MICROGEOGRAPHIC SONG DIALECTS IN THE ORANGE-TUFTED SUNBIRD (NECTARINIA OSEA)

by

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Summary

In a study of male song in the orange-tufted sunbird (*Nectarinia osea*) in an urban neighborhood in Ramat-Aviv, Israel, we discovered the occurrence of song variation on a microgeographic scale in the form of two distinct dialects with a sharp boundary between them. The main distinction between the two song dialects is the frequency of the trill, which comprises the terminal part of the song. A large difference of 2-3 kHz in the peak frequency of the trill was discovered between the two dialects, which could be easily distinguished by ear. Thirty-seven males were recorded singing the ‘low' dialect and 21 birds sang the ‘high' dialect. Four other birds sang both dialects or ‘hybrid' songs. Along the boundary that separated the two dialect populations, neighboring birds sang different dialect songs, although they were only 20-30 meters apart. All four ‘bilingual' birds occupied territories near the dialect boundary. The historical processes leading to the formation of this dialect system may result from the pattern of human settlement at the time of the establishment of this neighborhood in the early 1950's. The spatial distribution of the two sunbird dialect populations, and the apparent low dispersal rates of birds from their natal dialect area, suggest the existence of a mechanism, which currently maintains these dialects at the current boundaries.

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Introduction

Geographical variation in vocalizations has been documented in a wide variety of avian species (Mundiger, 1982). Some species show a geographical mosaic of local populations, each characterized by distinctive variants of a given vocalization. These different groups of individuals constitute ‘dialects' which may be defined as separate, adjacent aggregations of birds, with well-defined boundaries, and with different vocalizations (Rothstein & Fleischer, 1987). The variations in bird song may even occur on a microgeographic scale, between neighboring groups of birds, which might, at least potentially, interact or interbreed with each other (reviewed in Mundinger, 1982). Such microgeographic variation is synonymous with the term ‘local dialects' (McGregor, 1980). The most striking example of microgeographic variation in song is where birds have only one song type (or a very small repertoire) and there is close sharing between neighbors. In such cases not only may the songs present differ between localities, but it is also frequently found that the change from place to place is not gradual, rather a sudden switch from one dialect to another occurs at a particular place (Catchpole & Slater, 1995). The best known example of sharp dialect boundaries is in the sedentary race of the white-crowned sparrow (*Zonotrichia leucophrys nuttalli*), originally studied by Marler & Tamura (1964) and by Baptista (1975).

Explanations for these patterns of variation are historical accidents, *i.e.* non-adaptive cultural founder effects (Thielcke, 1969, 1973; King, 1972; Baker, 1975; Baptista, 1975, 1977; Mundiger, 1980; Payne, 1981), genetic differences between populations (*e.g.* Nottebohm, 1972; Baker & Cunningham, 1985), physical circumstances, *i.e.* different song types being more or less suitable in different habitats because of their acoustical properties (*e.g.* Morton, 1975; Wiley & Richards, 1978; Gish & Morton, 1981), and finally, social behavior, *i.e.* interactions between neighboring males (Payne, 1981, 1982, 1983; Rothstein & Fleischer, 1987; Payne *et al.*, 1988; Bell *et al.*, 1998).

The orange-tufted sunbird (*Nectarinia osea*) is a small (6-8 g), socially monogamous passerine, showing substantial sexual dimorphism in plumage colors and body size. It is territorial and sedentary throughout most of its range. At the beginning of the 20th century this sunbird was considered extremely rare in Israel, and was restricted mainly to the southern parts of the Jordan valley and desert oases near the shores of the Dead Sea at

Jericho and En-Gedi (Paz, 1986). Since the 1930's, it has expanded its range dramatically and today is a very common resident in gardens near human dwellings, throughout Israel. This expansion is attributed to the abundance of ornamental gardens, plentiful with cultivated nectar-secreting flowers year round.

