se presentaron en condiciones de silencio. Solo puedo especular que en esas condiciones los cantos extraños resultan llamativos. Las hembras se aproximaron en mayor medida a cantos más diversos cuando se presentaron con ruido, y en menor medida cuando se presentaron en condiciones de silencio, lo que sugiere que los cantos diversos pueden resultar más ventajosos al ser mejor percibidos cuando hay ruido porque se incrementa la posibilidad de que alguna sílaba resulte menos enmascarada que las demás.

Por último, corroboré lo encontrado en estudios previos -pero separados-acerca de la relación entre la frecuencia del canto de las aves y la complejidad del hábitat, la talla corporal y la forma del pico. Encontré que especies de gran tamaño y especies que habitan en sitios con vegetación densa emiten cantos con frecuencias menores que aves de tamaño menor y que aquellas que habitan espacios abiertos. Los cantos de especies que se encuentran en hábitats complejos tienen una anchura de banda relativamente baja, al tiempo que incluyen altas frecuencias mínimas. También mostré que aves con picos cortos y altos emiten cantos con frecuencias altas y con anchura de banda mayor. Un hallazgo novedoso e importante es que en hábitats cerrados como bosques, donde la transmisión acústica es limitada, se han seleccionado los cantos con menor versatilidad o más repetitivos.

Palabras clave: ruido antropogénico, urbanización, canto de aves, ajuste plástico, frecuencia mínima, gorrión mexicano

Abstract

In this Doctoral Thesis I provide evidence that anthropogenic noise affects the acoustic signals of the house finch (*Carpodacus mexicanus*). Firstly, I prove in an experimental and correlative way, that male house finches are capable of plastically adjusting the minimum frequency of their songs in response to urban noise, which probably improves the probability that the signals are not masked by low frequency urban noise. This study was one of the first to report this kind of plasticity in passerines. In addition, I found that house finches use the same syllables but emit them in a higher minimum frequency when they sing in noisy environments than in quiet areas. In a second study I found experimentally that the increase in the song's minimum frequency under urban noise is achieved mainly by frequency adjustment of low-frequency syllables of the song, and these syllables also tend to shorten in high level noise conditions. When birds substitute syllables for others, instead of adjusting the frequency, the length of those syllables are increased in comparison with the same ones uttered in less noisy conditions. All of this shows that this species has at its disposal different spectral and temporal strategies to deal with urban noise. I also showed that in response to noise, this species plastically adjusts both the peak and maximum frequency of the calls and the number of harmonics. These small changes may also facilitate the transmission of vocalisations when utteredin a noisy urban environment.

I experimentally evaluated the responses of female house finches to songs adjusted and unadjusted to noise, presented in a noisy and a quiet background. The females seemed to show more interest –evidenced by the frequency of approaches to the loudspeaker- in the songs when these were played in a noisy background than against a quiet background. This may be because the noise obligates the females to approach the source of the stimulus in order to perceive/evaluate it properly. In my experiment the females spent more time oriented towards unadjusted songs when presented in a noisy background. It would seem that these natural songs are attractive and despite the noise we added experimentally, they were properly perceived by the females that, however, were not interested in the adjusted songs. Surprisingly, the females showed more interest in adjusted songs when presented in quiet conditions. I can only speculate that under those conditions strange songs are striking. Females approached more to diverse songs when presented with noise, and less so when presented in quiet conditions, which suggests that diverse songs can be more advantageous to be better perceived when there is noise because of the possibility that any syllable may result less masked than others is increased.

Finally, I corroborated the findings in previous studies about the relationship between the song frequency of birds and the complexity of the habitat, body size and beak shape. I found that big size species and species inhabiting dense vegetation sites emit songs with lower frequencies than small size birds and those inhabiting open areas. Songs of species found in complex habitats have a relatively narrow bandwidth while including higher minimum frequencies. I also showed that birds with short and tall beaks emit songs with high frequencies and wide bandwidth. A novel and important finding is that in close habitats like forests where the sound transmission is limited, less versatile and more repetitive songs have been selected.

Keywords: anthropogenic noise, urbanization, birdsong, plasticity, minimum frequency, house finch

1.- Introducción General

1.1.- El proceso de la comunicación

La comunicación involucra dos individuos, un emisor y un receptor. El emisor produce una *señal*, la cual es el vehículo que provee la información. La señal es transmitida a través del ambiente y es detectada por el receptor. El receptor usa la información para ayudarse a tomar una decisión acerca de cómo debería responder. La respuesta del receptor afecta la adecuación del emisor, así como la propia (Bradbury & Vehrencamp, 1998).

Existen diferentes modalidades de comunicación animal; acústica, química, visual, y táctil. Las aves utilizan primordialmente la comunicación acústica y visual. Las señales visuales no operan en condiciones de poca luz o en ambientes muy estructurados, donde sí pueden operar señales acústicas, que pueden ser usadas para la comunicación a larga distancia. La comunicación sonora es de naturaleza veloz y transitoria; debido a esto las señales acústicas de las aves pueden transmitir cantidades grandes de información rápida y eficaz a través del canal de sonido (Catchpole & Slater, 2008).

1.2.- Las señales acústicas o vocalizaciones de las aves y su función

Las aves emiten dos tipos de vocalizaciones o señales acústicas; los cantos y los llamados (Catchpole & Slater, 2008). Los llamados se pueden definir como sonidos breves de estructura acústica simple, compuestos generalmente de uno o dos elementos conocidos como sílabas y son producidas por ambos sexos durante todo el año. Señalan alarma, necesidad de contacto, proximidad social, anuncian fuentes de comida y promueven la cohesión durante la migración; es decir, están más involucrados que los cantos en situaciones inmediatas de vida o muerte. También son empleados en cuestiones reproductivas, por ejemplo el mantener lazos de pareja (Thorpe, 1956; Welty & Baptista, 1988; Del Hoyo & Sargatal, 2001; Marler, 2004a). Los cantos son una exhibición o despliegue vocal que consiste en una serie de sílabas producidas por el ave en secuencias y patrones definidos en el tiempo. Por lo tanto, es una señal más compleja que un llamado, y la emiten principalmente los machos en ambientes templados durante la época reproductiva (Catchpole, 1982; Navarro & Benítez 1995; Catchpole & Slater, 2008). Las funciones del canto se han podido determinar gracias a un amplio cuerpo de evidencia, el cual confirma que éste tiene principalmente dos funciones: atracción de pareja (selección intersexual: se da entre individuos de diferente sexo) y competencia entre miembros de un mismo sexo por un recurso, por ejemplo el territorio, ya que usualmente tener uno es requisito para acceder a una pareja (selección intrasexual: se da entre individuos del mismo sexo; Catchpole & Slater 2008). Estas dos funciones pueden determinar que algunos individuos se reproduzcan más que otros, debido a los atributos de sus cantos, y que por consiguiente éstos se expresen en la siguiente generación (Gil & Garh, 2002).

Las aves canoras (Orden Passeriformes) incluye a los subórdenes Oscinos y Suboscinos (Catchpole & Slater, 2008). Los Oscinos entre otras características, presentan siringes más evolucionadas, cantos más diversos y complejos, y un mayor desarrollo de las estructuras del cerebro implicadas en la producción y aprendizaje del canto que el clado hermano, los Suboscinos (Catchpole & Slater, 2008).

1.3.- Propiedades acústicas de las vocalizaciones

El sonido se puede definir como el fenómeno producido por ondas sonoras longitudinales generadas por el movimiento vibratorio de un cuerpo (e. g. una cuerda que vibre o el músculo de la siringe de las aves), que se propagan por un medio elástico como el aire y que son captadas por un receptor (Bradbury & Vehrencamp, 1998; López, 2009). Una onda sonora es una variación local de la densidad o presión (P) de un medio continuo en función del tiempo (T). Dicha onda realiza un movimiento ondulatorio, y se define por los siguientes parámetros físicos: longitud de onda (λ), frecuencia (f), velocidad (c), período (T) y amplitud (A) (Bradbury & Vehrencamp, 1998; López, 2009). Período (T) es el tiempo que tarda en producirse un ciclo (lapso mínimo que separa dos instantes en el que la onda se encuentra exactamente en la misma posición, amplitud o estado) completo de la onda sonora, su unidad es el segundo (Figura 1). La frecuencia (f) es el número de ciclos que se realizan por segundo, y se mide en hercios (1 ciclo por segundo = 1 Hz; Figuras 1 y 2). El tono está determinado por la frecuencia fundamental de las ondas sonoras (es lo que permite distinguir entre sonidos graves, agudos o medios), y es medido en hercios (Hz) (Figura 1 y 2). La longitud de onda (λ) es la distancia entre dos puntos análogos en dos ondas sucesivas; se mide en metros (m) y está relacionada con la velocidad del sonido, frecuencia y período (Figura 1; Bradbury & Vehrencamp, 1998; López, 2009). La longitud de onda describe cuan larga es la onda; una longitud de onda larga corresponde a una frecuencia baja y viceversa; ver figura 2.

Velocidad (c), es el tiempo que tarda una onda acústica en propagarse a una distancia dada en un medio elástico. Se mide en metros/segundo (m/s). La intensidad es la cantidad de energía acústica que contiene un sonido; está determinada por la amplitud (Figura 1), y permite distinguir si el sonido es fuerte o débil; se mide en decibelios (dB). Por último, la duración es el tiempo de escucha de un sonido desde su emisión hasta su extinción (Bradbury & Vehrencamp, 1998; López, 2009).

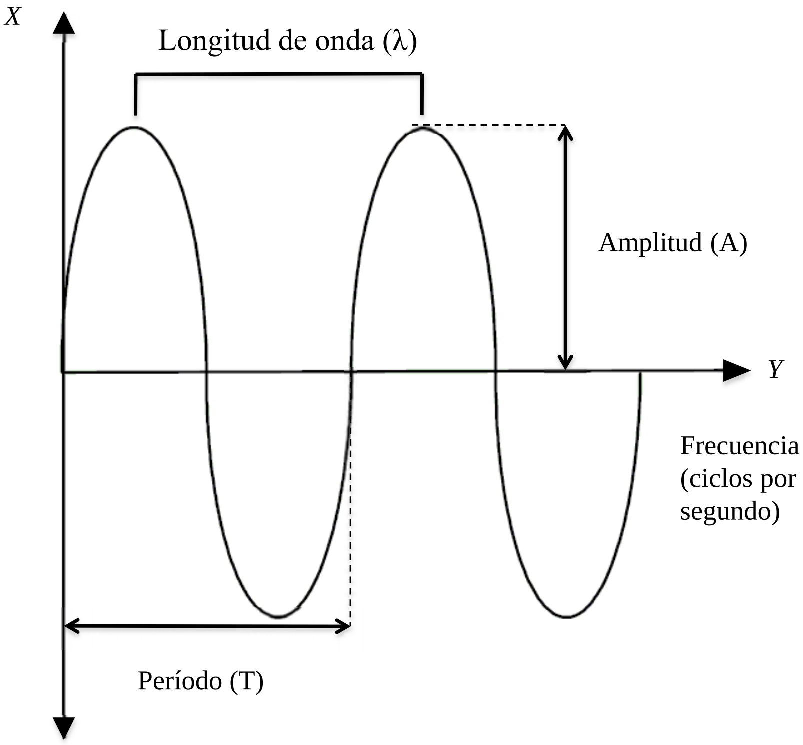

Figura 1.- Representación gráfica de una onda sinusoidal simple (distancia en línea recta que recorre un movimiento ondulatorio determinado en cada ciclo o período, curva que representa gráficamente la función seno). Este trazo se emplea para estudiar el sonido en una dimensión. En esta imagen vemos representada la longitud de onda (λ), la amplitud o intensidad (A), el período (T) y la frecuencia (f), ver detalles en texto.

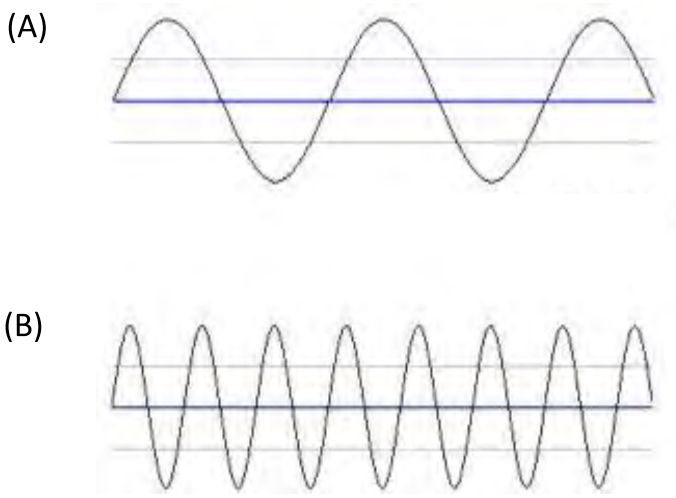

Figura 2.- Ondas sinusoidales que representan (A) longitud de onda larga, sonido grave (menor frecuencia; menos ciclos por segundo) y (B) longitud de onda corta; sonido agudo (mayor frecuencia, más ciclos por segundo).

1.4.- Influencia del hábitat en la comunicación acústica de las aves: el problema del ruido natural y urbano.

El hábitat es una fuente de presiones de selección que moldean las señales acústicas de las aves. Un factor selectivo es el ruido ambiental (Morton, 1975; Ryan & Brenowitz 1985). Éste puede interferir con la eficiencia de la comunicación acústica cuando la razón señal-ruido está por debajo del umbral de detección del receptor (Marten & Marler, 1977). Cuando la razón señal-ruido es baja ocurre enmascaramiento de la señal. Éste se puede definir como la reducción de la detección de la señal causada por la energía acústica de otros sonidos. Depende de la amplitud relativa de la señal y del ruido, pero también de la similitud en la distribución de las frecuencias (Klump, 1996). Los sonidos de enmascaramiento podrían ser producidos, por ejemplo, por aves vecinas y otros animales (factores bióticos) y por viento y lluvia, es decir por factores abióticos (Brumm & Slabbekoorn, 2005).

El ruido antropogénico es otro tipo de sonido que puede enmascarar las señales acústicas de las aves y que actualmente se ha incrementado de manera alarmante en todo el mundo debido a la expansión demográfica del ser humano y de sus tecnologías (Slabbekoorn & Peet, 2003; Brumm & Slabbekoorn, 2005; Warren et al. 2006). Este ruido es generado principalmente por el tráfico terrestre y aéreo, las industrias y los locales de ocio. El ruido antropogénico producido en las ciudades es conocido como “ruido urbano” (Raven et al., 2010). En décadas recientes el estudio del impacto del ruido antropogénico en la comunicación acústica de las aves ha recibido mucha atención (Brumm & Todt 2002; Brumm & Slabbekoorn 2005; Slabbekoorn & Peet, 2003; Francis et al., 2011; Slabbekoorn & Ripmeester, 2008; Potvin & Mulder, 2011; Ríos-Chelén et al., 2012). Una serie de investigaciones han reportado efectos negativos debido al ruido antropogénico, como la disminución en la densidad, riqueza, diversidad y éxito reproductivo de aves presentes en lugares ruidosos comparadas con las de lugares silenciosos (por ejemplo, lejos y cerca del ruido de tráfico de las carreteras; Reijnen & Foppen, 1994; Reijen et al. 1995; Reijnen et al. 1996; Rheindt 2003). Por otro lado se ha reportado el desarrollo de estrategias en diferentes especies de aves, que les permiten evitar el enmascaramiento de sus vocalizaciones (Brumm & Slabbekoorn, 2005, Patricelli & Blickley, 2006; Ríos-Chelén, 2009). Slabbekoorn y Peet (2003) mencionaron que el ruido antropogénico ha hecho que se cree una nueva presión de selección, la cual podría conducir a una disminución de las especies de aves que no sean capaces de adaptar sus señales acústicas al ruido.

1.4.1.- Estrategias que evitan el enmascaramiento de las vocalizaciones por ruido.

Las estrategias que evitan el enmascaramiento de las vocalizaciones por ruido se pueden clasificar en estrategias de corto o largo plazo (Brumm & Slabbekoorn, 2005). Las primeras están basadas en plasticidad, entendiendo ésta como los cambios en el fenotipo de un mismo individuo debido a los cambios en el ambiente. En estas estrategias las aves son capaces de ajustar sus vocalizaciones de manera flexible e inmediata ante los niveles cambiantes de ruido a los que se enfrentan. Las segundas están relacionadas a cambios evolutivos, en este caso el ruido es un factor de presión de selección que permite a cantos de una forma en particular ser favorecidos por selección, mientras que otros, son seleccionados en contra.

Una de las estrategias más comunes a corto plazo es conocida como Efecto Lombard. Es empleada por aves y mamíferos, incluído el hombre. Consiste en un incremento involuntario tipo reflejo de la amplitud de la vocalización en cuanto se elevan los niveles de ruido (Brumm & Todt, 2002; Brumm, 2004; Brumm & Slabbekoorn, 2005; Zollinger et al., 2012). Otra estrategia tiene que ver con el ajuste temporal de los atributos del canto. Se ha encontrado que algunas especies alargan y otras acortan sus vocalizaciones o los intervalos entre ellas lo que podría permitir aprovechar mejor las características temporales del ruido enmascarante. También pueden realizar repeticiones lo que podría incrementar la probabilidad de que las señales sean escuchadas (Fernández-Juricic et al. 2005; Brumm & Slater, 2006; Slabbekoorn & den Boer-visser 2006; Ríos-Chelén, 2009). Sin embargo, es necesario realizar más estudios para indagar si el cambio en las características temporales de las vocalizaciones es una estrategia general que las aves emplean para lidiar con el ruido.

Una tercera estrategia que ha generado mucho interés en años recientes y que es el tema central de este trabajo de Tesis, consiste en que las aves que habitan lugares ruidosos emiten cantos agudos o de frecuencia mínima (Hz) mayor que las que habitan zonas silenciosas, evitando así el enmascaramiento generado por las frecuencias bajas, características del ruido urbano (Slabbekoorn & Peet, 2003; Brumm & Slabbekoorn, 2005; Patricelli & Blickley, 2006; Ríos-Chelén, 2009). Las especies de aves en las que se ha encontrado el empleo de esta estrategia son: el carbonero común *Parus major* (Slabbekoorn & Peet 2003), el gorrión mexicano *Carpodacus mexicanus* (Fernández-Juricic et al. 2005), el gorrión cantor *Melospiza melodia* (Wood & Yezerinac, 2006), el mirlo común *Turdus merula* (Nemeth & Brumm, 2009) y el pájaro con anteojos *Zosterops lateralis* (Potvin et al., 2011).

En el primer capítulo de esta Tesis (ya publicado) evalué si en la Ciudad de México el gorrión mexicano (*Carpodacus mexicanus*) ajusta la frecuencia mínima de su canto en respuesta al ruido urbano, como lo reportó Fernández-Juricic (2005) para una población de California, Estados Unidos de Norteamerica. Formulé dos posibilidades no mutuamente excluyentes de cómo logran elevar la frecuencia mínima de sus cantos: 1) empleo de diferentes tipos de sílabas de acuerdo al nivel de ruido al que se enfrentaban, y 2) uso de los mismos tipos de sílabas en lugares ruidos y silenciosos. Por último en ese capítulo indagué si este gorrión es capaz de elevar la frecuencia mínima (Hz) de su canto en tiempo real al incrementarse repentinamente el ruido urbano. En los capítulos 2 (ya publicado como una de las primeras demostraciones de este fenómeno) y 3 probé experimentalmente si los gorriones mexicanos muestran plasticidad en la frecuencia mínima de sus cantos y llamados al exponerlos a diferentes niveles de ruido urbano.

1.4.2.- Impacto de los cantos de alta frecuencia de los machos en las preferencias sexuales de las hembras.

Las hembras emplean los atributos del canto de los machos para determinar si son una pareja potencial apropiada. Si los machos en áreas urbanas ajustan atributos como la frecuencia o características temporales de sus cantos evitando así el enmascaramiento por ruido, podrían ya no resultar atractivos para sus hembras y afectar el éxito reproductivo (Patricelli & Bickley, 2006). Por lo tanto, los machos podrían enfrentarse a una disyuntiva, ser escuchados o ser atractivos para las hembras (Patricelli & Bickley, 2006). La imposibilidad de garantizar simultáneamente ambas funciones podría explicar la reducción en la densidad, riqueza, y éxito reproductivo de aves en sitios ruidosos versus silenciosos (Reijnen & Foppen 1994; Reijnen et al. 1996; Rheindt 2003; Bayne, et al. 2008). Sin embargo, a la fecha existen pocos trabajos que muestran el impacto del incremento de la frecuencia mínima (Hz) de los cantos en respuesta al ruido, en las preferencias sexuales de las hembras (Halfwerk et al. 2011a; Halfwerk et al. 2011b). Uno de estos trabajos es el de Halfwerk y colaboradores (2011b) quienes encontraron que los machos de carbonero común (*Parus major*) cantan frecuencias bajas cuando la fertilidad de las hembras es más elevada, y que al emitir estas frecuencias sufren de menos pérdida de paternidad. También encontraron que las hembras de esta especie mostraron una preferencia mayor por cantos de frecuencias altas que por cantos de frecuencias bajas durante la señalización sexual en condiciones de ruido. Los autores mencionan que la eficiencia de la señal depende de la frecuencia del canto en presencia del ruido. Si bien las hembras parecen preferir cantos de frecuencias bajas, cuando son expuestas a ruido responden a cantos de frecuencias altas, lo que podría indicar que existe un costo involucrado.

En el capítulo 4 de esta Tesis quise evaluar si las hembras del gorrión mexicano responden de forma paralela al incremento de la frecuencia mínima del canto de los machos debido a los elevados niveles de ruido urbano. Para ello estudié experimentalmente las preferencias de las hembras del gorrión mexicano por cantos de frecuencias mínimas (Hz) altas o bajas en condiciones de silencio y de ruido urbano.

1.5.- Características morfológicas de las aves, estructura del hábitat y la frecuencia (Hz) del canto de las aves.

La evolución de los sistemas de comunicación acústica se ha moldeado a través de fuerzas selectivas y restricciones intrínsecas (morfológicas, fisiológicas) heredadas, que actúan en la producción, transmisión y detección de las señales acústicas (Ryan & Brenowitz, 1985). Se ha demostrado que la frecuencia del canto de las aves es afectada tanto por las características morfológicas del emisor (e. g. el tamaño corporal y del pico) como por la complejidad estructural de su hábitat (Morton, 1975; Wallschläger, 1980; Ryan & Brenowitz, 1985; Podos, 1997; 2001; Badyaev et al. 2008; Derryberry, 2009). Las características morfológicas afectan el proceso de producción de la señal, mientras las de complejidad estructural del hábitat afectan la transmisión de la señal.

Especies de aves de gran tamaño emiten cantos de frecuencia menor que las especies pequeñas (Wallschläger, 1980; Ryan & Brenowitz, 1985). Esto se explica porque las aves de gran tamaño tienen una siringe grande (Cutler, 1970) con membranas grandes, y que como consecuencia pueden vibrar a través de un rango de frecuencia más bajo que las membranas pequeñas que conforman las siringes de tamaño menor (Podos J. & Nowick S., 2004). La forma del pico también influye en la emisión de las frecuencias (Podos, 1997;

2001; Badyaev et al. 2008; Derryberry, 2009). Como ejemplo se ha encontrado una limitación en la producción de trinos, dada la dificultad de realizar repeticiones rápidas de notas, lo que hace que las aves de picos grandes produzcan trinos con tasas de repetición y anchos de banda menores que las aves con picos pequeños (Podos, 1997 ; 2001; Badyaev et al. 2008; Derryberry, 2009). Podos (2001), propuso que esto se debe a un compromiso en la biomecánica de la mandíbula, entre fuerza máxima y velocidad. Si el pico está adaptado para producir una fuerza mayor, estará limitado para realizar movimientos rápidos.

