臺灣師範大學生命科學系碩士論文

都市噪音對於白頭翁
(*Pycnonotus sinensis*)鳴聲的影響
Song adjustment of Chinese bulbuls
(*Pycnonotus sinensis*) in urbanized areas

研究生：洪貫捷
Kuan-Chieh Hung
指導教授：李壽先 博士
Dr. Shou-Hsien Li
劉小如 博士
Dr. Lucia Liu Severinghaus

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Abstract

Urban areas have sprawled recently, accompanied by dramatic alteration of abiotic and biotic environments. Therefore, to live in urban areas, wildlife must adjust their behavior to adapt to anthropogenic selection pressure. To reveal how birds modulate their vocal communication to accommodate noisy urban environment, advertising songs of 71 Chinese bulbuls (*Pycnonotus sinensis*) were recorded in two urbanized areas: Taipei City (TP) and Shenkeng Township (SK) of the Taipei County in Taiwan, during March to June, 2008. Sound characteristics, such as the peak frequency, maximum frequency, minimum frequency, delta frequency, and time span of each song were measured. The results showed that the minimum frequency of songs in Chinese bulbuls increased with the background noise level (multiple linear regression, $b= 942.46$, $t= 2.89$, $P=0.0052$) and such relationship was not different between TP and SK ($t_{1,65}=0.397$, $P>0.05$). In addition, I found that the peak frequency, maximum and delta frequency were spatially structured (Moran's I correlogram, $P<0.05$), but not for the minimum frequency (Moran's I correlogram, $P>0.05$). However, the spatial structures of the minimum frequency and background noise were similar in shape, and the residual minimum frequency had no spatial structure (Moran's I correlogram, $P>0.05$), implying the minimum frequency was highly correlated with background noise. These results suggested that the mechanism of song adjustment against noise might be due to behavioral plasticity for Chinese bulbuls.

中文摘要

都市地區的擴張改變了生物居住的環境，野生動物必須面對強烈地人為選汰壓力，才能成功生活在都市地區。本研究在 2008 年三月到六月於台北市區以及台北縣的深坑鎮錄取了 71 隻白頭翁(*Pycnonotus sinensis*)的領域宣示鳴聲，並測量每段鳴唱之主要頻率、最高頻率、最低頻率、頻寬及持續時間等特徵以及當時低頻噪音的音量，以瞭解鳥類如何改變聲音溝通模式，以因應人為產生之低頻噪音。結果顯示，白頭翁領域宣示鳴聲的最低頻率會隨著低頻噪音的音量增加而提升(multiple linear regression, b=942.46, t=2.89, P=0.0052)，且此趨勢在台北市區與深坑鎮間並無顯著差異(t=0.397, P>0.05)。同時在主要頻率、最高頻率以及頻寬上則存在空間結構 (Moran’s *I* correlogram, P<0.05)，但在最低頻率上並無空間結構的存在(Moran’s *I* correlogram, P>0.05)。然而最低頻率與背景噪音的空間結構相似，且最低頻率的殘差也沒有空間結構(Moran’s I correlogram, P<0.05)，代表最低頻率與背景噪音音量有緊密的關係。本實驗結果顯示都市地區的白頭翁會改變鳴唱之最低頻率的方式來抵抗低頻噪音的遮蔽效應，其機制可能來自於鳴唱行為的可塑性，且與鳴聲的學習過程應無直接的關係。

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Introduction

Worldwide urbanization has homogenized the physical environment, producing similar anthropogenic habitats, and resulting in few dominant species (Blair 1996; Marzluff et al. 2001; McKinney 2006). Urbanization usually rises the noise levels, which would pose a new threat to animals (Ariel and Ríos-Chelén1 2009; Slabbekoorn and Ripmeester 2008). Therefore, how animals modify their behaviors to cop to man-made habitat changes is critical to survive in urbanized regions.

In birds, songs are important acoustic traits used to communicate with each others (Gil and Gahr 2002). To achieve successful acoustic communication, signalers must produce signals which can be properly heard and interpreted by receivers (Endler 1992). Therefore, the acoustic adaptation hypothesis (AAH, Morton 1975) proposed that individuals of different populations that inhabit different habitats might have different song characteristics to optimize song transmission (reviewed in Boncoraglio and Saino 2007). For example, because lower frequency songs could better transmit through dense vegetation, great tits (*Parus major*) use higher frequency songs in open woodlands but lower frequency songs in closed forest (Hunter and Krebs 1979).

As an unique habitat, the urbanized area has its characteristic acoustic properties: e.g. high volume of low-frequency noise usually produced by human activities such as traffic as well as many cliff-like structures caused by high density of buildings and roads (Warren et al. 2006). In light of the AAH, birds in urban areas may adopt song structure different from that used in forest or other kinds of natural habitats to maximize the effectiveness of acoustic communication. For example, great tits across ten Europe cities were observed to use songs with different attributes, such as higher minimum frequency of whole song and of the first syllables than that of adjacent forest populations (Slabbekoorn and den Boer-Visser 2006). Consequently, differences of bird songs between urbanized areas and adjacent natural habitat could be attributed to the distinct habitat structure and background noise composition.

Even with the same habitat, different background noises such as wind, stream or other animals would also mask acoustic signals differentially (Klump 1996; Slabbekoom 2004). Signalers should maximize their active space, which is the distance from the source over which signal amplitude remains above the detection threshold of potential receivers, to improve their communication effectiveness by adjusting signals structures or changing singing behaviors even under noise interference (Brenowitz 1982; Marten and Marler 1977). In urbanized areas, birds might adjust their song structure against anthropogenic background noise by increasing singing amplitude, changing frequency structure, altering temporal structure or timing of vocalization (reviewed in Patricelli and Blickley 2006; Warren et al. 2006). For instance, nightingales (*Luscinia megarhynchos*) in one urban population tend to increase the sound level of their songs to maintain desirable signal-to-noise ratio against noise (Brumm and Todt 2002). Great tits increase their minimum frequency of the song with increased volume of background noise (Slabbekoorn and Peet 2003). Song sparrows (*Melospiza melodia*) increase their singing amplitude of low frequency part in noisier conditions (Wood and Yezerinac 2006).

