

Syllable sharing and inter-individual syllable variation in Anna's hummingbird *Calypte anna* songs, in San Francisco, California

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A b s t r a c t. We examined the song sharing and variation pattern of 44 Anna's hummingbird males at syllable level in San Francisco, California. Full songs of Anna's hummingbird were composed of repeated blocks of phrases. Each male sang from three to six syllable types and syllable repertoire size averaged 5.1. A total of 38 syllable types were identified in songs of the population examined, which can be classified into five basic syllable categories. Each syllable category exhibited different variability among individuals. We quantified the variation of each category and found the variability was highest in the first phrase of song. Using Jaccard's similarity coefficient, we found the syllable sharing among birds was significantly greater within one sample site than between sites. Using Mantel tests, we demonstrated that syllable sharing among birds tended to decline with the increase of inter-individual geographic distance. A microgeographic song variation pattern that nearest neighbours tend to sing more similar songs than non-neighbours was supported in these analyses. However, hierarchical cluster analysis suggested not all individuals singing the most similar songs were nearest neighbors. It might be due to possible postbreeding immigration and song learning pattern that syllable is a unit of learning in this species.

Key words: syllable type, inter-individual variability, syllable sharing

Introduction

In contrast to the extensive studies in vocalizations of oscines, few detailed analyses of hummingbird songs have been reported so far, especially studies in acoustic characteristics, song structure, organization, repertoire, variation and function of hummingbird vocalizations (e.g. sparkling violet-ear *Colibri coruscans* and green violet-ear *C. thalassinus*, G a u n t et al. 1994; blue-throated hummingbird *Lampornis clemenciae*, F i c k e n et al. 2000; amethyst-throated hummingbird *Lampornis amethystinus*, O r n e l a s et al. 2002; wedge-tailed sabrewings *Campylopterus curvipennis*, G o n z á l e z & O r n e l a s 2005; sombre hummingbird *Aphantochroa cirrhochloris* and rufous-breasted hermit *Glaucis hirsute*, J a r v i s et al. 2000 and F e r r e i r a et al. 2006).

S n o w (1968) documented microgeographic song variation in little hermits (*Phaethornis longuemareus*) in which neighbouring males had similar songs that differed from other groups in the same singing assembly. G a u n t et al. (1994) demonstrated that in sparkling violet-ear and green violet-ear males of a neighbourhood sang the same song type and those of distant neighbourhoods had different song types. Similar patterns of microgeographic

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song variation in other hummingbird species have been described in quite a few studies (e.g. Snow 1977, Stiles & Wolf 1979, Vielliard 1983, González & Ornelas 2005), which can be considered as indirect evidence of song learning in these species (Kroodsmá 1982, Kroodsmá & Baylis 1982).

Anna's hummingbird (*Calypte anna*) is most abundant in California, resident from northern California southward. Mirsky (1976) found songs of populations from Island Guadalupe, Mexico were quite different from those from mainland California. Baptista & Schuchmann (1990) also mentioned in Anna's hummingbird nearest neighbours tended to share similar syllable types, rhythms and syntax which differed from those from other localities. But they only put forward an example from wild populations in California that songs of two adult males recorded at Half Moon Bay shared similar syllables, but differed from songs of another two males recorded at San Francisco who also shared similar syllable types. They demonstrated by experiments on males raised by hand (single isolate and group isolate) that songs of Anna's hummingbird were the result of acquisition by vocal learning, together with the indirect evidence from wild populations. Neuro-anatomy evidence also suggested that songs were probably all learned in this species, as well as some other hummingbirds, because of the remarkable similarity in forebrain areas that are similar in morphological appearance, location, and connectivity to the song control areas of oscine passerines in which songs are learnt (Gahr 2000).