Cramp & Perrins (1993) describe orange-tufted sunbird song as a sweet sibilant warble, composed of a few introductory notes followed by a rapid hard musical trill. However, apart from this short description, the song of the orange-tufted sunbird has never been studied thoroughly. Virtually nothing is known of dialects, of other spatial song variations or of inter-individual variation.

The aims of this study are (1) to describe the song of the orange-tufted sunbird and (2) to examine patterns of geographic variation in the song of this species.

Methods

The study was carried out at Ramat-Aviv, a suburban neighborhood of Tel-Aviv, Israel (32°05′N, 34°47′E) during 1997-1999. The study site is about 1.5 km^2, situated in an urban area, with a mixture of private gardens, lawn and park areas between residential buildings and private homes. Most vegetation consists of many introduced nectar-secreting plants, which attract sunbirds (*e.g. Hibiscus* spp., *Malvaviscus arboreus*, *Tecomaria capensis*, *Aloe* spp., *Callistemon* spp., *Erythrina* spp.).

This particular sunbird population has been the subject of continuous behavioral research for more than 10 years (Goldstein *et al.*, 1986, 1987; Goldstein & Yom-Tov, 1988; Markman *et al.*, 1995, 1996; Zilberman *et al.*, 1999). Therefore, most birds recorded were color-banded allowing individual recognition. The sunbird's tolerance to human presence in urban areas, allowed for relatively easy observations and song recordings without any apparent disruption of sunbird behavior.

Vocalizations of 63 territorial male orange-tufted sunbirds were recorded extensively during the entire length of the three breeding seasons (February-September 1997-1999). This included 51 males that were present on their territories for the entire three year duration and 12 males that were present for at least one breeding season (5 of which replaced males that had disappeared).

All recordings were made within close proximity to singing birds (5-10 m) using a Sennheiser ME-67 ‘shotgun' microphone and a Sony WM-D6 cassette recorder. Songs were downloaded to a computer from a Sony TC-KE500S 3-head stereo cassette deck and were digitized at 22050 Hz with 16 bit precision, band-pass filtered from 2 to 10 kHz to eliminate urban background noise and stored as individual computer files. Spectrograms used for measurements were produced with a 512-pt. FFT (frequency resolution 55 Hz, time resolution 2.90 ms, Hamming window and 87.5% overlap) using Avisoft SASLab Pro for Windows Version 3.4 (Avisoft© 1998). All measurements were taken using Avisofts'

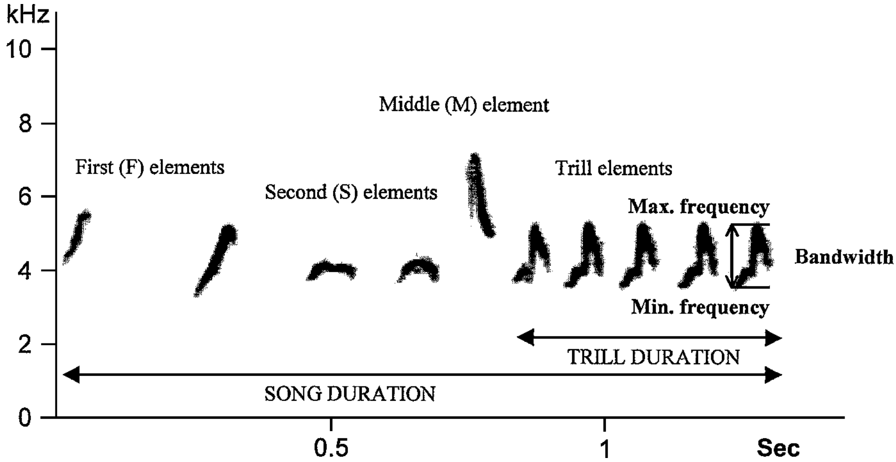

Fig. 1. Spectrogram of a typical male orange-tufted sunbird song. Detailed are the four phrases in the song as well as the method of calculation of acoustical variables noted in Table 1.

built-in measurement cursors. 711 songs from 63 territorial males were recorded and used in the analyses. Between five and 41 songs were recorded from each individual ($\bar{x} \pm$ SE = 11.85 $\pm$ 1.34 songs/bird, $N = 63$).