This study is aimed to investigate how anthropogenic noise affects bird songs within urban habitats. I chose Chinese bulbuls (*Pycnonotus* *sinensis*), which is dominant in urbanized area of lowland Taiwan, as target species. They breed in the cultivated area such as orchards, farmlands or highly urbanized areas like parks in downtown areas from March to August, (Hsu and Lin 1994). The low-frequency advertising songs (900 - 4200 Hz) which male Chinese bulbuls used to attract female and defend territories in breeding seasons (Lin 1991), would be measured in two adjacent urban areas with different human population density. The level and characteristic of background noise of these two areas would be measured, too. I expect that the background noise level should be higher in urban areas, especially that with higher population density. Second, owing to the relatively low-frequency advertising songs of Chinese bulbuls, I expect that song characteristics of Chinese bulbuls, especially the minimum frequency, would be affected by the instant background noise. Existence of spatial structure could potentially complicate the results of this study. The spatial autocorrelation of song would be examined by Moran’s *I* statistics (Moran 1948) to describe the pattern of geographical variation of song characteristics.

Methods

Study sites

My study sites included two urbanized areas with different human population density: Taipei City (TP, 25.02°N, 121.53°E) and nearby Shenkeng Township (SK, 25.00°N, 121.62°E) of Taipei County, Taiwan (Figure 1). Both TP and SK were composed by high density of buildings and road systems, but with different human population densities (TP: 9677 /km^2; SK: 1096 /km^2). Both study sites are about 4 km in diameter, separating by about 4 km apart. Consequently the sampling of this study can be classified into two geographic scales: the within-area scale (0 - 4 km) and between-area scale (4 – 10 km).

Song and ambient noise recording

Thirty-nine individuals in TP and 32 individuals in SK were recorded from March to June, 2008. All recordings were taken on weekdays because of relatively stable pattern of traffic noise. I recorded bird songs in the morning between 05:30-10:00 am and in the afternoon between 14:00-17:30 pm. Only songs from birds that were observed with unobstructed view were recorded. To avoid pseudoreplication, I only visited each recording site once and each recording site was at least 100m apart. Locations of each recording site were recorded in Taiwan Datum 1967 (TWD67) cadastral coordinate systems which is one of 2-degree transverse Mercator coordinate systems with global position system (Garmin Rhino 120). Bird songs and ambient noise were recorded simultaneously through left and right channels of the Nagra V digital recorder (frequency response: 30 to 20000 kHz, sampling rate: 24bit 48kHz in Wave from audio format, sensitivity: 2mv/Pa) with two microphones: one directional microphone (Sennheiser MKH-70, frequency response: 60 - 20000 Hz, sensitivity: 15mv/Pa) with windscreen (Sennheiser MZW-701 blimp windscreen) and the other omnidirectional microphone (Sennheiser ME62, frequency response: 20 - 20000 Hz, sensitivity: 31mv/Pa), respectively. The directional microphone for bird songs was mounted on a tripod at 150 cm height to avoid hand vibration, and the omnidirecterional microphone for ambient noise was hand-held at the same height. The mike level potentiometers (maximum gain) for both channels of the digital recorder were set to the 0.2 mV/hPa sensitivity for the subsequent noise level calibration. For example, while the potentiometer was set to 90dB, the 0 dB in the modulometer was corresponding to an acoustic level of 90 dB. I also recorded other potential abiotic and biotic factors, such as the ambient temperature, relative humidity and presence of sympatric singing bulbuls, that might influence the song characteristics.

Song characteristics and noise measurements

The number of songs of each bird varied from 1-22 (*N*=478). Two to five successive songs and noise with best-quality of recording (relatively low background noise, low distortion of songs and elements, and high purity of the sound trace on the spectrogram) were chosen for the subsequent analysis by visually assessing the spectrograms. Then I used the mean of the song characters of the same bird to represent song characteristics of each individual. In order to calibrate the loudness before song measurement, all the left channel of recordings were subjected to a low-pass band filter set at 900 Hz to eliminate any low frequency background noise and then normalized the amplitude of the recording to 0 dB by the software *CoolEdit Pro 2.0* (Syntrillium Software Corporation).

For song measurements, I considered five song characters: maximum frequency (the highest frequency of the whole song), minimum frequency (the lowest frequency of the whole song), peak frequency (the frequency with the most energy), delta frequency (the maximum frequency minus the minimum frequency) of the song in Hz and the time span of the song (the lasting time of one song) in seconds (Figure 2). For the background noise, I measured the average power from 20 - 24000 Hz in dB (i.e. dB(A)) for one second in the right channel of recording right after each song phrase had terminated in left channel, to assure exclusion of bird songs from ambient noise. All background noise levels of TP and SK areas were averaged to represent the noise level of two urbanized areas. In order to compare noise profile of TP and SK, I measured noise spectra, which were the average power ranges from 20 to 8000 Hz at 1000 Hz intervals of urban and suburban areas. For both bird song and noise measurement, I used the software *Raven Pro 1.3* (Cornell Laboratory of Ornithology, Ithaca, NY, USA) with the following settings to document song characters: a hamming analysis window, a filter bandwidth of 61 Hz, a frame length of 512 points, a grid resolution of 10.7 ms, an overlap of 50%, a frequency of 46.9 Hz and a fast Fourier transformation (FFT) size of 1024 points. The unit of average power in dB was calibrated by a synthesized 2 kHz pure tone created by *CoolEdit Pro 2.0*, replaying it in a quite room and measured the sound level with a sound pressure level (TES-1350A, frequency range: 31.5 – 8000 Hz, range: 35-130 dB). All dB values given in this study were referred to 20μPa.