Por su parte, el hábitat preferido por distintas especies difiere con respecto a la densidad y tipo de vegetación, resultando en diferentes presiones de selección sobre las señales acústicas, como consecuencia de la forma en la cual los sonidos se atenúan y degradan al penetrar en el ambiente físico (Morton, 1975). Se ha reportado que las frecuencias bajas y las señales con menores anchos de banda se transmiten mejor que otras señales cuando se emiten en sitios de vegetación densa, pero no cuando se emiten en sitios con vegetación escasa. Ello está asociado a cantos con una frecuencia promedio más baja, y con menores anchos de banda en aves que habitan bosques, con respecto a las que viven en áreas abiertas (Morton, 1975; Ryan & Brenowitz 1985; Sorjonen, 1986; Wiley, 1991; Dabelsteen et al., 1993; Derryberry, 2009; Cardoso & Price 2010). En el quinto capítulo de la Tesis investigué cómo se relacionaban los parámetros de frecuencia del canto de especies paseriformes con las características de su hábitat, tamaño corporal y forma de pico. Usé aves de la península Ibérica por contar con descripciones adecuadas de su hábitat, suficientes buenas grabaciones de sus cantos, y acceso a ejemplares de museo de un número razonable de pares de especies -lo que permitiría realizar contrastes filogenéticos independientes-.

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Capítulo 1

Strategies of song adaptation to urban noise in the house finch: syllable pitch plasticity or differential syllable use?

Strategies of song adaptation to urban noise in the house finch: syllable pitch plasticity or differential syllable use?

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Summary

The influence of ambient noise in shaping birdsong attributes has received much attention lately. Recent work shows that some birds sing higher-pitched songs in noisy areas, which may allow them to avoid acoustic interference; yet it is not clear how this is achieved. Higher-pitched songs may be produced either by using the same syllable types in quiet and noisy areas, but singing them at a higher frequency in the latter (syllable pitch plasticity), or by using different syllable types in silent and in noisy circumstances (differential syllable use). Here we explored both strategies in the Mexico City population of house finch (*Carpodacus mexicanus*), a species known to possess a repertoire of several hundreds of syllable types. Birds produced songs with higher minimum frequencies in noisy than in quiet areas. This was mostly due to the minimum frequency of some syllable types being higher in noisy areas than in quiet locations. Also, males modulated the minimum frequency of the same syllable type during momentary increases of noise. Our results can help explain the high success of house finches at colonizing urban areas, while providing evidence of syllable pitch plasticity.

Keywords: house finch, *Carpodacus mexicanus*, urban noise, birdsong, pitch plasticity.

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Introduction

The influence of ambient noise in shaping birdsong attributes has received much attention recently (e.g., Brumm & Todt, 2002; Slabbekoorn & Peet, 2003; Brumm, 2004, 2006; Leader et al., 2005; Brumm & Slater, 2006; Patricelli & Blickley, 2006; Slabbekoorn & den Boer-Visser, 2006; Wood & Yezerinac, 2006; Fuller et al., 2007). Some of these studies have shown that the song of birds in situations of high levels of noise show particular adaptations to favour signal transmission, such as increase in sound amplitude (Brumm, 2004), number of same song types within a bout before changing to another song type (Brumm & Slater, 2006), and increased minimum song frequency (Slabbekoorn & Peet, 2003; Fernández-Juricic et al., 2005; Wood & Yezerinac, 2006). With respect to the latter, singing high-pitched songs in noisy areas may lead birds to reduce noise interference. This is because ambient noise, whether naturally produced (e.g., wind) or anthropogenic (e.g., automobile traffic), is commonly composed of low frequencies, with its energy diminishing towards higher frequencies, and certain types of anthropogenic noise like car traffic can easily reach frequencies that overlap with the frequencies of birdsong (e.g., 2 kHz). Therefore, producing songs above these frequencies could prevent noise masking. As birdsong is known to play an important role in sexual selection processes (reviews in Searcy & Anderson, 1986; Catchpole & Slater, 1995; Gil & Gahr, 2002), avoiding noise masking may have important fitness consequences.

Indeed, some studies suggest that noise has negative effects on bird populations. For instance, several studies have found a reduction in density of breeding birds in the proximities of noisy roads and highways (e.g., Reijnen & Foppen, 1994; Reijnen et al., 1996), and a negative association between noise level and bird density (Reijnen et al., 1995). While it is not clear how high noise level may be related to population decline, some data suggest that the latter may be a consequence of noise masking birdsong (Rheindt, 2003), which in turn may impair processes of sexual selection, erode pair preferences (Reijnen & Foppen, 1994; Swaddle & Page, 2007), or disrupt bird vocal communication in general.

Since anthropogenic noise is a widespread phenomenon, particularly strong in or around cities, airports and highways, often reaching levels beyond those allowed by current legislation on public health (especially in big cities), it is important to study whether birds are able to deal with this kind of pollution. A positive correlation between anthropogenic noise level and frequency of birdsong was first reported in the great tit (*Parus major*, Slabbekoorn & Peet, 2003). This study was subsequently followed by additional work by Fernández-Juricic et al. (2005) in the house finch (*Carpodacus mexicanus*) and Wood & Yezerinac (2006) in the song sparrow (*Melospiza melodia*), who reported similar correlations. The consensus of these studies is that the typically low-pitched urban noise would favour higher-pitched songs since these would be more readily detected by conspecifics.

Yet the strategy by which birds achieve higher frequency songs in noisy areas is far from clear, and at least two non-mutually exclusive hypotheses can be envisaged. First, birds may use different syllable types according to the level of noise, that is, they may include in their song more high-frequency syllable types in noisy areas than in quiet areas (differential syllable use). Such a strategy may be reinforced through differential learning by young birds, since by definition those syllables better suited to noisy environments would have a higher chance of being heard and learnt, by young birds (Hansen, 1979). Second, birds may use the same syllable types in noisy and in quiet areas, yet produce this syllable type with a higher minimum frequency in noisy environments (syllable pitch plasticity). A change in frequency could in fact be a side effect of an increase in song amplitude (the Lombard effect, Quedas et al., 2007), which is a well-known strategy that organisms use when facing noise (e.g., Cynx et al., 1998; Brumm & Todt, 2002; Brumm, 2004; Brumm et al., 2004). It is also unknown whether the positive correlation between noise intensity and minimum song frequency is the relatively slow, and long-term, result of selection favouring males whose song is less masked by environmental noise, or whether it results from the individuals being able to modulate the minimum frequency of their songs, thus being a short-term change due to behavioural plasticity (Brumm & Slabbekoorn, 2005). If the former is true we would expect individuals to sing high-pitched songs in noisy areas irrespective of current noise levels. A long-term change process has probably occurred in great tits (*Parus major*) from noisy environments, which even during some particularly quiet periods continue to sing high-pitched songs (Slabbekoorn & Peet, 2003). Indeed, recent data show that in this species the song adaptation to urban conditions is based on song-type selection and not on spectral shifts or note deletion (Slabbekoorn & den Boer-Visser, 2006).

However, Slabbekoorn & den Boer-Visser (2006) study focused on between-population differences (city vs. forest) and, thus, individual adaptation could be masked by population differentiation and drift. In the present study we have taken a more direct approach and have analysed differences in syllable use and pitch plasticity within the same population with respect to different urban noise levels. In addition, by comparing minimum song frequencies in relation to changing levels of noise in particular moments, we tested whether individuals are capable of modulating their songs when facing sudden increases of background noise.

We studied a Southern population of house finches in Mexico City, one of the biggest and presumably noisiest cities in the World. Our objectives were three-fold: (1) to establish whether previous results reporting higher minimum frequencies in noisy areas in this species (Fernández-Juricic et al., 2005) also apply to our population; (2) to determine whether higher-pitched songs are produced in noisy areas through either differential syllable use or syllable pitch plasticity; and (3) to investigate whether house finches are capable of real-time modulation of the minimum frequency of their songs in response to changes in background noise levels.

Methods

Study site and song recordings

From May 17 to July 7, 2006, between 0800 and 1400 h, songs of 35 male house finches were recorded in 26 different locations in southern Mexico City. Spontaneously (not enticed by playback) singing males were recorded while perched from a distance of 5–10 m. We did not register whether recorded birds were interacting with other (male or female) individuals. To avoid recording each male more than once, the distances between recorded subjects were at least 1 km apart, which is larger than the maximum expected home range size of house finches (Manley & Schlesinger, 2000). Only one male was recorded on each location, except when several individuals could be recognized by differences in plumage colouration. This was the case at seven locations where two individuals were recorded and in one location in which three males were recorded. Following the study by Pytte (1997), who showed that five songs per individual are sufficient to establish a representative individual's syllable repertoire, we recorded at least five songs for each male. We analysed (see below) an average of 21 songs per male (SE = 2.38, range = 6–71). Songs were recorded on audio cassettes (TDK SA60), using a directional microphone (Sennheiser ME66) connected to a Marantz PMD221 cassette recorder. Recordings were digitized on a PC computer using an Intel® 5.10 Sound card with 16 bits accuracy, and sampled at a rate of 22 kHz using the Avisoft SASLab Pro software.

Measuring the songs and constructing a syllable catalogue

For each song we measured minimum frequency of each syllable (kHz), maximum frequency of song (kHz) and song length (s). Spectrograms were obtained using the Avisoft SASLab Pro software (FFT length, 256; frame size, 100%; window, Hamming; frequency resolution, 86 Hz; temporal resolution, 8 ms). Frequency and temporal measures of songs were conducted manually on the spectrograms, always by the same person, with the on-screen free moveable reticule cursor available in Avisoft SASLab Pro software. Only those songs whose minimum frequencies were discernible from the background noise were measured and subject of analyses. Figure 1 shows an example of a song recorded in a very noisy site and one song recorded in a quieter site.

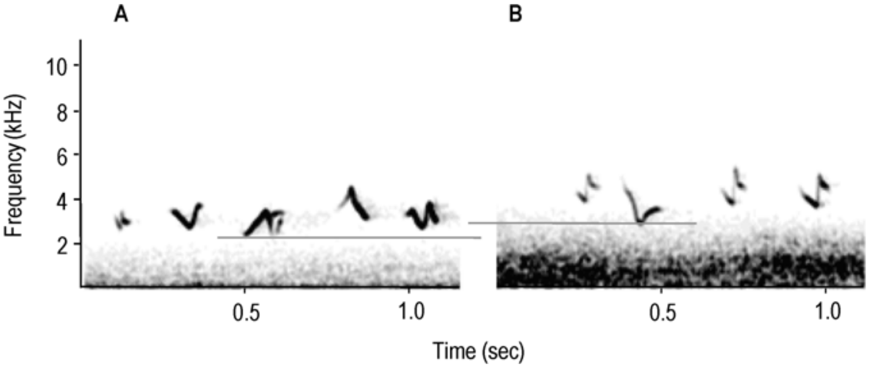

Figure 1. Two examples of house finches song recorded at two locations with low (A) and high (B) levels of noise. (A) A song recorded in Instituto de Biología, UNAM. (B) A song recorded in Gabriel Mancera Avenue. This figure exemplifies that even in noisy locations, the minimum frequency of songs could reliable be measured. The spectrogram of the song at the quiet location shows a lower minimum frequency than the song recorded at the noisy location. The line in A and B shows the minimum frequency of the song in A and B, respectively.

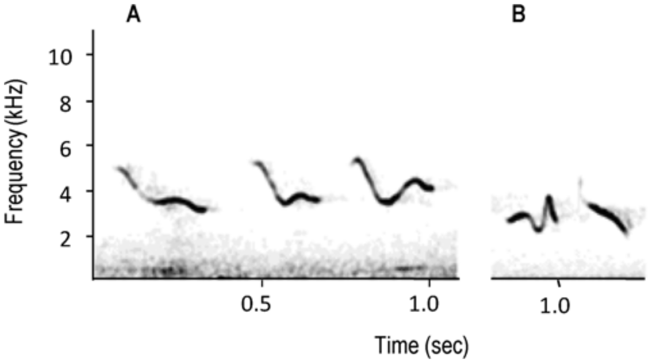

Figure 2. Examples of discrete and continuous variation in syllable types. (A) An example of three syllables with continuous variation; that is, with variation resulting in intermediate forms. These three syllables are considered as the same syllable type. (B) An example of two syllables that show discrete variation. These two syllables always showed these two discrete forms and, thus, were considered as different types.

In order to establish whether house finches increase syllable pitch or differentially use high-pitched syllable types in noisy areas, a catalogue of syllables was compiled. Syllables were classified into several types according to their shape. Variation between syllables was either discrete (i.e., a syllable type was clearly differentiated by its shape from other types) or continuous (i.e., there was a smooth transition in the shape of similar syllables). Following Pytte (1997), syllables with discrete variability were grouped in the same type if they shared the same general shape, whereas syllables that showed continuous variability and were similar in shape were grouped as the same type (Pytte, 1997). Thus, under these criteria, if the syllable decreased in bandwidth but kept its basic shape we considered it as the same syllable type. Figure 2A shows an example of a syllable showing continuous variability. Following these criteria, a total of 261 different syllable types were recognized in our sample.

Measuring noise

Noise level (dB SPL re 20 μPa) was measured at the same locations where songs were recorded, using a SEW® 2310 SL digital sound level meter (range, 30–130 dB; weight, A, fast response, ANSI S1.4 Type II) between September 1 and October 25, 2006. Since, because of logistic reasons, this work could not be done at the same time of the song recordings, we choose to measure noise in September, thus avoiding the Mexican holiday period during which noise levels are typically reduced. To have a representative measure of noise, we measured it at the same time-span during which songs were recorded (there were six intervals: 8–9, 9–10, 10–11, 11–12, 12–13 and 13–14 h). We measured noise at each interval following a modified version of Brumm's (2004) protocol. Briefly, Brumm's protocol consisted of registering the highest value of ambient sound level, measured during 10 s at repeated times, at each of four directions of the compass. We measured noise at 2 m above the ground during 5 min; 1 min was used for each of five different directions in a clockwise direction (North, East, South, West and Upwards (i.e., towards the sky)). Each minute, noise was measured every 10 s (6 measurements/min). We flipped a coin to randomize the direction in which we started to register noise (North or South). West was always followed by Upwards. For each recorded male, noise level was registered at the same location where the bird was recorded. This means that even for those males that were recorded in the same location we registered independent noise levels for each one of them. Sound levels were averaged for each site, and these values used in further analyses.

Because we measured ambient noise levels in different months than when songs were recorded, we decided to test the repeatability of noise measures. For this purpose, we obtained new noise measures in a sub-sample ($N = 10$) of the 26 sites where songs were recorded in October 2008 and compared it with the first measurements. This sub-sample encompassed places of low, moderate and high noise levels.

Data analyses

Parametric tests were used when data conformed to normal distributions. Otherwise, non-parametric statistics were used. Whenever the same data set was analysed more than once, a sequential Bonferroni correction was performed to correct the level of significance (Rice, 1989).

Differential syllable use

To determine whether house finches sing different syllable types in relation to noise level (i.e., differential syllable use), we first catalogued all syllables as 'high frequency syllable (HFS)' or 'low frequency syllable (LFS)' depending on whether their average frequency was, respectively, above or below the overall mean syllable frequency. The mean frequency of each syllable type was calculated by obtaining the mean frequency of each syllable type per male, and then averaging the mean frequencies of each syllable type across all males. From these mean frequencies of syllable types we obtained the overall mean syllable frequency. If birds use different syllables types depending on background noise, we expected a positive correlation between the proportion of HFS and noise level.

Syllable pitch plasticity

To determine whether house finches use the same syllable types, but sing them at a higher frequency in noisy areas (i.e., syllable pitch plasticity), we compared the minimum frequency of the same syllable types between locations that differed in noise level. This comparison was designed to maximise the variance in the independent variable (differences in noise levels), and each bird was used only once in order to avoid pseudoreplication. We proceeded by first ranking the different birds according to the measured noise levels, then we paired male 1 (from the noisiest location) with male 35 (from the less noisy place), male 2 with male 34, and so on until 17 pairs were formed (leaving one male out of the analysis). We then calculated pair-wise differences in noise level (always subtracting quiet from noisy) as well as the average difference in minimum frequency of shared syllables types. Under the syllable pitch plasticity hypothesis we predicted a positive correlation between the difference in noise level and the difference in minimum frequency of shared syllables types.

Since the above procedure is open to the possibility that whatever result it yields is only valid for that particular set of pairs, we performed, in addition, a Mantel test in which all possible pairs ($N = 595$) were included. Again, we calculated for each pair both the difference in ambient noise and the average difference in the minimum frequency of shared syllables. Inevitably this procedure generates a much more scattered association but has the advantage of a greater external power than the previous one.

Real-time modulation of song pitch in response to current changes in noise level

A further criterion required under the syllable pitch plasticity hypothesis is to demonstrate that house finches are able to modulate the minimum frequency of their songs according to different noise levels (i.e., short-term change, Brumm & Slabbekoorn, 2005). We took advantage of the fact that, while we were recording, there were sudden bursts of noise due to cars passing close by. This gave us the opportunity to investigate whether males are able to increase the minimum frequency of their songs during these moments of increased noise level with respect to quieter moments. We searched our song files for cases in which, at the same time when the focal male was singing, a sudden and evident increase of noise occurred (as determined by an increase in the density of the spectrogram's trace between 0 and 2 kHz). Provided that we had also a recorded song for this focal male (in the same sound file) in a moment of lower noise level, we could compare both songs. We had 13 such cases. We compared the minimum frequency of a song in the low noise level condition with the minimum frequency of another song from the same individual in the high noise level condition. To test whether there were significant differences in minimum frequencies between both conditions, we used a paired t test. An additional criterion was to choose the first song that precisely matched the same type of song (i.e., same sequence of syllables, same number of syllables, etc.) as the song in the noisy condition. This is because we wanted to compare the same syllable types to see if house finches modulate their frequency, and the same syllable type is easier to find in a song of the same type. This meant that we compared the minimum frequencies of the same syllable type in both conditions. This criterion was chosen after knowing the results of the previous analyses and was conducted in order to confirm the use of syllable pitch plasticity by male house finch. Unless specified otherwise, values are reported as mean ± SE.

Results

Urban noise

Urban noise was mostly represented by cars and vehicles that passed far away (i.e., around 1 km away, in quite areas) or near (i.e., as close as 1 m to the place where noise was registered, in noisy sites). Mean urban noise levels significantly differed among sites (Kruskal–Wallis test: $^{2} = 146$, df $= 25$, $p < 0.001$), and ranged between sites from 40 dB(A) SPL to 74 dB(A) SPL. Mean noise level in our study sites was 58 ± 2 dB(A) SPL. Noise level was not correlated with number of recorded songs (Pearson correlation: $r = 0.15$,

$N = 35$, $p = 0.367$) nor with number of syllables (Pearson correlation: $r = 0.04$, $N = 35$, $p = 0.782$), showing that our data were comparable between locations differing in noise level. Additionally, we found a highly significant correlation ($r = 0.94$, $N = 10$, $p < 0.001$) between our measures of noise level obtained in September–October 2006, and our measures of noise levels obtained in October–November 2008. The repeatability value for this sub-sample of 10 sites was 0.94.

House finch songs

In exploratory analyses, we found that longer songs had lower minimum frequencies (Pearson correlation: $r = 0.45$, $N = 35$, $p = 0.006$), and higher maximum frequencies (Pearson correlation: $r = 0.49$, $N = 35$, $p = 0.002$). Maximum and minimum song frequencies were not correlated ($r = 0.28$, $N = 35$, $p = 0.104$).

We found an average of 27 ± 1.6 different types of syllables per male in our sample. When comparing places of high and low noise levels, we found that only an average of 7.5 ± 0.8 syllable types were shared among males. The mean house finch song duration in our sample ($N = 35$) was 2.02 ± 0.10 s, range 0.99–3.93 s. The mean minimum frequency of songs was 2221 ± 31.30 Hz (range 1916–2697 Hz), and the mean maximum frequency was 5873 ± 103.42 (range 4630–7032 Hz).

House finch songs and urban noise

We found a positive correlation between noise level and minimum frequency of song ($r = 0.42$, $N = 35$, $p = 0.012$), which remained significant after Bonferroni correction. This result supports previous findings with this species (Fernández-Juricic, 1985), in which a positive correlation between noise level and minimum frequency of song was also found. We failed to find a significant correlation between noise level and maximum frequency ($r = 0.23$, $N = 35$, $p = 0.176$), and between noise level and song length ($r = 0.27$, $N = 35$, $p = 0.11$). In other words, as noise levels increases, the minimum frequency of songs increases as well, but not their maximum frequencies or their lengths. This results in syllables being 'compressed' in the frequency axis (Figure 5).

The relative use of high-pitch over low-pitch syllable types was not significantly related to noise levels, although there was a non-significant trend

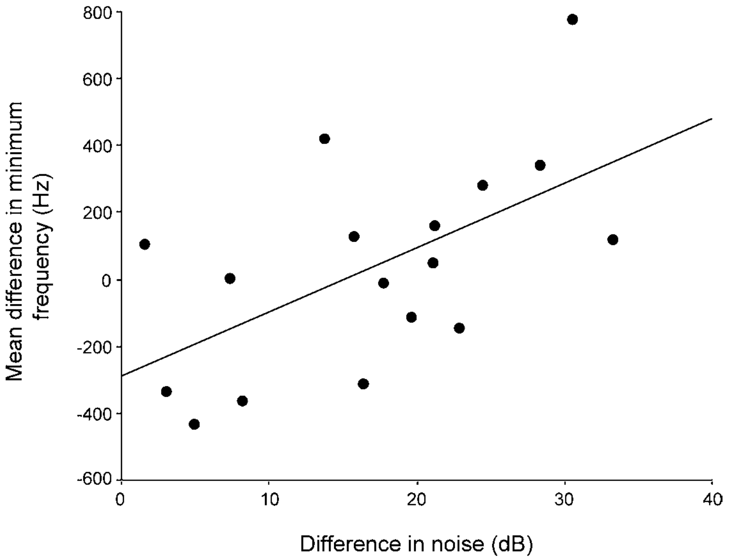

Figure 3. Relation between difference in noise intensity and difference in minimum frequency of syllables shared between songs. As the difference in noise level between two locations increases, the difference in minimum frequency of shared syllable types between two males in these locations also increases. For this analysis the difference in minimum frequency of syllable types shared between two locations was averaged across syllables types. See text for statistics.

for a higher use of high-pitched syllables in noisier environments (Pearson correlation: $r = 0.30$, $N = 35$, $p = 0.07$), suggesting that differential use of syllable types may be a subsidiary strategy in song adaptation to noise. However, we found stronger evidence for the alternative hypothesis, syllable pitch plasticity, as shown by a significant positive correlation between difference in noise intensity and mean difference in minimum frequency averaged for same syllable types (Pearson correlation: $r = 0.58$, $N = 17$, $p = 0.014$, Figure 3). This pattern obtained with our set of pairs was also supported by the results of the Mantel test using all possible ($N = 595$) pairs ($r = 0.19$, $p = 0.001$).

