Homogenization of birdsong along a natural-urban gradient in Argentina

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One of the clearest examples of animal adaptation to urban habitats is the variation in their vocalizations driven by anthropogenic noise. A behavioural process that has received less attention in urban habitats is how anthropogenic barriers influence animal spacing behaviour and communication. I addressed the effects of the distribution of bird territories in urban habitats and the pattern of song differentiation over distance among neighbouring birds. I studied natural and suburban populations of the white-crowned sparrow *Zonotrichia capensis* in Argentina. This songbird dwells in gardens, but is here less abundant and more regularly spaced than in open woodlands. Neighbouring birds in garden suburbs sang songs that were more similar to each other than neighbouring birds in natural habitats. Song differentiation was greater within natural habitats than within suburbs at distance < 400 m. At larger distances differences among habitats were no longer significant. Neighbour songs were more homogenous where territories were more regularly spaced, considering all habitats or urban ones only. Selection for individual recognition of neighbours through songs and greater male-male interactions could have enhanced acoustic differentiation in natural habitats. Conversely, weak territorial interactions in suburbs with abundant landmarks may have constrained song output, resulting in song homogenization. This study points to differences in variability that may be more difficult to detect than differences in acoustic properties *per se*, and suggests that the effects of urbanization on animal communication can be underestimated if inter-individual variation is not properly addressed.

KEY WORDS: *acoustic differentiation, birdsong, spatial behaviour, urban bioacoustics, urban ecology, urban architecture*

INTRODUCTION

Habitat alteration due to urbanization is drastic, widespread, and rapidly exceeding that provoked by other land uses (MARZLUFF & EWING 2001). Urban development can extirpate native species, promote the invasion of exotic ones, decrease species diversity, alter food web dynamics and condition animal communication (SLABBEKOORN & PEET 2003; SHOCHAT et al. 2006; PARRIS & SCHNEIDER 2009; BARBER et al. 2009). With respect to the latter phenomenon, ‘urban bioacoustics’ provides several examples of how animal vocalizations change following the conditions generated by urban habitats (KATTI & WARREN 2004). There is evidence of both European and North American cities in which urban birds have shifted song frequencies (as examples SLABBEKOORN & PEET 2003; WOOD & YEZERINAC 2006; BERMUDEZ-CUAMATZIN et al. 2010), amplitudes (NEMETH & BRUMM 2009) and timing (BERGEN & ABS 1997) as a consequence of urban noise. The song of many successful urban dwellers, although not of all, has acoustically adapted to the evolutionarily novel habitat represented by cities, a shift that has been made possible by song learning processes, although microevolutionary (genetic) change cannot be excluded (RABIN & GREENE 2002; BRUMM 2006; SLABBEKOORN & RIPMEESTER 2008, EVANS et al. 2010). Luther and Baptista (2010) in their study on white crowned sparrow *Zonotrichia leucophrys* showed that acoustic variation in urban birds can occur in very short times (30 years).

Noise pollution is only one factor among many that affects how animal communication systems may respond to urbanization (WARREN et al. 2006). By altering the spatial distribution of suitable resources and by installing or removing barriers, urban habitats alter bird movements, and vary the spatial distribution of individuals (FERNÁNDEZ-JURICIC & TELLERIA 1999). As spatial distribution is known to affect

individual interactions, behaviours and social life, we can expect it to ultimately influence the way birds communicate (SERRANO & TELLA 2007; LAIOLO et al., in press). Anthropogenic habitat barriers, by isolating individuals, can diminish the rate of their social interactions and the transmission of song units among separated nuclei, generating song differentiation over distance, i.e. the increasing accumulation of inter-individual differences in song over geographic distances (LAIOLO & TELLA 2006 and 2007; BRIEFER et al. 2010, PETRUSKOVA et al. 2010;).