Data analyses

I compared the noise spectrum, song characteristics and averaged noise levels between urban and suburban areas with two-tailed student's t-test when the data fitted normal distribution and with equal variance, and Wilcoxon rank-sum test when otherwise. Normal distribution was tested by Shapiro–Wilk test; the equal variance was tested by Levene's test.

The two-sample Kolmogorov-Smirnov test was use to compare the shape of noise spectrum. Using multiple linear regression models, I examined whether song characteristics were affected by sites (TP or SK), temperature, relative humidity, present of conspecies, and background noise level. I detected the spatial structure in song measurements, instant background noise level by Moran's *I* statistics (1948). The null hypothesis of Moran's *I* is that the variance of a particular variable is randomly distributed in space, i.e. there are no spatial autocorrelation for that variable. To calculate Moran's *I* coefficient, the number of distance classes was determined using Sturge's rule (Legendre and Legendre 1998): number of classes = $1 + 3.3 \log_{10}(m)$; where m is the number of sampling site. Because there were 71 recording sites in this study, number of classes is equal to 7.109. I rounded the value to 7 classes and opted for equal sample size across classes instead of equal distance intervals, in order to obtain sufficient statistical power. The critical *P*-value of all statistical tests was set at 0.05. I used software *JMP 5* (The SAS Institute) for student's t test and Wilcoxon rank-sum test, *R* 2.8.1 (R Development Core Team 2008) for stepwise multiple linear regression and two-sample Kolmogorov-Smirnov test and *PASSaGE 2.0* (Rosenberg 2009) for Moran's *I* spatial autocorrelation test.

Results

Characterization of songs and noise in two urbanized areas

The average noise level across all sampling sites was 61.79 ± 4.9 dB(A) (N=71). The average noise level (mean ± SD) in TP was significantly higher than in SK (Figure 3, TP: 63.35±4.07 dB, SK: 60.21±5.27 dB, *S*=928.5, *Z*=-2.57709, *P*=0.0100, Wilcoxon rank-sum test). The average noise spectrum between 1 and 8 kHz at 1 kHz interval were similar between two areas (*D*=0.375, *P*=0.660, two-sample Kolmogorov-Smirnov test): both areas had strong noise levels in the lower frequency region and low noise levels in the higher frequency range. However SK turned out to be noisier than TP in the high frequency range (5 to 8 kHz) (Figure 4, 4-5 kHz, *Z*=-2.22615, *P*=0.0260; 5-6 kHz, *Z*=-2.05227, *P*=0.0401; 6-7 kHz, *Z*=-2.38858, *P*=0.0169; 7-8 kHz, *Z*=-2.81750, *P*=0.0048, Wilcoxon rank-sum test) but not in low-frequency ranges (0 to 4kHz) (Figure 4; 0-1 kHz, *Z*=0.91611, *P*=0.3596; 1-2 kHz, *Z*=1.61751, *P*=0.1058; 2-3 kHz, *Z*=-0.32475, *P*=0.7454; 3-4 kHz, *Z*=-1.42613, *P*=0.1538, Wilcoxon rank-sum test). The sources of low-frequency noise were alike in both areas: the automobile traffic. In addition, in SK, cicadas, birds, and other insects often produced high-frequency noise.

The average minimum frequency, maximum frequency, peak frequency, delta frequency and time span (mean ± SD) of Chinese bulbuls' songs were 1300.58 ± 74.16 Hz, 3612.14 ± 307.03 Hz, 2710.60 ± 335.51 Hz, 2311.56 ± 306.82 Hz, 1.38 ± 0.55 s, respectively (*N*=71). Results of the multiple linear regression (Table 2) suggested that background noise level significantly affected the minimum frequency of

Chinese bulbuls' songs in both urban areas (Table 2, Figure 6, t= 2.89, P=0.0052). Besides, there were some song variances between two sites: the site factor significantly affected the maximum frequency (t_5= 2.92, P= 0.0048), the peak frequency (t= 2.79, P= 0.0070) and the delta frequency (t= 2.85, P= 0.0059), but not the minimum frequency (t=0.40, P=0. 6929) of the Chinese bulbul's song. Except the minimum frequency, all these song characteristics were higher in TP than in SK (Figure 5. All $P<0.05$; maximum frequency: TP 3732.17±45.08 Hz, SK 3465.84±48.57 Hz, t_{69}=4.0093, P=0.0002, t-test; peak frequency: TP 2831.54±56.65 Hz, SK 3563.20±43.29 Hz, S=837 Z=-3.63462, P=0.0003, Wilcoxon rank-sum test; delta frequency: TP 2424.72±47.15 Hz, SK 2173.65±46.96 Hz, t_{69}=3.7347, P=0.0004, t-test;). The minimum frequency and time span showed no difference between sites (Table 2, both $P > 0.05$; Figure 5, minimum frequency: TP 1307.45±13.22Hz, SK 1292.20±11.09 Hz, t_{69}=0.8604 P=0.3926, t-test; time span: TP 1.313±0.136 sec, SK 1.459±0.745 sec, S=1164.5 Z=0.13868 P=0.8897, Wilcoxon rank-sum test). The relative humidity affected time span (t= 2.02, P= 0.0048), but the overall model was not significant ($F_{5,65}$=1.282, P=0.2825).