In addition to song recordings in the Ramat-Aviv study site, we made a few recordings of male sunbird song in the surrounding neighborhoods as well as at a few localities throughout Israel.

Methods of analyses

To describe acoustic variation in the songs from different individuals, we divided each song into different phrases as shown in Fig. 1. The terms we used to describe song are illustrated in Fig. 1 and follow the terminology of Catchpole & Slater (1995). An element is a continuous trace on a spectrogram, separated by at least 3 ms from other traces. A syllable is a repeated unit of one or more element.

We measured 24 acoustical variables on each song (Fig. 1, Table 1). After examining the correlation matrix, we entered the variables into a principal components analysis. A principal component analysis creates a small set of summary variables that efficiently summarize the variation present in the original set of 24 variables.

Results

Song characteristics

In the Ramat-Aviv study site, once territories are established, male orange-tufted sunbirds start singing a single stereotyped ‘full song' delivered from

TABLE 1. *Acoustical variables measured in spectrograms of the 'high' and 'low' dialects in the Ramat-Aviv sunbird population*

Variables	Method of calculation
SFLFREQ	Min. frequency of 'First' element (kHz)
SSLFREQ	Min. frequency of 'Second' element (kHz)
SMLFREQ	Min. frequency of 'Middle' element (kHz)
STRLFREQ	Min. frequency of 'Trill' element (kHz)
SFHFREQ	Max. frequency of 'First' element (kHz)
SSHFREQ	Max. frequency of 'Second' element (kHz)
SMHFREQ	Max. frequency of 'Middle' element (kHz)
STRHFREQ	Max. frequency of 'Trill' element (kHz)
SFBAND	Frequency bandwidth of 'First' element (kHz)
SSBAND	Frequency bandwidth of 'Second' element (kHz)
SMBAND	Frequency bandwidth of 'Middle' element (kHz)
STRBAND	Frequency bandwidth of 'Trill' element (kHz)
SFMODUL	Frequency modulation of 'First' element (Δ kHz /Δ s)
SSMODUL	Frequency modulation of 'Second' element (Δ kHz /Δ s)
SMMODUL	Frequency modulation of 'Middle' element (Δ kHz /Δ s)
STRMODUL	Frequency modulation of 'Trill' element (Δ kHz /Δ s)
STOTALTIME	Total song duration (s)
STRILLTIME	Duration of 'Trill' element (s)
SFIRST	No. of 'First' notes
SMIDDLE	No. of 'Second' notes
SSECOND	No. of 'Middle' notes
STRILLS	No. of 'Trill' notes
SNNOTES	Total no. of notes
TRILLRATE	No. of 'Trill' notes /duration of 'Trill' element

high vantage points such as tree-tops or overhead wires. Males continue to sing throughout the breeding season (February-September). Mean rate of song delivery of males was 2.56 $\pm$ 0.23 songs/min. (range 1-15, N = 60 males). Singing is most pronounced during the nest building stage, during which time males sing from a high song-post just above the nest, while the female is busy collecting nesting material. Males are aggressive in defense of their territory at this time and launch attacks from these song-posts at approaching male rivals, as territories are especially prone to trespass by males seeking extra-pair fertilizations a few days before the resident female starts laying (Goldstein & Yom-Tov, 1988).

Two distinct variations or dialects of this song were discovered in the study area, which were maintained during three breeding seasons (see below; Fig. 2).