Males facing a sudden increase in noise (high noise condition) increased the minimum frequency of the song emitted during that moment in comparison with the same type of song produced during a quieter moment (paired t-test: $t = 3.80$, df $= 12$, $p = 0.002$, Figure 4). This was achieved by increasing the minimum frequency of the same syllable type. During these bursts of noise, the background noise was increased from a mean of

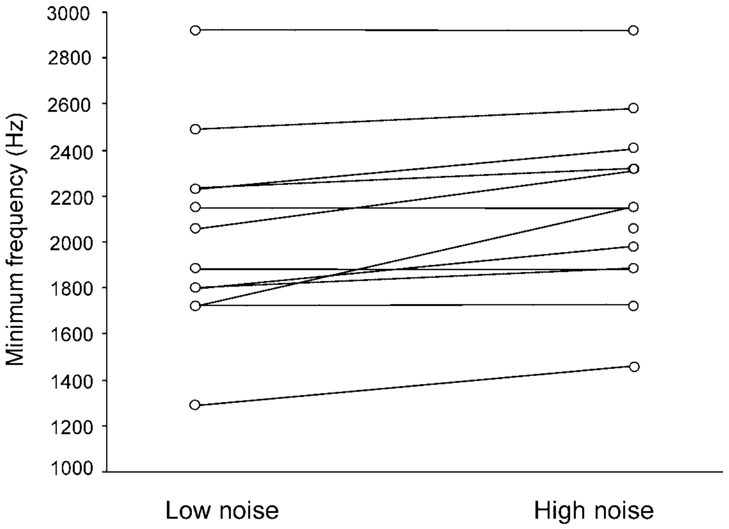

Figure 4. Minimum frequency of songs emitted during a moment of relative low noise level (Low noise) and during a sudden increase of noise level (High noise). Nine out of 13 males increased the minimum frequency of their songs during a moment of noise increment in comparison to another moment of lower noise. See text for statistics.

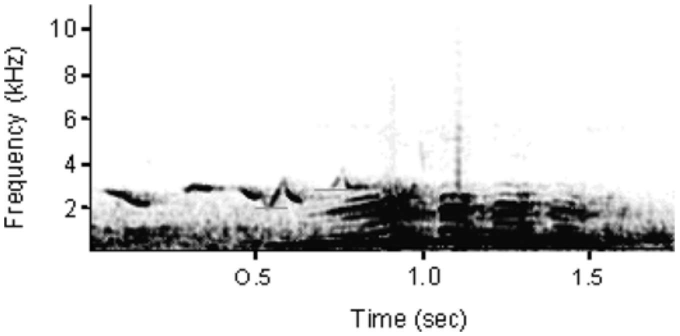

Figure 5. A house finch song when the male producing it faces a sudden burst of noise. The minimum frequency of the same syllable type was increased, within the song, from 1890 to 2750 Hz when a motor vehicle passed nearby, momentary increasing the background noise level. Also note that this syllable type was 'compressed' as a result of its minimum frequency being increased to a much grater extent than its maximum frequency. Lines show minimum frequencies of the same syllable type.

64 ± 10 dB to 71 ± 10 dB, as measured in the song files. This increase in noise was significant (paired t-test: $t = 6.24$, df $=$ 12, $p < 0.001$). Figure 5 shows an example in which a house finch increases the minimum

frequency of the same syllable type (in this case within a single song) during a sudden rise in noise.

Discussion

Our results confirm previous studies that show that house finches and other songbirds sing higher-pitched songs in noisy areas (e.g., Slabbekoorn & Peet, 2003; Fernández-Juricic, 2005; Wood & Yezerinac, 2006), a pattern that may be an adaptation for living in noisy environments (but see Leader et al., 2005). By increasing the minimum frequency of their songs, house finches in Mexico City appear to be producing songs that are less likely to be masked by urban noise.

Besides ambient noise, habitat structure is another potential factor that may influence the structure of bird song. For instance, Slabbekoorn et al. (2007) found a relationship between habitat structure and minimum frequency in dark-eyed juncos (*Junco hyemalis*). They showed that males sing higher-pitched songs in an urban habitat than their counterparts in natural forest. Thus, it can be argued that the relationship between ambient noise and minimum frequency that we found may be confounded by differences in habitat structure. We believe, however, that habitat structure is not as important a factor as ambient noise in shaping song properties in our study. First, we limited our sample to an urban population and, thus, possible effects of different habitat structure on song frequency are expected to be minimized. Second, we avoided recording birds in parks, where habitat structure (i.e., close habitat) is typically different from other parts of the city (i.e., open habitat). Finally, the study by Fernández-Juricic et al. (2005), with house finches in urban parks, unmasked the relationship between several ambient factors, including ambient noise and micro-habitat structure, and different song attributes. While they showed a significant correlation between ambient noise and song minimum frequency, they failed to report any relation between habitat structure and song attributes (e.g., minimum frequency, frequency range, number of notes), suggesting that ambient noise is a more important factor in shaping the structure of house finches song than micro-habitat structure.

Producing high-pitched vocalizations in the presence of high levels of noise can lead to the production of unexpectedly high frequencies for an oscine bird. Perhaps the most extreme example of an oscine bird producing high frequency vocalizations in places with high levels of noise is the one reported by Narins et al. (2004). They showed that both a frog (*Amolops tormutus*) and a songbird (*Abroscopus albogularis*) living near streams emit acoustic signals containing ultrasonic harmonics. These harmonics reached maximum frequencies of up to 54 kHz in the case of the passerine. Although we did not look for ultrasonic sounds in our study, a different phenomenon appears to emerge with the house finch: as opposed to the minimum frequency of songs, the maximum frequency was not higher with increasing levels of ambient noise. This resulted in some syllables being 'compressed' (Figure 5). Wood & Yezerinac (2006) report a similar relation between noise amplitude and the minimum frequency of song sparrows (*Melospiza melodia*) songs, but a lack of relationship with 'high frequency of song'.

The fact that we found a highly significant correlation between the measures of noise levels obtained in September–October 2006 and October–November 2008, and a high repeatability value for these measures, demonstrates that noise intensities were consistent between different months and years. That is, a place with a high or low noise level remains a place with a high or low noise level, respectively, regardless of the month or year when the measure is taken.

Our data allow us to draw conclusions about the strategies that are used by birds to achieve song adaptation. We failed to find convincing evidence that singing higher-pitched songs in noisy areas is due to increasing the proportion of high frequency syllables types in these locations, as predicted by the differential syllable use hypothesis. However, a marginally significant tendency in that direction implies that we cannot completely rule-out the hypothesis that male house finches sing different syllable types according to local noise levels. On the other hand, we provide robust evidence that higher-pitched songs in noisy areas are the result of uttering the same shared syllable types in quiet and in noisy circumstances, but with a higher minimum frequency when there is more noise (i.e., they show syllable pitch plasticity). This, however, does not annul the possibility that other syllables (i.e., non-shared syllables) may have also increased their minimum frequency. Additionally, our results indicate that house finches are able to adjust in real time the minimum frequency of their songs to changes in noise level and, thus, the observed pattern of minimum frequency in relation to noise can be explained in terms of plasticity and may be viewed as a short-term adaptation.

This result does not discard the possibility that a long-term adaptation is, as well, in process (Brumm & Slabbekoorn, 2005). Since this modulation was achieved by increasing the frequency of the same syllable type, this latter result provides further support for the syllable pitch plasticity hypothesis. This plasticity may well be related to the great success with which house finches have colonized different cities. Our results do not mean that house finches are unable to individually select different syllable types when sudden bursts of noise occur. To our knowledge, there is only another study that has proved vocal plasticity in a bird in relation to frequency song parameters and noise (Tumer & Brainard, 2007). This laboratory study used white noise in a reinforcement contingency procedure, whereby Bengalese finches (*Lonchura striata* var. *domestica*) were conditioned to change the fundamental frequency of a particular syllable in their songs. By applying bursts of white noise to a specific targeted syllable, Tumer & Brainard (2007) demonstrated that Bengalese finches are able to increase or decrease the fundamental frequency of this specific syllable, without changing the fundamental frequency of other syllables types within the same song. This proves that, like the house finch (this study), Bengalese finches display syllable pitch plasticity when noise result in auditory disruption or compromise acoustic communication.

Nolan & Hill (2004) provide experimental evidence that female house finches prefer longer over sorter songs in laboratory conditions. On the other hand, Mennill et al. (2006) found that male house finches singing longer songs (i.e., with more syllables) had an earlier nest initiation date, which is a good predictor of reproductive success. We found that higher-pitched songs were also shorter, but, on the other hand, we failed to find a negative correlation between noise level and song length, casting doubts on the idea that house finches sing shorter songs in noisy places. If this is true, house finches in our studied population may not be facing a trade-off between singing to attract a female and making their signals heard in a noisy place, as was suggested for another studied population in California (Fernández-Juricic et al., 2005). With respect to song length, our results on syllable pitch plasticity, coupled with the fact that only an average of 7 syllable types were shared between compared males, support the idea that males do not need a large repertoire of syllables to deal with noise. Since males adjust the frequency of the same syllable types that are produced in noisy and in quiet conditions, a few learnt syllables may be enough to produce a song adapted to noise.

To conclude, besides corroborating the results of Fernández-Juricic et al. (2005) we show that the observed pattern of noise amplitude and minimum frequency of house finch songs is a result of singing the same syllable types that are found in quiet and noisy conditions, but with a higher frequency in the latter case. We also show that individuals are able to instantaneously adjust the minimum frequency of their songs to deal with contemporary changes in noise levels. More studies (e.g., on female choice) are needed to assess whether, and how, noise pollution has an effect on house finches populations, a bird species that appears to settle particularly well in cities. Finally, it is worth studying whether this plasticity is shared by species that use less variable and complex songs and are perhaps less capable of song plasticity, since this might limit the capacity to cope with the acoustic challenges posed by human activities.

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Capítulo 2

Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird.

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Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird

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Research has shown that bird songs are modified in different ways to deal with urban noise and promote signal transmission through noisy environments. Urban noise is composed of low frequencies, thus the observation that songs have a higher minimum frequency in noisy places suggests this is a way of avoiding noise masking. Most studies are correlative and there is as yet little experimental evidence that this is a short-term mechanism owing to individual plasticity. Here we experimentally test if house finches (*Carpodacus mexicanus*) can modulate the minimum frequency of their songs in response to different noise levels. We exposed singing males to three continuous treatments: low–high–low noise levels. We found a significant increase in minimum frequency from low to high and a decrement from high to low treatments. We also found that this was mostly achieved by modifying the frequency of the same low-frequency syllable types used in the different treatments. When different low-frequency syllables were used, those sung during the noisy condition were longer than the ones sang during the quiet condition. We conclude that house finches modify their songs in several ways in response to urban noise, thus providing evidence of a short-term acoustic adaptation.

Keywords: house finch; *Carpodacus mexicanus*; birdsong; urban noise; acoustic adaptation

1. INTRODUCTION

In acoustic communication, noise can be defined as any sound that reduces the ability of a receptor to detect acoustic signals [1]. Noise is ubiquitous in nature; however, human activities have increased the amount of noise that animals are exposed to, and evidence suggests that urban noise is a selective pressure that has shaped the song of birds inhabiting sound-polluted environments (reviews in [1,2]).

Selection has promoted several mechanisms that enhance the effectiveness of signal detection under noisy conditions. A first mechanism, the Lombard effect, is characterized by an increase in sound amplitude as a response to noise [3–5]. Additionally, birds can increase the redundancy of signals so that the message has an increased chance of getting across in noisy environments [6], or sing at times when noise level is lower [7]. Another possibility is to sing higher pitched songs to reduce their acoustic overlap with low-frequency noise [8–11]. A recent study has shown that urban populations of great tits (*Parus major*) have an increased minimum frequency in comparison to the countryside populations, and that this modification is best explained as a response to noise perturbation [12]. However, there is still little evidence disentangling the relative contribution of natural selection, differential learning and individual plasticity in generating this noise-dependent change in frequency (but see [13] for a case of cultural evolution). In a previous correlative study in the house finch (*Carpodacus mexicanus*), we found that males modulated the frequency of their song by increasing the minimum frequency of certain syllable types, when bursts of urban noise occurred during the recording session, suggesting that immediate, real-time responses are possible in this species [8]. In the great tit, it has been shown that when confronted with low-frequency urban noise, males sing, for longer times, song types with higher low-frequency notes [14].

Here we set out to experimentally test the hypothesis that house finches can plastically modify the frequency of their songs, by exposing singing males with different levels of urban noise in controlled captivity conditions.

2. MATERIAL AND METHODS

We obtained birds from authorized local suppliers in Mexico City, which had been captured as adults in different areas of Mexico, including Mexico City and San Luis Potosí. Birds were kept in individual cages, and fed with an ad libitum combination of seed mix and fruit. Light/dark cycle was kept at 12 : 12. Before the experiment, all males were implanted with testosterone to induce singing. Twenty one males were used in this experiment.

The experiment was run in March–April 2009, in the mornings 8.00–14.00 and afternoons 16.00–18.00. Individually caged males were placed outdoors in an arena set in a quiet open area of the Universidad Nacional Autónoma de México (UNAM) campus. Males were flanked at approximately 10 cm by two individually caged females to induce singing. Males were visually separated from females, but could interact vocally. Four females were changed between males to avoid habituation. This set of three cages was presented with a loudspeaker (Mineroff SME-AFS, frequency response: 100 Hz–12 kHz) from which the acoustic stimuli were broadcast using a laptop (HP Pavilion dv1000), while the experimenter was hidden from the birds at a distance of 3.5 m from the arena (figure 1).

All males were sequentially exposed to two different sound stimuli: low (44–57 dB) and high (56–65 dB; see below) levels of urban noise, in a 'sandwich' fashion of playbacks: low–high–low. Each bird received a different noise recording to avoid pseudoreplication. Treatments were prepared from atmospheric recordings at a busy avenue near UNAM, Mexico City, with a microphone Sennheiser ME66 connected to a Marantz PMD221 tape recorder, using TDK SA60 tapes. From a 2 h recording, 30 s segments of noise were randomly selected, normalized to the same amplitude and prepared using Avisoft SAS-Lab Pro v. 2.0. Since sound pressure was not even through any given segment, noise level during each playback was not a fixed value, but rather a range, which we kept at the values indicated above.

The experimental procedure started by taking the females from their home cages and placing them in the flanking cages of the arena, where they were left to habituate for 15 min. Then a male was taken from his cage and placed in the experimental cage. A continuous recording began once he started singing. After it had produced five songs under ambient noise (31–39 dB), playbacks of

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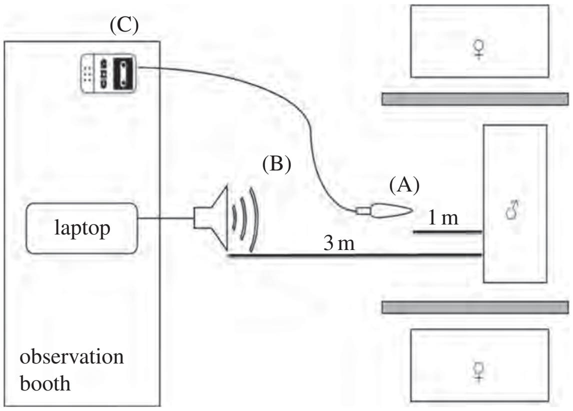

Figure 1. Song recording arena. The cages of experimental individuals are represented by rectangles on the right. The divisions between cages are observed in grey. The microphone (A) is shown connected by a cable to the recorder (C). The loudspeaker (B) is shown connected to a laptop.

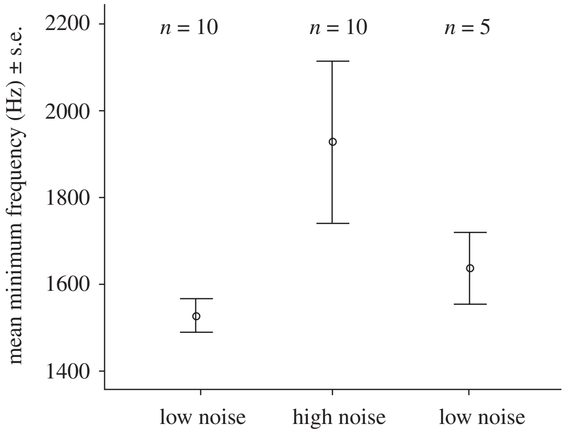

Figure 2. Mean minimum frequency in the three treatments. Males increased the minimum frequency of their songs from low to high and then decreased it from high to low. See text for statistics.

noise stimuli were broadcasted until we obtained a minimum of three songs under each of low, high and low noise conditions. The recordings of the songs were made with a Sennheiser ME66 directional microphone connected to a Marantz digital recorder PMD660.

Noise intensity was measured with a digital sound pressure meter (SEW 2310 SL, ANSI S1.4 Type II), with a frequency range of 30–130 dB, A-weight mode, and slow-response setting.

Of a total of 21 males, 10 males sang during the first (low) and second (high) playbacks, and only five continued singing during the third playback (low). As data were normally distributed, we used a paired-*t*-test to compare the change from low to high in those 10 males, and a Wilcoxon matched-pairs test to compare the songs of those five males that kept on singing from high to low.

We measured song length, minimum and maximum frequencies of songs, and length of each syllable within songs. Additionally, we made a syllable catalogue to analyse whether birds used the same or different minimum-frequency syllable types in different treatments. These minimum-frequency syllable types were classified as shared or non-shared, depending on whether or not they were used by an individual in the different treatments.

Table 1. Percentages of shared-syllable types and shared syllables among songs produced by males during treatments. Since the percentage of shared-syllable types and shared syllables is not 100%, this means that the songs produced in different treatments had non-shared-syllable types also.

male	% shared-syllable types	% shared syllables
1	33.3	60.0
2	60.0	83.3
3	12.5	30.0
4	22.2	35.7
5	50.0	83.3
6	20.0	47.0
7	16.6	25.0
8	14.2	41.6
9	16.6	64.2
10	33.3	55.5

3. RESULTS

We found a significant increase in minimum frequency from low to high ($t = -3.71$, d.f. $= 9$, $p = 0.005$; figure 2). Neither song duration ($t = 1.30$, d.f. $= 9$, $p = 0.22$) nor maximum song frequency ($t = 0.17$, d.f. $= 9$, $p = 0.86$) changed between treatments. The mean length of syllables within songs did not differ between treatments ($t = 0.21$, d.f. $= 9$, $p = 0.83$). In the sample of males that also sang in the third playback (low), we found a significant decrease in minimum frequency from high to low ($Z = -2.023$, $n = 5$, $p = 0.04$; figure 2). As expected, noise had a strong low-frequency component (peak frequency, mean ± s.e. $= 231 \pm 28$ Hz, range $= 184$–475 Hz).

Males sang both shared- and non-shared-syllable types during noise exposure (table 1). We found a strong significant increase in song frequency when we analysed only the songs with shared-syllable types ($t = -5.587$, d.f. $= 9$, $p < 0.001$, see the electronic supplementary material), but the effect fell short of significance when we analysed those with non-shared-syllable types ($t = -2.035$, d.f. $= 7$, $p = 0.08$). We found that the songs with shared syllables were shorter during noise exposure ($t = 2.531$, d.f. $= 9$, $p = 0.03$). This was not the case for songs with non-shared syllables ($t = 0.858$, d.f. $= 7$, $p = 0.41$). Finally, non-shared-syllable types were longer than the syllables they replaced ($t = -2.605$, d.f. $= 7$, $p = 0.03$); whereas shared-syllable length did not vary between treatments ($t = 1.435$, d.f. $= 9$, $p = 0.18$).

4. DISCUSSION

Our experiment shows that house finch males shift the minimum frequency of their songs in response to an increase in the amplitude of urban noise. This dynamic change is indicative of real-time plasticity, as suggested by correlative data in the same species [8].

Frequency shifts as a response to urban noise have been found in several bird species, and evidence suggests that it is a widespread strategy used by oscines to increase the salience of their songs in noisy urban environments [8–10,12,15], leading to interpopulation song divergence [16].

Song styles are markedly different among species, and thus it is not surprising that those species that achieve this shift differ in the mechanisms used to accomplish it. In the great tit, song frequency differences between noisy and quiet populations seem to be owing to differential use of song-types, so that in noisy situations birds may favour the use of high-pitched songs [12]. In the house finch, a species with more versatile songs, we have found that the same syllable types are used in noisy and quiet areas, and that birds can modify the minimum frequency of a given syllable type depending on the noise level [8, this study], but that males also use other novel minimum syllable types (this study). The fact that the frequency shift was stronger when we considered only those songs with shared syllables suggests that the frequency shift is achieved mostly by increasing the pitch of shared-syllable types, which is in accordance with previous correlative findings [8]. A study in the Bengalese finch (*Lonchura striata*) has shown that birds are able to increase or decrease the frequency of a given syllable in response to aversive conditioning, suggesting that minor variations in frequency of a given note can be perceived and controlled [17].

Here we also show that house finches' songs can be classified into two distinct groups in relation to their response to noise; those with shared-syllable types and those with non-shared-syllable types. The former have a stronger effect in frequency shifts and are shortened during noise exposure. In contrast, non-shared-syllable types, whose role in frequency shifts is at best marginal, are elongated during noise exposure. Thus house finches have at their disposal two strategies to deal with urban noise: frequency increase, and temporal elongation. A similar temporal change in vocalization elements have been previously reported by Brumm *et al.* [18] in the marmoset (*Callithrix jacchus*). It remains to be studied whether the ability to shift song frequency in response to noise is a widespread passerine ability or whether it is limited to those species that learn their songs.

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Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird

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Capítulo 3

Evidencia experimental del incremento en tiempo real de los atributos de frecuencia de los llamados del gorrión mexicano (*Carpodacus mexicanus*) en respuesta al ruido urbano.

Evidencia experimental del incremento en tiempo real de los atributos de frecuencia de los llamados de gorrión mexicano (*Carpodacus mexicanus)* en respuesta al ruido urbano

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Resumen

Los niveles elevados de ruido urbano han dado lugar a que diferentes especies de aves presentes en ambientes antropogénicos hayan desarrollado diversas estrategias que presumiblemente les ayudan a evitar que sus cantos sean enmascarados. Una de estas estrategias consiste en el incremento de la frecuencia mínima del canto cuando aumentan los niveles de ruido. Se ha encontrado de manera correlativa y experimental que esta estrategia es empleada por el gorrión mexicano (*Carpodacus mexicanus*) al emitir sus cantos. Aquí nos propusimos indagar si estos gorriones también pueden ajustar en tiempo real la frecuencia mínima de sus llamados en función del ruido. También investigamos si existe plasticidad en algún otro atributo de los llamados. Sometimos experimentalmente a machos provenientes de zonas ruidosas y silenciosas a dos tratamientos: grabaciones de bajo y alto nivel de ruido urbano. En presencia de ruido urbano, ni los individuos procedentes de zonas silenciosas ni los de ruidosas incrementaron la frecuencia mínima de sus llamados al exponerlos a altos niveles de ruido urbano, pero sí incrementaron la frecuencia pico, la frecuencia máxima y el número de armónicos. El origen de los machos en función del nivel de ruido al que habían estado expuestos se asoció con diferencias en la frecuencia máxima y en la frecuencia pico de los llamados entre tratamientos. Nuestros resultados demuestran plasticidad en los llamados del gorrión mexicano en respuesta al ruido urbano; lo que puede al menos en parte favorecer el mantenimiento de sus poblaciones urbanas.