Spatial structure analysis

The Moran's I coefficients of song characteristics were represented as Moran's I spatial correlograms (Figure 7). Results of Moran's I correlograms showed that spatial structures existed in the maximum frequency, the peak frequency and the delta frequency of Chinese bulbuls' songs, but in different scales (Figure 7b-d, all $P<0.001$). The minimum showed near-significant spatial structure (Figure7a, P=0.017). However, significantly positive Moran's I coefficient in within-area scale still indicated that nearby individuals tended to have similar minimum frequency (Figure 7a). Similarly, background noise level had a within-area spatial structure similar to that of the minimum frequency (Figure 7e, $P<0.001$). However, the Moran's I correlogram of residual minimum frequency, calculated from the linear regression model of minimum frequency on background noise level ($b=5.73$, $F_{1,69}=11.61$, $R^2=0.1317$, $P=0.001$), showed no spatial structure (Figure 7f, $P=0.392$). These results implied that the variance of the minimum frequency was mostly contributed by the variation of noise. The maximum frequency and the delta frequency showed clear within-area and probable between-area spatial structure (Figure 7c-d, $P<0.001$). It indicated that neighboring individuals also tended to use similar maximum, peak and delta frequency. However, only peak frequency showed clear spatial structure in between-area scale (Figure 7b, $P<0.001$): it implied that microgeographic song variation exists in this scale.

Discussion

The acoustic signal should be masked if its frequency range overlaps with the background noise (Klump 1996). Birds in urban areas should adjust their minimum frequency of their songs against low frequency anthropogenic noise (Rabin and Greene 2002). In this study, I found that the minimum frequency of the Chinese bulbul's song did increase with background noise level (Table 2, Figure 6), that is consistent with previous findings in house finches (*Carpodacus mexicanus*, Fernández-Juricic et al. 2006), great tits (Slabbekoorn and Peet 2003), chaffinches (*Fringilla coelebs*, Brumm and Slater 2006) and song sparrows (Wood and Yezerinac 2006). All these studies did not find any correlation between noise and other frequency-related characters such as the maximum frequency or the peak frequency, suggesting these birds only changed the masked minimum frequency according to background noise. However, the Chinese bulbul has the lowest frequencies (1-4 kHz) songs among these birds (e.g. house finch: 2-15 kHz, great tits: 3-7 kHz, chaffinches: 1.4-7.5 kHz and song sparrow: 2-9 kHz). It implied that if urban noise has an adverse effect on acoustic communication, Chinese bulbuls would suffer more than other species.

Female mate choice in song birds is partly influenced by characteristics of male singing behavior such as song frequency, singing rate or repertoire size, which sometimes can indicate male quality directly or indirectly (Andersson 1994; Catchpole and Slater 2008; Gil and Gahr 2002). Besides, it had been shown that the pairing success of zebra finches (*Taeniopygia guttata*) and the vigilance level of chaffinches (Quinn et al. 2006; Swaddle and Page 2007) would decrease in noisy situations. Presence of anthropogenic noise was known to stress the physiology and psychology of humans and animals (Wright et al. 2007). Although there has no research revealing how female Chinese bulbuls choose male by male songs, I suspect that noise should impair their communication efficiency and result in decreasing fitness.

Three kinds of mechanism of song modification in birds have been proposed: short-term adjustment, long-term adjustment (through song development), and evolutionary adjustment (through genetic processes) (Ditchkoff et al. 2006). Moreover, Brumm and Slabbekoorn (2005) proposed the regulation of singing amplitude and adjustment of frequency structure could be contributed to short-term and long-term adjustment respectively. The best known example of short-term song adjustment may be the nightingale, which can increases song amplitude with increasing background noise level (Brumm 2004; Brumm and Todt 2002). For long-term song adjustment, if young passerines exposed to songs masked by noise during song development period, they could develop abnormal song structures (Rabin and Greene 2002). However, my results revealed similar spatial structure between background noise and the minimum frequency (Figure 7a and 7e) as well as no structure on the residual minimum frequency (Figure 7f) in Chinese bulbul suggest that instant noise did affect the minimum frequency and the regulation of the minimum frequency might be attributed to short-term adjustment.

The capability for a plastic and short-term vocal adjustment of crystallized song to current noise intensities has been demonstrated for the Bengalese finchs (*Lonshura striata var. domestica*, Tumer and Brainard 2007). In this laboratory experiment, Bengalese finchs rapidly shifted the pitch of particular syllable in an adaptive fashion to avoid disruption of noise, demonstrating the adaptive plasticity of crystallized adult birdsong. This short-term adjustment of frequency could potentially explain how the minimum frequency varied in this study. Except for noise interference, the minimum frequency of bird songs could be affected by body size, peak size and vicariant isolation. (Koetz et al. 2007; Podos et al. 2004; Ryan and Brenowitz 1985). However, the influence of body size and peak size in Chinese bulbuls is unknown due to lack of morphological data.

Singing in high pitch might be a strategy to counter the interference of low-frequency traffic noise. Rheindt (2003) showed that bird species with higher peak frequency songs had higher population density in noisy forest close to the highway. In this study, I found that Chinese bulbuls in TP tended to have higher peak, maximum and delta frequencies of the song than in SK (Figure 5), it coincided with the pattern of average noise level recorded in both urbanized areas that TP was slightly but significantly noisier than SK. The peak frequency of Chinese bulbuls' song (2.4-2.7 kHz) overlapped with the range of low-frequency background noise, but it did not correlate with its instant background noise level, implying that the peak frequencies of two urbanized areas were influenced by long-term noise interferences.

In conclusion, this study might be the first one to compare the effect of noise on bird song in two urbanized areas with different population density. My results suggested that possible mechanisms for the variation of the minimum frequency in the Chinese bulbul song might be due to short-term adjustment; in contrast, other frequency characters, such as the peak frequency, might be modulated by long-term adjustment. Taken together, these findings shed new lights on how Chinese bulbuls adapt to urbanized areas successfully. Further researches that focus on the fitness consequence of acoustic adaptation in urbanized region are needed.