In spite of the interest in the consequences of habitat fragmentation on individual-level features, few studies have analysed the spatial patterns of birdsong variation in urban habitats, where barriers to individual interactions are an ordinary occurrence. Leader et al. (2000) found that city (and garden) expansion contributed to create contact zones between formerly separated dialect systems in the orange-tufted sunbird (*Nectarinia osea*), causing the origin of ‘hybrid songs’ at dialect borders. Changes in dialect composition in the Puget Sound white-crowned sparrow (*Zonotrichia leucophrys pugetensis*) were also attributed to the expansion of human settlements in a study by Chilton & Lein (1996). Apart from these studies that deal with contact among populations rather than with isolation between individuals, no evidence has been gathered on within-population variation in urban versus control/natural habitats. This is an important topic since song mediates individual interactions and may have direct bearings on fitness through its control over reproduction (LAIOLO 2010).

In this study I analyse how urban habitats affect the pattern of song diversification among neighbours of the rufous-collared sparrow (*Zonotrichia capensis*). In a habitat gradient including natural open woodlands and garden suburbs in Argentina, I address the effects of geographic distance and urbanization on song diversification, to examine

fine-scale song variation patterns in the transition of natural to urban, and highlight the behavioural consequences of spatial and social alterations provoked by urbanization.

METHODS

Study species

The rufous-collared sparrow is a small territorial songbird inhabiting a wide range of altitudes in the Neotropics. The species includes both sedentary and migratory (altitudinal or latitudinal) populations, and occupies a variety of habitats, from open grasslands to shrublands and woodlands (KING 1974). It occurs with higher relative abundance in the less managed woodlands, although it can tolerate grazing and persist after fire and habitat conversion to open habitats (NOTTEBOHM 1975). The species also inhabits suburban and periurban areas, although at lower densities (LEVEAU & LEVEAU 2005).

Studies on the song of the rufous-collared sparrow males provided some of the first demonstrations of the ‘acoustic adaptation hypothesis’ (NOTTEBOHM 1969, 1975). This hypothesis proposes that acoustic signals are structured to maximize their performance under the constraints of the environmental acoustics of the habitats (ROTHSTEIN & FLEISCHER 1987).

The rufous-collared sparrow learns its song by imitation of conspecifics within the first 40 days after hatching and then tends to maintain this song in a stable manner (KING 1972; TUBARO et al. 1997), although detailed studies on song learning process in the wild are lacking. The song is made up of two distinctive portions, described by Nottebohm (1975): “the introductory whistles (the ‘theme’) often vary considerably between individuals singing at the same locality. [....] The terminal portion of the song,

the ‘trill’, can remain relatively homogeneous over vast areas, and its characteristics tend to be shared by all birds at one locality, thus determining the “dialect” sung by a bird”. The acoustic structure of the ‘theme’ therefore varies little within the individual but differs between individuals, and characterizes individual identity. Conversely, the ‘trill’ does not vary to a great extent among individuals of the same population but does vary among populations, and characterizes ‘dialect’ units (NOTTEBOHM 1975; HANDFORD 1988; HANDFORD & LOUGHEED 1991; TUBARO & SEGURA 1994).

Study area

This study was carried out in the southern, Atlantic Argentinean range of the rufous-collared sparrow distribution, in Bahía Blanca (Buenos Aires province: 38° 42’ S -62° 15’ W) and Viedma (Rio Negro province, 41° 01 S -62° 48 W) in November and December 2006. The study was designed to encompass a gradient of rural-urban habitats with a moderately wooded aspect, either natural or anthropogenic in nature, in a buffer of 5 km radius from the cities (Fig. 1). The sampling methodology consisted of walking transects of up to 1.2 km length, and when one bird was heard singing, it was approached and recorded (see below), along with its neighbours using a procedure similar to territory mapping. Singing post position was established with a GPS Garmin eTrex Legend Navigator (Fig. 2A, B).

Three habitat typologies were considered (Fig. 1):

(1) Open woodland remnants located at 2.5-5 km from town fringes, characterized by scattered trees less than 3 meters high (Chañar *Geoffroea decorticans* and Caldén *Prosopis caldenia*) with a grassy understorey. Cattle grazing may occur in forest gaps, although livestock is concentrated in surrounding pastures. Four transects were walked to record birds in this habitat, two in Bahía Blanca and two in an analogous habitat in

the surroundings of Viedma. These transects constitute the 4 natural sampling sites of the study.