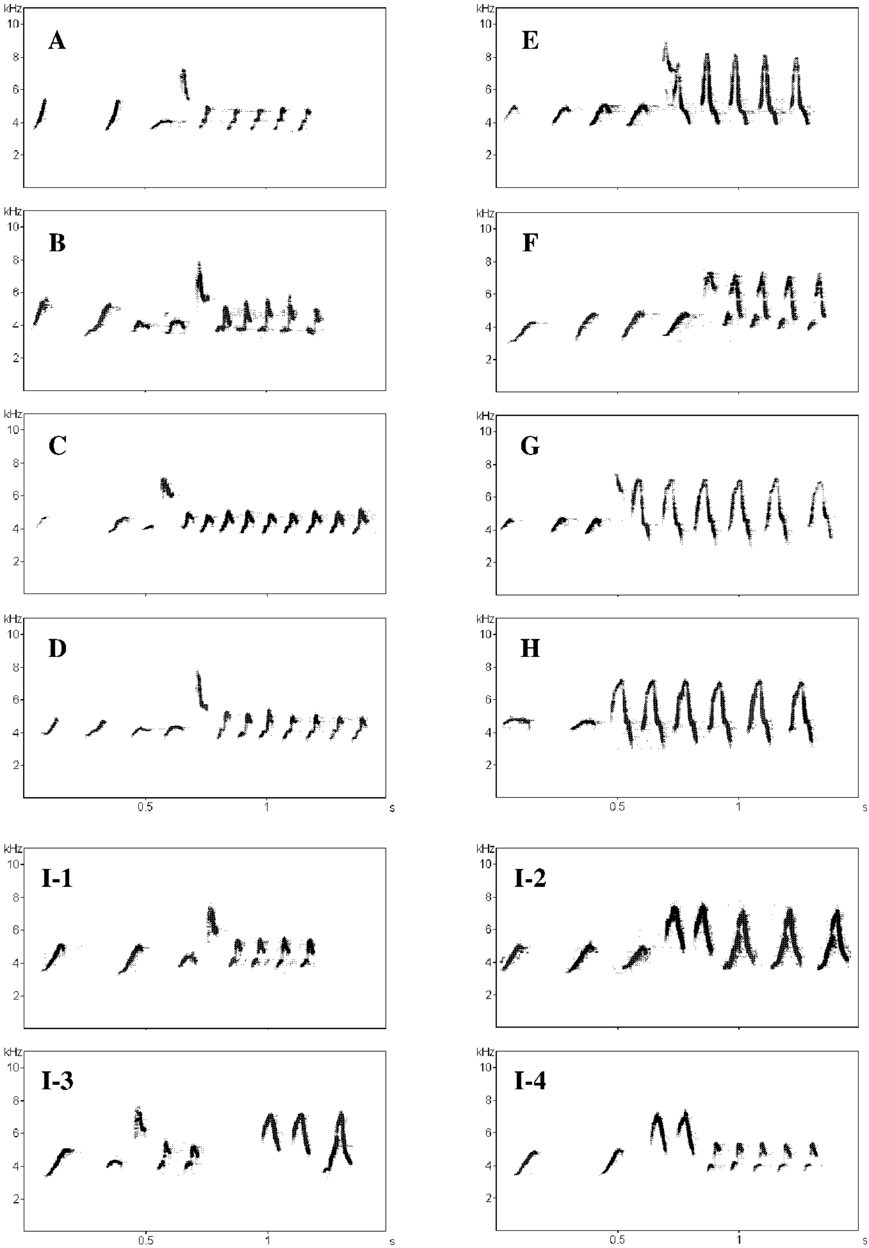

Fig. 2. Spectrograms of orange-tufted sunbird song dialects in Ramat-Aviv: (A-D) 'low' dialect song; (E-H) 'high' dialect song; (I) example of a 'bilingual' male. This male was recorded singing 'low' (I-1) and 'high' dialects (I-2) and mixed dialect songs (I-3, I-4) in one continuous song-bout.