Palabras clave: llamados, ruido urbano, plasticidad espectral, gorrión mexicano, *Carpodacus mexicanus*

Introducción

El notable incremento de ruido generado por los humanos ha hecho que las especies que emplean señales acústicas puedan ver afectada su comunicación. Sin embargo, en décadas recientes investigaciones bioacústicas han revelado que las aves no están indefensas al enmascaramiento de sus señales al observar que han desarrollado una variedad de estrategias que les ayudan a contrarrestar el problema del ruido ambiental (Brumm & Slabbekoorn, 2005; Patricelli & Blickley, 2006; Ríos-Chelén, 2009). Una de estas estrategias consiste en emitir cantos de elevada frecuencia mínima (Hz) que evitan su enmascaramiento por las frecuencias bajas típicas del ruido urbano (Slabbekoorn & Peet, 2003; Fernández-Juricic et al., 2005; Wood & Yezerinac, 2006; Nemeth & Brumm, 2009; Bermúdez-Cuamatzin et al., 2009; Potvin et al., 2011; Ríos-Chelén et al., 2012). En la población del gorrión mexicano (*Carpodacus mexicanus*) presente en la ciudad de México se encontró tanto de manera correlativa como experimental que un mismo individuo es capaz de elevar la frecuencia mínima de sus cantos al incrementarse repentinamente los niveles de ruido urbano (Bermúdez-Cuamatzin et al., 2009; Bermúdez-Cuamatzin et al., 2011). Sabemos entonces que este gorrión puede moldear una de sus señales acústicas en función del ruido urbano, lo que es consistente con nuestros conocimientos respecto a la plasticidad de los cantos de las aves oscinas (Slabbekoorn & Peet, 2003; Fernández-Juricic et al., 2005; Wood & Yezerinac, 2006; Nemeth & Brumm, 2009; Bermúdez-Cuamatzin et al., 2009; Potvin et al., 2011; Ríos-Chelén et al., 2012). En cambio, la evidencia de que los oscinos pueden también ajustar los atributos de sus llamados a las condiciones acústicas imperantes es escasa (Potvin et al., 2011; Potvin & Mulder, 2012). Los llamados son señales estereotipadas frecuentemente relacionadas con la transmisión de señales que requieren respuestas rápidas, como alarma frente a depredadores, señalizar fuentes de comida, contacto social (p. ej. durante la migración), por lo que es posible que se trate de señales poco plásticas (Catchpole & Slater, 2008; Marler, 2004).

Existe una serie de estudios sobre el impacto del ruido en los llamados de las aves. Lengagne et al. (1999) encontraron que los pingüinos rey (*Aptenoydes patagonicus*) responden al incremento del ruido generado por su colonia y por la velocidad del viento aumentando el número de sílabas en sus llamados. Lengagne & Slater (2002) observaron que el búho cárabo común (*Strix aluco*) durante las noches húmedas deja de llamar cuando los niveles de ruido de la lluvia se incrementan. También se sabe que las aves evitan el sobrelapamiento de sus llamados impidiendo así el enmascaramiento al alternar las vocalizaciones entre conespecíficos (Evans, 1991).

Leonard y Horn (2005) estudiaron el efecto del ruido en los llamados de solicitud de los polluelos y en la respuesta de sus padres a estos llamados. Encontraron que en campo los pollos de la golondrina bicolor (*Tachycineta bicolor*) incrementan la longitud, la amplitud (dB) y el rango de frecuencia (Hz) de sus llamados cuando se elevaba el nivel de ruido ambiental en el nido, aunque en el laboratorio únicamente aumentaron la amplitud de sus llamados en respuesta al playback de ruido blanco. Los padres expuestos a playbacks de llamados de polluelos respondieron más a los que habían incrementado la amplitud en respuesta al ruido ambiental. Más recientemente Leonard y Horn (2012) encontraron en esta misma especie que los polluelos que habitan lugares ruidosos fallaron más al responder con llamados de solicitud a sus padres cuando arribaron al nido con comida que aquellos que se encuentran en ambientes menos ruidosos, sugiriendo que los polluelos podrían ser menos receptivos bajo condiciones de ruido. Schroeder y colaboradores en el 2012, encontraron que la adecuación del gorrión inglés (*Passer domesticus*) en una población ruidosa de la isla Lundy es menor que en zonas silenciosas control; las hembras anidando en zonas ruidosas alimentaron con menor frecuencia a sus crías que las de zonas silenciosas, posiblemente porque el ruido enmascara la comunicación padres-progenie.

Potvin y colaboradores (2011) dieron evidencia por primera vez que individuos de un ave oscina, el pájaro con anteojos (*Zosterops lateralis*) presente en lugares con ruido urbano mostraban una frecuencia mínima mayor en sus llamados que los individuos de zonas rurales. Posteriormente, Potvin y Mudler en el 2013 demostraron también por primera vez la capacidad plástica de esta misma especie en sus llamados en función del tipo de ruido al que eran expuestos. En primer lugar fueron sometidos a ruido de frecuencias bajas (característica del ruido urbano) y los machos respondieron emitiendo llamados de frecuencia mínima elevada. Posteriormente se les expuso a ruido de frecuencias altas y esta ave respondió con cantos de frecuencias mínimas bajas, evitando así el enmascaramiento.

En este trabajo evaluamos si los machos de gorrión mexicano *(Carpodacus mexicanus*) ajustan de manera plástica algún atributo temporal o espectral de sus llamados en respuesta al ruido urbano y si las condiciones de ruido del lugar donde proceden influyen en dicha plasticidad.

Métodos

Captura y mantenimiento de los individuos en cautiverio.

Entre el 25 de febrero y el 9 de mayo, durante la temporada reproductiva del gorrión mexicano, capturamos mediante redes de niebla y trampas cerca de comederos, un total de cinco hembras y 26 machos adultos de *C. mexicanus* en el sur de la ciudad de México, en zonas de bajo (media ± EE = 49.94±0.42 dB; dos hembras y ocho machos) y alto nivel de ruido urbano (media ± EE = 60.28±0.54 dB; tres hembras y 18 machos). Las aves fueron mantenidas en jaulas individuales dentro de un aviario en el Instituto de Ecología, UNAM, donde recibieron comida (mezcla comercial de semillas y frutos) y agua *ad libitum*, y estuvieron sujetos a iluminación artificial que contenía luz UV, en un fotoperiodo de 12/12 luz/obscuridad y a temperatura ambiente.

Protocolo

Las pruebas las realizamos del 11 de septiembre al 10 de octubre, diariamente de 8:00 a 14:00 h y de 16:00 a 19:00 h en un cuarto equipado con lámparas que emitían el espectro de luz de día (incluyendo UV), y 3 jaulas con agua y alimento; una central para el macho, flanqueada por 2 jaulas con una hembra en cada una (Figura 1) para estimular al macho a emitir llamados. Antes de una prueba cada trío fue aclimatado por 2 horas en el cuarto de pruebas. Los tríos estuvieron compuestos por individuos del mismo origen (los tres provenientes o bien de zonas ruidosas o bien de zonas silenciosas).

Todos los machos (de cada una de las procedencias) fueron expuestos a dos tratamientos de ruido urbano. El primero consistío en presentarles una grabación de ruido urbano de baja intensidad (40 - 45 dB), y el segundo, fue la misma grabación de ruido pero a mayor intensidad (65 - 70 dB). Cada tratamiento se reprodujo durante 15 minutos. El orden de presentación de los tratamientos fue alternada entre individuos (la mitad fue expuesta primero a bajo ruido y luego a alto, y la otra mitad alrevés) e inmediatamente después de reproducir un tratamiento se reprodujo el siguiente. La reproducción de cada uno de los tratamientos se realizó con la opción denominada "playback special (looped)", del programa Avisoft SASLab™ Pro V. 2.0 en una computadora laptop HP Pavilion dv1000 (con una tarjeta de sonido Conexant Cx20551 @ Intel 82801GBM ICH7-M conectada a un altavoz Mineroff SME-AFS situado a 2.5 m de los individuos (Figura 1). La función "playback special (looped)" nos permitío repetir constantemente las grabaciones de ruido de 30 segundos (ver detalles abajo) hasta completar los 15 minutos de tratamiento.

Las grabaciones de ruido empleadas se obtuvieron grabando el ruido de tráfico de una avenida ruidosa cerca del Instituto de Ecología, con ayuda de un micrófono direccional Sennheiser™ ME66 y una grabadora Marantz™ PMD221 con casetes TDK SA60 tipo 2. El ruido fue grabado por 2 horas, posteriormente digitalizamos en una computadora PC utilizando una tarjeta de sonido Intel ® de 5,10 con 16 bits de precisión, y se tomaron muestras a una velocidad de 22 kHz utizando el software Avisoft SASLab™ Pro V. 2.0. Editamos las grabaciones para obtener 30 grabaciones distintas de ruido, normalizadas y de 30 segundos de duración. Asignamos aleatoriamente las grabaciones a los sujetos. Para determinar la amplitud a la que se tendrían que reproducir las grabaciones empleamos un medidor de presión de sonido digital SEW® 2310 SL (rango de respuesta de 30 a 130 dB, peso de frecuencia “A”, y en una tasa de respuesta rápida).

Durante cada tratameinto grabamos durante los 15 minutos todos los llamados emitidos por el ave focal con un micrófono direccional RODE™ NTG-2 conectado a una grabadora Marantz™ digital PMD660 (formato WAV, tasa de muestreo de 44.1 kHz, 16 bits). El micrófono fue colocado frente a la jaula central para evitar grabar a las hembras, las cuales se mantuvieron en los extremos distales mediante divisiones en sus jaulas (Figura 1).

Las aves fueron liberadas después de las pruebas, tras permitirles recuperar condición de vuelo durante dos semanas, en las que estuvieron sueltas en una habitación de 2.60X1.50X2.20 m con perchas, agua y comida *ad libitum*.

Análisis de datos

Analizamos las grabaciones de los llamados en Avisoft SASLab™ Pro V. 2.0. Cinco de los 26 machos no emitieron llamados en ninguno de los dos tratamientos, por lo que se eliminaron de los análisis. Usamos toda la muestra (todos los llamados de 21 machos en ambos tratamientos) para clasificar los llamados por su forma siguiendo los criterios de Pytte (1997) de acuerdo a los cuales la variación en la forma puede ser discreta (cuando la forma es claramente distinta se clasifican en diferentes tipos, si la forma es idéntica se clasifican como el mismo tipo) o contínua (cuando existe una transición suave entre sílabas similares se clasifican como el mismo tipo).

Encontramos ocho diferentes tipos de llamados (Figura 2), sin embargo no todos los tipos fueron emitidos por todos los individuos en ambos tratamientos, solamente los tipos 1, 2 y 4 fueron emitidos con suficiente frecuencia como para ser incluidos en los análisis. Siete de ocho individuos capturados en zonas silenciosas emitieron llamados del tipo dos (el octavo emitió llamados tipo 4), mientras que 16 de los 18 machos provenientes de zonas ruidosas emitieron el tipo 1 (los restantes emitieron llamados tipo 2). Para determinar qué tipo de llamados empleaban los individuos según su procedencia, únicamente se tomaron en cuenta los tipos de llamados más frecuentes en todos los individuos, el tipo 1 y 2 (descartando el tipo 4, al ser emitido sólo por un individuo). También comparamos los atributos de estos dos tipos de llamados en cada tratamiento. Estos dos análisis se llevaron a cabo a través de pruebas de t pareada.

Por otro lado, realizamos un conteo del total de llamados emitidos por cada macho y seleccionamos al azar 20 de cada tratamiento para ser medidos, con excepción de tres individuos de los que se midieron menos (18, 19 y 19, debido a que fue la cantidad máxima que emitieron del tipo elegido). De cada llamado se midió la frecuencia mínima, frecuencia máxima, frecuencia pico, ancho de banda, duración y número de armónicos. Cada individuo fue representado en los análisis por el promedio de cada variable en cada tratamiento. Comparamos las variables de los llamados emitidos en cada tratamiento mediante un ANOVA de medidas repetidas con tratamiento y procedencia del individuo (zona ruidosa o silenciosa) como factores fijos, seguido de una prueba post-hoc Holm-Sidak cuando era justificado. El ANOVA se realizó usando SigmaPlot™ v. 11. Los análisis con pruebas de t se hicieron con SPSS™ v. 17.

Resultados

Tipos de llamados

Los machos procedentes de zonas ruidosas produjeron una mayor cantidad de llamados tipo 1 en relación a los llamados tipo 2 (media ± EE; tipo 1, 216.77±43.37 llamados; tipo 2, 34.69±20.8 llamados; t = 3.32, df = 12, p =0.006). Por otro lado los individuos de lugares silenciosos emitieron más llamados tipo 2 en relación a llamados tipo 1 (media ± EE; tipo 2, 403.5±96.44 llamados; tipo 1, 20.13±16.43 llamados; t = -4.10, df = 7, p =0.005). Con estos resultados comparamos los atributos de los llamados tipo 1 (emitidos mayormente por individuos procedentes de zonas ruidosas) y tipo 2 (emitidos en mayor medida por individuos provenientes de zonas silenciosas) separadamente por cada tratamiento. Cuando fueron emitidos en el tratamiento de mucho ruido, los llamados tipo 2 tuvieron mayor frecuencia pico que los llamados tipo 1 (media ± EE; tipo 1, 3169.01 ± 55.67 Hz; tipo 2, 3485 ± 112.15 Hz; t= -2.804, df= 16, p= 0.013).

En el tratamiento de poco ruido, los llamados tipo 2 tuvieron una mayor frecuencia pico que los llamados tipo 1 (media ± EE; tipo 1, 3033.83 ± 67.68 Hz; tipo 2, 3510.91 ± 81.55 Hz; t= -4.459, df=16, p < 0.001). La frecuencia máxima también fue mayor para el tipo 2 comparado con los del tipo 1 (media ± EE; tipo 1, 3753.36 ± 104.29 Hz; tipo 2, 4093.78 ± 89.23 Hz; t= -2.28, df=16, p= 0.037). Por último, hubo una tendencia a que el ancho de banda fuera mayor para los llamados tipo 2 que para los llamados tipo 1, sin embargo esta diferencia no fue significativa (media ± EE; tipo 1, 1303 ± 69.1 Hz; tipo 2, 1618.86 ± 167.62 Hz; t= -1.10, df=16, p= 0.063).

Comparación de los llamados en tratamientos

No hubo diferencias en la frecuencia mínima de los llamados emitidos en ambos tratamientos (ANOVA, $F_{1,20}$= 1.88, p= 0.19). Los individuos de ambas procedencias (zona ruidosa y silenciosa) emitieron llamados con frecuencias mínimas similares ($F_{1,20}$= 0.11, df= 1, p= 0.75).

Los machos emitieron llamados de frecuencia máxima menor cuando estuvieron expuestos a elevados niveles de ruido (media ± EE; alto nivel de ruido, 4028.11 ± 61.42 Hz; bajo nivel de ruido 3920.12 ± 72.07 Hz; ANOVA, $F_{1,20}$ = 10.30, p= 0.005; Figuras 3A y 4A). La procedencia de los individuos muestreados no influyó significativamente en el incremento de la frecuencia máxima ($F_{1,20}$ = 3.01, p= 0.09). Sin embargo la interacción tratamiento-procedencia sí fue significativa ($F_{1,20}$= 4.732, p= 0.042). Durante el tratamiento de alto nivel de ruido encontramos que la frecuencia máxima fue mayor en los individuos procedentes de zonas silenciosas (media ± EE; procedencia de silencio, 4126.47 ± 76.42; procedencia de ruido, 3967.57 ± 85.20; Post-Hoc, t= 4.36, df= 1, p= <0.001). En el tratamiento de bajo nivel de ruido no encontramos diferencias significativas en la frecuencia máxima entre las procedencias (Post-Hoct; t= 0.66 df= 1 p= 0.52). Al comparar a los individuos procedentes de ruido en los dos tratamientos no encontramos diferencia significativa en la frecuencia máxima (Post-Hoct; t= 1.21 df= 1 p= 0.239). Comparando los individuos provenientes de zonas de bajo nivel de ruido encontramos que la frecuencia máxima fue mayor en el tratamiento de alto nivel de ruido (media ± EE; bajo nivel de ruido, 4096.5 ± 77.32; alto nivel de ruido, 4126.47 ± 76.42; Post-Hoct; t= 2.17 df= 1 p= 0.04).

El ancho de banda de los llamados no difirió entre tratamientos (ANOVA, $F_{1,20}$ = 2.33, p= 0.14). Sin embargo los individuos provenientes de áreas silenciosas tuvieron un ancho de banda mayor que los individuos de procedencia de ruido (media ± EE; zonas silenciosas, 1595.663 Hz; zonas ruidosas 1336.716 Hz; $F_{1,20}$ = 4.578, p= 0.046; Figura 4B). La interacción tratamiento-procedencia no fue significativa ($F_{1,20}$ = 2.27, p= 0.15).

La frecuencia pico incrementó del tratamiento de bajo nivel de ruido al de elevado nivel de ruido (media ± EE; bajo nivel de ruido, 3246.79 ± 66.49 Hz; alto nivel de ruido, 3331.98 ± 60.81 Hz; $F_{1,20}$= 8.02, p= 0.01; Figura 3B). Los individuos de procedencia silenciosa presentaron una frecuencia pico mayor que los machos de áreas ruidosas (media ± EE; zonas silenciosas, 3498.35 Hz; zonas ruidosas, 3160.79 Hz $F_{1,20}$ = 10.13, p= 0.005). La interacción tratamiento-procedencia fue significativa ($F_{1,20}$ = 11.46, p= 0.003). En el tratamiento de ruido, mostramos que la frecuencia pico fue mayor en individuos procedentes de áreas silenciosas (media ± EE; zonas silenciosas, 3491.87± 97.37; zonas ruidosas, 3233.59 ± 66.59; Post-Hoct, t= 5.04 df= 1 p= <0.001). En el tratamiento de bajo nivel de ruido no encontramos diferencias significativas entre las procedencias (Post-Hoc; t= 0.35 df= 1 p= 0.729). Comparando a los individuos de lugares ruidosos damos evidencia de que la frecuencia pico fue más elevada en el tratamiento de elevado nivel de ruido (media ± EE; bajo nivel de ruido, 3088 ± 67.69; tratamiento de alto nivel de ruido 3233. 59 ± 66.59; Post-Hoc; t= 2.38 df= 1 p= 0.03). Entre los machos de áreas silenciosas la frecuencia pico fue superior para el tratamiento de bajo nivel de ruido (media ± EE; bajo nivel de ruido, 3504.82 ± 70.89; alto nivel de ruido, 3491.88 ± 97.37; Post-Hoct; t= 3.84 df= 1 p= <0.001).

La duración de los llamados no difirió entre tratamientos ($F_{1,20}$= 0.61, p= 0.44). La procedencia tampoco tuvo ningún efecto en la duración de los llamados ($F_{1,20}$= 3.49, p= 0.08). El número de armónicos fue mayor en el tratamiento de elevado nivel de ruido (media ± EE; bajo nivel de ruido 1.55 ± 0.20; alto nivel de ruido, 2.10 ± 0.18; $F_{1,20}$ = 11.03, p= 0.004; Figura 3C y 4C). La procedencia no fue significativa ($F_{1,20}$ = 0.17, p= 0.69), ni la interacción entre tratamiento y procedencia ($F_{1,20}$ = 1.72, p= 0.21).

Discusión

Reportamos por primera vez para una población mexicana de *Carpodacus mexicanus* una clasificación de llamados de ocho diferentes tipos. De estos tipos de llamados fue interesante encontrar que los individuos muestreados procedentes de zonas ruidosas emplearon en mayor medida el llamado tipo uno, mientras que los procedentes de zonas silenciosas emitieron en mayor porcentaje el tipo dos. Hallamos que los dos tipos de llamados difirieron durante el tratamiento de alto nivel de ruido en la frecuencia pico, mostrando valores más elevados en los individuos procedentes de silencio. Por otro lado, en el tratamiento de bajo nivel de ruido también encontramos diferencias entre los dos tipos de llamados; nuevamente en la frecuencia pico, marginalmente en el ancho de banda y además en la frecuencia máxima; y todos estos atributos tuvieron valores más altos para los machos de zonas silenciosas. Los machos de zonas ruidosas presentan menores frecuencias máximas y anchos de banda, lo que incrementa las posibilidades de hacerse escuchar, ya que como se sabe en situaciones ruidosas los sonidos con menores anchos de banda se transmiten mejor (Lohr et al. 2003); al mismo tiempo si estos dos parámetros se reducen la frecuencia pico también tenderá a disminuir.

Nuestros resultados sugieren que los gorriones mexicanos no cuentan con plasticidad que les permita modificar en tiempo real la frecuencia mínima de sus llamados, aun cuando sí la tienen para ajustar sus cantos (Bermúdez-Cuamatzin et al., 2011). Este hallazgo difiere con lo encontrado por Potvin y Mundler (2013) en el pájaro con anteojos, ya que estos individuos lograron incrementar la frecuencia mínima de sus llamados al exponerlos a ruido de bajas frecuencias. Sin embargo, encontramos que los gorriones mexicanos son capaces de incrementar facultativamente la frecuencia pico y la frecuencia máxima de sus llamados cuando hay altos niveles de ruido urbano. En el pájaro de anteojos no se encontró esta plasticidad en la frecuencia pico y frecuencia máxima (Potvin & Mundler, 2013). Esto nos puede estar hablando de diferentes estrategias espectrales que están empleando distintas especies de aves, de acuerdo a sus capacidades fisiológicas o anatómicas en la plasticidad de sus vocalizaciones para contrarrestar el efecto del ruido en sus vocalizaciones. La frecuencia pico es importante porque en ella se concentra la mayor cantidad de energía, y el concentrar una gran cantidad de energía en una frecuencia relativamente alta podría hacer al llamado sobresalir del transfondo de ruido urbano. Si bien tanto los individuos procedentes de zonas de ruido como de silencio incrementaron la frecuencia pico al aumentar el ruido, los machos procedentes de zonas silenciosas realizaron un incremento mayor, quizá como una sobre-reacción frente a una circunstancia poco común en sus sitios de origen. Esto es consistente con el hecho de que en nivel de ruido bajo los machos de ambos orígenes emiten llamados con frecuencias pico similares.

La frecuencia máxima de los llamados también se elevó al aumentar el ruido urbano, lo que podría ayudar a evitar el enmascaramiento; este efecto fué mayor en aves procedentes de zonas silenciosas lo que nuevamente podría ser resultado de que reaccionaban frente a un nivel de ruido atípicamente alto. El ancho de banda de los llamados no difirió entre alto y bajo nivel de ruido pero si en función del origen de los machos; aquellos de zonas ruidosas usaron anchos de banda menores en sus llamados, lo que permite una mejor transmisión de sus llamados en condiciones de ruido, como lo indican los trabajos de psicoacústica de Lohr y colaboradores (2003).