(2) New-built garden suburbs, made up of regular rows of houses surrounded by wide gardens still connected by unpaved roads (mean garden size 0.26 ha; 36 gardens measured). Four transects were walked in the neighbourhoods of Bahía Blanca, representing the 4 new suburb sites of the study.

(3) Older and inner garden suburbs comprising a larger proportion (40-100%) of paved roads and smaller gardens (0.12 ha, 30 gardens measured). Three transects were walked in the neighbourhoods of Bahía Blanca, constituting the 3 old suburb sites of the study.

The typical suburban garden in the study area included a lawn, and several trees and bushes, often of exotic origin (*Cupressus chamaecyparis*, *Eucalyptus* spp, *Magnolia grandiflora*, *Araucaria* spp, etc.) fencing garden edges. The new-built suburbs visited for this study have been progressively replacing former open, agricultural grasslands during the last 15 years. The study habitat matrix also included open croplands and agricultural grasslands, where the species was absent, and plantations of eucalypt and poplar trees. The latter were inhabited by the rufous-collared sparrow, but were excluded from sampling because their size and the number of territories included was too small for the purposes of this study (<4 singing birds per patch).

When considering tree species composition, variation within habitats was small as compared to variation among habitats, and greater tree diversity was found in the study gardens than in the natural habitats. All habitats presented a typical 'open-savannah' structure with grassy understorey; tree density was slightly greater in natural habitats although differences were not significant (mean distance among trees: 6.9 m $\pm$ 0.9 SE in

natural habitat, 6.4 ± 1.4 in old gardens and 9.4 ± 1.0 in new gardens; $F_{2,27} = 2.93$, $P = 0.07$; 10 measurements per habitat).

Sound recording and analysis

Birds were recorded in their territories during dawn or dusk song chorus in the breeding season; I was located in front of the singing individual at a distance of < 20 meters.

Sampled males were not marked, but were recorded in their territories during a single visit only, thus avoiding the problems of individual identification in successive days (LAILOLO & TELLA 2006). Recordings were made on analog cassette tapes using a Sennheiser ME67 microphone (frequency response 50 -20000 Hz) and a Sony walkman recorder WM-GX680 (bandwidth 40 - 15000 Hz). Forty-two rufous-collared sparrows were recorded in the four natural sites (i.e. 4 transects), 42 in the four new-built garden suburb sites (4 transects), and 44 in the three old garden suburb sites (3 transects), totalling 128 birds from 11 study transects.

The rufous-collared sparrow usually sings one song type only (NOTTEBOHM 1969, HANDFORD & NOTTEBOHM 1976). In this study only two birds out of 128 uttered two different song types. The theme of recorded songs was made up of 2- 8 notes and the trill was composed of up to 16 steeply descending stereotyped notes. Digitized songs sampled at 22050 Hz frequency were analysed with Avisoft SASLab Pro 3.91 by Raimund Specht (Berlin), performing a Fast Fourier Transform (FFT length 512, time resolution 8.9 msec, frequency resolution 43 Hz, Window Function: Bartlett). In the time domain, I measured total song duration, the duration of the theme, of the trill, of the first two notes of the theme, of the first note of the trill and the time interval between theme and trill; in the frequency domain, I quantified the minimum, maximum and range of frequencies of the theme, the trill, the first two notes of the theme and the first

note of the trill (Fig. 3). The number of notes of the theme and the trill were also measured, as well as their note rate (number of notes of the theme and the trill per second). Overall, 26 acoustic parameters were measured in each individual song.

The rufous-collared sparrow is known to show scarce intra-individual variation in song features, to the extent that its song has been used to identify males for the study of territory turnover and survival (TUBARO 1999). Here, I tested for acoustic individuality by performing a discriminant function analysis, a multivariate technique employed to analyze the consistency of grouping categories and inter-group variability when using independent song units (LAILOLO et al. 2007). I entered in the analysis 120 songs from 18 individuals that were recorded > 5 times and 26 acoustic variables. Prior probability of individual membership was selected so that any given song sequence was equally likely to be classified to any individual bird (prior $P = 0.055$). The analysis correctly classified 100% of songs to the individual from which they were recorded, and the first 3 discriminant functions explained 99.69% of overall data variation, had eigenvalues > 365, and Wilks' Lambda values < 0.49 ($P < 0.001$). The highest loadings on discriminant functions were provided by temporal and spectral features of the theme. In light of this constancy in individual song structure, only measurements of one song per individual were used to analyse the spatial patterns of song differentiation.