Four different elements have been identified, appearing in most individuals' song (Figs 1 and 2). These elements appear in well-defined syllables and syntax is retained in all songs. Most songs start with a first syllable consisting of 1-8 frequency-modulated elements (F element). Individual F elements are often given throughout the year as calls, however males start producing them in an organized syllable form just before the beginning of the breeding season, as a precursor to full song. The second syllable type consists of 1-4 less frequency modulated whistle elements (S element). This syllable is sometimes absent especially in the 'high' dialect song. The third syllable type consists of a high-pitched element preceding the trill (M element). In the Ramat-Aviv population this syllable is sometimes absent in the 'high' dialect song, and consists of only one element in the 'low' dialect song (only one bird was recorded giving 2-3 M elements). In other locations, this syllable may consist of 1-3 M elements. The last part of the song always consists of a slow trill made up of 1-12 elements and is very variable in quantity between males.

The main distinction between the two dialects found in the study population is the frequency of the trill. Trill elements of both dialects start at about 3.6-3.8 kHz, yet the 'low' dialect's peak trill frequency reaches a mean of 5.1 kHz (4.7-5.4), whereas that of the 'high' dialect reaches a mean of 7.3 kHz (6.9-7.9). There is thus no overlap in peak frequencies and all songs could be assigned unequivocally to one of the two groups. This large frequency difference of 2-3 kHz between the two dialects can be distinguished by ear while in the field.

Thirty-seven males were recorded singing the 'low' dialect and 21 birds sang the 'high' dialect. Four birds sang both dialects or 'hybrid' songs (Fig. 2). Song types did not vary within males over the breeding season or from year to year. In all the cases where a territorial male disappeared either during or after the breeding season, the new male that occupied the territory sang an identical song type.

Quantitative analysis of acoustic variation

In a principal components (PCA) analysis the first three principal components extracted explained 30.1%, 14.5% and 10.7% of the total variation in the data set, whereas the remaining four explained less than 10% each (8.2%, 7.5%, 6.0% and 4.5%). Together, these seven components account for 81.6%

TABLE 2. *Details of principal components analysis performed on 24 acoustical measures of sunbird song*

PC	Eigenvalue	% total variance	Cumul. %
1	7.23	30.1	30.1
2	3.49	14.5	44.7
3	2.58	10.7	55.4
4	1.98	8.2	63.6
5	1.80	7.5	71.1
6	1.43	6.0	77.1
7	1.07	4.5	81.6

Seven principal components were extracted. Eigenvalues greater than one show principal components that explain more variance than a single original variable.

of the total variance in these data. Although the first principal component may account for the most variation, it may not be the axis of most biological interest (McGregor, 1992). Table 2 shows all seven principal components extracted having Eigenvalues in excess of one.

Seventeen of the 24 variables had correlations greater than 0.7 with the seven principal components (Table 3). PC1 corresponds to an axis primarily of increasing bandwidth of the trill (mainly due to rising maximum trill frequency), decreasing trill rate and fewer S elements. PC2 corresponds to an axis primarily of decreasing trill length and fewer trill elements. Increasing values on PC3 correspond to increasing total song length, increasing number of F elements and decrease of minimum frequency of F elements. PC4 shows increasing bandwidth of type F elements and decreasing frequency modulation of type S elements. PC5 shows decreasing values of minimum and maximum frequencies of S elements. PC6 corresponds to an axis of decreasing values of bandwidth of F elements, their maximum frequency, and decreasing frequency modulation of F elements. PC7 shows increasing values of the maximum frequency of M elements.

t-tests between dialects (Table 4) showed significant differences for PC1, PC5, PC6 and PC7. No difference between dialects was found for PCs 2, 3, and 4.