Baptista & Schuchmann (1990) described the microgeographic song variation pattern with only examples, and no statistical evidence has been used to demonstrate this pattern from wild populations so far. The purpose of this study is to give a detailed examination on the inter-individual song sharing and variation pattern in Anna's hummingbird in San Francisco, California. Since most previous studies mentioned a general and relatively simple song syntax in this species and an inter-individual syllable-level variation is more remarkable (Mirsky 1976, Stiles 1982, Baptista & Schuchmann 1990), we examined the songs at the syllable level rather than at the whole song type level. We first describe the song structure, syllable types and repertoire size of Anna's hummingbird. We then survey the inter-individual song sharing and variation in this region to assess whether the same microgeographic song variation pattern exists in Anna's hummingbird as Baptista & Schuchmann (1990) mentioned.

Materials and Methods

Song recordings

Songs of 47 adult male Anna's hummingbirds were recorded at the Golden Gate Park (GP, 38 birds), Golden Gate Bridge (GB, five birds), Lake Merced (LM, two birds) in San Francisco, California, and at Filoli Garden (FG, two birds) which is 40 km south of San Francisco (Fig.1a). Recordings were made from 20 April to 16 May (the end of Anna's hummingbird's breeding season (Russell 1996)) in 1999.

During our field work, recordings were made when the bird was singing while perching. Since Anna's hummingbirds are highly territorial and defend their singing territories by chasing away intruding individuals, individuals could be identified easily by their perch position (Stiles 1973). Exact locations of each male's territory were available from the recorder. Distribution of all birds in GP was demonstrated in the map (Fig.1b). Between two to 74 songs ($\bar{x} = 26.6 \pm 2.5\text{SE}$) recorded per male were included in the analysis.

All the recordings were made using a Nagra tape recorder with an omnidirectional ME-20 microphone mounted on a Sony parabolic reflector. Spectrograms were produced using Avisoft SASlab Pro (sampling rate 44.1 KHz, sample size 16 bits, FFT length = 512 points, overlap 87.5%, 86 Hz frequency resolution, 1.45 ms temporal resolution, FlatTop window). Spectrograms were visually inspected by two independent observers to obtain a syllable type catalog for each male which was used for the measurement of syllable repertoire size and for comparison among individuals, and then a syllable type pool for all individuals studied was obtained in this way.

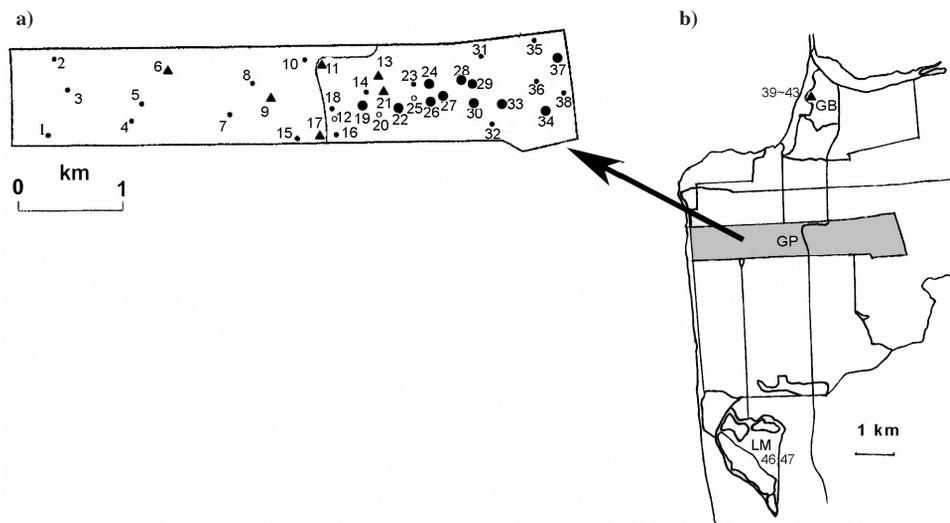


Fig. 1. (a) Locations of recording sites in San Francisco, California. GP: Golden Gate Park, GB: Golden Gate Bridge, LM: Lake Merced (FG: Filoli Garden, which was not marked in the map). Numbers indicated individuals recorded in GB and LM; (b) Distributions of each male's territory in GP, numbers indicated recorded individuals in GP including the three rejected males denoted with a circle (bird 12, 20, 25). Bigger dots: males sharing dominant syllable repertoire, Ba-ba-Ca-Za-Da; Triangle: males sharing Bb-ba-Ca-Za-Da; Smaller dots: other individuals in GP. Totally 35 individuals in GP were analyzed in the study.