Differences in spectrotemporal features among habitat types and geographic locations were already analyzed in many studies on the rufous-collared sparrow in Argentina. In this study I address within population variation (i.e. differences in the songs of neighbouring birds), testing whether natural and urban sites were characterized by a different degree of song differentiation among neighbours. Thus, the song dissimilarities calculated in this study were always extracted from birds that were

located < 1148 m from each other, and shared the same habitat. A quantification of the acoustic characteristics of rufous-collared sparrow songs in the three habitat types is provided in Table 1.

Statistical analysis

To test for differences in nearest neighbour distances (NND) among habitats, I used a Kruskal Wallis ANOVA. A non-parametric test was performed because normality and homoscedasticity assumption were violated, being variability in neighbour distances in natural habitats greater than in the suburbs (Fig. 2 C, D).

Using the individual values of each spectrotemporal variable, I built an ‘individual × acoustic variable’ matrix (individuals in rows, acoustic variables in columns). From this multivariate matrix, I derived a measure of acoustic variability among individuals, expressed in terms of Euclidean distances (pair-wise song dissimilarity matrix).

Geographic distance was expressed as pair-wise geographic distances (Euclidean, i.e. straight line distances) between recorded individuals within sites. These geographic distances were then grouped in bins with a lag distance of 100 m (see also Fig. 4). For each distance lag (multiple of 100m-bin), the mean song dissimilarity was computed. By focusing on mean song dissimilarities over bins instead of raw dissimilarities over distance, the problem of inflated sample size due to large numbers of pair-wise comparisons (913 in this study) was circumvented (LAILOLO 2008). All in all, each of the eleven transects (4 in wooded areas, 4 in new-built garden suburbs, and 3 in old garden suburbs), was characterized by a mean value of acoustic dissimilarity per distance class.

To analyze song differentiation through distance, I performed generalized linear mixed models (GLMM) with a normal distribution of errors and an identity link

function, using R 2.10.1. As independent variables, I entered habitat typology (natural, new-built and old suburbs) and distance lag; site identity was entered as random factor, and geographical coordinates as covariate. The latter two variables were entered to control for the influence of geographical variation on acoustic dissimilarities, and for the potential non-independence of data collected within random sampling areas. As dependent variables, I used log-transformed song dissimilarity values.

Nonmetric multidimensional scaling was performed to inspect the spectrotemporal similarity among and within habitats. This multivariate ordination technique involves the construction of an ordination space from the pair-wise song dissimilarity matrix in which the habitat type positions are rearranged until a strong correspondence between the separation of groups (habitat types) and song dissimilarities is generated. The measure of goodness of fit is called the stress value and, although there is no sampling distribution for the stress value, a “good” fit is generally obtained with a value less than 0.1 (KRUSKAL & WISH 1978). One measure of multivariate dispersion (variability) within a group is to calculate the average distance of group members to the group centroid (multidimensional group average). Here I calculated the distance of individual songs from the group centroid within each habitat type, to derive a measure of song variability within habitats, and tested whether distances significantly differ among habitats by means of GLMM. Distances to the group centroid were modelled entering habitat type as a fixed effect and locality as a random variable.

RESULTS

The spatial organization of male rufous-collared sparrow differed among the three habitat types. The number of male territories varied from 2.8 ± 1.5 per ha in wooded

areas to 1.0 ± 0.4 and 1.5 ± 1.3 per ha in new-built and old suburbs, respectively. Nearest neighbour distances progressively increased from woodland to old and new garden suburbs (median values = 46.7, 74.2 and 93.9 m respectively; Kruskal Wallis ANOVA, $\chi^2 = 11.35$, $P=0.0034$; Fig. 2C). These median NND values were used to scale individual distance within each habitat type. In urban habitats, NND was correlated to garden size, i.e. it decreased in suburban sites characterized on average by small gardens (Spearman $r = -0.79$, $n = 7$ suburban sites, $P<0.05$).