El número de armónicos fue mayor durante la exposición a altos niveles de ruido, quizá como consecuencia del incremento de frecuencia y amplitud del llamado que se genera con el aumento de ruido (revisar en Nemeth et al. 2013). Por último, la duración de los llamados no fue diferente entre niveles de ruido altos o bajos y esto coincide con nuestros trabajos previos con el canto de este gorrión donde encontramos que dichos cantos no disminuyen su longitud en presencia de altos niveles de ruido urbano (Bermúdez-Cuamatzin et al. 2009). Sin embargo, esto difiere con lo reportado por Potvin y Mudler (2013) en el pájaro de anteojos, en el que encontraron que sus llamados disminuyen 14 % en longitud durante ruido de frecuencias altas respecto al tratamiento de silencio. Igualmente, Leonard y Horn (2005) encontraron que los llamados de solicitud de los polluelos de la golondrina bicolor (*Tachycineta bicolor*) son de longitud mayor, cuando se incrementa el nivel de ruido ambiental en el nido. Una posible explicación es que ambas estrategias permiten contender con el ruido. Por un lado las señales acústicas de mayor longitud pueden ser mejor detectadas en condiciones de ruido, ya que incrementan la oportunidad de escucharse al menos una parte cuando ocurren ventanas de silencio (Brumm & Slabbekoorn, 2005; Fernández-Juricic et al. 2005). Sin embargo, también es posible que una señal corta sea captada en condiciones de ruido ya que puede escucharse en su totalidad durante alguna ventana de silencio (Slabbekoorn & den Boer-visser 2006; Ríos-Chelén, 2009).

Anteriormente se pensaba que los llamados eran señales acústicas estereotipadas y determinadas mayoritariamente en forma congénita (Marler, 2004). Esto parece menos cierto de lo que se pensaba, ya que se han descrito dialectos en los llamados de algunas especies, lo que sugiere plasticidad en el desarrollo de los llamados (Baptista, 1990; Marler, 2004). Dicha plasticidad se confirma con el ajuste facultativo de las características espectrales de los llamados del gorrión mexicano; y las temporales y espectrales de los llamados del pájaro de anteojos (Portvin & Mudler, 2013) para hacer frente al ruido de frecuencias bajas de los ambientes urbanos.

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Figura 1.- Diagrama de grabación de llamados. En la parte inferior vemos representada la computadora (A) desde donde se reprodujeron los tratamientos de ruido, la cual se conectó a un altavoz (B). La grabadora (C) se conectó al micrófono (D). Se observa la disposición de las jaulas (E), donde se colocaron cada uno de los individuos empleados durante las pruebas, un macho en la parte central de la arena flanqueado por dos hembras. Dentro de las jaulas de las hembras se pueden observar las divisiones (F) que permitieron mantener a las hembras en los extremos distales de las jaulas.

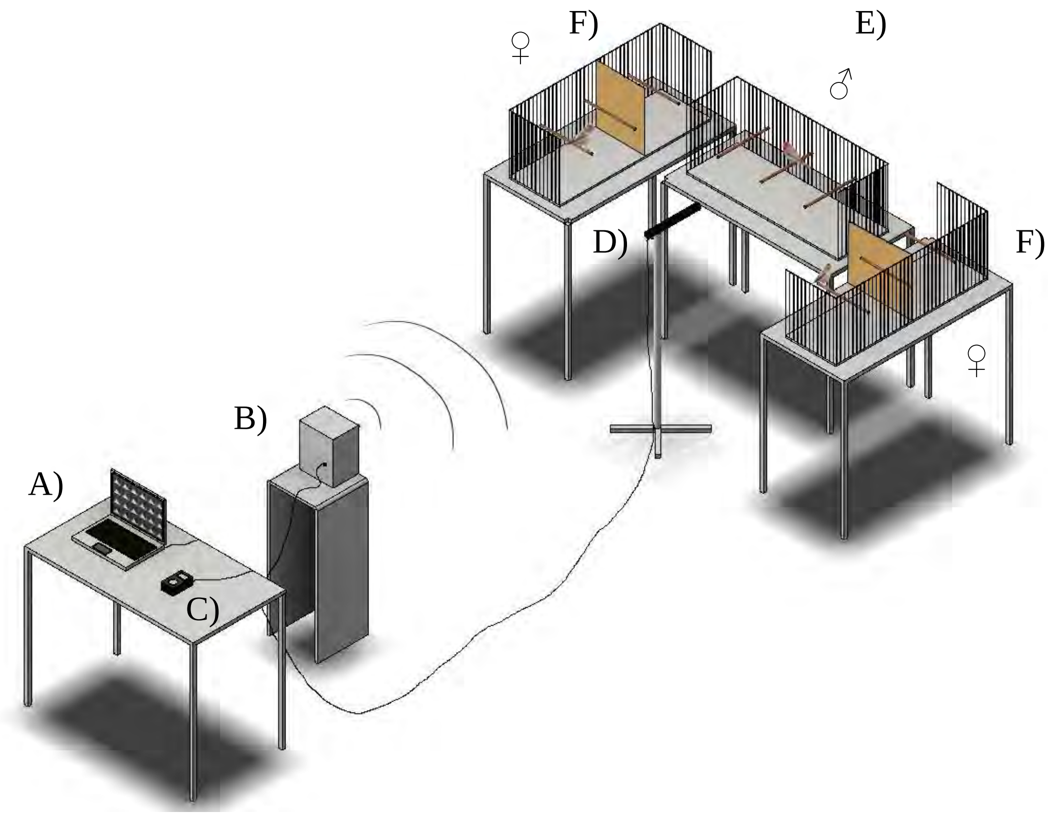
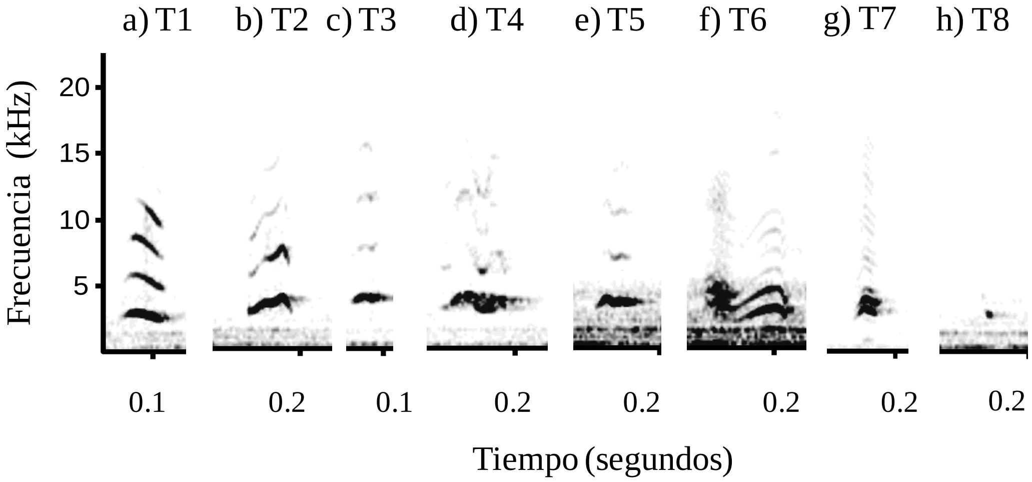


Figura 2.- Tipos de llamados. Espectrogramas de los ocho tipos de llamados encontrados en la muestra de veintiún individuos. El inciso a corresponde al tipo 1, el b al tipo 2 y así sucesivamente. Los tipos empleados para el análisis de los datos fueron el tipo 1, 2 y 4.



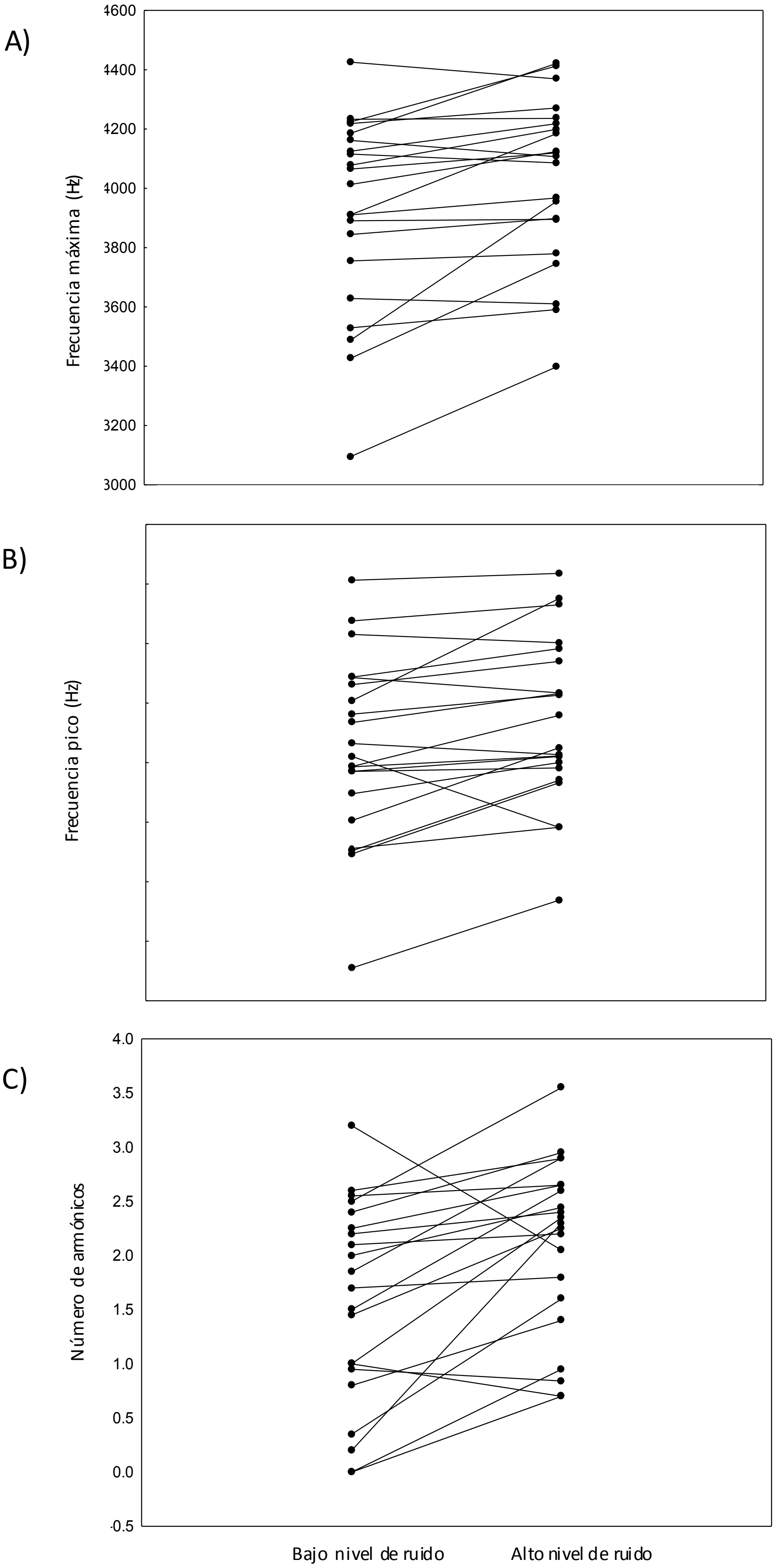
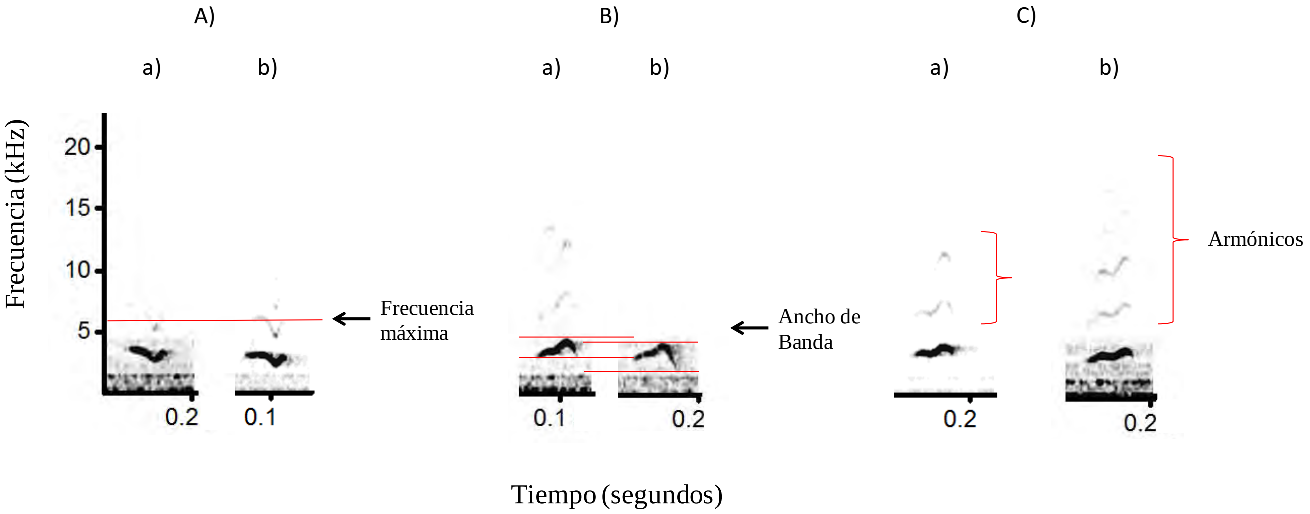


Figura 3.- Comparación entre bajo y alto nivel de ruido urbano de 3 atributos de los llamados. Incremento de la frecuencia máxima **A)**, frecuencia pico **B)** y número de armónicos **C)** del tratamiento de bajo a alto nivel de ruido. Diecisiete de 21 individuos realizaron el incremento significativo de frecuencia máxima y pico; y 17 de 21 individuos aumentaron también significativamente el número de armónicos (ver estadística en texto).

Figura 4.- Ejemplos del cambio en los atributos de los llamados en función del ruido urbano al que fueron expuestos o a la procedencia de los individuos. **A)** Incremento de frecuencia máxima del llamado tipo 1 (mismo individuo (a y (b procedente de zona de ruido) en alto nivel de ruido. a) muestra un llamado con frecuencia máxima mayor de 3840 Hz (indicada por la línea roja) durante el tratamiento de alto nivel de ruido urbano, en comparación con b) donde el llamado presenta una frecuencia máxima menor, de 3370 Hz durante el tratamiento de bajo nivel de ruido. **B)** El ancho de banda del llamado en a) (perteneciente a un individuo de zona silenciosa) con 2350 Hz, es mayor que el llamado en b) (individuo de zona ruidosa), el cual tiene un menor ancho de banda de 1600 Hz. Ambos llamados están tomados del tratamiento de elevado nivel de ruido. **C)** Los dos espectrogramas a) y b) pertenecen al mismo individuo procedente de una zona ruidosa. Se observa que el llamado a) presenta únicamente 2 armónicos debido a que se emitió durante el tratamiento de silencio, mientras que el llamado en b) muestra 4 armónicos, ya que fue emitido en el tratamiento de elevado nivel de ruido.



Capítulo 4

Noise-adjusted songs face females with a puzzle

“Noise-adjusted songs face females with a puzzle”

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Abstract

Evidence from an increasing number of species shows that birds raise the minimum frequency of their songs in response to urban noise. This reduces spectral overlap with noise, but evidence that it improves communication is scant. Here we ask how female house finches (*Carpodacus mexicanus*) respond to adjusted songs produced by males in noisy environments. We manipulated recorded songs to mimic the upward shift in song pitch made by males when singing in noisy conditions, and exposed recently-captured females to two different versions of their song: a) adjusted and b) intact songs, played against a noisy or a quiet background. Females approached the speakers more often when the songs were played along with urban noise. Females spent more time oriented towards the intact song in noisy condition, and also spent more time oriented towards the adjusted songs when played in a quiet condition. Our playback songs did not evoke female copulation solicitation, thus our results do reflect social, and not necessarily sexual female responsiveness. Nevertheless, it appears that females need to pay more attention to intact songs -particularly the normal, presumably attractive ones- when heard against a noisy background, and we speculate that their apparent interest on adjusted songs when played in quiet conditions is because they sound strange when heard out of context. Individualized recordings varied in their syllable diversity, and we found that females approached diverse songs more frequently in background noise than in the quiet condition. This may mean either that the complex songs are attractive in noisy environments, perhaps because they are easier to detect than simpler songs, or that complex songs require more attention from the receiver, particularly in noisy conditions. We report in *C. mexicanus*, that song frequency adjustment leads to differential female responsiveness, as this is not a mere by-product of increased song amplitude, further research should investigate the function of such adjustment in house finch communication.

Keywords: female preferences, noise adjusted song**,** urban noise, sexual selection, oscine bird

Introduction

In recent years, many studies have investigated the effects of the anthropogenic noise in the acoustic communication in birds (Brumm & Todt 2002; Brumm & Slabbekoorn 2005; Patricelli & Bickley, 2006; Slabbekoorn & Ripmeester, 2008; Ríos-Chelén et al. 2012). Some studies show that birds in noisy areas sing in a differently to their counterparts in quieter places, presumably to reduce masking by environmental noise (Slabbekoorn & Peet 2003; Brumm 2004; Slabbekoorn & Boer-Visser 2006, Ríos-Chelén et al. 2012). For instance, birds may have higher minimum song frequency in noisy places, which may prevent spectral overlap with low-pitched urban noise (Slabbekoorn & Peet 2003; Fernández-Juricic et al. 2005; Wood & Yezerinac, 2006; Bermúdez-Cuamatzin et al, 2009; Potvin et al, 2011; Ríos-Chelén et al., 2012). Recent investigations found that great tit (*Parus major*), chiffchaffs (*Phylloscopus callybita*), reed buntings (*Emberiza schoeniclus*), house finches (*Carpodacus mexicanus*) and silvereyes (*Zosterops lateralis*) exhibit behavioural plasticity in their use of this strategy; that is, males are capable of singing higher pitch songs immediately when exposed to experimental noise (Halfwerk & Slabbekoorn 2009; Verizijden et al. 2010; Gross et al. 2010; Bermúdez-Cuamatzin et al. 2011; Potvin & Mulder, 2013). This strategy could represent a short-term adaptation that allows birds to inhabit anthropogenic environments despite the high noise levels. Singing modified songs in noisy conditions can potentially carry costs if these songs are less attractive to females, or if they are less efficient at deterring intruders from the territory. However, the consequences of producing modified songs in noisy conditions are largely unknown. To our knowledge there is only one study that has investigated the impact of the use of higher pitch songs in the sexual preferences of females. This research found that great tits males (*Parus major*) sing lower frequencies when female fertility is highest and also that these males suffer from less paternity loss (Halfwerk et al. 2011b). Coupled with this, and using an indirect measure of female preference, they found evidence that females prefer low-pitched songs but under noisy conditions they are more responsive to, presumably less masked, high-pitched songs (Halfwerk et al. 2011b).

Males that adjusted their vocalizations in response to urban noise may face a trade-off between signal transmission efficiency and signal attractiveness (Patricelli & Bickley, 2006). Increasing song pitch may make males less attractive to females in species in which females are attracted to low-frequency songs. On the other hand, this could also increase signal transmission efficiency and improve the chances of attracting females (Patricelli & Bickley, 2006).

Some studies have shown the negative impact of noise on the attractiveness of male bird songs. Swaddle & Page (2007) showed in the laboratory, that high levels of white noise erode female zebra finch (*Taeniopygia guttata*) pair bonds, either because of masking of the male calls, or because the females cannot recognize them. Similarly, Habib et al. (2007) found that ovenbirds (*Seiurus aurocapilla*) from a disturbed area near a noise-generating compressor station had lower pairing success than birds in a less noisy site. They also found that more inexperienced first-year breeders were found at the noisier habitat (Habib et al. 2007). Human-produced noise has consequences at higher levels, as shown by reports of reduced bird species richness, abundance, density and breeding success in noisy places (Rheindt 2003; Bayne et al. 2008), such as near motorways (Reijnen & Foppen 1994; Reijnen et al. 1995; Reijnen et al. 1996). That this may be linked to traffic noise, because Rheindt (2003) found that species with a higher pitch song were more abundant near a motorway than birds with low frequency songs. This tallies with the findings of Parris and Schneider (2009), who found that at Australian roadside sites, the Shrike-thrush (*Colluricincla harmonica*) produces a lower-frequency song than the Grey Fantail (*Rhipidura fuliginosa*), but the latter sang at a higher frequency under traffic noise conditions. More recent work showed that female great tits (*Parus major*) laid smaller clutches with fewer chicks fledged in noisy areas in the vicinity of a Dutch motorway than in quiet zones (Halfwerk et al., 2011a). Their study also revealed that traffic noise and bird vocal activity overlap in time and frequency.

Song adjustment in response to acoustic pollution has been described in the house finch (*Carpodacus mexicanus*: Fernández-Juricic 2005; Bermúdez-Cuamatzin et al. 2009), whose males modify in real time the frequency of their songs in response to urban noise (Bermúdez-Cuamatzin et al. 2011). Here we evaluated the responses of unmated adult female house finches to adjusted and intact male songs, when played back with and without a background urban noise. Females were exposed to two dichotomous preference tests under controlled conditions at the onset of the breeding season.

Methods

Experimental design

We used mist-nets to capture 21 female house finches from January 13 to February 11, 2011, at two sites in the city of Puebla, México, that were flanked by noisy motorways. The birds were transported to an outdoor aviary at the Centro Tlaxcala de Biología de la Conducta in nearby Tlaxcala, where they were kept in individual cages, fed a combination of seed mix and fruit *ad libitum*, and exposed to the natural light/dark cycle, at room temperature.

The experimental design consisted of exposing the females to two-preference trials (Figure 1). In the first preference trial against a silent acoustic background, females were exposed to one treatment of an un-manipulated low-frequency song (*intact song*), and a second treatment of a manipulated high-frequency song (*adjusted song*) in which we increased the pitch of the syllable or syllables with the lowest minimum frequency. In the second preference trial, we compared the female's response to the intact and adjusted song, but with an acoustic background of noise. The intact song in this trial was considered a *masked song*, because low frequency syllables in the song were masked by an urban noise recording; to emulate urban conditions. In the same way, the adjusted song was termed *non-masked song*, because the song was above the low frequency of the noise recording.

Stimuli

We obtained the songs used for treatments from our previous study with this species (Bermúdez-Cuamatzin et al. 2009). These recordings were obtained opportunistically in natural conditions in México City. The females used in the trials had not previously heard these songs. To avoid pseudoreplication we used a song from a different male, for each female. We chose songs of different lengths (N = 21, mean ± SE= 2.486 ± 0.236 s, range= 1.138-4.748).

To construct adjusted songs, we measured the minimum frequency of the syllable or syllables with the lowest and highest minimum frequency in the song, and calculated the average of these measures. We then subtracted from this average the minimum frequency value of the syllable or syllables that we wished to adjust. The measure obtained before was the number of hertz that we increased to the adjusted syllable or syllables. If this amount of hertz was higher to the maximum frequency of the song, we only increased 689.9 Hz, because this value was the maximum increase of minimum frequency song that we observed in the house finch song in our previous research (Bermúdez-Cuamatzin et al. 2011). We used Avisoft SAS-Lab Pro v. 5.1.16 software to modify the songs.

We used one stimulus for each trial. The stimulus was composed of 10 repetitions of the song for each treatment. These songs were intercalated and separated by 2.5 seconds intervals (average obtained from a subsample of 5 song intervals from 10 males (Bermúdez-Cuamatzin et al. 2011). We constructed the stimuli in Adobe Audition version 3.