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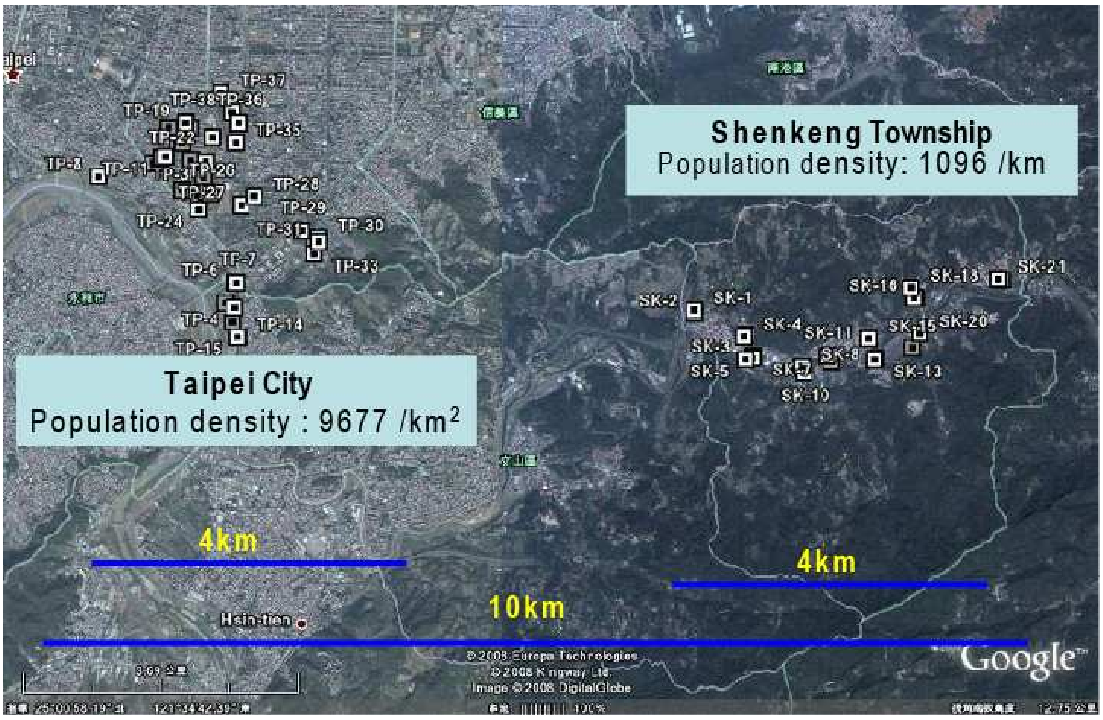

Figure 1. Recording sites in Taipei City (N=39) and Shenkeng Township (N=32). Each recording site is labeled by half-filled square.

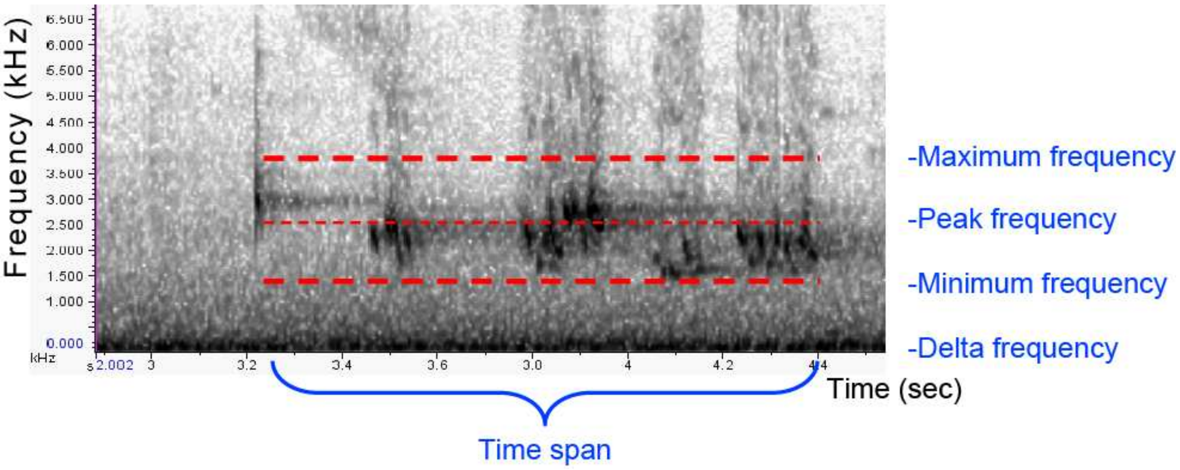

Figure 2. Spectrographic view of the typical songs of the Chinese bulbul (*Pycnonotus sinensis*).