Acoustic dissimilarities among individuals varied according to habitat typology, and peaked in woodland habitats (overall dissimilarities= 9.13 *versus* 3.2 and 3.4 of old and new suburbs; GLMM $F_{2,69} = 4.40$, $P= 0.016$). When considering song variation over metric distance, no trends of increasing or decreasing dissimilarities with distance can be found, although habitat type affected song differentiation over distance (GLMM, habitat type $\times$ distance: $F_{2,69} = 3.47$, $P= 0.050$ when considering the three habitat types, $F_{1,70} = 6.10$, $P= 0.0016$ when considering natural *versus* urban habitats, i.e. clumping old and new suburbs in a single category) (Fig. 4). Geographic coordinates (defining area location) did not significantly affect the extent to which song varied within areas (all $P > 0.23$).

Song dissimilarity within transects was related to the variability in nearest neighbour distance (as represented by its coefficient of variation CV): transects where average song dissimilarities among individuals was greatest showed the greatest variability in neighbour distances (Fig. 5, $r_s = 0.94$, $n=11$ transects, $P<0.05$). The association was significant also when considering urban habitats only (Fig. 5, $r_s = 0.89$, $n=7$ transects, $P<0.05$).

Figure 6 shows the results of nonmetric multidimensional scaling, where the song dissimilarity matrix is reproduced in a plot with two axes (dimensions), with the greatest song dissimilarity resulting in the greatest separation among individual songs. Songs from different groups (habitat types) were not clearly separated, and the stress value was 0.6, greater than the 0.1 threshold. The scatter of points around their centroid was significantly greater in natural habitats, suggesting once again greater spectrotemporal variability with respect to urban sites (average distance from the group centroid: natural habitat: 0.66 ± 0.12 , new suburbs: 0.34 ± 0.05 , old suburbs: 0.33 ± 0.03 , GLMM: $F_{2,119} = 27.93$, $P=0.0075$). Notably, songs from urban birds appear to be a subset of those sampled in natural habitats, as they are included within the range of variation of natural populations (Fig. 6). Distances among group centroids were not statistically different from distances within groups (i.e. from one individual point to its group centroid) (0.44 versus 0.45 respectively; Mann-Whitney U test, $U=3306$, $P=0.41$, $n=180$ distances), suggesting that acoustic variation among groups was not greater than that within groups, and that no clear geographic differentiation in acoustic properties characterized the study zones (see also Table 1).

DISCUSSION

Greater abundances of the rufous-collared sparrow and smaller inter-individual distances were found in open-wooded habitats compared to urbanized sites. These results are in line with previous research that highlighted the species' preference for wooded periurban habitats over the suburbs of large cities in Argentina (LEVEAU & LEVEAU 2005). When considering only man-made habitats, old suburbs supported slightly greater bird abundances and closer territories than new suburbs, in spite of their

greater degree of urbanization (smaller gardens and larger percentages of paved roads). This can be explained by taking into account the older age and greater diversity of trees, shrubs and lawn in old compared to new gardens, along with the smaller size of buildings, which could favour the occurrence of the rufous-collared sparrow (CUETO & LOPEZ DE CASENAVEZ 2000).

A significant decline in song differentiation among neighbouring birds appears in urban habitats, with greater acoustic overlap among birds inhabiting garden suburb sites than among neighbours in wooded sites. The latter habitats were, on the other hand, inhabited by neighbouring birds singing songs with more varied acoustic structure. This is in spite of the fact that woodland and urban populations appear to belong to the same dialectal units, as highlighted by the similarities in within- and among-group variation in multidimensional scaling analysis.

When analyzing within-habitat variability in greater detail, it appears that habitat typology affected the differentiation of birdsong through distance, i.e. the diversification of song acoustic structure among birds sharing the same habitat and in neighbouring territories. In natural habitats song differentiation reaches maximum values among very close birds, in a radius of 400 m. In urban habitats, no differentiation with distance was found.