Statistical analyses

To determine the amount of syllable sharing among birds, we used Jaccard's similarity coefficient: $S_j = a / (a + b + c)$ (Krebs 1989, Tracy & Baker 1999), where a = the number of syllable types shared by both bird A and B, b = the number of syllable types in B's repertoire but not A's, and c = the number of syllable types in A's repertoire but not B's.

The presence (1) or absence (0) of a certain type in the syllable type pool was scored. In this way, we calculated the S_j value for each bird compared with all other birds in this study and generated a matrix of similarity values using SPSS 14.0 (Distances-Binary measure-Jaccard). And then a hierarchical cluster analysis was performed based on the similarity coefficient values (SPSS 14.0). In the resulting dendrogram, degree of similarity between individuals is represented by the proximity of branches with the individuals possessing the most similar syllable repertoire closest to one another.

We then averaged each bird's S_j values over birds from different sites so as to make a comparison within a site and between sites. Since the number of birds sampled in each site other than GP was no more than five, we only compared S_j of GP birds over birds within the

same site with S_j of GP birds over birds at all other sites (two independent samples t -test, SPSS 14.0).

A measurement of inter-individual geographic distance was obtained from the map (FG was not included in this analysis because it was not marked in the map and no exact distance measurement was available), and a matrix of bird-bird distance (except the two birds in FG) was achieved in this way.

To determine whether the amount of syllable sharing was correlated with the geographic distance between individuals, we performed Mantel test, which is used to test whether there are correlations between two matrices (Mantel 1967, Manly 1991, Guant et al. 1994). Here the matrix of similarity values and the corresponding matrix of bird-bird geographic distance were put to test. The Mantel test uses multiple random permutations of the observed data to generate the chance expectation and produces an r -value between -1 and $+1$ that can be interpreted like a correlation coefficient (Molles & Vehrencamp 1999). XLSTAT-Pro 7.5.3 was used for the analysis with 1000 permutations per run.

Results

Song structure, syllable types and repertoire size

In this study, all Anna's hummingbird individuals shared a general song syntax. Syllables are grouped together into phrases or sets (Mirsky 1976, Stiles 1982, Baptista & Schuchmann 1990, Goldberg & Ewald 1991). A typical song consisted of three different phrases: phrase A containing three (two or four less often) squeaky syllables sounding like "Bzz-bzz-bzz", Phrase B composed of two different syllables which sounded like "chur-ZWEE" and phrase C containing two "dz!" syllables (Stiles 1982, Fig. 2). Phrase A may also occur alone with or without repetitions. Such phrase A songs appeared in all male's recordings. Among 1249 songs recorded, 521 (41.7%) were typical songs containing all the three phrases, 86 (6.5%) were typical songs but losing a whole or part of phrase B or C and these songs were all considered as "full" songs. Another 642 (51.4%) were phrase A songs.

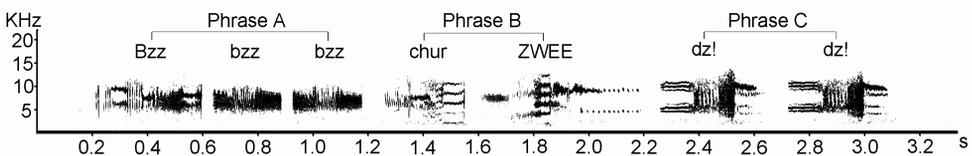


Fig. 2. A full song of Anna's hummingbird with all three phrases containing only one song block sounding like "Bzz-bzz-bzz chur-ZWEE dzi! dzi!" (bird16).