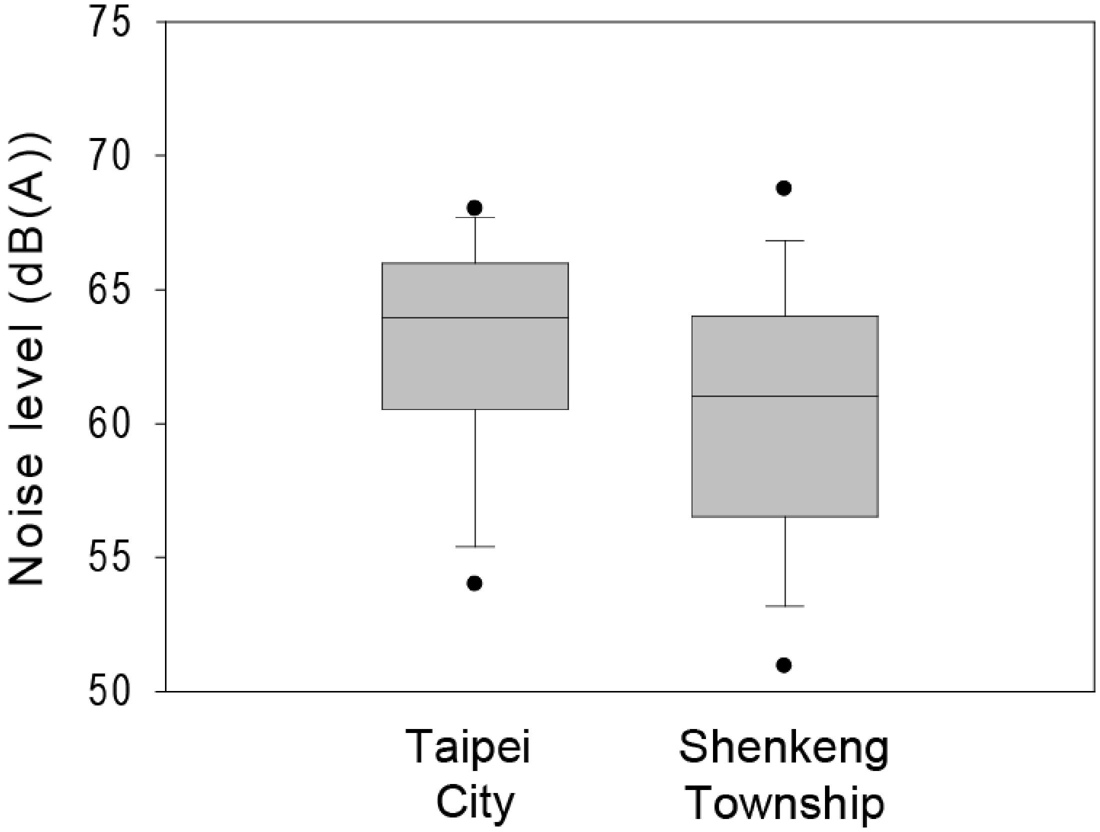

Figure 3. The box plots of background noise level (dB(A)) averaged over all sampling site in Taipei City (TP) and Shenkeng Township (SK). The solid line indicated medium. Noise level in TP was significantly higher than SK (*S*=928.5 *Z*=-2.57709 *P*=0.0100, Wilcoxon rank-sum test).

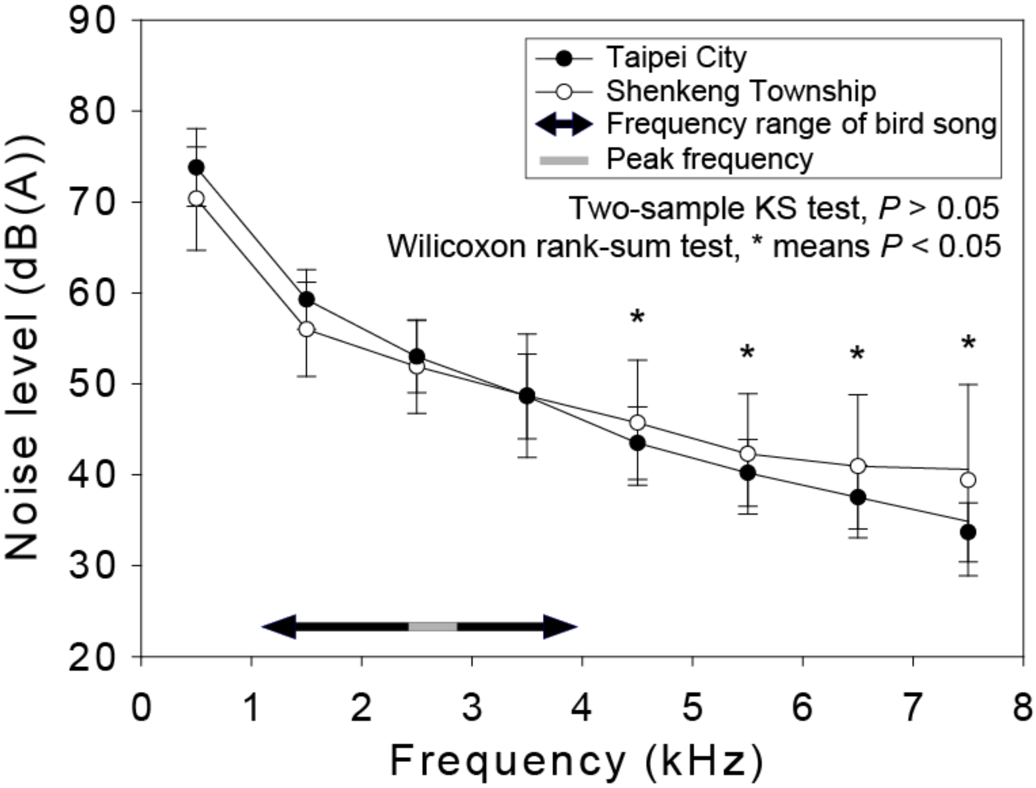

Figure 4. Average noise spectrum in Taipei City (solid circle, TP) and Shenkeng Towhship (empty circle, SK) at 1 kHz interval (mean ± SD). SK was significantly noisier at the 4-8 kHz range than TP. However, the shape of the two spectrums did not differ (two-sample Kolmogorov-Smirnov test, P>0.05). The range between two black arrows indicated the frequency range of the Chinese bulbul’s song; and the bold grey line was the range of peak frequency.