In many bird species, song matching of neighbours is an integral component of territory settlement, and determines an increase of song dissimilarities with distance, an opposite pattern to that found here (SLABBEKOORN et al. 2003; KOETZ et al. 2007). Song matching behaviour has been described in the Nuttall's white-crowned sparrow (*Zonotrichia leucophrys nuttalli*) (BELL et al. 1998) but not in the rufous-collared sparrow. In the latter species, high levels of theme individuality may have evolved to

favour acoustic differentiation among interacting neighbours, an effective adaptation in habitats where visual stimuli are poorly effective (TUBARO 1999; CAMPBELL & HAUBER 2010). Vocal individuality may therefore be one of the factors that explain why close birds sing the most diverse songs in natural habitats (Fig. 4). Outside the radius of neighbouring birds, interactions may be weaker with the result of decreasing song dissimilarities at a fine-scale. Young rufous-collared sparrows in the wild might listen to and learn several song types in their sensitive phase (they learn a repertoire early in life; TUBARO et al 1997), but may establish a definitive song only when settling in their first territories. Individuality may thus be achieved by adopting a distinctive song from that of neighbours (by selective attrition), as documented in the congener white-crowned sparrow (NELSON 2000). Lachlan and Slater (2003) found that chaffinches *Fringilla coelebs* had a significant preference for learning songs not from immediate neighbours, but from males about 500 m away. This behaviour would result in greater song differentiation among close birds than among those at greater distances, and greater acoustic diversity in habitats where male abundance is greatest. Greater abundance may increase the rate of encounter among males and the occurrence of social interactions, which in turn would drive song diversification. This differentiation can be then used by females to compare male songs and better appraisal their quality. Since song choruses enable female songbirds to assess multiple individual simultaneously and guide mate choice (MCGREGOR 2005), it can be hypothesised that anthropogenic homogenization in male bird communication network might affect reproductive processes. These potential consequences are important to address, in order to deepen our knowledge on the fitness consequences of urban life for wildlife.

If selection for acoustic individuality may determine the observed spatial pattern of song differentiation in natural sites, why should urban birds show such a poor song differentiation? First, it can be argued that natural habitats have a great fine-scale structural complexity that would drive acoustic divergence (to facilitate sound transmission in woodland microhabitats). Under this hypothesis, however, similar values of song divergence would be expected at all distance classes in natural habitats, or greater diversity at longer distance classes. Contrary to these expectations, song variability peaks among close birds, i.e. those individuals supposedly inhabiting the same microhabitat. As an alternative hypothesis, suburbs may have been recently colonized by rufous-collared sparrows, and songs may still be poorly diversified there ('founder effect hypothesis'). If the song is learned from males that are not immediate neighbours, close birds will not diverge to a great extent because of the homogeneity of suburb song pools at all distance classes. In addition, selection for song individuality can be reduced by low rates of social interactions, due to low abundance of territories and to the structure of the gardens themselves. All gardens in fact present regular tree/shrub distribution (i.e. a tree line fencing a lawn around the house) that act as a landmark for territory borders, and in turn reduce territorial interactions and turnover (LAMANNA & EASON 2003). This idea is supported by the positive correlation between garden size and nearest neighbour distance, and by the fact that songs are more homogeneous where territories are more regularly spaced.

All in all, this study shows that *acoustic differences among habitats* (e.g. average spectrotemporal variables) are not marked, but the *magnitude of acoustic variation within habitats* (e.g. variability) changes to a greater extent between natural and urban habitats (Fig. 4, Table1). The latter may be more difficult to detect than differences in

mean values, and if not properly addressed can be underestimated in urban bioacoustics studies, which generally points to song structural differences and adaptations (or lack adaptations) to the novel acoustic habitat represented by towns.

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Figure captions

Fig. 1 Aerial pictures of the study sites in Bahía Blanca, Argentina. (A) Natural habitat (open woodland), (B) new-built garden suburbs, (C) old gardens.

Fig. 2. A) Example of the territory locations of rufous-collared sparrow males in a natural habitat site; B) Example of the territory locations of rufous-collared sparrow males in a new suburb site; C) Median nearest neighbor distance among territories of the rufous-collared sparrow in different habitat types; D) Coefficient of variation of the nearest neighbor distance among territories of the rufous-collared sparrow in different habitat types.