Actually in Anna's hummingbird, songs may be delivered on the wing ("dynamic songs") or while perching ("static songs") (Wells et al. 1978, Baptista & Matsui 1979). Aerial songs consist of only "bzz" elements, that is, they are phrase A songs. Static songs typically are more elaborate than aerial songs and contain different phrases (Baptista & Schuchmann 1990), which were considered as full songs here. But songs from perched birds may also consist of only "bzz" elements, they are like some aerial songs (Russell 1996). So static songs include both full songs and phrase A songs. Recordings in this paper were all static songs. And sampling of three males recorded only

with phrase A songs were supposed to be insufficient. They were rejected in the following analysis, so totally 44 males were analyzed in the subsequent study.

The three different phrases appeared in a given sequence and long songs were composed of repeated blocks of phrases (ABC) (Fig. 3). Syllable number of each recorded full song were between seven, which contained only one song block (bird16, ABC) (Fig. 2), to 42 (bird9, AAAABCABCAABCABCA) ($\bar{x} = 19.8 \pm 0.58SE$). Syllable number of full songs also varied within individual, e.g. syllable number in bird16 varied from seven to 12 ($\bar{x} = 10 \pm 0.95SE$); while in bird9 varied from 12 to 42 ($\bar{x} = 22.8 \pm 2.37SE$). Phrase A appeared much more frequently than phrase B and C in full songs, which occupied an average of 56% ($\pm 0.01SE$) of all phrases in each full song.

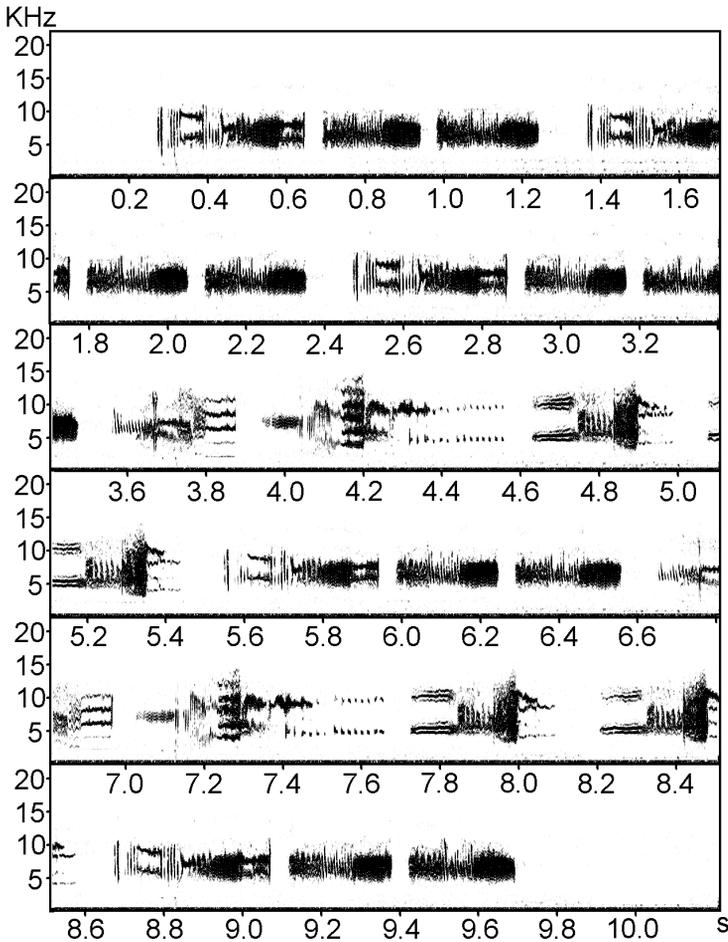


Fig. 3. A long full song composed of repeated blocks of phrases (bird27, AAABCABCA).

Each male sang from three (males lost phrase B) to six syllable types and repertoire size averaged 5.1 ($\pm 0.091SE$). Syllables are stereotyped in structure and vary little between songs within the repertoire of an individual, as was mentioned in previous studies (Wells et al. 1978, Baptista & Schuchmann 1990). So the syllable repertoire size had no relationship with the number of full songs recorded per male ($r = -0.023, P > 0.05$).