To summarize, the major distinctions between the dialects are that the high dialect has a much higher peak trill frequency, larger trill bandwidth and decreased trill rate. The high dialect also has a lower peak frequency of the F element, as well as decreased bandwidth and frequency modulation of the F element, a higher peak frequency of the M element, and fewer S

TABLE 3. *Correlation coefficients between acoustic variables and the seven principal components*

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7
SFLFREQ	– 0.08	– 0.04	*– 0.79*	0.23	– 0.07	0.04	0.13
SSLFREQ	0.19	0.05	– 0.09	– 0.30	*– 0.90*	0.06	0.10
SMLFREQ	0.36	– 0.05	0.09	– 0.26	– 0.21	0.34	*0.71*
STRLFREQ	0.07	0.41	0.05	– 0.06	– 0.60	0.14	0.39
SFHFREQ	– 0.37	0.16	– 0.31	0.11	0.04	*– 0.78*	– 0.06
SSHFREQ	0.18	0.01	– 0.04	0.14	*– 0.89*	0.08	0.12
SMHFREQ	0.14	0.04	0.03	0.16	– 0.27	– 0.12	*0.85*
STRHFREQ	*0.84*	0.01	0.06	– 0.05	– 0.29	0.20	0.33
SFBAND	– 0.31	0.22	0.29	– 0.09	0.08	*– 0.82*	– 0.13
SSBAND	0.14	– 0.12	0.02	*0.83*	0.14	0.11	– 0.11
SMBAND	– 0.18	0.09	– 0.17	0.62	– 0.02	– 0.43	– 0.14
STRBAND	*0.89*	– 0.09	0.05	– 0.04	– 0.18	0.19	0.27
SFMODUL	– 0.13	0.03	– 0.03	– 0.04	0.11	*– 0.91*	– 0.04
SSMODUL	– 0.31	0.16	0.02	*0.72*	– 0.01	0.03	0.33
SMMODUL	– 0.27	– 0.09	– 0.13	0.05	0.06	– 0.35	0.08
STRMODUL	0.59	– 0.09	– 0.20	– 0.22	– 0.40	0.15	0.30
STOTALTIME	0.11	– 0.34	*0.81*	0.16	0.04	0.12	0.08
STRILLTIME	0.41	*– 0.85*	– 0.01	0.02	0.04	0.20	– 0.07
SFIRST	0.19	0.28	*0.74*	0.02	0.03	0.32	0.39
SMIDDLE	– 0.23	0.38	0.41	0.13	– 0.09	– 0.31	– 0.34
SSECOND	*– 0.77*	0.01	– 0.22	0.16	0.01	– 0.38	– 0.09
STRILLS	– 0.01	*– 0.97*	– 0.01	– 0.07	0.07	0.05	– 0.03
SNNOTES	– 0.39	– 0.68	0.54	0.07	0.08	0.00	0.14
TRILLRATE	*– 0.88*	0.09	– 0.02	– 0.06	0.06	– 0.24	0.09
Expl. var	4.35	2.81	2.64	2.03	2.44	3.14	2.16
Prp. totl	0.18	0.12	0.11	0.08	0.10	0.13	0.09

Variables with $r > 0.70$ are in italics.

elements in the song, which if they exist, have a higher peak frequency and also begin at a higher frequency.

Geographical variation

The Ramat-Aviv population is separated into two distinct areas, each with a distinct dialect and a sharp boundary (Fig. 3). The ‘high-low' dialect border appears to run in a straight line from NW to SE. The border comprises a recreational park (composed mainly of *Tipuana tipu* trees), high-school grounds and a shopping center, areas which are lacking suitable nectar-

TABLE 4. *t-test of principal factors between 'high' and 'low' dialects*

PC	Mean low	Mean high	*t*	*p*
PC1	– 0.691	0.994	– 10.61	< 0.000001
PC2	– 0.051	– 0.151	0.36	0.716
PC3	– 0.067	0.053	– 0.42	0.675
PC4	0.046	– 0.107	0.55	0.581
PC5	0.254	– 0.354	2.24	0.029
PC6	– 0.187	0.393	– 2.12	0.039
PC7	– 0.229	0.540	– 3.02	0.004

$N_{\text{high}} = 21, N_{\text{low}} = 35$.