Trials

Trials took place in March-April 2009, from 0800-1140 and from 1730-1830, in an indoor experimental arena (Figure 2) consisting of one central cage identical to the female home cage flanked by two speakers (Mineroff SME-AFS, with a frequency response: 100 Hz – 12 kHz) placed 1 m apart. The speakers were connected to a MacBook Aluminio laptop. Female behaviour during trials was recorded on a video camera (SONY™ Carl Zeiss™ Vario-Tessar 60X Optical Zoom) placed 2.5 m in front of the cage. The cage contained three perches, one at the centre (no preference), and one at each extreme of the cage (preference perches). The cage also contained two feeders and two water dishes at each of the preference perches.

The order of the trials for the first female was random and for the consecutive females we alternated the order. Females had an acclimatization time of 30 minutes. Trials started when we introduced the female into the experimental arena, in the central cage (Figure 2). At this moment we started the video recording and finished one minute later after the stimulus was over. In the trials all the stimuli were played to the same amplitude, which was 70 dB measured at a distance of 1 m. We took this measure with a digital sound level meter SEW® 2310 SL, before initiating the test in the cage where the female was placed.

The songs of the two treatments were reproduced one in each speaker, alternating their reproduction in the Adobe Audition, version 3. This software can broadcast each kind of song through the left and the right channels (left and right speaker). For the second trial, the recording of background noise was played through a third channel with a third speaker to emulate urban background noise. For the first female we randomized the song treatments reproduced in each speaker; for the consecutive females we simply altered the order of the song treatments to have a balanced design.

Behaviour analysis

We registered two types of behaviours in the videos: 1) approach, and 2) orientation to the stimulus. In both behaviours we measured frequency of occurrence and duration. We know from a previous study that these behaviours are good indicators of mate preferences in female house finches (Nolan & Hill 2004). We defined the *approach to the stimulus* behaviour as displacements through hops or flutters among the perches, feeders, and bars of the cage, moving towards one of the stimuli. To establish the stimulus preference by the females, we considered the number of approaches to the left or right side of the cage, and amount of time spent in one of these sides of the cage. The *orientation to the stimulus* behaviour occurred when females moved their head or body in direction toward one of the two stimuli (left or right). This behaviour not involves a displacement in the cage. We registered behaviour as neutral when the bird looked or positioned its body to the front (i. e. to neither stimulus). The behavioural response of females in the videos was recorded by an observer who did not know which stimulus was broadcasted by each speaker, and data were analysed with The Observer version 2.0 software. We also recorded one minute of female behaviours prior to the preference test. We recorded a total of 84 videos, of which 42 were preference trial videos (21= quiet background, and 21= noisy background) each with a pre-test (n = 42) video.

Data Analysis

We subtracted the values of frequency and duration of approach and orientation behaviours of females during the pre-trial from values of behaviours preference trial to obtain a single value for each variable. We conducted a two way ANOVA, where one factor was treatment (intact and adjusted song) and the other was the condition (silent or noisy acoustic background). Whenever necessary, we conducted post hoc tests (Bonferroni). We performed the analysis with NCSS^{TM} (2007, Kaysville, UT) software. Descriptive data are presented with mean ± standard error, and we applied $P < 0.05$ significance level.

We explored the associations between the females behavioural variables measured in our experiment with the variable *Song diversity* of the songs broadcasted. This index was obtained using the formula of the Shannon Diversity Index. Instead of taking the number of different species, we consider the number of different syllables in each song.

Results

In the video analysis only 12 out of the 21 females showed approach and orientation behaviours, therefore only these females were considered in the statistical analysis.

Approaches

We found a marginally significant tendency for females to approach the stimuli more frequently in the noisy condition than in the quiet condition (ANOVA: $F_{1,11}$= 3.87, p= 0.055). We found no treatment effect (adjusted or intact songs: $F_{1,11}$= 0.16, p= 0.69), and the interaction was not significant ($F_{1,11}$= 0.56, p= 0.46).

Neither treatments, condition nor their interaction had a significant effect on the duration of approaches (ANOVA; treatments: $F_{1,11}$ = 1.25, p= 0.27; condition: $F_{1,11}$ = 0.22, p= 0.64; interaction: $F_{1,11}$ = 0.22, p= 0.97).

Orientation to the stimulus

We failed to find an effect of condition ($F_{1,11}$= 0.26, p= 0.61) or treatment ($F_{1,11}$ = 0.54, p= 0.46) on the frequency of orientation towards the stimuli. The interaction between condition and treatment also was not significant ($F_{1,11}$= 0.98, p= 0.33).

The duration of orientation towards the stimuli showed a significant interaction between treatment and condition ($F_{1,11}$ = 9.91, p= 0.002). Females spent more time oriented towards the intact song when played against a noisy background, and more time towards adjusted songs in the quiet condition (Figure 3).

Song diversity

Females approached diverse songs significantly more times in noisy for both treatments (intact and adjusted songs), and approached complex songs significantly less in the quiet condition ($F_{1,11}$= 2.76, p= 0.024; Figure 4). We did not find a significant relation between approach duration and song diversity ($F_{1, 11}$= 0.27, p= 0.95), or for frequency of orientation towards the stimulus and song diversity ($F_{1,11}$= 0.48, p= 0.85).

Discussion

The marginally significant tendency of females to approach the speaker playing songs against a noisy background suggests that females use proximity as a means to overcome signal masking. This hitherto ignored mechanism to avoid the interference caused by urban noise is in line with the findings of Lohr et al. (2003), that noise reduces the distance over which songs can be heard (i.e. the active space).

Females spent more time oriented towards the intact song when played together with noise, and more time oriented towards the adjusted songs in quiet conditions. These results run against our expectations; the only published study that we are aware of showed that in noisy conditions female great tits (*Parus major*) have a reduced responsiveness to un-adjusted songs than to adjusted (Halfwerk et al 2011b). It is possible that the spectral attributes of house finch songs are sexually selected attributes preferred by females, but this is at odds with our finding that in quiet conditions the same females were more attracted to adjusted songs. We can only speculate that strange songs also draw the attention of females, particularly when unmistakably strange (in quiet conditions).

The association between female's responses and song complexity mimics the unexpected link between female responses and song frequency. We found that songs (adjusted and intact) with greater diversity of syllables are attended to (approached) more often by females when played in the presence of noise; in a quiet environment females approached more often the simpler songs. We suspect that complex songs are more audible and thus easier to detected under noisy conditions (Brumm & Slater, 2006; Slabbekoorn & den Boer-visser 2006; Ríos-Chelén, 2009). This effect would not occur in quiet places, but it is unclear why simpler songs were more attractive in these latter conditions.

Females responded to songs with behaviours that may indicate interest, but not necessarily sexual preference. Nevertheless, differential responsiveness to male signals would lead to either differential encounter rates with potential partners (when unpaired), or to differential responsiveness to the partner's vocalizations, both of which could have fitness consequences. Our experimental set-up ensured that detectability was not an issue, thus it may still be the case that adjusted songs can be detected at further distances. Yet *C. mexicanus* often sings within centimeters of the female, thus we believe that the patterns found here reflect female responses to spectral, temporal and structural variables of the perceived -i.e. detected- songs. They suggest that the almost universal avian response to noise -increasing the vocalization's lower frequency- does not improve female responsiveness. Thus the question of whether this is a consequence of the Lombard effect, (which is subject of actual debate; Nemeth & Brumm, 2010; Nemeth et. al., 2012; Cardoso & Atwell, 2011; Cardoso & Atwell, 2012; Zollinger et. al. 2012; Slabbekoorn et. al., 2012; Nemeth et. al., 2013), or of other process (es) such as improving acoustic feedback to the performing male, remains open.

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Figure 1. – Sonograms preference trials. In the first trial, females faced to treatment 1 *intact song* (low frequency song, in **a**) to treatment 2 *adjusted song* (high frequency song, in **b**) with silence background. The red lines in **a** and **b** indicates the minimum song frequency. To construct adjusted song, we elevated the minimum frequency of the syllable with lower minimum frequency of the song (show in **a**). The spectrograms in **c** and **d** show the songs that conform the second preference trial (noisy background). The *masking song* (in **c**) the noise masked the syllable with lower minimum frequency of the song. In *No-masking song* (in **d**) the syllable increased in frequency to avoid masking.

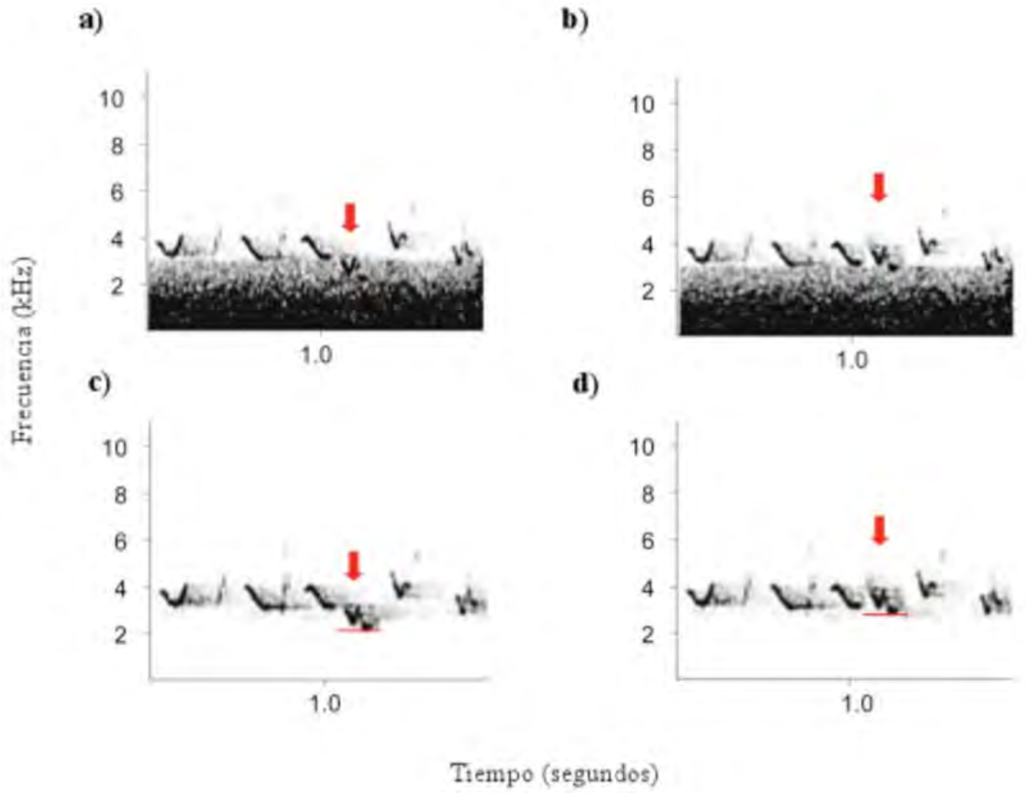


Figure 2. - Experimental arena preference tests. In the central arena we can observe the cage (A) where females was tested. The cage was flanked by two speakers (B) connected to the laptop (C). We put the video camera (D) in front of the cage to 2.5 m.

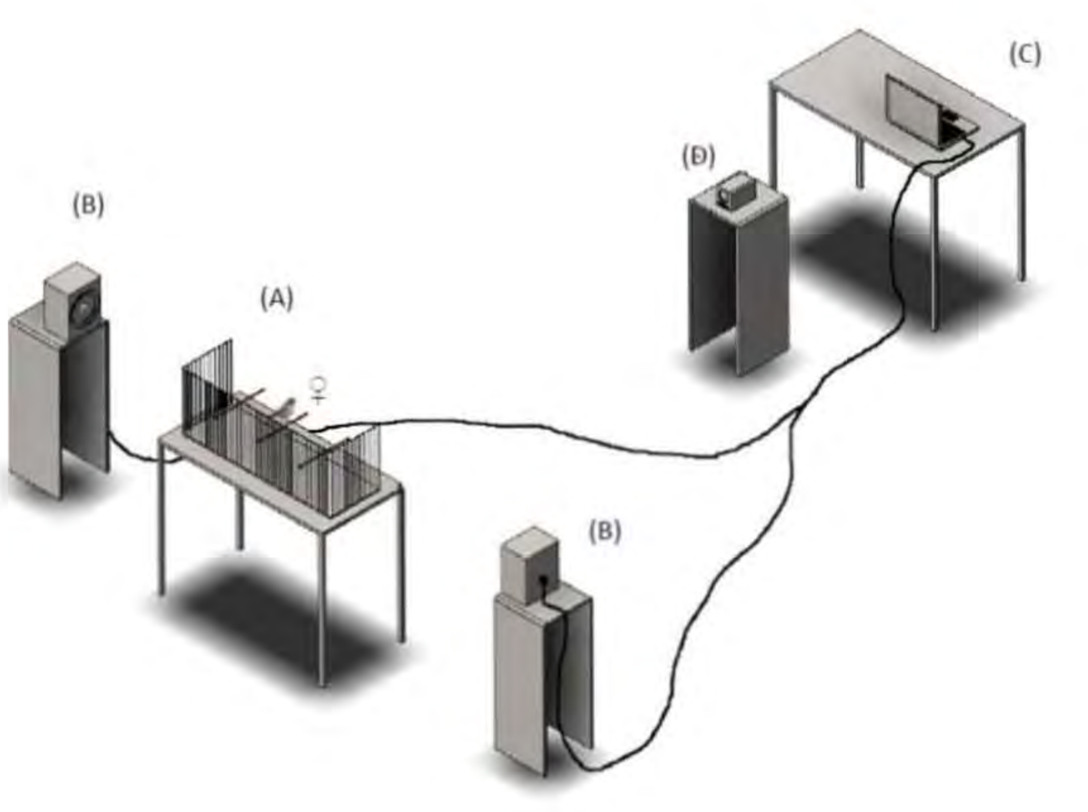


Figure 3. – Interaction between condition and treatment in the mean difference (during trail – pre-trial) in duration of orientation of females towards the stimuli of intact or adjusted songs in quiet and noisy conditions.

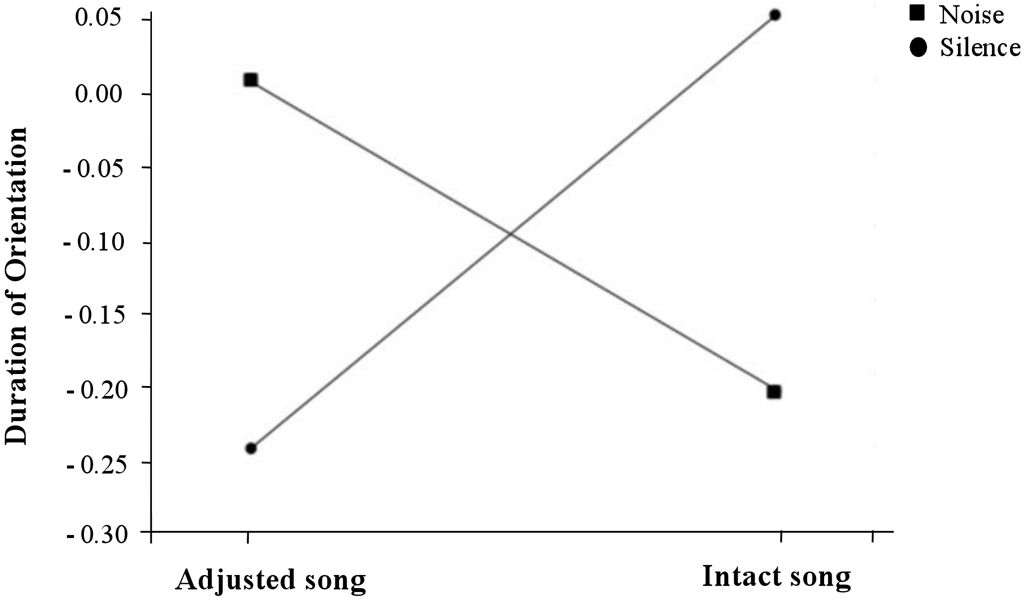
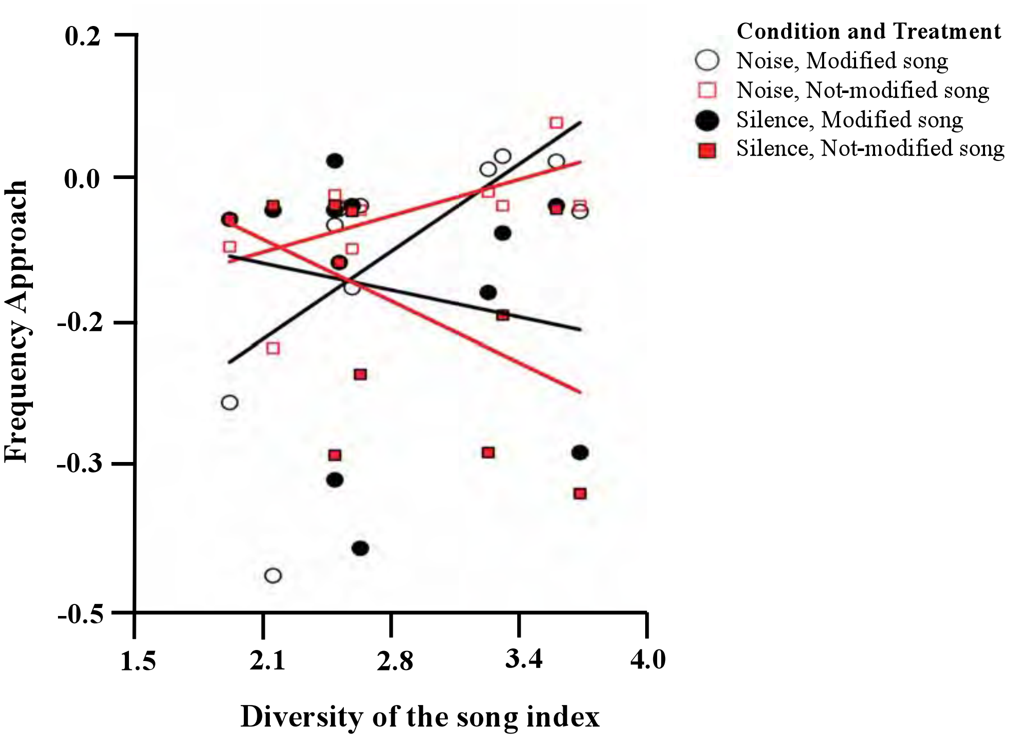


Figure 4 - Relation between mean difference (during trail - pre-trial) in approach frequency of females and diversity of song index.



Capítulo 5

Morphology and habitat characteristics influence song frequency attributes and song versatility in European passerines.

Morphology and Habitat Characteristics Influence Song Frequency Attributes and Vocal Versatility in Songbirds

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Abstract. It has been shown that the structure of bird songs -a major component of bird communication- is a function of the environment in which they communicate, with those produced in open habitats being normally more complex and higher-pitched than songs produced by in close environments. Morphology also constraints bird song; for instance, larger birds produce deeper songs than smaller species, and long thin beaks limit the production of rapid thrills. Habitat use, bird size, and beak shape are all linked through ecology, yet the simultaneous influence of these factors on bird song has been largely ignored. Using phylogenetically-corrected contrasts we evaluated the relative effect of habitat type, bird size and beak shape on the pitch (frequency parameters, including bandwidth) and versatility (diversity of elements that constitute the song) of the songs produced by 55 passerine species from the Iberian Peninsula. We confirm the negative association between vegetation density and song frequency and bandwidth, and demonstrate an independent effect of beak shape; deeper beaks are associated with wider song bandwidths. Additionally, we found that versatility is higher in open habitats, lending support to the idea that redundancy -the opposite of versatility- is promoted when signal transmission is hampered.

Key words: Bird song, beak shape, acoustic constraints, song complexity, Passeriformes, independent contrasts

Introduction

The evolution of acoustic communication systems has been shaped by selective forces and by constrains acting on the production, transmission and detection of the acoustic signals (Ryan and Brenowitz, 1985). A large number of studies have investigated the role of these evolutionary factors on the evolution of bird song, mostly on song frequency attributes. Those studies have shown that bird song frequency is affected by morphological features of the sender such as body size and beak shape, and by the structural complexity of the habitat where the communication takes place (Morton, 1975; Wallschläger, 1980; Ryan and Brenowitz, 1985; Podos, 1997; 2001; Palacios and Tubaro 2000; Podos et al. 2004; Badyaev et al. 2008; Derryberry, 2009); morphology influences the attributes of the signal that is produced, while habitat structure imposes a selective regime on signal transmissibility.

General body size is the morphological feature whose influence on song frequency has been most often demonstrated. Given the physical relationship between the length of the vibrating membranes and the fundamental frequency they produce (Podos and Nowicki, 2004), large birds, which also have a large syrinx (Cutler, 1970), produce lower frequencies than small species (Bowman 1979; Wallschläger, 1980; Ryan and Brenowitz, 1985), leading to a negative association between body size and song frequency.

A morphological factor that has received comparatively less attention is beak shape, although several studies show that beak size and shape have an influence in song frequency. In the family Emberizidae, for instance, species with large beaks are not capable of producing songs with a rapid repetition of notes and a narrow frequency bandwidth (Podos, 1997; 2001; Badyaev et al. 2008; Derryberry, 2009). Podos (2001) and Herrel et al. (2009) suggested that this constraint is caused by a biomechanic trade-off between maximum mandible power and agility: beaks adapted to produce a great force would be at a disadvantage when performing quick movements. In addition, recent research has found that beak gape width needs to increase significantly when notes of increasing frequency are produced (Westneat et al. 1993; Podos et al. 2004; Riede and Suthers 2009). This pattern is due to beak movements influencing the resonance properties of the vocal tract through varying its physical dimensions (Nowicki and Marler, 1988). Accordingly, some studies have found that birds with longer, deeper, and wider beaks produce songs with significantly lower minimum frequencies, maximum frequencies and reduced frequency bandwidths (Huber & Podos, 2006; Palacios and Tubaro, 2000). Since beak/gape attributes are a consequence of (mostly feeding) ecology, and given that bird songs are involved in mate choice and species recognition, these physical constraints may provide a link between ecology and speciation as recently evidenced in a group of Neotropical forests birds (Derryberry et al 2012).

Classical models of song production emphasize the role of the syrinx membranes in the determination of frequency spectra (e.g. Brackenbury 1982). However, more recent studies have shown that frequency is affected by both structural and dynamic attributes of the suprasyringeal tract, including vocal tract filtering (Nowicki 1988), modification of throat space by hyoid movements (Riede and Suthers 2009) and beak movements that track the different frequency modulations produced at the syrinx (Hoese et al 2000). Across species, several studies have found that vocal agility (rapid trills with ample frequency modulation) is restricted to species with slender beaks (Podos et al 2004, Derryberry 2009). To our knowledge, only one study (Palacios and Tubaro 2000) has examined a general relationship between vocal frequency and beak size, finding that in the family Dendrocaliptidae there is a negative association between fundamental frequency and beak length.