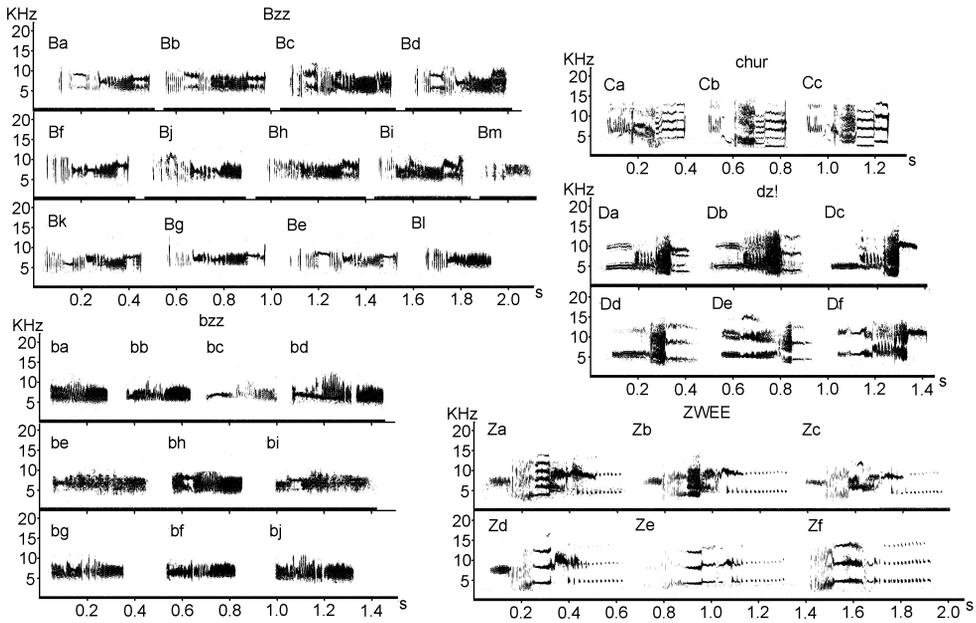


Fig. 4. Catalogue of 38 syllable types belonging to five categories: “Bzz”, “bzz”, “chur”, “ZWEE” and “dz!”.

A total of 38 syllable types were identified in songs of the 44 males studied, which could be classified into five basic syllable categories, “Bzz”, “bzz”, “chur”, “ZWEE” and “dz!” (Fig. 4). The 38 types actually were 38 syllable variants of the five categories possessed by different individuals. We considered these variants as specific syllable types, since difference between most variants were discrete though not so distinct as between categories. In cases where syllables had subtle variations, we took a conservative approach and did not distinguish these in the catalog. And the little syllable variation within the repertoire of an individual was too subtle to be distinguished, as was compared with variations between individuals.

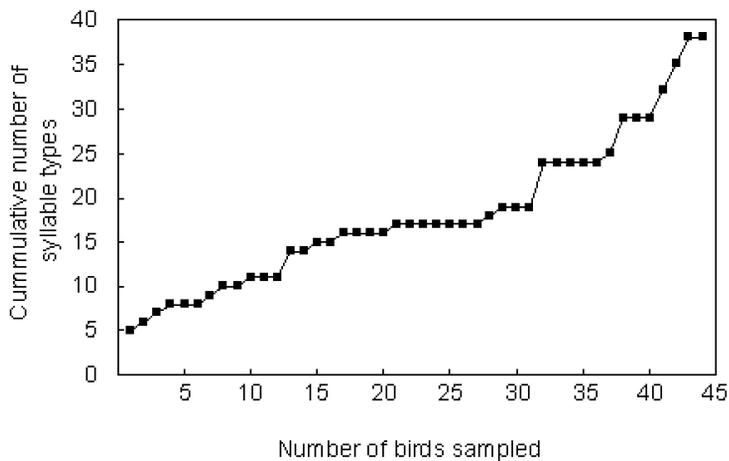


Fig. 5. Cumulative number of syllable types detected in individuals against the number of sampled males in random order.