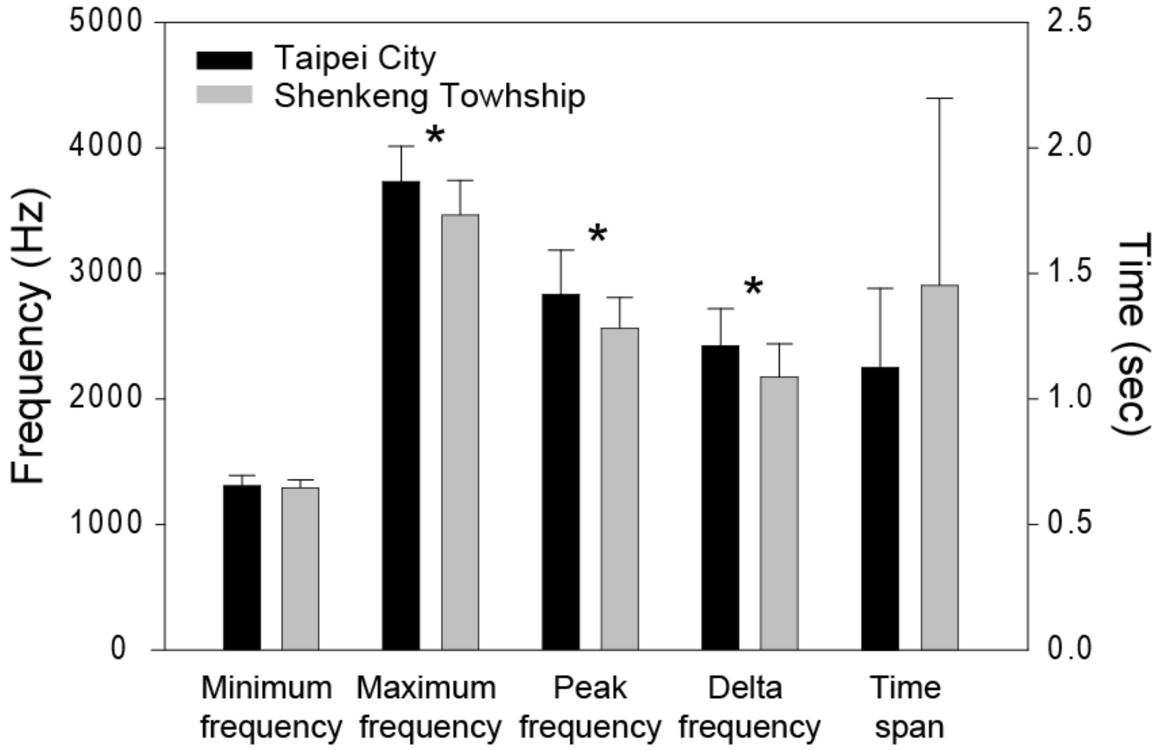

Figure 5. Acoustic measurements (mean ± SD) of Chinese bulbuls' (*Pycnonotus sinensis*) songs in Taipei City (TP) and Shenkeng Towhship (SK). Songs recorded in TP and SK were labeled by black and gray bar respectively. * means P<0.05.

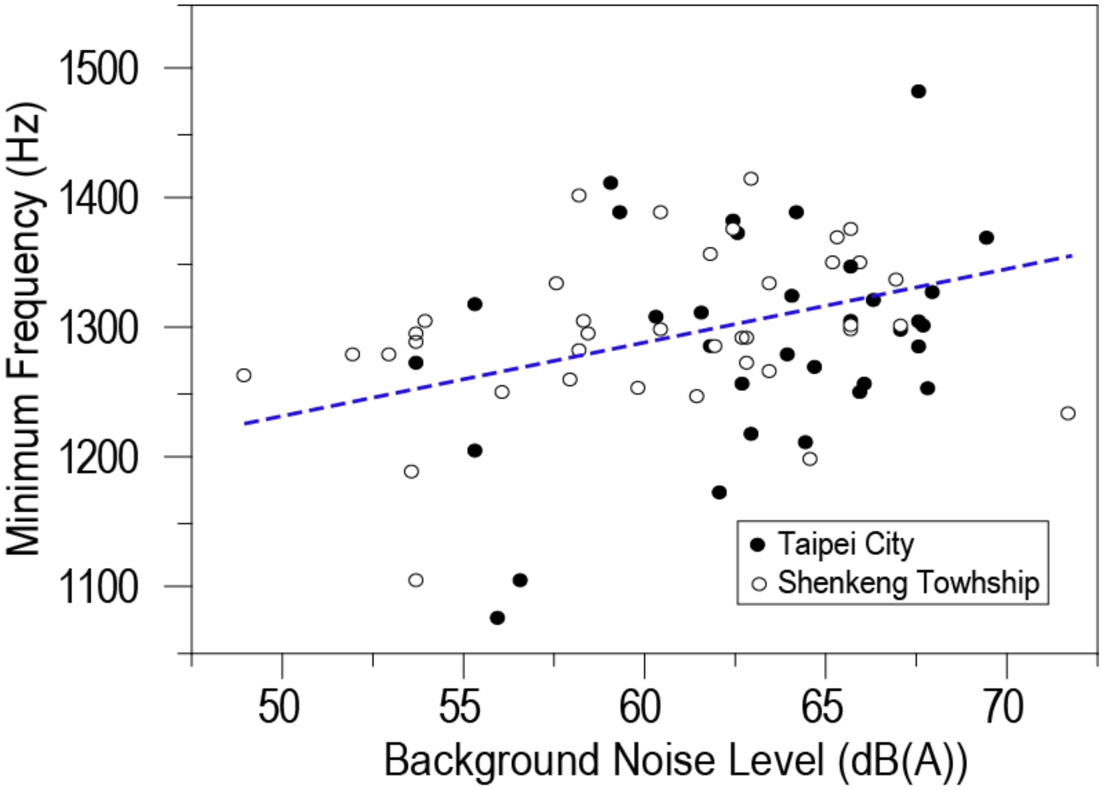

Figure 6. Relationship between the minimum frequency (Hz) and background noise level (dB(A)) (multiple linear regression, $b=5.47\pm1.89$, $t_{1,65}=2.89$, $P=0.\ 0052$). But the slope of Taipei City (solid circle) and Shenkeng Towhship (empty circle) were not different ($t_{1,65}=0.397$, $P=0.\ 6929$).