The attributes of the bird song are also consequence of the environment in which they are produced, since its acoustic properties favour the transmission of vocalisations with particular structures and frequencies. Habitats differ in topography and in type and density of vegetation, thus imposing different selection pressures on acoustic signals as a result of the way in which sound is attenuated and degraded (Morton, 1975). As expected from the physics of sound transmission, it is recurrently found that in dense vegetation, low frequencies and narrow bandwidths are transmitted more efficiently than high frequencies. Indeed, forest bird species produce songs with lower frequency and a narrower bandwidth that species living in open areas (Morton, 1975; Ryan and Brenowitz 1985; Sorjonen, 1986; Wiley, 1991; Dabelsteen et al., 1993; Derryberry, 2009; Cardoso and Price 2010).

Whereas the structure of the habitat and the mechanical density of the objects that make it determine the rate at which sounds attenuate, and thus differentially favour songs with specific pitch and structure, the sounds that are normally encountered in a place differentially mask segments of the songs and thus influence signal composition. For instance, chaffinches (*Fringilla coelebs*) living near noisy torrents in Scotland produce more redundant songs bouts than finches elsewhere (Brumm and Slater 2006). By extrapolation, it could be predicted that species living in habitats that constrain sound transmission, such as dense forests, should produce more redundant songs that species living in open habitats.

In this study we analysed whether and how body size, beak shape and habitat structural complexity simultaneously affect the frequency and song characteristics of bird song in a sample of 55 passerines common in the Iberian Peninsula. We used habitat characteristics empirically defined in the national Spanish bird atlas, and collected song data from commercial sound recordings. Beak shape data were directly obtained from Museum specimens.

Methods

Species

We selected 55 bird species commonly found in the Iberian Peninsula using inclusion criteria designed to maximise habitat differences between closely related taxa (e.g. *Phoenicurus ochrurus* vs. *P. phoenicurus, Anthus trivialis vs. A. campestris*, etc.; see phylogeny in Fig. 1).

Song data

We used song recordings from different Spanish and European commercial bird songcollections (Llimona et al. 1995; 2000; 2001; Matheu, 2001; 2003; Roché y Jérôme, 2001; Schulze, 2003; Márquez y Matheu, 2004), available at the Fonoteca Zoologica of the Spanish Museum of Natural Sciences (MNCN, CSIC) in Madrid. Most samples were recorded from Spanish populations, but a high and significant within-species repeatability of song characteristics (mean repeatability = 0.66, range 0.32 - 0.95; mean p= 0.003, range 0.00 - 0.012) allowed us to add recordings from other European populations for those species with limited Iberian recordings. We analysed 326 songs -on average 2.28 songs per individual (SD= 0.57, range = 1-4)- and a total of 139 males- on average 2.52 males per species-. We measured song attributes in Avisoft SASLab Pro software; the spectrograms were obtained using the following settings: FFT length, 256; frame size, 100%; window, Hamming; frequency resolution, 86 Hz; temporal resolution, 8 ms).

Song attributes directly measured were song length, total number of syllables, number of different syllable types, minimum frequency, maximum frequency, emphasized frequency and bandwidth. We also measured minimum frequency, maximum frequency and bandwidth of each syllable within the song, and additionally calculated vocal versatility as the ratio of number of different syllable types to total number of syllables. The syllable-specific data were used to derive an index of within-song frequency variation, since we predicted that species with a greater variety of frequencies in their syllable repertories would be able to exploit a larger diversity of habitats. Species estimates of maximum and minimum frequencies based on means of 1) complete songs, or 2) song elements, were virtually identical (all Pearson's $r > 0.85$, $P < 0.001$), and thus we only used the former in the analyses. Element-wise frequency data were used to calculate a mean coefficient of variation (CV) of frequency per song, and we averaged this per species to provide an estimate of vocal range variation. Principal components analyses (PCA) were performed separately for frequency and repertoire characters, so that the large number of variables could be reduced to a handful of orthogonal (uncorrelated) factors.

Habitat

As a measure of habitat openness we used the index of *structural complexity* reported for each species in the Spanish Breeding Bird Atlas (see Carrascal & Lobo 2003 for a detailed explanation). We selected as representative of each species the habitat where it showed the highest density, and took the index of structural complexity of that habitat for the analysis.

This index uses six habitat categories: 0 (lacking or very sparse vegetation cover); 1 (grasslands); 2 (scrublands with sparse vegetation cover made up of bushes lower than 0.5 m); 3 (thick scrublands with bushes higher than 0.3 m in height); 4 (parklands, narrow riparian woods, hedgerows and young forests); and 5 (dense mature forests with trees usually higher than 12 m). Our measure of diversity of habitat used was the estimate of *habitat amplitude* reported for of each species in the Spanish Bird Atlas (Carrascal and Lobo, 2003).

Morphology

Body morphological data came from Cramp et al. (1982-1994). Mean body mass, wing length, tarsus length and tail length -whenever possible for males- were obtained from the nominal species in Spanish or Mediterranean populations (data taken throughout the year). Beak shape was directly measured from 165 museum specimens held at the MNCN (then the average from n = 3 individuals per species was used). We measured beak length (exposed culmen), beak width at the anterior end of the nostril, and beak depth in a vertical plane at the anterior end of nostrils over both mandibles.

We estimated body size as the first principal component of the 7 morphological characters ($PC1_7$). To remove the effect of bird size on beak height, we calculated a similar canonical variable in which all morphological variables except beak height were entered. This $PC1_6$ is almost identical to the previous estimate ($PC1_7$) considering all measurements ($F_{1,53}$ = 1939, $P < 0.0001$; $r^2 = 0.97$). Then, we calculated the residuals of the regression of beak height on body size (i.e. on $PC1_7$; $F_{1,53} = 39.06$, $P < 0.001$; $r^2 = 0.42$; B (SE) = 0.10 (0.07)). The residuals from this model were then used as size-free estimates of beak height.

Comparative análisis

We built a global phylogeny for our taxa by collating several sources of molecular information (Fig.1). The structure at the family level was taken from a robust study by Barker et al (2002) which shows that all the families of the Passeriformes parvorder Passerida are monophyletic and the result of a radiation that took place once their common ancestor expanded from their ancestral Australian distribution. Relationships between species within families were obtained from available sources.

Species estimates cannot be treated as independent data points because of common descent. Therefore, we calculated independent contrasts (Felsenstein, 1985) using the software CAIC (Purvis and Rambaut, 1995) to control for possible phylogenetic drift. Analyses were based on lineal regression of independent contrasts through the origin (Falsenstein 1985).

Statistics

We used principal component analysis to reduce complexity of suites of traits to a smaller number of uncorrelated factors. Multiple regression models were then built with those predictors that were included in the hypotheses, and non-significant terms were removed stepwise.

Results

Song attributes

Frequency. Analysis of frequency attributes revealed a complex pattern. The first component has a straightforward interpretation, indicating common variance of all frequency measurements, but chiefly loaded by maximum and peak frequencies: species whose songs have a high maximum frequency also sing songs with high peak frequencies, relatively wide bandwidths and high minimum frequencies (Table 1). We will refer to this component as *pitch1*. In contrast, the second component showed a bipolar pattern, revealing negative covariance between minimum frequency and band width. This factor captures additional variance aside from *pitch1*, distinguishing between birds with relative high minimum frequencies and small bandwidths, and birds with relatively low minimum frequencies and large bandwidths (Table 1). We will refer to this component as *pitch2*.

Repertoire. The results of the PCA analysis of variables measuring song element diversity, versatility and output have a straightforward interpretation (Table 2). A first principal component is loaded in the same direction by number of syllables (total and different) and song duration. We will refer to this component as *repertoire size*. The second component is loaded almost singly by song versatility, and will refer to it as *vocal versatility*.

Habitat and morphology

We built a multiple regression model for each song component, adding as predictors both morphological and habitat measurements, since we expected song to be simultaneously affected by both.

Song frequency

As expected, overall song frequency -as expressed by *pitch1*- was negatively related to body size and to habitat structural complexity ($F_{2,52} = 7.66$, $P < 0.001$; $r^2 = 0.228$; body size: $B \pm SE = -0.53 \pm 0.15$, $P < 0.001$, Fig. 2a; habitat structural complexity: $B \pm SE = -0.26 \pm 0.10$, $P = 0.014$, Fig. 2b). Beak height dropped from the model ($P > 0.12$), and this was not due to co-linearity (tolerance = 0.93, FIV = 1.075). As seen in Fig. 2a, there is a relative scarcity of large bird species singing at high frequencies and of small birds singing at low frequencies.

Pitch2 showed a positive association with habitat structural complexity and a strong negative association with size-corrected beak height ($F_{2,52} = 7.80$, $P < 0.001$; $r^2 = 0.23$; habitat structural complexity: $B \pm SE = 0.24 \pm 0.10$, $P = 0.027$, Fig. 3a; beak height: $B \pm SE = -0.75 \pm 0.21$, $P < 0.001$, Fig. 3b). *Pitch2* was not related to body size, which dropped from the model ($P > 0.5$), and showed no co-linearity (tolerance = 0.90, FIV = 1.10). The negative link between beak height and *pitch2* is not due to the extreme beak height contrast between *Prunella* sp *and P. petronia* (leftmost datum in the graph; not a bi-variate outlier), since the results were not modified when we ran a new analysis removing *Prunella* from the data set ($F_{2,51}$ = 5.86, P = 0.005; r^2 = 0.18; habitat structural complexity: B ± SE = 0.24 ± 0.10, P = 0.026; beak height: B ± SE = -0.76 ± 0.27, P = 0.007).

Song repertoire

Repertoire size was negatively related to habitat structural complexity ($F_{1,53}$ = 5.38, P = 0.024; r^2 = 0.09; B ± SE = -0.25 ± 0.10). However, this relationship was due to an outlier (the contrast between *Alauda arvensis and Lullula arborea,* which is extreme because of the repertoire size of *Alauda*, the largest of all taxa considered). When *Alauda* is removed from the analysis, the significance of the relationship disappears ($F_{1,51}$ = 2.17, P = 0.14; r^2 = 0.04; B (SE) = -0.14 (0.09)).

Still, vocal versatility was negatively associated with habitat structural complexity, and in this case models with and without *Alauda arvensis* yielded similar results: (with *Alauda*: $F_{1,53}$= 7.22, P = 0.01; r^2 = 0.12, B ±SE = -0.30 ±0.11; Fig.4; without *Alauda*: $F_{1,51}$ = 4.78, P = 0.033; r^2 =0.09; B ± SE = -0.27 ± 0.12). This relationship is not due to positive covariance of versatility with *pitch1*, since both factors are not intercorrelated ($F_{1,53}$ = 0.10, P = 0.75), and suggests that the removal of *Alauda* in the analysis of vocal versatility may be conservative, and that habitat structural complexity does influence attributes of the song repertoire.

Discussion

As predicted, we found that bird song attributes related to frequency are associated to both habitat structural complexity -which sets up the conditions under which song attributes operate- and beak morphology, which we expected that may constrain some of the attributes of the song in much the same way as the vocal cavity in humans controls the quality of the voice that is produced. This last finding seems to indicate that song pitch is determined by both the size of the syrinx (Ryan and Brenowitz 1985) and the beak morphology, thus implying two independent structures in the control of song pitch, which may synergistically promote the production of very variable and complex songs (Suthers et al., 1999 Suthers, 2004).

Overall frequency characteristics (*pitch1*) were negatively correlated with body size and habitat structural complexity. Essentially, large species and species that inhabit dense woodlands produce songs with lower overall frequencies than small species and that birds living in open areas. The association with habitat is a pattern found in many studies with a wide variety of species (Morton, 1975; Ryan and Brenowitz 1985; Sorjonen, 1986; Wiley; 1991; Dabelsteen et al., 1993; Derryberry, 2009; Cardoso and Price 2010; Weir et al 2012). A possible functional explanation is that low-frequency sounds have long wavelengths and thus are less attenuated -mainly because they can better diffract around small obstacles such as foliage- than high-frequency sounds with shorter wavelengths (note also that in some cases ground attenuation in open habitats may greater for lower than for higher frequencies; see Wiley and Richards 1978). Additionally, may be that birds in tropical forests sing at low frequencies to escape masking by high-frequency insect songs (Weir et al 2012). As a proximal explanation, we also found that body size limits frequency song emission. This can be explained if birds with a relatively large body have a correspondingly large syrinx (Cutler 1970) and, as a general rule, produce lower-pitched vocalizations (Bowman 1979; Wallschläger 1980; Ryan & Brenowitz 1985).

In addition to overall frequency, a second component chiefly loaded by frequency bandwidth and minimum frequency is also explained by morphology (beak height) and habitat. Woodland species have relatively narrow bandwidths associated with higher minimum frequencies. Narrow bandwidth songs are common in species singing in close habitats (e.g. Hunter and Krebs, 1979; Shy, E. 1983; Tubaro and Segura, 1995; Weir et al 2012), but it is not clear why this should be so. One proposal is that reverberations in such environments enhance the transmissibility of notes with a narrow bandwidth (Slabbekoorn et al, 2002) in comparisons with frequency-modulated notes. This, however, does not explain why the bandwidth of the whole song is narrow in forest-dwelling species. Wiley and Richards (1978) suggested that producing songs with narrow frequency ranges in dense habitats allows birds to broadcast greater power at each frequency. Additionally, scatter may make wide-band songs more difficult to interpret by receivers. Dense vegetation scatters acoustic signals through refraction, deflection and diffraction (see Wiley and Richards 1978), and different wavelengths within a song will be scattered differently. Therefore different elements will reach the receiver with different delays and attenuations, making a signal with a wide frequency band more difficult to decode than a narrow-band signal of a comparable temporal structure.

The proximal, mechanical explanation of the fact that taller beaks allow a wider frequency range may relate to our finding that short beaks are also taller. Indeed, recent studies show that birds with short beaks have a large opening angle and thus can produce high frequencies not available to birds with long beaks (Palacios and Tubaro, 2000). Thus birds with short and tall beaks have a large opening angle and can produce (and modulate) a larger frequency range (see also Podos 1997).

Finally, we present a novel result suggesting that limited acoustic transmission in woodlands has selected for lower versatility (i.e. more repetitive songs). This relates to the function of songs for information transfer hypothesis; by repeating the same song type several times, a bird may increase the probability that the signal will be successfully transmitted (Brumm and Slater, 2006). A comparable result was reported in the chaffinch (*Fringilla coel coelebs*) which in noisier areas sings longer bouts of the same song type than elsewhere (Brumm and Slater 2006), suggesting that birds increase serial redundancy to transmit their songs through noisy environments. Our data suggest that the proposal of Brumm and Slater (2006) holds generally for forest-dwelling birds.

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Table 1.- Factor loadings of frequency variables obtained by principal component analysis (PCA). Factor loading above > 0.70 in **bold**.

Variable	*pitch1*	*pitch2*
Minimum frequency	0.575	**0.779**
Maximum frequency	**0.925**	-0.319
Frequency bandwidth	0.590	**-0.805**
Peak frequency	**0.849**	0.379

Table 2.- Loading of repertoire variables in the principal component analysis. Factor loading above > 0.70 in **bold**.

Variable	Repertoire	Versatility
Song versatility	0.423	**0.898**
Total number of syllables	**0.865**	-0.428
Number of different syllables	**0.933**	0.267
Song duration	**0.857**	-0.302

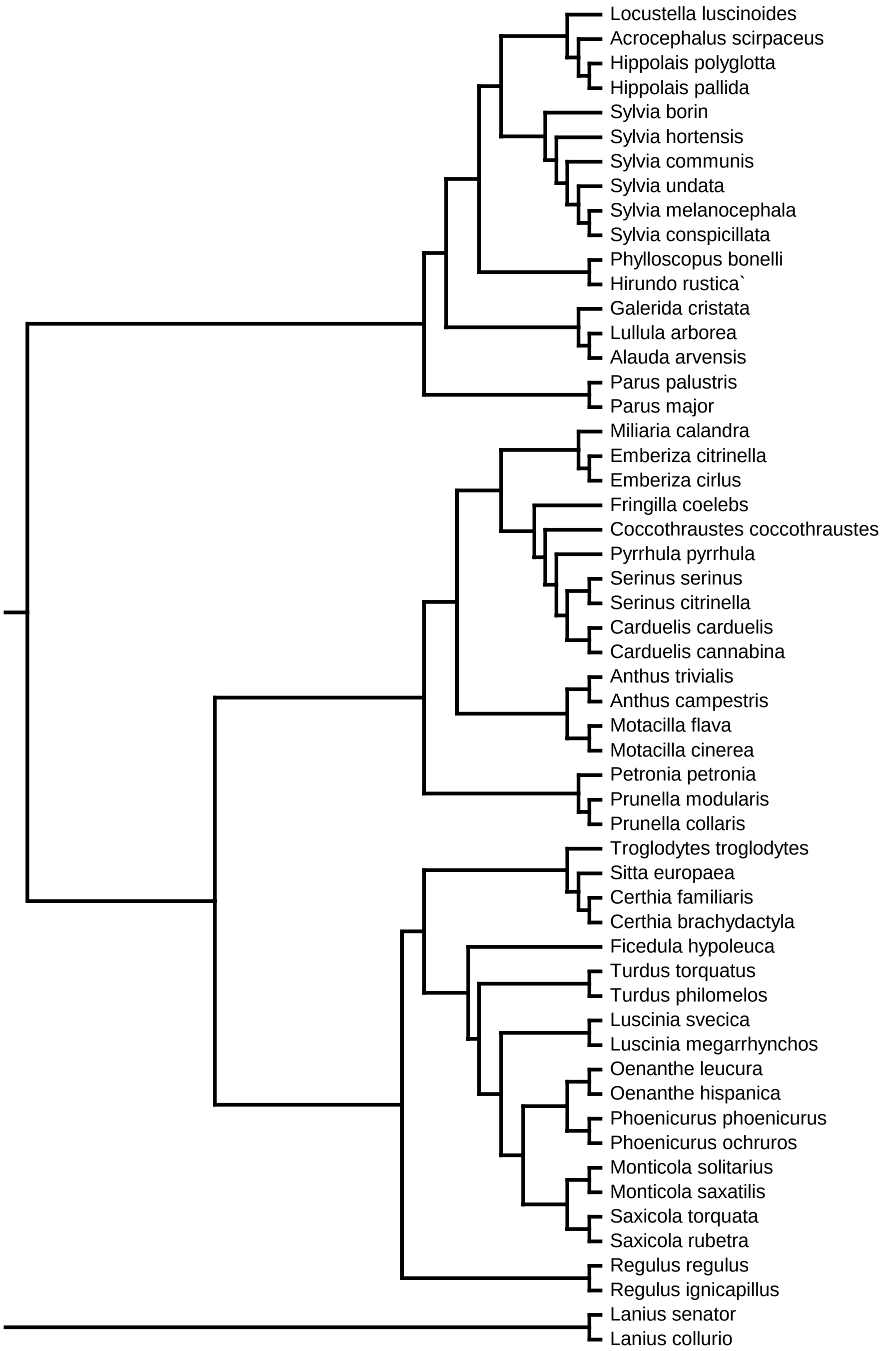

Figure 1.- Phylogeny of fifty five european passerine species studied, obtained by collating data from several sources of molecular information (see text for sources).

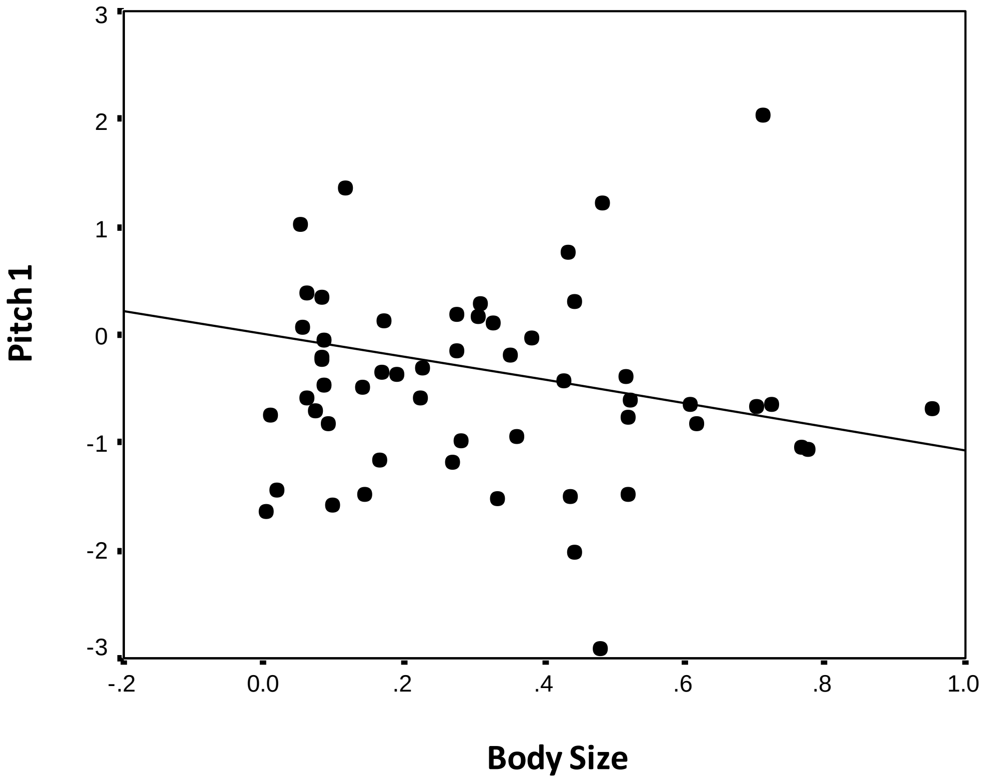

Figure 2a.- There was a significant negative association between contrast of body size and contrast of *pitch 1*. As body size increase *pitch 1* decreases (see text for statistics).

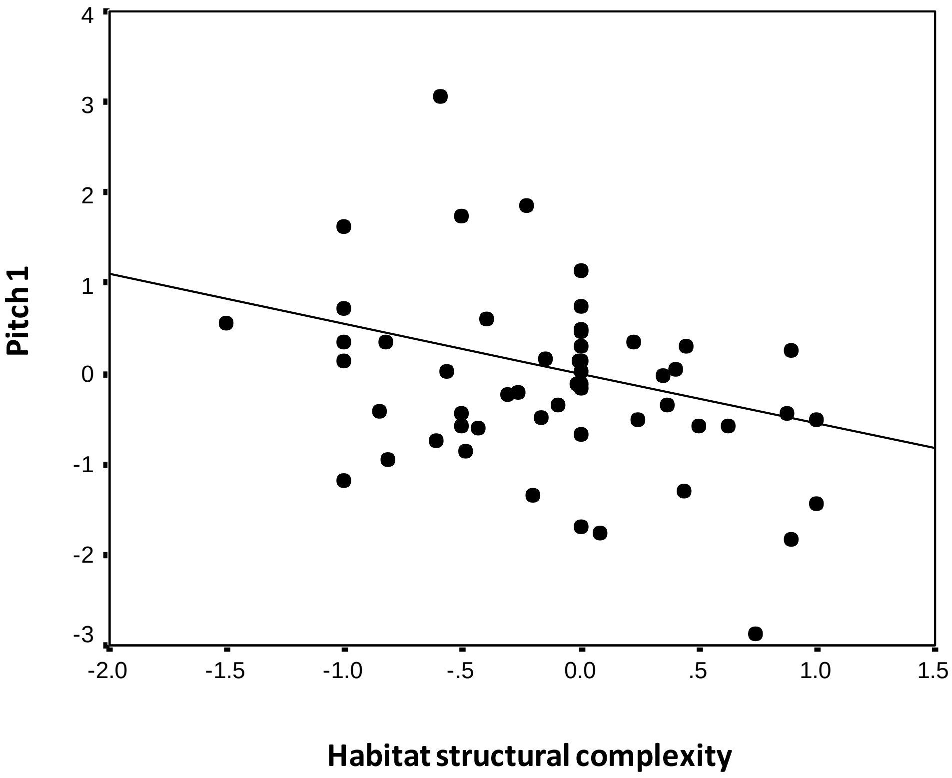

Figure 2b.- We found a negative association between contrasts of habitat structural complexity and contrast of *pitch 1*.