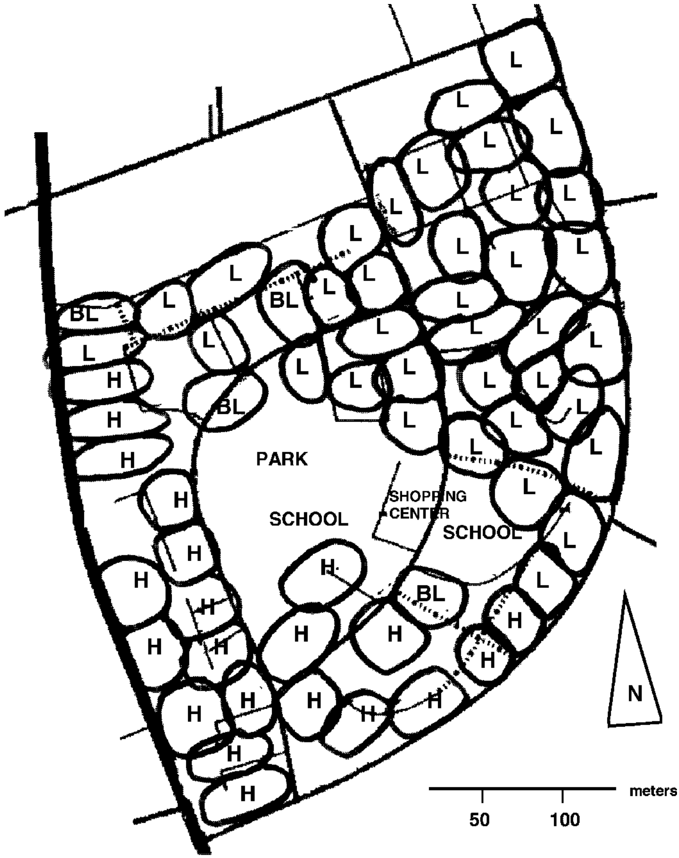

Fig. 3. Map of the Ramat-Aviv study showing the territorial boundaries of orange-tufted sunbirds in 1998. (L) 'low' dialect; (H) 'high' dialect; (BL) bilingual male.

secreting plants for sunbirds. At the NW as well as the SE corners, however, both sides of the border contain suitable territories and neighboring birds can be heard singing different dialect songs, although they are only 20-30 meters apart. All four ‘bilingual' birds singing both dialects or ‘hybrid' songs, occupied territories near the dialect border.

The two dialects seem to be confined to the study area and do not continue into neighboring areas. Recordings made adjacent to the NE corner of the study site (Tel-Aviv University campus grounds and the Afeka neighborhood) reveal different patterns of song. Preliminary recordings from a number of locations in Israel reveal the occurrence of distinct dialects on a macrogeographic scale, some varying in tempo, syntax, frequency and the shape of elements. This finding is less surprising, as most populations are isolated from one another by large areas of unsuitable habitat.

We found very low rates of dispersal outside the dialect areas. Of 21 marked birds singing the low dialect, 16 were banded as adults between 1989 and 1998 in the study area, three were banded as first year birds and two as nestlings. Of these only three birds (14%, one adult, one first year bird and one nestling) were banded outside the current dialect boundaries. Of nine marked birds singing the high dialect, seven were banded as adults between 1994 and 1998, and 2 were banded as first year birds. None of these birds were banded outside the current dialect boundaries. One male (OAWY) banded in 1997 as a nestling in the high dialect area, occupied a territory at the boundary in 1998 and sang a mixed dialect song.

Discussion

The main findings of our study are that the songs of the orange-tufted sunbird show marked microgeographical variation within a small area. Two adjacent and distinctive local dialect populations are present with a sharply defined boundary between the different dialect areas. Bilingual males, singing both dialects, occupy territories on the boundary. This close geographic association of birds singing the same basic song and the lack of variability within groups is characteristic of local dialects (McGregor & Thompson, 1988).