Fig. 3. Song of a randomly chosen rufous-collared sparrow, illustrating the acoustic measurements taken Waveform (top), sonogram (left), mean power spectrum of the theme and the trill song portions (right) and of the notes 1,2 of the theme and 1 of the trill (bottom) Numbers in the sonogram indicate the notes of the theme and the trill Time and frequency variables were measured on the waveform and power spectrum, respectively

Fig. 4. Relationship between mean pair-wise song dissimilarities and inter-individual distances in the rufous-collared sparrow. For each distance class, a mean of song dissimilarities was calculated in the 11 sampling sites. Pair-wise song dissimilarities per habitat type per distance class were then calculated by averaging site song dissimilarities (mean of 4 values per distance class in wooded areas, 4 in new-built suburbs, and 3 in old suburbs). Standard errors are also shown.

Fig. 5. Relationship between mean pair-wise song dissimilarities and the coefficient of variation of nearest neighbour distance within transects. The main graph represents the

whole data set of 11 transects, the small box depicts the relationships in urban habitats (in both cases the trend is significant)

Fig. 6. Bi-dimensional plot of nonmetric multidimensional scaling based on the dissimilarity matrix of the acoustic features of the rufous-collared sparrow song. Different symbols and colours are associated with the eleven study transects (natural habitats: ▲◆■●; new suburbs: △◇□○; old suburbs: ▲■●, centroids of the eleven transects: ●)

Table 1. Mean and variance values of the acoustic features of the songs of the rufous-collared sparrow in the study habitats.

Acoustic features	Natural habitats		New-built suburbs		Old suburbs	
	mean	variance	mean	variance	mean	variance
No. notes in the theme	3.53	1.25	3.03	0.39	2.96	0.26
No. notes in the trill	7.55	16.86	5.23	1.39	5.06	1.67
Song duration (s)	1.61	0.05	1.79	0.07	1.73	0.04
Theme duration (s)	1.11	0.04	1.09	0.04	1.03	0.03
Trill duration (s)	0.45	0.05	0.65	0.03	0.64	0.03
Minimum theme frequency (kHz)	2.94	0.15	2.93	0.10	3.04	0.08
Maximum theme frequency (kHz)	6.55	0.19	6.80	0.24	7.00	0.25
Minimum trill frequency (kHz)	2.87	0.79	2.84	0.03	2.92	0.04
Maximum trill frequency (kHz)	6.07	2.74	6.81	0.12	6.83	0.14
Theme frequency range (kHz)	3.61	0.37	3.87	0.39	3.96	0.32
Trill frequency range (kHz)	3.20	1.33	3.96	0.14	3.90	0.16
duration of the first note of the theme (s)	0.18	0.01	0.28	0.01	0.27	0.01
duration of the second note of the theme (s)	0.27	0.01	0.33	0.01	0.33	0.00
duration of the first note of the trill (s)	0.06	0.00	0.10	0.00	0.10	0.00
time interval between theme and trill (s)	0.06	0.00	0.06	0.00	0.07	0.00
minimum frequency of the first note of the theme (kHz)	4.08	0.31	4.05	0.16	4.24	0.11
maximum frequency of the first note of the theme (kHz)	4.83	0.33	4.69	0.17	4.78	0.13
minimum frequency of the second note of the theme (kHz)	3.62	0.39	3.57	0.10	3.68	0.09
maximum frequency of the second note of the theme (kHz)	5.86	0.98	6.27	0.47	6.24	0.36
minimum frequency of the first note of the trill (kHz)	2.93	0.85	2.88	0.02	2.94	0.04
maximum frequency of the first note of the trill (kHz)	5.99	2.63	6.63	0.14	6.75	0.12
note rate of the theme (1/s)	3.19	0.74	2.82	0.25	2.89	0.22
note rate of the trill (1/s)	19.12	227.45	8.33	1.94	7.95	0.46
frequency range of the theme first note (kHz)	0.75	0.57	0.65	0.35	0.54	0.24
frequency range of the theme second note (kHz)	2.24	1.60	2.70	0.57	2.56	0.53
frequency range of the trill first note (kHz)	3.06	1.27	3.75	0.18	3.82	0.18

Fig. 1

Fig. 2.

Fig. 3

Fig 4

Fig 5

Fig 6