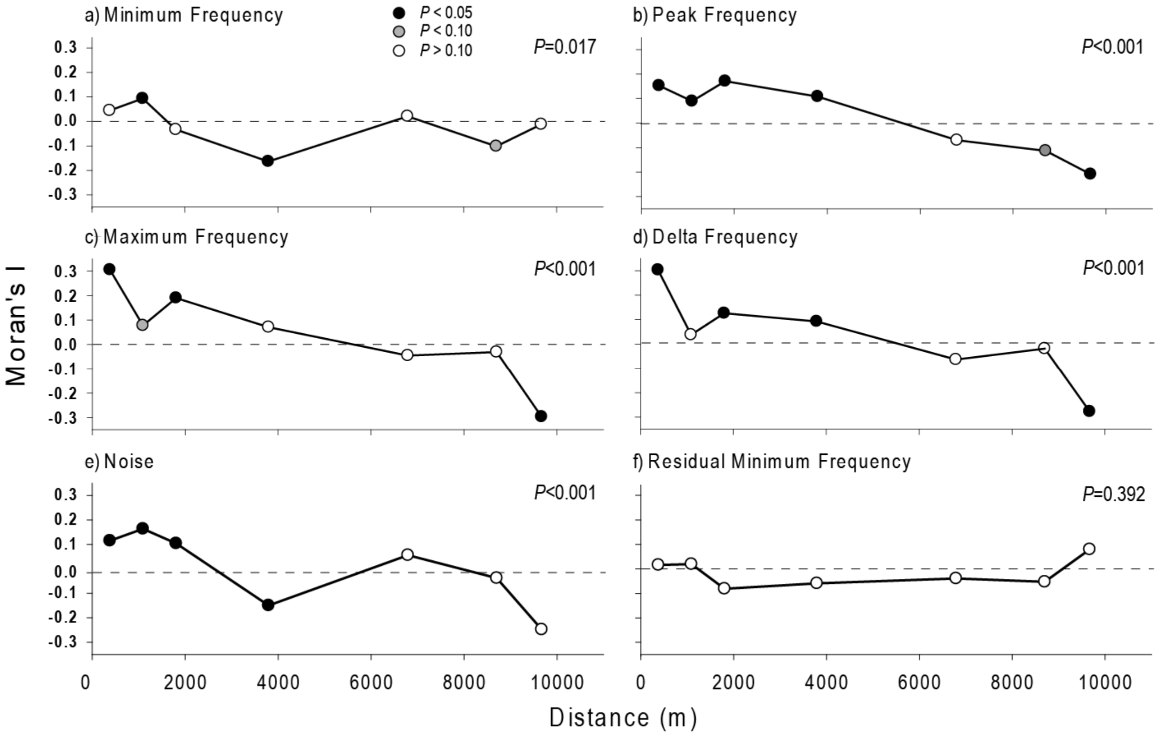

Figure 7. Moran's *I* spatial correlograms of a) minimum frequency, b) peak frequency, c) maximum frequency, d) delta frequency, e) noise and f) residual minimum frequency, calculated from the linear regression model of minimum frequency on background noise level. Correlograms represented the variation in the score of Moran's *I* spatial autocorrelation coefficient (Y axis) with increase in the separation distance (X axis) with equal sample size of 310 pairs ranged per interval from 0 km – 10.12 km. Black circle indicated the Moran's *I* coefficient is significant (P<0.05), grey circle indicated the Moran's *I* coefficient is nearly significant (P<0.1) and empty circle showed the Moran's *I* coefficient was not significant.

Table 1. Quantities of field recordings

No. of sequential songs measured per individual	No. of individuals in TP and SK	No. of individuals in TP	No. of individuals in SK
2	6	4	2
3	7	4	3
4	12	7	5
5	46	24	22
Total	71	39	32

Table 2. The results of multiple linear regression of all acoustic measurements of Chinese bulbuls (*Pycnonotus sinensis*) with all environment and biotic factors. Each cell indicates slope ± SE. The sample size = 71.

Respond	Intercept	Site	Temperature	Relative humidity	Present of conspecific	Background noise level	$F_{5,65}$	P	R^2	Adjusted R^2
Minimum frequency	942.46± 130.48***	8.35± 21.06	2.42± 2.39	-0.50± 0.65	-15.33± 21.67	5.47± 1.89**	2.743	0.026	0.174	0.111
Maximum frequency	3882.92± 519.45***	244.70± 83.83**	-9.05± 9.52	0.42± 2.57	126.98± 86.29	-5.12± 7.54	4.023	0.003	0.236	0.178
Peak frequency	1934.18± 573.92***	258.21± 92.62**	3.58± 10.52	-1.37± 2.84	143.21± 95.34	8.37± 8.33	3.652	0.006	0.219	0.159
Delta frequency	2940.46± 513.88	236.36± 82.93**	-11.48± 9.42	0.92± 2.54	142.31± 85.36	-10.59± 7.46	4.37	0.002	0.252	0.194
Time span	1.04± 1.02	-0.05± 0.16	0.01± 0.02	0.01± 0.01*	0.07± 0.17	-0.01± 0.01	1.282	0.283	0.090	0.020

*: P<0.05, **: P<0.01, ***: P<0.001