The 38 types included 13 types of “Bzz”, 10 types of “bzz”, three types of “chur”, six types of “ZWEE” and six types of “dz!” (Fig. 4). We generated a plot of the cumulative number of syllable types detected in individuals in random order, which indicated that new syllable types would be detected in new samples (Fig. 5).

Syllable sharing and inter-individual variation

To quantify the variation scale of each syllable category, we introduced the Shannon-Wiener diversity index: $H_s = -\sum p_i \ln(p_i)$, where $p_i = n/N$, n is the number of birds possessing the i th syllable type of a category, and N is sum of number of birds possessing each syllable type

Table 1. Details of inter-individual syllable variation of the five basic syllable categories.

Syllable category	Number of birds possessing each category	Number of syllable types	H_s	Number of dominant types	Number of syllable types unique to one individual	Number of birds possessing dominant type
“Bzz”	44	13	2.0166	2	7	13,13
“bzz”	43	10	1.2422	1	5	36*
“chur”	41	3	0.2287	1	2	39
“ZWEE”	42	6	0.6331	1	4	36
“dz!”	44	6	0.6111	1	4	38

* Among the 36 males singing dominant syllable type “ba”, four males also sang one another type of “bzz”, only 32 males’ 2nd and 3rd “bzz” were both “ba”.

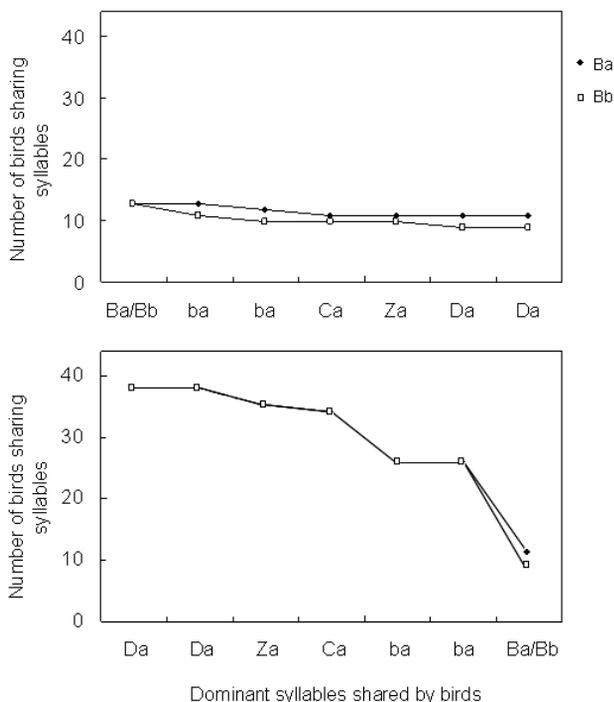


Fig. 6. Number of males sharing dominant syllables declined as the increase of syllable number in a typical song block. The bottom graph illustrated it in a reversed syllable order of the song block.

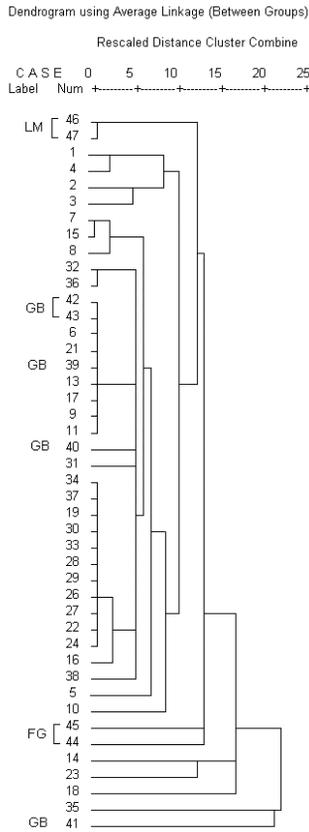


Fig. 7. Dendrogram generated from the hierarchical cluster analysis and males from GB, LM and FG were marked with their recording sites. Unmarked birds were from GP.

of the category. The more types each syllable category possesses and types distribute among individuals more evenly, the higher syllable category variability is.