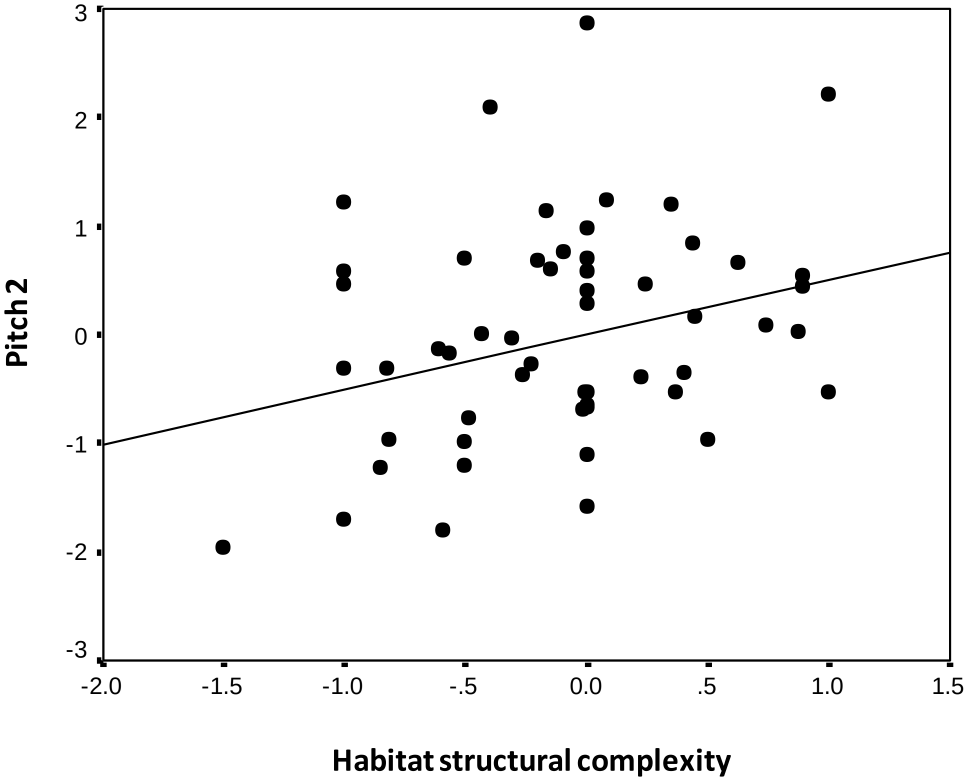

Figure 3a.- Habitat structural complexity contrasts was positively related to *pitch 2* contrast.

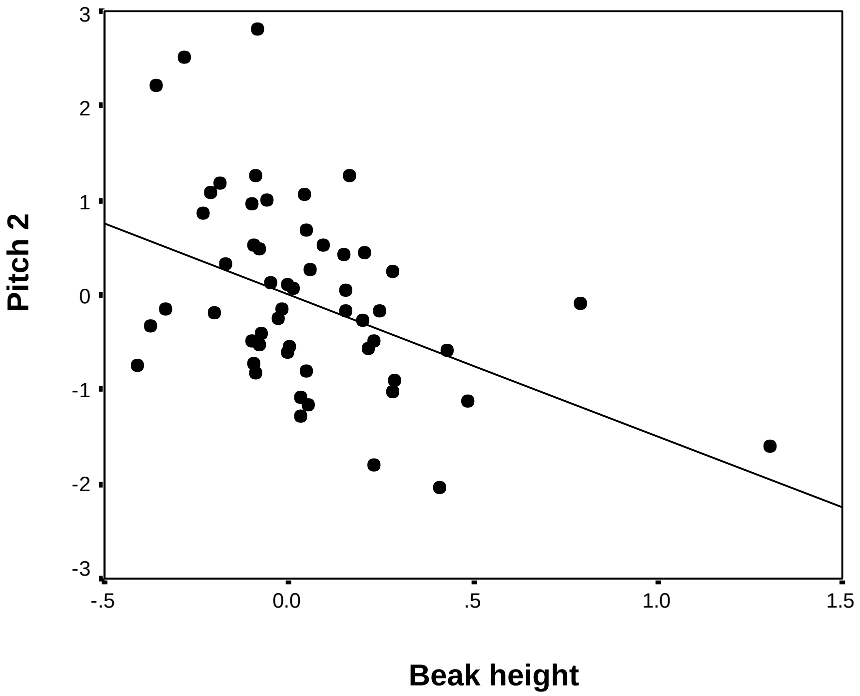

Fig. 3b.- Beak height is negatively related to *pitch 2* contrast.

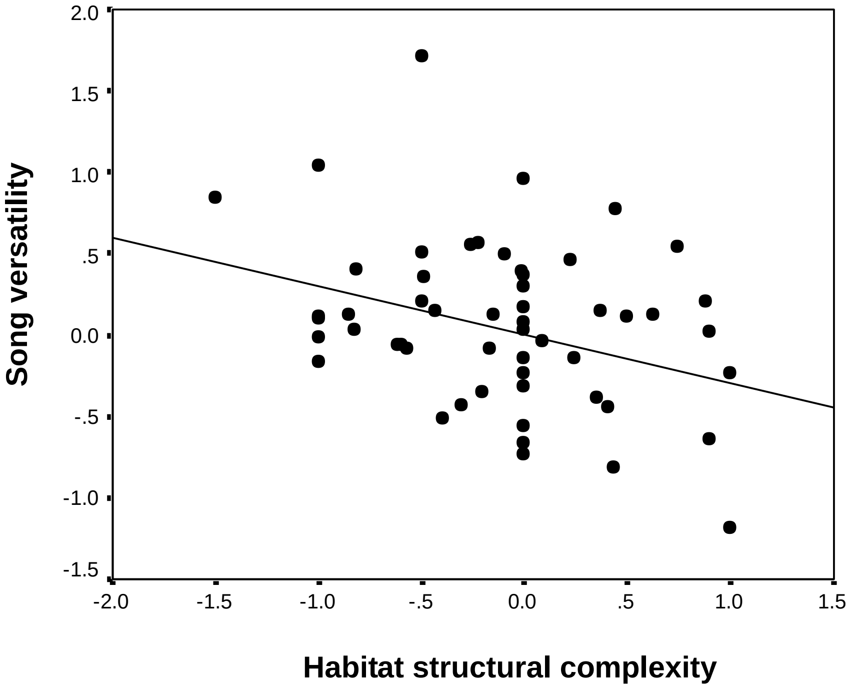

Fig. 4.- Habitat structural complexity contrasts is negative related to song versatility contrasts; birds in habitats with high structural complexity have low song versatility

7.- Discusión General

El crecimiento desmedido de las áreas urbanas ha sido percibido por algunos como una posibilidad para realizar “experimentos naturales” en los cuales se pueden estudiar las modificaciones o ajustes de las señales acústicas de las aves en respuesta a las rápidas alteraciones del entorno acústico. Algunas de las preguntas que han surgido en estos estudios son: ¿Qué parámetros de las vocalizaciones de las aves han sido modificados para reducir el enmascaramiento por el ruido antropogénico? ¿Qué características fisiológicas de las aves son necesarias para que puedan llevar a cabo estos ajustes de las vocalizaciones? y ¿Cuáles son las consecuencias de dichos ajustes en la adecuación individual y la persistencia de las poblaciones de las aves? Las respuestas a estas preguntas dependen de los fundamentos morfológicos, ontogenéticos y de comportamiento de las aves, así como también del contexto ecológico en el cual se emplean las vocalizaciones. El conocimiento de la fisiología, la neurobiología del desarrollo, el comportamiento animal y la ecología del comportamiento, contribuyen a la comprensión de cómo las aves pueden o no modificar sus vocalizaciones en respuesta al cambio antropogénico. Los principales parámetros de las vocalizaciones de las aves donde se han encontrado cambios en respuesta al ruido urbano son: de frecuencia (i.e. qué tan grave o agudo es una vocalización), de amplitud y temporales (Brumm & Slabbekorn, 2005; Patricelli & Blickley, 2006; Ríos-Chelén, 2009). En la presente tesis estudié los ajustes temporales y espectrales de las vocalizaciones del gorrión mexicano (*Carpodacus mexicanus*) en función del ruido urbano. También evalué la respuesta de las hembras de este gorrión al incremento de la frecuencia mínima del canto de los machos debido a los elevados niveles de ruido urbano. Por último, investigué cómo se relacionaban los parámetros de frecuencia del canto de especies paseriformes con las características de su hábitat, tamaño corporal y forma de pico.

En primer lugar, me propuse indagar si los machos de gorrión mexicano de la Ciudad de México, que se encontraban en lugares ruidosos cantaban con una frecuencia mínima mayor que los individuos de zonas silenciosas (Capítulo 1). Mostré de manera correlativa que los individuos presentes en lugares ruidosos emiten cantos de frecuencia mínima mayor que los de sitios silenciosos (Bermúdez-Cuamatzin et al. 2009), lo que se ha interpretado como una estrategia que permite a las aves urbanas evitar el enmascaramiento de sus cantos por las bajas frecuencias del ruido urbano. Esto se ha hallado en varias especies citadinas (Slabbekoorn & Peet 2003; Wood & Yezerinac, 2006; Nemeth & Brumm, 2009; Fernández-Juricic et al. 2005; Potvin et al., 2011; Ríos-Chelén et al., 2012). En esta investigación también reporté que mientras en zonas ruidosas la frecuencia mínima del canto se incrementaba, la frecuencia máxima del canto no lo hacía, lo que indica que el canto presenta un ancho de banda menor; se sabe por estudios de psicoacústica que los sonidos con esta característica se transmiten eficientemente en ambientes ruidosos (Lohr et al. 2003). Además, propuse dos estrategias que podrían estar empleando los gorriones para elevar la frecuencia mínima de sus cantos en lugares ruidosos. Estas dos estrategias, no mutuamente excluyentes, fueron el uso de diferentes tipos de sílabas (variación inter-sílaba) y el uso del mismo tipo de sílabas (variación intra-sílaba). Los resultados mostraron que este gorrión emplea las mismas sílabas, pero a una frecuencia mínima mayor en lugares ruidosos, lo que es indicativo de plasticidad. Por último, en este capítulo encontré de manera correlativa que un mismo individuo es capaz de elevar la frecuencia mínima de su canto al incrementarse súbitamente el nivel de ruido urbano (Bermúdez-Cuamatzin et al. 2009). Este estudio fue de los primeros en reportar dicha capacidad plástica en una especie de ave. Esta estrategia es considerada como una adaptación a corto plazo. Previo a esta investigación no existía mucha información acerca de la escala de tiempo en la cual estos cambios conductuales tomaban lugar (Slabbekoorn & Peet, 2003; Brumm & Slabbekoorn, 2005; Patricelli & Blickley, 2006; Verzijden et al., 2010).

A pesar de haber mostrado en el capítulo previo la capacidad plástica de los gorriones mexicanos en la emisión de sus cantos debido al incremento súbito de ruido urbano, quise corroborar este hallazgo experimentalmente al exponerlos a diferentes niveles de ruido urbano (Capítulo 2). Encontré que al incrementar el nivel de ruido urbano los individuos elevaron la frecuencia mínima de sus cantos. Posteriormente, al disminuir el nivel de ruido, los gorriones redujeron la frecuencia mínima de su canto. Con estos resultados demostré que los machos de *Carpodacus mexicanus* modulan plásticamente de manera instantánea la frecuencia mínima de sus cantos en base al nivel de ruido que experimentan (Bermúdez-Cuamatzin et al. 2011). Otras especies de aves en las que se ha reportado el ajuste a corto plazo de la frecuencia mínima del canto por el incremento del ruido, son: el carbonero común (*Parus major*; Halfwerk & Slabbekoorn, 2009), el mosquitero común (*Phylloscopus collybita*; Verzijden et al. 2010), el escribano palustre (*Emberiza schoeniclus*; Gross et al. 2010), el carbonero de capucha negra (*Poecile atricapillus*; Godwin & Podos, 2013) y el petirrojo (*Erithacus rubecula*; Montague et al. 2013).

Entre especies los estilos de canto son diferentes, por lo que también son distintos los mecanismos para lograr el ajuste plástico de la frecuencia mínima. Los carboneros comunes al enfrentarse a niveles de ruido altos de frecuencias bajas, emiten por más tiempo tipos de canto de frecuencias mínimas elevadas. Sin embargo, cuando son expuestos a niveles de ruido elevados pero de frecuencias altas emiten tipos de cantos con menor frecuencia máxima (Halfwerk & Slabbekoorn, 2009). A diferencia de los carboneros comunes, los gorriones mexicanos tienen cantos más complejos y variados, y emplean el mismo tipo de sílabas de sus cantos tanto en condiciones de niveles de ruido elevados como en niveles de ruido bajos (Bermúdez-Cuamatzin et al. 2009; Bermúdez-Cuamatzin et al. 2011). Además, pueden modificar la frecuencia mínima de un mismo tipo de sílaba en función del nivel de ruido urbano, aunque también encontré que utilizan otros tipos de sílabas nuevas (Bermúdez-Cuamatzin et al. 2009; Bermúdez-Cuamatzin et al. 2011). Así mismo, mostré que el incremento de la frecuencia mínima de los cantos era mayor cuando sólo consideramos aquellos cantos con el mismo tipo de sílabas de frecuencia mínima del canto menor, denominadas sílabas compartidas (Bermúdez-Cuamatzin et al. 2011). Esto sugiere que el cambio de frecuencia se logra principalmente mediante el aumento de la frecuencia mínima del mismo tipo de sílabas. Este resultado indicativo de plasticidad en la frecuencia de las sílabas, concuerda con lo hallado por Tumer y Brainad (2007) en el pinzón capuchino de lomo blanco (*Lonchura striata var. domestica*). Esta ave tiene la capacidad de modular la frecuencia de una determinada sílaba en respuesta a un acondicionamiento aversivo de ruido blanco. Por último, reporté que los cantos de gorrión mexicano se pueden clasificar en dos grupos en función del ruido urbano. Los cantos que tienen tipos de sílabas compartidas, poseen un mayor efecto en los cambios de frecuencia y se acortan durante la exposición al ruido. Por otro lado, están los cantos de tipos de sílabas no compartidas, cuyo papel en los cambios de frecuencia es marginal y estas sílabas se alargan durante la exposición al ruido. El tití (*Callithrix jacchus*) muestra un cambio temporal similar al del gorrión mexicano en los elementos de sus vocalizaciones respecto al incremento del ruido (Brumm et al., 2004). Con este estudio, concluyo que el gorrión mexicano tiene a su disposición dos estrategias al emitir sus cantos cuando se enfrenta al ruido urbano: el aumento de la frecuencia y el alargamiento temporal.

Entre las preguntas diversas que surgieron de los resultados del primero y segundo capítulo, una de ellas fue si los machos de gorrión mexicano ajustan de manera plástica algún atributo de sus llamados en respuesta al ruido urbano y si las condiciones de ruido del lugar donde proceden influyen en dicha plasticidad (Capítulo 3). Demostré que estos gorriones no incrementan la frecuencia mínima ante niveles de ruido elevados como lo hacen con sus cantos (Bermúdez-Cuamatzin et al., 2011). Por otro lado, evidenciamos que estas aves muestran plasticidad al elevar en tiempo real la frecuencia pico y la frecuencia máxima de sus llamados ante niveles de ruido urbano elevados; lo que puede evitar el enmascaramiento de los llamados al concentrar la mayor cantidad de energía a frecuencias más elevadas. El ancho de banda no mostró diferencias entre nivel de ruido bajo y alto, en cambio sí hubo diferencias respecto a la procedencia de los individuos, siendo menor en los machos provenientes de zonas ruidosas respecto a los de zonas silenciosas. El número de armónicos aumentó durante el nivel de ruido alto, lo que puede estar relacionado con el incremento de frecuencia y amplitud del llamado que se produce cuando se eleva el ruido (Nemeth et al., 2013). La longitud de los llamados no difirió entre nivel de ruido bajo y alto; esto concuerda con nuestro trabajo previo en el que hallamos que el canto de esta ave no disminuye su duración debido al ruido urbano (Bermúdez-Cuamatzin et al. 2009). El presente trabajo es uno de los primeros en mostrar en un ave oscina la capacidad de ajustar parámetros espectrales de sus llamados en respuesta al ruido urbano (Potvin & Mulder, 2013; Bermúdez-Cuamatzin et al. en prep.).

Otra pregunta que se desprendió de los hallazgos presentados en el primer y segundo capítulo fue si las hembras del gorrión mexicano prefieren cantos de frecuencias altas o bajas en presencia de ruido. Investigué a través de un par de pruebas dicotómicas qué tipo de canto preferían las hembras (Capítulo 4). Encontré que las hembras se aproximaban a un estímulo más veces en condición de ruido que en silencio. Esto puede suceder porque el ruido antropogénico obliga a las hembras a acercarse a la fuente de los cantos para evitar su interferencia (Lohr et al. 2003; Brumm & Slabbekoorn, 2005;

Patricelli, & Bickley, 2006). También, las hembras muestran preferencia por cantos de frecuencia baja o cantos no modificados sobre los de frecuencia alta (modificados) durante la condición de ruido. Estos resultados fueron contrarios a lo que esperábamos, debido a que Halfwerk y colaboradores (2011) encontraron que las hembras de *Parus major* muestran preferencia por cantos de frecuencia alta en presencia de ruido. Esto podría indicar que los cantos de frecuencias altas mejoran la comunicación entre hembras y machos al reducir la superposición espectral con el ruido de fondo. Mis resultados pueden deberse a que los cantos de frecuencia baja no los modificamos como los de frecuencia alta. Tal vez, la modificación del canto los hizo percibir como extraños. Por otro lado, las hembras prefieren cantos de frecuencia alta en la condición de silencio probablemente porque sin el ruido urbano interfiriendo, exploran los cantos modificados. Durante las pruebas reprodujimos a la misma amplitud los cantos de frecuencia baja y alta, esto pudo afectar la respuesta de las hembras, pues se sabe que el incremento de la frecuencia en los cantos es acompañado por un aumento en la amplitud en ambientes ruidosos (Nemeth et al. 2013). También, reporté que las hembras prefieren cantos más diversos en la condición de ruido.

Por último, resultó interesante investigar cómo se relaciona la emisión de las frecuencias del canto de las aves paseriformes con las características morfológicas y de complejidad de su hábitat. Encontré que aves de gran tamaño y aves que habitan vegetaciones densas emiten cantos con frecuencias menores que aves de tamaño menor y aves que habitan espacios abiertos. Muchos estudios han reportado esta misma asociación entre la frecuencia del canto y la complejidad del hábitat (Morton, 1975; Ryan & Brenowitz 1985; Sorjonen, 1986; Wiley, 1991; Dabelsteen et al., 1993; Derryberry, 2009; Cardoso & Price 2010; Weir et al 2012). Esto puede explicarse porque los sonidos de frecuencia baja poseen una longitud de onda mayor, por lo que su atenuación es menor que en los sonidos de frecuencias altas con longitudes de onda menores (Wiley & Richards 1978) en hábitats complejos. Con respecto a las implicaciones del tamaño corporal y el ruido podemos inferir que aves de gran tamaño tendrían dificultades mayores para lidiar con las frecuencias del ruido urbano debido a sus restricciones fisiológicas. Sin embargo, estas aves pueden emplear otro tipo de estrategias para contrarrestar los efectos del ruido.

Las especies de aves que se encuentran en hábitats complejos como los bosques, tienen anchos de banda relativamente menores asociados con frecuencias mínimas altas. Wiley y Richards (1978) sugieren que esto sucede porque la producción de cantos con anchos de banda menores permite a las aves transmitir una energía mayor en cada frecuencia. Además, la dispersión puede hacer que los cantos de anchos de banda mayores sean más difíciles de interpretar por los receptores. La vegetación densa dispersa las señales acústicas a través de la refracción, deflexión y difracción (ver Wiley & Richards, 1978), y las longitudes de onda diferentes dentro de un canto se dispersan de manera diferente. Por lo tanto, elementos distintos del canto llegarán al receptor con retardos y atenuaciones diferentes, haciendo una señal con un ancho de banda amplio más difícil para decodificar que una señal de ancho de banda menor. En base a estas conclusiones puedo inferir que un ambiente urbano podría considerarse como un hábitat complejo debido a la cantidad de construcciones humanas y se podría deducir que las aves presentes en estos hábitats presentarán anchos de banda menores y frecuencias mínimas elevadas lo que les ayudaría a una transmisión más eficiente de sus señales acústicas a través de este medio (Bermúdez-Cuamatzin et al. 2009; 2011).

La explicación mecánica de por qué las aves con picos más altos poseen una gama de frecuencias más amplia, puede relacionarse con nuestro hallazgo de que los picos cortos también son más altos. Estudios recientes muestran que las aves con picos cortos tienen un gran ángulo de apertura y por lo tanto pueden producir altas frecuencias que no están disponibles para las aves con picos largos (Palacios & Tubaro, 2000). Entonces, aves que tienen picos cortos y altos poseen un ángulo de apertura grande que les permite producir y modular un rango de frecuencias amplio (ver también Podos 1997). Por lo tanto, aves con este tipo de picos serán menos vulnerables a ambientes ruidosos, puesto que al tener la capacidad de generar un rango de frecuencias amplio podrían emitir el tipo de frecuencias que más les convenga según las frecuencias y la amplitud del ruido ambiental al que se enfrenten para evitar que sus cantos sean enmascarados. Un hallazgo que resultó novedoso e importante plantea que en hábitats cerrados como bosques donde la transmisión acústica es limitada se han seleccionado los cantos con versatilidad menor o más repetitivos. Esto concuerda con la hipótesis que nos dice que al repetir la misma señal acústica muchas veces un ave puede incrementar la probabilidad de que dicha señal sea transmitida eficazmente (Brumm & Slater, 2006).

7.1.- Futuros trabajos

Estudios futuros deben centrarse en indagar si la capacidad de ajustar la frecuencia del canto en respuesta al ruido es una habilidad ampliamente propagada en paserinos o si se limita a aquellas especies que aprenden sus cantos (oscinos). Aunque los primeros trabajos apuntan a que los oscinos son menos vulnerables a la contaminación acústica que los suboscinos a quienes se les considera con menor capacidad para colonizar ciudades o hábitats novedosos acústicamente (Ríos-Chelén et al. 2012). También se debe continuar la investigación acerca de cómo las señales acústicas cambian en respuesta a las alteraciones rápidas en su entorno acústico. Esto nos podrá dar pauta para conocer cómo evolucionan dichas señales acústicas y podremos indagar el impacto en la adecuación de las especies. La comprensión de estos procesos tiene implicaciones importantes para su conservación, ya que a partir de éstos se pueden realizar propuestas para mitigar los efectos del ruido antropogénico en la comunicación de las aves.

7.2.- Referencias

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