Dialects and geographical song variation has also been discovered in another species of sunbird, the splendid sunbird, *Nectarinia coccinigaster*

(Grimes, 1974; Payne, 1978) and probably exist in at least two other sunbirds species, *Nectarinia kilimensis* and *Nectarinia chalybeus*, as well (Grimes, 1974).

Colonization of new areas by songbirds is thought to be one process through which regional differences in song may arise (Baker & Cunningham, 1985). Sunbird settlement in many parts of Israel appears to be dependent on nectar producing ornamental bushes and trees planted by people in gardens. One can speculate on the historical processes leading to the formation of the Ramat-Aviv dialect system. This neighborhood was established in the early 1950's and has slowly expanded throughout the years. Old aerial photographs reveal that the neighborhood grew out of two concentrations of homes, separated by vacant, barren areas. Apparently, at least two founding populations of sunbirds settled near these homes and gardens in different parts of Ramat-Aviv. Each population could have sung a different variant of the song, based on the place they originated from. Young birds would have settled in vacant territories near their natal territories and would start singing the local song, learned from their fathers and immediate neighbors. This would persist, resulting in small clusters of sunbird territories around private homes and gardens existing at the time, each cluster of birds singing a different dialect. Human expansion through the years will have slowly connected the two neighborhoods and thus connected the two sunbird concentrations, leading to a seemingly homogenous population today, yet with two dialects.

Interestingly, aerial photographs clearly show the neighborhood was fully built and inhabited by people, with well-developed gardens, as early as 1963. Thus, it seems odd that whilst it took probably less than 10 years for these sharp dialect boundaries to arise due to a geographical barrier, an additional 35 years would have gone by after the isolating barrier had been lifted, without them diffusing.

The issue of how local dialects are maintained and whether they have significant evolutionary consequences has been the subject of intense interest and controversy in recent years (summarized in Kroodsma *et al.*, 1984; Baker & Cunningham, 1985; Rothstein & Fleischer, 1987).

Catchpole & Rowell (1993) have shown that in the case of local dialects in a population of the European wren (*Troglodytes troglodytes*), a small yet significant natural boundary, such as a 200 meter wide lake, is all that is needed for separate song traditions to develop. According to them, such boundaries are clearly insignificant in terms of dispersal, but may form an effective social barrier between both populations (Catchpole & Rowell, 1993).

In our study, the area along the boundary which is unoccupied by sunbirds (a recreational park, school grounds and a shopping center; Fig. 3), is not only smaller, it also does not provide a complete separation between the two dialect populations. In our case, however, it seems that dispersal outside the dialect area is uncommon. This is consistent with earlier findings of a high degree of relatedness between neighboring individuals in our study area, as evidenced from high proportions of band sharing discovered in genetic analysis of this sunbird population (Zilberman *et al.*, 1999).

The spatial distribution of the two sunbird dialect populations in Ramat-Aviv, together with the observed dispersal patterns strongly suggest the existence of a mechanism, which is not merely the consequences of a nonadaptive cultural founder effect 50 years ago, that currently maintains these dialects at the current boundaries. Moreover, if such a mechanism does indeed exist, it is natural to assume that one of its main characteristics is the ability of birds to discriminate between their 'home' dialect and foreign dialects. Indeed, preliminary results from playback experiments on male sunbirds have revealed a significant differential behavioral response by males to playbacks of low and high dialects. Such behavioral discrimination implies the capability to recognize differences between the two dialects by the birds.

The pronounced differences we have discovered between these two adjacent sunbird dialects in the peak trill frequency (2 to 3 kHz), seem substantial compared to those reported in many published song dialect studies on other songbird species. The sunbird dialect system in Ramat-Aviv is also unique in that it is recent and based mainly on human impact on colonization. We are currently researching the stability and function of these dialects in two avenues: (1) investigating the genetic composition of males of the two dialects, which will help us to establish the rate of gene flow between the two dialect areas, and to determine if and how the song dialects reported here affect gene flow in this species; and (2) conducting playback experiments in order to investigate discrimination capability and differential responses of males and females to different song dialects.

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