Among the five syllable categories, “Bzz”, the introductory category, was the most variable one which had a highest value of Shannon-Wiener diversity index (Table 1). Two dominant “Bzz” types (Ba & Bb) were both shared by 29.5% (13/44) of all males (Table 1). Category “bzz” had the second highest H value. Thus phrase A, composed of category “Bzz” and “bzz”, was more variable than phrase B and C. “chur” was the most stable category with a lowest H value (Table 1).

Number of sharing birds declined as number of shared syllables increased (Fig. 6). Syllable types Ca-Za-Da, i.e. a dominant phrase B & C, were shared by 34 males from all the four recording sites. Two dominant syllable repertoires (Ba/Bb-ba-Ca-Za-Da), i.e. two dominant song blocks (Ba/Bb-ba-ba Ca-Za Da-Da), were respectively shared by 25% (Ba, 11/44) and 20.5% (Bb, 9/44) of all males.

The 11 males sharing repertoire Ba-ba-Ca-Za-Da were all from GP. Among the nine males sharing Bb-ba-Ca-Za-Da, six were GP birds and the other three were from GB (Fig. 1b). Not all males sharing repertoires were nearest neighbours (Fig. 1b). Dendrogram generated from hierarchical cluster analysis also suggested that individuals at closest branches singing the most similar syllables were not all neighbors (Fig. 7). Bird 44,45 from

FG which had the largest distance from GP were gathered together with GP birds, while bird 41 from GB and bird 14,18,23,35 from GP sang the most different song (Fig. 7).

S_j values for bird versus bird comparisons ranged from 0 to 1. All the birds analyzed in this study had different amount of syllable sharing, except bird35&41 which both had a S_j value of zero with all the other males. Similarity coefficient was significantly greater among birds within GP than that between GP and the other sites (mean S_j value within GP (35 vs 35): $0.530 \pm 0.028SE$, $N = 35$; mean S_j value of GP birds over birds at all other sites (35 vs 9): $0.408 \pm 0.025SE$, $N = 35$; two independent samples t -test: $t = 3.238$, $P < 0.01$). Since sample number from GB, LM or FG was no more than five, we didn't make a comparison within and between these sites.

We put a Mantel test on birds within GP population (35 birds) first. There was a negative correlation between the similarity matrix and the geographic distance matrix, but the relationship was weak (Mantel $r = -0.283$, $P = < 0.01$). For Mantel test on all individuals (except the two birds from FG whose measurements of geographic distances were not available), the relationship became a little stronger (Mantel $r = -0.314$, $P = < 0.01$).

Discussion

Different studies all suggested a typical and relatively simple song type in Anna's hummingbird (M irsky 1976, Stiles 1982, B a p t i s t a & S c h u c h m a n n 1990, G o l d b e r g & E w a l d 1991). Results of field observation and sonogram inspection in this study consisted with the previous reports. Typical full songs are composed of repeated song blocks and only three to six syllable types were recognized in each individual. Males from all the four recording sites had different amount of syllable sharing, which exhibited no distinct microgeographic song dialect in the studied area.

Among the five syllable categories of Anna's hummingbird, inter-individual variability was the highest in category "Bzz" and "bzz", i.e. phrase A. This variability may benefit individual recognition, as suggested by C i c e r o & B e n o w i t z - F r e d e r i c k s (2000) in the insular populations of Lincoln's sparrow (*Melospiza lincolni*). In songs of this species, individual variability was the highest in the terminal elements of songs and this terminal variability may promote individual recognition. Individual variability concentrated in the later parts of the song is also found in song sparrow (*Melospiza melodia*) (H o r n i n g et al. 1993). Considering the large proportion (51.4%) of phrase A songs in all songs recorded and its higher employ frequency in full songs, there is a possibility that the most variable phrase A play a more important role in individual recognition than phrase B and C do.

Birds sharing a dominant syllable type and the number of sharing birds varied with syllable category (Table 1). In a male's syllable repertoire, each syllable type may be shared with different other individuals in the population, e.g. bird 2 shared syllable "bc" with bird 3, whereas it shared "Bb" with bird 1, 4, 9, etc but not bird 3. We may reach a conclusion that syllable is a basic unit of song sharing in Anna's hummingbird. Since songs of Anna's hummingbirds have been proved to be the result of learning (B a p t i s t a & S c h u c h m a n n 1990, G a h r 2000), syllable can be regarded as a unit of song learning in this species.

Studies of mechanisms of song learning in some bird species also support this conclusion, which indicate that not the overall song pattern but certain song components, e.g. syllable, are the unit of song learning, at least in some species (e.g. Northern cardinal

Cardinalis cardinalis, Lemon 1975; swamp sparrows *Melospiza georgiana*, Marler & Peters 1977; Nuttall's white-crowned sparrow *Zonotrichia leucophrys nuttalli*, Nelson et al. 1996; house finches *Carpodacus mexicanus*, Tracy & Baker 1999). An individual may learn certain syllable from some of its tutors while another syllable in its repertoire comes from some other tutors. The successfully dispersing males may learn from multiple tutors and produce syllable repertoire hybrids which could explain the syllable repertoire variation among individuals (Slabeckorn et al. 2003).

Results of similarity coefficient comparison suggested that syllable sharing among Anna's hummingbird individuals were much greater within site GP than between sites, which supported the microgeographic song variation pattern that nearest neighbours tend to sing more similar songs than non-neighbours, as documented by Baptista & Schuchmann (1990). Mantel test results were consistent with this conclusion though no strong correlation was discovered between the song similarity and inter-individual geographic distance in this sample area. However, the dendrogram generated from hierarchical cluster analysis showed that not all individuals singing the most similar songs were nearest neighbors, which seemed to be a contradiction to the former conclusion.

Father/son learning is unlikely in Anna's hummingbirds since this species is promiscuous and fathers take no part in the reproductive process other than inseminating the females (Stiles 1973), so young Anna's hummingbirds are more likely to learn songs from males other than fathers (Baptista & Schuchmann 1990). If young birds settled on their territories for the first time and learn songs from males in neighbourhood, nearest neighbours tend to sing more similar songs. Birds singing the most different songs with their neighbours might have learnt their songs before arriving in the breeding area and then taken no account of neighbour songs when settling (Catchpole & Slater 1995), i.e. there is possibility that these males are immigrants. In this study, recordings were made at end of Anna's hummingbird's breeding season. This species typically nests from December to May. Following the nesting season, many (if not most individuals) migrate, but they may be replaced by other birds, leading the impression of year-round residency (Russell 1996). And the inter-individual song variation pattern might be different at beginning of the breeding season since previous banding data suggest breeding site fidelity in this species (Russell 1996). Speculation that syllable is a basic unit of song learning in Anna's hummingbird could also explain why nearest neighbors didn't share a whole syllable repertoire, but they did share certain syllable types.

Analysis in this study was based on a visual syllable classification system. Though more objective approaches to syllable classification are available, this visual technique has been proved to be sufficient in many studies, e.g. Tracy & Baker (1999) used visual classification successfully in analyzing the geographic variation in syllables of house finch (*Carpodacus mexicanus*) songs, and a more time-consuming digital technique for analyzing black-capped chickadee (*Poecile atricapillus*) vocalizations provided similar results to a visual system (Nowicki & Nelson 1990).

Though Mantel test results indicated that syllable sharing among birds tended to decline with the increase of inter-individual distance, the r -values were too low to suggest any significant relationship. The majority of males analyzed in this paper were all from one recording site, GP. Such a small population restricted within an area of a park (4.1 km²) was insufficient to reflect the relationship between song similarity and inter-individual geographic distance. And the cumulative plot indicated that new syllable types would be

detected in new samples, which also suggested that our sampling was insufficient to capture all acoustic variation in this species because of the limited sampling area. If a larger sample from the other three localities were taken, a better correlation result and more evidences on acoustic variation would be obtained. Then we would focus on the song sharing and variation pattern among populations of Anna's hummingbird rather than among individuals in this paper, which are to be achieved in further studies.

A c k n o w l e d g e m e n t s

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